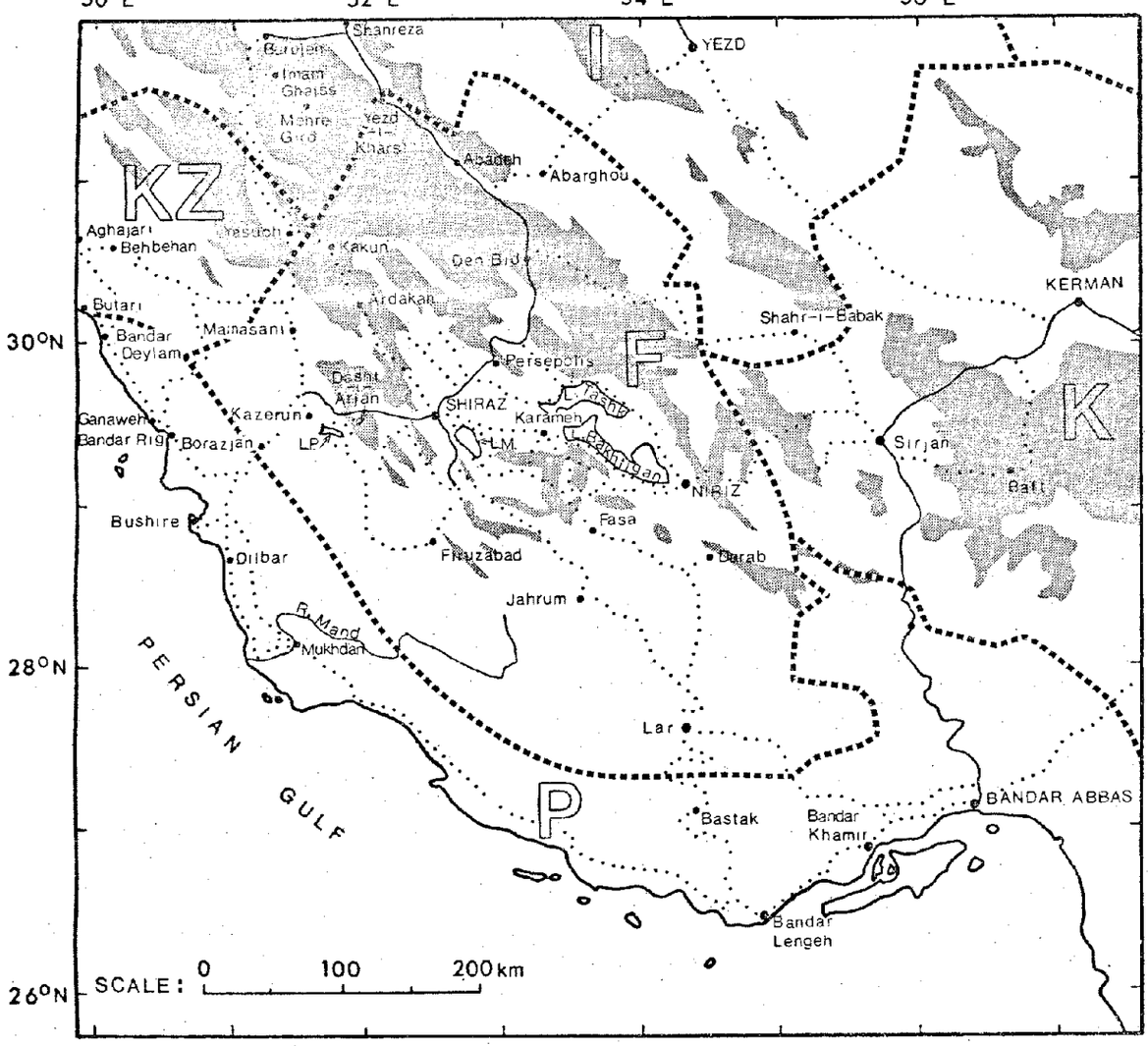

KEY

▭ – Land above 2,100m	F – Fars
~~ – Asphalt roads	I – Isfahan
····· – Gravel roads	K – Kerman
▪▪▪▪▪ – Provincial boundaries	KZ – Khuzistan
LM – Lake Maharlu	P – Persian Gulf and Sea of Oman Ports and Islands
LP – Lake Perishan	

Provinces:

S. W. Iran showing most of the places mentioned in the text, but for study areas see figure 7 page 42 and for topographic features see figure 4 page 17.

THE COMPARATIVE ECOLOGY OF ELEVEN SPECIES OF WHEATEAR (GENUS OENANTHE) IN S. W. IRAN

BY

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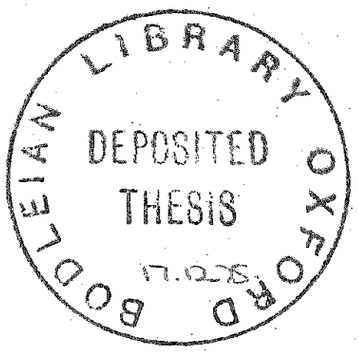
(Trinity College)

Thesis presented in the University of Oxford
for the Degree of Doctor of Philosophy.

September 1975



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ABSTRACT

Wheatears, genus Oenanthe, are small chat-like thrushes (family Muscicapidae, sub-family Turdinae). Eighteen species have been recognised of which four are confined to Africa while the remaining 14 have largely Palaearctic breeding distributions. They are all similar in size and morphology and some are alike in plumage. Their behaviour and ecology are also, broadly speaking, similar. They typically inhabit open, barren plains and hillsides which are often stony and boulder-strewn. They feed chiefly on insects and other small invertebrates which they catch largely on bare ground, mainly by making rapid pursuits on foot or by pouncing from elevated watch-posts. Most nest in rock crevices, under boulders or in holes in the ground. Suitable habitat is found particularly in the arid zone to which 11 of the 14 Palaearctic species are largely confined. Some species differ in their altitudinal ranges, geographical distributions and/or habitats but the majority have contiguous or overlapping ranges so that in many areas, particularly in North Africa and the Middle East, several species occur. Indeed different species of wheatear have often been reported side by side in the same habitat.

The wheatears present two main problems which have received little attention and which are considered in this study:

1) In view of the similarity of their ecology, species of wheatear that occur side by side in the same habitat present problems in relation to Gause's hypothesis, which is now generally accepted, that two species can coexist indefinitely only if they differ sufficiently in ecology that their numbers are limited by different environmental factors; that is, if they are ecologically isolated. The first problem, therefore, is how are species of wheatear, that apparently overlap in distribution and ecology, ecologically isolated?

2) The second main problem concerns the factors that influence the ranges and habitat distributions of wheatears. These factors are of interest for two main reasons: a) The ranges and habitat distributions of wheatears tend to end rather abruptly and the factors that limit them are often obscure since the boundaries seldom coincide with any obvious deficiency or restraint in the environment. b) Many species of wheatear differ in range and/or habitat and the factors that account for these differences are rarely obvious since all species of wheatear are similar in size, morphology and, broadly speaking, in their ecological requirements.

These two main problems were investigated within the context of S. W. Iran, where wheatears had not previously been studied in detail, and where the problems could be investigated with particular advantage for the following reasons: a) The genus Oenanthe is better represented in S. W. Iran than anywhere else. Eleven species breed or may breed, of which eight do so commonly; and seven species winter or probably winter, of which three are common. b) A preliminary survey showed that the pattern of coexistence between the various species was particularly complex, with some species differing in geographical distribution, altitudinal range and/or habitat while others were found side by side in the same habitats. The species considered in the study are as follows: Hume's Wheatear (O. alboniger), Desert Wheatear (O. deserti), Finsch's Wheatear (O. finschii), Black-eared Wheatear (O. hispanica), Isabelline Wheatear (O. isabellina), Mourning Wheatear (O. lugens), Hooded Wheatear (O. monacha), Common Wheatear (O. oenanthe), Eastern Pied Wheatear (O. picata), Pied Wheatear (O. pleschanka), and Red-tailed Wheatear (O. xanthoprymna).

As background for studying the two main problems the thesis begins, after the introduction, with five largely descriptive chapters. These are briefly reviewed below:

Chapter II. The environment of S. W. Iran. The topography, climate and vegetation of S. W. Iran are described and it is shown that for a relatively small area (approximately 400,000 km^2) in the arid zone it is exceptionally varied in all three respects. Indeed bioclimatic zones are recognised which range from sub-desert, through steppe and xerophilous

ABSTRACT

forest to montane. This diversity is due in large measure to the varied topography. The area is traversed from northwest to southeast by the Zagros Mountains which rise to 4,404 m above sea level. These mountains, which are relatively well watered and often forest clad at higher altitudes, separate the hot, arid coastal plain of the Persian Gulf from the steppes and deserts of the high plateau of central Iran.

Chapter III. Fieldwork and methods. Fieldwork was carried out on 842 days over a period of nine years. It consisted mainly of a) a broad survey of distribution and habitat selection; and b) detailed studies of phenology, territoriality, interspecific relationships, habitat utilization and feeding ecology which were carried out in 19 study areas which were visited regularly. Coverage and the techniques used for mapping territories, recording the activities of wheatears and sampling their food supplies are described.

Chapter IV. Distribution and status. All available records of wheatears in S. W. Iran are summarised in maps and tables and used as a basis for deducing the distribution and status of each species in the area. The world range and status of each species is also briefly described to give perspective to the situation in S. W. Iran.

Chapter V. Habitat. The habitat distributions of the various species of wheatear that occur in S. W. Iran are described and for each species habitat features which may be important in habitat selection are considered.

Chapter VI. Feeding ecology. This chapter is divided into three parts: a) Food supply: An attempt was made to measure diurnal, seasonal, regional and inter-habitat variations in the abundance, size distribution and taxonomic composition of arthropods that were available to wheatears. Three direct methods were employed: pitfall trapping and 100 m transects on bare ground, and sweep-net sampling from vegetation. In addition inferences about arthropod availability were made from data on ground surface temperatures. The results are reported and the following conclusions drawn: i) In cold weather arthropods are active mainly during the middle of the day while in hot periods they tend to be active in the early morning and late afternoon; ii) peak food supply coincides with the spring flush of vegetation; iii) lean periods occur in winter in cold highland areas and in summer in the hot lowlands; iv) other factors being equal food supplies are probably generally better in wetter than drier areas, better on piedmonts and in valley bottoms than on plains and better on plains than on hillsides; and v) the most abundant arthropod taxa available are Orthoptera, Araneida and particularly Coleoptera and Formicidae (workers). b) Foraging: The foraging patterns of wheatears in S. W. Iran are described. It is shown that prey is taken mainly from bare ground and that most species employ predominantly one or other of two main foraging patterns: i) the perch and pounce foraging pattern where birds search for quarry mainly from elevated watch-posts whence they launch aerial attacks and ii) the dash and jab foraging strategy in which birds search for and pursue their prey mainly on foot. The adaptive significance of these foraging strategies are considered in chapter VIII. Some data on foraging rates and rhythms are given. c) Diet: Two types of data on the diets of wheatears in S. W. Iran are presented: i) the results of 91 field observations in which wheatears of nine species were seen to take food items that were identified; and ii) analyses of the gut-contents from 226 wheatears of 11 species. Where possible items were placed in size classes and identified to order or family. Difficulties in the use of gut-contents as indicators of diet are discussed and in the case of S. W. Iranian wheatears it was concluded that the results probably give a fair indication of what the birds had actually eaten. The diets of the various species are compared and shown to overlap considerably both in the size distribution and the taxonomic composition of the items taken. The majority of the items eaten by wheatears were 2-10 mm in length and were in the following taxonomic groups: winged Hymenoptera, Isoptera, Hemiptera, Embioptera, insect larvae, seeds, berries and particularly Coleoptera and Formicidae (workers). The size distribution and taxonomic composition of arthropods taken by wheatears and of arthropods that were available in wheatear habitat were broadly similar, and it is tentatively suggested that wheatears eat any prey item that they encounter as long as it is large enough to be worth fetching and not too large to handle.

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Ecological isolation is considered in chapter VII where careful comparisons of the ranges and habitats of the various species of wheatear that occur in S. W. Iran showed that, although the pattern of coexistence between the different species is complex, most avoid interspecific competition by living in different places from other species. This spatial separation is achieved largely by interspecific differences in altitudinal range, geographical distribution and/or habitat. However where different species occurred side by side in the same habitat spatial separation was brought about by interspecific territoriality. Since the various species of wheatear have similar ecological requirements they would probably compete, particularly for food, if they occupied the same ground for any length of time. Their spatial separation is therefore consistent with Gause's hypothesis. However where different species of wheatear held territories close together in the same habitat they appeared to have very similar ecology and initially this led me to believe that they were imperfectly ecologically isolated. However when viewed in the context of their total ranges and habitat distributions it was found that such cases of ecological overlap were relatively few and occurred mainly where the ranges and/or habitats of different species overlapped marginally. Furthermore such ecological overlap was observed only in places where there was some, apparently suitable, ground that was unoccupied by wheatears, which suggested that interspecific competition was unlikely to have been severe. Therefore, since competitive exclusion is a theoretical necessity only when two species compete for a limited resource, these cases of ecological overlap did not contravene Gause's hypothesis.

Factors that influence the ranges and habitat distributions of wheatears in S. W. Iran are investigated in chapter VIII (and habitat features that may be important in habitat selection are considered in chapter V). The chapter is divided into two parts. In the first, factors that are likely to influence distributions are considered in general terms and in the second, the factors influencing the distribution of each species are examined in turn. Factors that are considered are reviewed below:

1) Climate and adaptations to climate: a) Temperature and rainfall: The range of ambient temperature in areas where the various species of wheatear occurred was found to be similar for all species (approximately 5° - 28°C estimated mean daily). It was therefore concluded that interspecific differences in temperature tolerance are unlikely to play an important role in determining the distributions of wheatears in S. W. Iran. However evidence is presented which suggests that temperature, in conjunction with rainfall, probably has a strong indirect influence on the distribution of wheatears through its influence on vegetation and the availability of arthropod prey. Furthermore in hot areas and in hot seasons wheatears are confined to habitats where shade is available which suggests that high temperatures are a limiting factor in such situations. At high and middle altitudes shade is probably important only as an escape from the midday heat, but in lowland areas general shade is probably also important in providing ground where arthropod prey is not inhibited by high ground surface temperatures and where birds can feed without jeopardizing their heat balances. b) Humidity: It was shown that ambient humidities in July within the ranges of the various species of wheatear in S. W. Iran vary considerably and that some are confined to areas with dry air while others are found only in areas with moist air. Since ambient humidity strongly influences the rate at which evaporative cooling can be effected it is postulated that capacity to thermoregulate in relation to ambient humidity may influence the distributions of some species.

2) Competition: It is suggested that interspecific competition probably influences the distribution of some species of wheatear in S. W. Iran. This suggestion is based on the following evidence: a) All wheatears have similar ecological requirements and hence are potential competitors. b) The pattern of coexistence between the various species is complex and in many areas several species occur side by side. c) Where different species were found side by side their territories were largely non-overlapping. This was brought about by various sorts of territorial behaviour, including interspecific aggressive encounters. The results of 223 such encounters are reported and these show that interspecific relationships are largely hierarchical which suggests that in the event of interspecific competition the

ABSTRACT

dominant member of each pair of species would prevail. d) Some species, for example O. deserti and O. isabellina, show contiguous allopatry which is strong circumstantial evidence for interspecific competition influencing distribution. e) Ecological release: Evidence is given which suggests that O. lugens occurs in a wider range of habitats in the absence than in the presence of O. finschii. O. finschii is dominant to O. lugens in clashes and it is postulated that where the two species occur together the habitat distribution of the former is restricted by competition from the latter.

3) Habitat requirements: Habitat requirements are considered in chapter V. Two criteria were used to identify habitat features which may influence habitat distributions of wheatears: a) correlations between the occurrence of a species and a habitat feature; and b) the use of habitat features by birds during such essential activities as foraging, thermoregulation, nesting, roosting, avoiding adverse weather and escaping from predators. Evidence is presented which suggests that the availability of the following features may influence habitat selection, at least in certain cases: i) relatively level bare ground which is where wheatears mainly forage; ii) elevated perches which are used for example during foraging, thermoregulation and as song posts; iii) boulder-strewn, rocky areas which provide shade, nest-sites, roost-holes, cover where birds can escape from predators and adverse weather, and variegated dark and light backgrounds against which black and white wheatears can be cryptic; iv) shade (see under temperature and rainfall above) and v) rodent holes which are used as nest-sites and roost-holes.

4) Adaptations to habitat: The adaptive significance of the coloration, the foraging strategies and the weight and morphology of the various species of wheatear for life in their respective habitats is considered. a) Coloration: Ideas about the adaptive significance of the coloration of wheatears are reviewed and the following conclusions reached: i) Dun-coloration in wheatears probably has survival value in two main ways: first concealment from predators in open habitats; and second reduction of heat load when temperatures are above the thermoneutral point. Both these factors are probably important in enabling dun-coloured wheatears to survive in open habitats, particularly in areas with little cover. ii) Black and white, and grey and black and white plumage in wheatears probably has survival value in three main ways: first concealment from predators in habitats with dark, and with variegated dark and light backgrounds; second reduction of the metabolic costs of staying warm when ambient temperatures are below the thermoneutral point; and third facilitating territorial defence and mate selection. The price of these advantages is probably restriction of these wheatears to habitats with cover, usually in the form of stones, rock-outcrops and boulders which, in addition to providing hiding places, furnish backgrounds against which they can be cryptic. b) Foraging strategies: It is postulated that the perch and pounce foraging strategy has two main advantages: i) Sitting on elevated watch-posts enables birds to search large areas of ground for prey with little expenditure of energy and hence is advantageous where food is patchy or scarce. ii) Pursuing prey on the wing enables birds to cross ground which would be difficult or impassable on foot. This strategy is therefore seen as an adaptation to life in arid regions where food is scarce and to life on steep rocky ground or in areas subject to dense flushes of vegetation where food is patchy and pedal locomotion difficult. The dash and jab foraging strategy is seen as an adaptation for life on featureless flat ground where elevated perches are scarce. c) Weight and morphology: The weights, tarsi, wings and tails of the various species of wheatear are compared to determine whether they show adaptive differences that might be associated with their respective patterns of habitat utilization. The main findings are as follows: i) Species that often use flimsy perches are lighter than species that usually sit on firm objects. The ability to use flimsy perches depends in part on low weight and therefore it is postulated that low weight is an adaptation to life in habitats where the use of flimsy perches is an advantage. ii) Largely cursorial species have longer tarsi than species that usually use flighted locomotion while in their habitats. It is suggested that the difference is adaptive since long legs increase the fields of view of cursorial birds and allow them to cover ground more quickly. iii) Species that often use non-rigid perches have shorter tarsi than species that usually sit on stable objects. It is suggested that this difference is adaptive as

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short tarsi facilitate maintenance of balance which is a problem when sitting on non-rigid perches. iv) Species that use short flights as their main means of locomotion while foraging and moving around their habitats tend to have longer tails and more rounded wings with lower wing loadings and more emargination than the more cursorial species. It is suggested that these differences are adaptive since long tails facilitate landing and manoeuvre while low wing loadings and well developed emargination provide high lift at slow speeds which is an advantage during the energetically expensive process of repeated take-offs and in manoeuvre. The influence of migratory status on the aerodynamic properties of the wings of wheatears is also considered and it is shown that long distance migrants tend to have longer, more pointed wings with higher aspect ratios than species that make shorter migrations or are relatively sedentary.

CHAPTER I

INTRODUCTION

BACKGROUND:

Wheatears, genus Oenanthe, are small chat-like thrushes (family Muscicapidae, sub-family Turdinae). The English substantive name Wheatear is given to all members of the genus and it is used in Britain without qualification for Oenanthe oenanthe which is otherwise known as the Common Wheatear. The name is derived from the earlier form "white arse" which alludes to the conspicuous white rump of most species (O. E. D.). Oenanthe spp. are also known as "chats" which refers to their "chacking" call notes, but this term is less precise than wheatear as it is shared by various members of related genera and other groups. Ripley (1952, 1964) recognised 18 species of Oenanthe. Four are confined to Africa and the remaining 14 have mainly Palaearctic breeding distributions.

The various species of wheatear are similar in size and morphology and some are also alike in plumage. Indeed several species are difficult to identify in the field while others at certain times of year can be safely distinguished only in the hand. They are all about the size of a House Sparrow (Passer domesticus) and have short, insectivorous bills and rather long, slender legs. The appearances of the species that occur in S. W. Iran are portrayed in plate 1 and some measurements of these species are given in table 1.

The ecology and behaviour of the different wheatear species are also, broadly speaking, similar. Most live on desolate, open, often rocky hills or plains with little vegetation while a few species occur in poor cultivation, in country with scattered bushes or even in sparse woodland. They feed chiefly on insects and other small invertebrates which they catch mainly on bare ground by swift



Plate 1. The eleven species of wheatear that occur in S. W. Persia.

1.	O. picata	(a) ♂, (b) ♀
2.	O. alboniger	♂ or ♀
3.	O. xanthoprymna	♂ or ♀
4.	O. lugens	(a) ♂, (b) ♀
5.	O. finschii	(a) ♂, (b) ♀
6.	O. pleschanka	(a) ♂, (b) ♀
7.	O. hispanica	(a) ♂, (b) ♀
8.	O. oenanthe	(a) ♂, (b) ♀
9.	O. monacha	(a) ♂, (b) ♀
10.	O. isabellina	♂ (the ♀ is similar but lacks the black lores)
11.	O. deserti	(a) ♂, (b) ♀

(From a watercolour by D. I. M. Wallace)

SPECIES		N	WING LENGTH (mm)		BILL LENGTH (mm)		TARSUS LENGTH (mm)		TAIL LENGTH (mm)		WEIGHT (gm)	
			Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
O. alboniger	♂	12	103.9	1.6	20.4	1.0	26.7	1.0	69.4	2.1	25.6	1.5
	♀	15	97.6	1.5	19.3	0.8	25.5	0.6	65.2	2.4	24.8	1.9
O. oenanthe	♂	7	98.8	2.9	17.8	1.1	27.8	1.2	57.5	4.0	21.9	2.5
	♀	5	93.8	4.1	17.6	0.6	26.3	1.5	54.1	2.7	21.8	2.8
O. isabellina	♂	23	98.7	2.9	19.5	0.9	30.6	1.0	57.3	2.3	28.3	2.0
	♀	19	95.6	2.3	19.0	0.9	29.8	1.3	55.0	2.2	27.6	2.8
O. monacha	♂	1	98		22.5		21.5		70			
	♀	1	104		22.0		24.0		78		22.5	
O. lugens	♂	7	94.7	2.1	18.6	0.4	25.6	0.7	62.8	1.8	22.3	0.9
	♀	4	91.0	1.8	18.6	1.0	25.1	0.9	61.9	3.0	22.6	2.3
O. pleschanka	♂	22	94.7	2.0	16.8	0.7	23.3	0.6	61.8	2.0	16.9	2.8
	♀	13	90.8	2.7	16.7	0.8	23.1	0.9	57.8	2.6	18.3	2.4
O. xanthoprymna	♂	8	94.0	2.3	19.0	0.9	26.3	0.9	60.1	1.5	24.4	1.8
	♀	4	89.3	3.3	19.0	0.8	24.8	0.5	59.0	3.9	22.3	2.1
O. deserti	♂	11	92.1	2.6	17.6	0.8	25.4	0.9	62.8	3.0	17.9	1.2
	♀	10	90.9	2.2	17.7	0.9	25.5	0.8	61.1	2.6	17.5	1.0
O. hispanica	♂	19	90.8	2.8	16.5	0.7	22.6	0.6	61.9	2.5	16.5	1.8
	♀	22	89.0	2.7	16.7	0.6	23.0	0.8	58.8	3.0	18.2	2.9
O. finschii	♂	36	90.6	2.3	18.0	0.9	25.9	1.0	61.3	2.2	26.1	3.2
	♀	9	85.6	2.0	17.7	0.9	24.9	0.7	58.5	3.9	24.4	2.2
O. picata	♂	15	89.3	1.7	17.1	0.8	24.4	0.8	63.3	2.8	19.6	2.2
	♀	6	85.3	1.5	17.0	0.5	23.8	0.4	61.0	2.3	19.5	2.6

Table 1. Measurements of wheatears from S. W. Persia using the methods of Witherby et al. 1938 and arranged in order of wing length of males.

(Bill measurements are from the cranio-facial hinge to the tip.

N = size of sample. S. D. = standard deviation.)

pedestrian dashes or by pouncing from some vantage point such as a boulder, thistle or clod. Sometimes they catch prey on the wing like a flycatcher. Most nest in rock crevices, under boulders or in holes in the ground, often rodent or rabbit burrows. However O. deserti sometimes nests at the foot of a shrub (Blanford 1876, Whitaker 1905, Johns 1970) and O. hispanica at times under a tussock of grass (Whitaker 1905).

Suitable habitat for wheatears is found particularly in dry country and 11 of the 14 Palaearctic species are largely confined to the arid zone (cf. fig. 1 and fig. 3), where, along with the larks (Alaudidae) and sandgrouse (Pteroclidae), they are among the commonest and most widespread birds. Two species (O. hispanica and O. leucura) breed mainly in areas with a Mediterranean climate and only O. oenanthe extends into the wetter areas of Eurasia during the breeding season and Africa during the winter. The ranges of most[1a] species overlap or are contiguous so that in many regions, particularly in North Africa and the Middle East, several species occur (fig. 1). For example in Israel with an area about the same as Wales (approximately 21,000 km^2) nine species breed and six winter while in an area of similar size in Morocco, seven species breed and five winter. The genus is best represented in S. W. Iran where, within an area also the size of Wales, nine species breed, one species probably breeds, one species may breed occasionally, five species winter, and two species probably winter (fig. 2).

---

[1]Comparisons on a species to species basis, of the available information on the ranges and habitat distributions of the 14 Palaearctic species of wheatear show: a) that of the 91 combinations of pairs of species the members of 79 (87%) have overlapping or contiguous ranges; and b) that of the latter 79 pairs of species the members of 36 pairs of species (46%) live mainly in habitats that are obviously different, which leaves 43 pairs of species (47% of the total 91) where the members apparently occur in the same areas and live in similar habitats, at least at certain times of year.

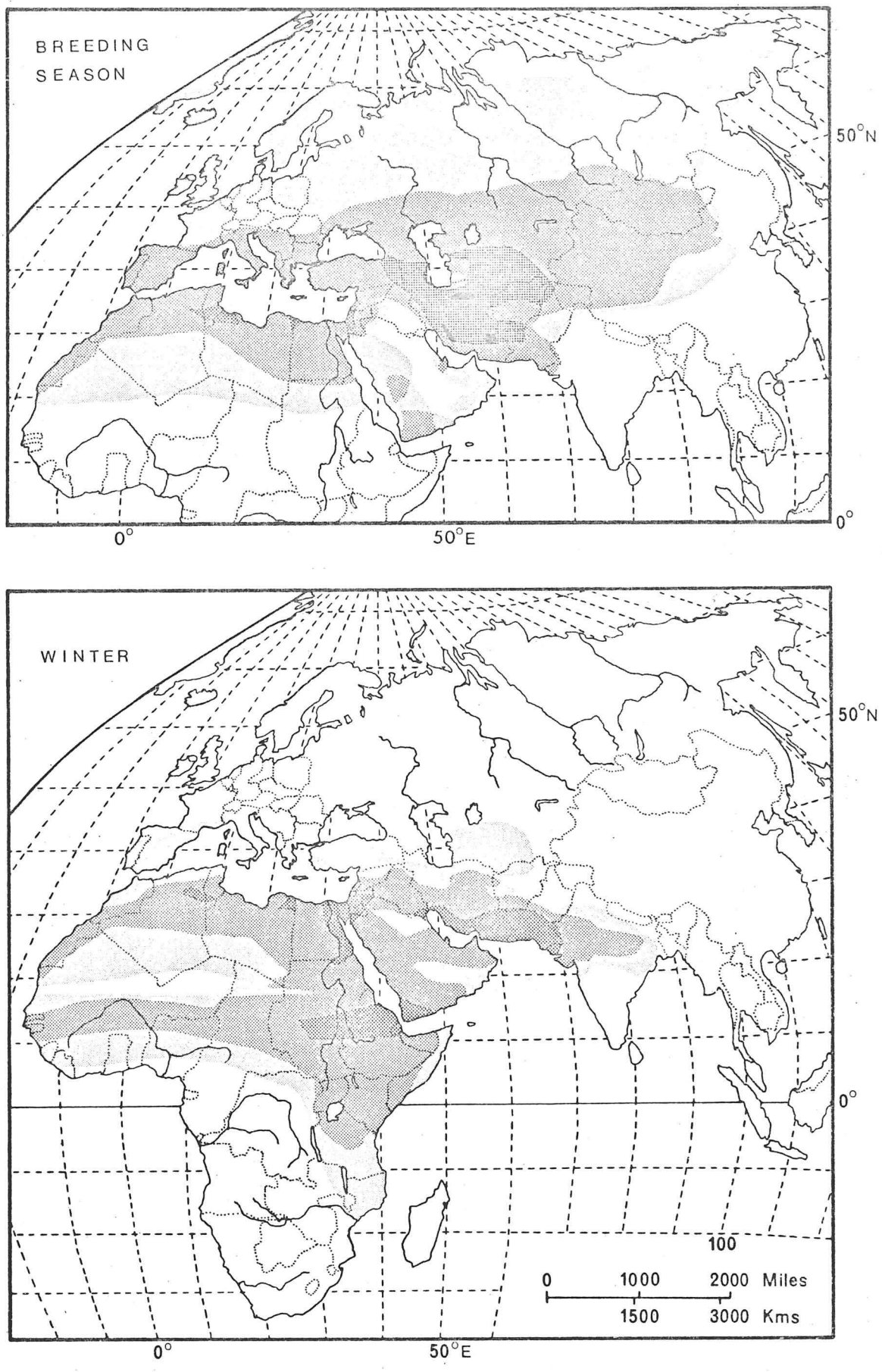

Figure 1. Breeding and winter distributions of the fourteen species of wheatear that breed in the Palaearctic Region. (N. B. one of these species, O. oenanthe, also breeds in western Greenland, north-eastern Canada and Alaska).

8 species. 2-4 species.

5-7 species. 1 species.

(Based on data from: Grote 1937; Meinertzhagen 1954; Vaurie 1959; Voous 1960; Ripley 1961; Etchécopar and Hüe 1967; Dementiev and Gladkov 1968; Hüe and Etchécopar 1970; Stresemann, Portenko and Mauersberger 1967 and 1971; Moreau 1972; and recent observations in Iran by L. Cornwallis and D. A. Scott.)

INTRODUCTION

In a few areas where several species of wheatear occur all or most have been shown to differ in geographical distribution, altitudinal range, and/or habitat. For example Lack (1971) compared the distributions and habitats of the four species of wheatear that breed in Europe and showed that they differ as follows: O. oenanthe and O. hispanica both breed on open, barren, stony or sandy hillsides (rarely steep) or plains, the latter sometimes in places with scattered bushes and trees. However O. oenanthe breeds mostly to the north of O. hispanica and where they meet in southern Europe O. oenanthe occurs at higher altitudes than O. hispanica. A third species, O. pleschanka, replaces O. hispanica in similar habitats in the extreme east of Europe, while a fourth species, O. leucura, is restricted to steep, rugged mountains with cliffs and screes in Spain and southern France and so differs in distribution and habitat from the other three species. Similar patterns of coexistence have been reported from other areas, for example: between six species that breed in Algeria (Rothschild and Hartert 1912); between most of the seven species that breed in Morocco (Brosset 1961); between four species that breed in Anatolia (Wadley 1951); between the seven species that breed commonly in Israel (A. Zahavi and Y. Yom-tov pers. comm.); and between some of the six species that winter in Sind (Ticehurst 1922).

However over most of their ranges only the broad outlines of the distribution and ecology of the various species of wheatear have been recorded and many,[1b] according to present information, overlap in both range and habitat. Detailed studies might reveal differences between many of these, but some have been reported side by side in the same habitat. Some examples are given below:

a) Overlap in the breeding season: Whitaker (1905) often found O. moesta and O. deserti near one another in semi-arid districts of Tunisia. From the same area Bannerman (1927) reported that O. deserti

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[1b] See footnote p. 4.

and O. moesta "...were usually found on the same ground". In several localities in Badakhshan, E. Afghanistan, Paludan (1959) found O. pleschanka occurring together with O. picata (mostly of the colour phase opistholeuca and a few of the colour phase picata) and was "...unable to find any difference in their habitats which for both species are most typically desolate, stony stretches with scattered boulders and more seldom fallow fields at the border of small cultivated areas". Eggebrecht (1943) reported a clear case of overlap in habitat and interspecific competition between O. oenanthe and O. pleschanka from the southern Ukrain in May where he observed an O. oenanthe establish a territory by usurping parts of the territories of two O. pleschanka and successfully defending it against them.

b) Overlap in winter: In Sind (Ticehurst 1922) and Kutch (Ali 1945) O. deserti and O. isabellina occur side by side in vast, arid plains with scanty vegetation. In N. W. India and W. Pakistan, Ali and Ripley (1973) found that in flat, stony or sandy semi-desert, often with sparse xerophytic bushes, and at the feet of rocky hillsides O. xanthoprymna is "...almost everywhere in direct food competition with the more domineering O. picata by which it is mercilessly chivvied and chased". Chapin (1953) referring to O. oenanthe and O. isabellina in the Congo wrote that "...during their winter period the behaviour and haunts of the two species are exactly similar". Hartley (1949) and Simmons (1951) described situations in Egypt where O. leucopyga, O. lugens and O. monacha occupied similar, adjacent and mutually exclusive territories. Moreau (1972), discussing the six Palaearctic species of wheatear that winter in Africa south of the Sahara, noted that "...their segregation in Africa appears to be imperfect,..." and Lack (1971) considering these species wrote that several of them "...coexist to an unusual extent for congeneric species". However he noted that there are some habitat differences and suggested that "...possibly the extent of their overlap would be found to be less than now thought if critical study had been made of their natural habitats.... Even so, several species are commonly seen side by side".

INTRODUCTION

PROBLEMS:

The wheatears present two main problems which have received little attention and which are considered in this study:

1) Ecological isolation:

The first problem concerns species which apparently overlap in both range and ecology. Gause's hypothesis[1] (Lack 1944a, 1947, 1971) or the principle of competitive exclusion (Hardin 1960), which is now regarded as axiomatic (Hutchinson 1957), asserts that two species can coexist indefinitely only if they differ sufficiently in ecology that their numbers are limited by different environmental factors; that is, if they are ecologically isolated (= ecologically segregated). The numbers of most birds are probably limited by food (Lack 1966), and Lack (1971), reviewing ecological isolation in birds, showed that species which occupy the same area usually take different foods, feed in different places, or live in separate habitats, at least at certain times of year, while those with similar requirements are segregated by range. As shown above, in many areas several species of wheatear coexist. Therefore according to Gause's hypothesis, they must differ in ecology at least when resources are limiting. Some species differ in their habitat requirements but others occur (some side by side) in the same or at least very similar habitats and the means of ecological segregation is obscure since the bills and feeding ecology of the various species seem too similar for it to be likely that they are segregated by taking different foods or by using different feeding stations, as has been

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[1] Gause's hypothesis, also referred to as the Volterra-Gause principle (Hutchinson 1957) is the logical consequence of the following ideas:

a) Different species, being genetically independent, have evolved separately and hence the chance is negligible that two species will be equally well adapted to exploit any given set of environmental conditions. Indeed Hutchinson(1957), considering the possibility of two species occupying identical niches,stated that "...this is so unlikely that the case is of no empirical interest".

b) Therefore if two species compete for a limited resource, one will eventually prevail. This principle was implicit in the mathematical models of competition by Lotka (1925, 1932) and Volterra (1926) and has since been supported by many laboratory (e. g. Gause 1934, Park et al. 1941, Park 1948 and Crombie 1947) and field studies (e. g. Lack 1944a, 1971; Cooper and Dobzhansky 1956).

shown, for example, for some British finches (Fringillidae) by Newton (1967). The first problem, therefore, is how are species, that apparently overlap in distribution and ecology, ecologically segregated?

2) Factors that influence the ranges and habitat distributions of wheatears:

The second main problem that is considered in this study concerns the factors that influence the ranges and habitat distributions of wheatears. These factors are of interest for several reasons which will be briefly outlined below:

a) The ranges and habitat distributions of wheatears tend to end rather abruptly and the factors that limit them are often obscure since the boundaries rarely coincide with any obvious deficiency or restraint in the environment. This problem was noticed in Palestine over a hundred years ago by Canon Tristram who, in 1867, described it admirably in the following words: "...in the case of the resident chats, their extremely restricted habitat is remarkable. Often within very narrow limits they are numerous, yet do not occur beyond these in districts apparently as well suited for their development."

b) Many species of wheatear differ in range and/or habitat and the factors which account for these differences are not immediately clear since all species of wheatear are rather similar in size, morphology and broadly speaking in their ecological requirements.

c) Since the various species of wheatear have similar ecological requirements and hence are potential competitors, and since evidence of competition between different species of wheatear has been reported by a number of workers (e.g. Eggebrecht 1943; Hartley 1949,1950; Stresemann 1950; Simmons 1951; Ali and Ripley 1973) it seems likely that interspecific competition may be an important factor in shaping the ranges and habitat distributions of wheatears.

AIMS OF STUDY:

In this study the two problems outlined above were investigated

within the context of S. W. Iran where wheatears had not previously been studied in detail (see below) and where the problems could be investigated with particular advantage for the following reasons:

a) As shown on p. 4 the genus Oenanthe is better represented in S. W. Iran than anywhere else (see also fig. 1).

b) A preliminary survey showed that the pattern of coexistence between the various species was particularly complex, with some species differing in geographical distribution, altitudinal range and/or habitat while others were found side by side in what appeared to be the same or at least very similar habitats.

c) Some degree of interspecific competition was implied by frequent clashes between different species.

The 11 species that occur in S. W. Iran, together with their status in the area, are listed in fig. 2.

The main aims of the study may be summarised as follows:

1) to describe the distribution, status and ecology of wheatears in S. W. Iran (Chapters IV, V and VI);

2) to determine the means of ecological segregation between the various species (Chapter VII);

3) to investigate the factors that influence their ranges and habitat distributions (Chapter VIII).

PREVIOUS WORK ON WHEATEARS IN S. W. IRAN:

The distribution and ecology of wheatears in S. W. Iran have received little detailed attention and published information is limited to lists of specimens and/or sight records with brief notes on habitat and/or status that appeared in systematic lists, the most important of which were by the following workers: Blanford (1876), Sharpe(1886), Witherby (1903), Zarudny and Härms (1926), Capito (1931), Koelz (1954) and Erard and Etchécopar (1970).

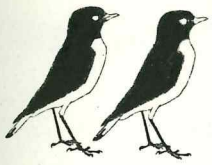
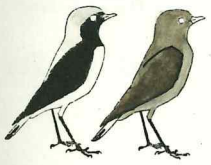
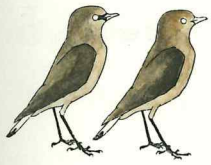
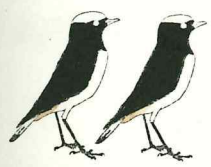
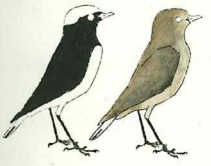
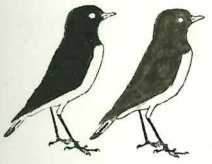
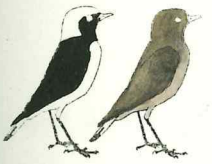
BREEDING PLUMAGE ♂ ♀	NOMENCLATURE	STATUS IN S.W.PERSIA			
		Breeding	Winter	Spring passage	Autumn passage
	O. alboniger (Hume's Wheatear)	+	+		
	O. deserti atrogularis (Desert Wheatear)	+	(+)?	(+)	(+)
	O. finschii finschii (Finsch's Wheatear)	+	+		
	O. hispanica melanoleuca (Black-eared Wheatear)	+			
	O. isabellina (Isabelline Wheatear)	+	(+)?	+	+
	O. lugens persica (Mourning Wheatear)	+		(+)	(+)
	O. monacha (Hooded Wheatear)	(+)?	(+)		
	O. oenanthe oenanthe (Common Wheatear)	+		+	(+)
	O. picata (picata phase) (Eastern Pied Wheatear)	(+)	(+)		
	O. pleschanka pleschanka (Pied Wheatear)	(+) ??		+	+
	O. xanthoprymna chrysopygia (Red-tailed Wheatear)	+	+	(+)	(+)

Figure 2. Plumage, nomenclature and status of the wheatears occurring in S. W. Persia, arranged alphabetically. + = common in suitable localities, (+) = small numbers, ? = unconfirmed. ?? = may breed occasionally.

INTRODUCTION

NOMENCLATURE:

For nomenclature I follow Vaurie (1959, 1965) and throughout I use the scientific names of the wheatear species as these, in their abbreviated forms, are shorter and, I believe, less easily confused than the English equivalents. These equivalents, together with the specific and subspecific names of the wheatears that were studied in S. W. Iran, are listed in figure 2.

LOCATION OF PLACES:

Most of the places in S. W. Iran that are mentioned in the text are marked on the map inside the front cover of this volume, but for the locations of topographic features see figure 4, p. 17 and for the locations of study areas see figure 7, p. 42.

CONVENTIONS ADOPTED:

References in the text to figures, tables and plates are made by number only (e. g. fig. 1, etc.) where the reference and the figure, table or plate are close together but where they are widely separated and likely to be difficult to find a page reference is added.

Where several species of wheatear are discussed in the text or appear in a figure or table they are treated in alphabetical order of their specific names unless there are good reasons for using a different order.

ACKNOWLEDGEMENTS:

During this study I have been helped by a great many people and several institutions and it is a pleasure to record my debt and gratitude to them.

My fieldwork in Iran was carried out while I was employed, first as a biology instructor and then as museum curator (part-time

in the last year), in the Biology Department at Pahlavi University in Shiraz which throughout provided generous logistic support and a secure base without which the fieldwork would have been exceedingly difficult and probably impossible. I enjoyed, and I mean enjoyed, free use of excellent office, laboratory and library facilities. I was allowed considerable liberty to plan my university commitments to fit in with fieldwork and I always travelled with official university backing which allayed the suspicions and ensured the cooperation of local authorities throughout S. W. Iran. I would like to thank all my friends at Pahlavi University very warmly for their unstinted support and many kindnesses and especially three successive Departmental Chairmen: M. Gettner, Dr. F. Hosseinie and Dr. S. Jahromi; and Hamid Assadi who accompanied me on many expeditions and helped with mist-netting and taxidermy.

I really enjoyed my fieldwork and this was in large measure due to the helpfulness and friendliness of the local people, particularly all those shepherds who skillfully manoeuvred their flocks between my mist-nets and all those mechanics who smilingly and cheaply kept my faithful old Land Rover on the road. It was equally due to many friends who accompanied me at different times and who helped in innumerable ways. These included: my late father; Dr. T. Butterfield; H. Grell; D. A. Ferguson; Dr. M. P. L., Dr. P. A. and S. C. L. Fogden; P. A. D. Hollom; Dr. C. B. Kepler; Dr. D. A. Scott; Dr. M. E. Taylor and throughout the last year my assistant Navarzollah Khalidge and my wife.

During the planning, interpretation and writing-up of the study I received much encouragement, advice and assistance from numerous people to whom I am extremely grateful. I would particularly like to thank my supervisor, the late Dr. D. Lack, F. R. S. for his guidance and encouragement during the greater part of the work and for making available the facilities of the Edward Grey Institute. I also wish to acknowledge with gratitude the profound influence his teaching has had on my interpretation of the distribution and ecology of wheatears in S. W. Iran. In addition I would like to extend special thanks to the following:

Dr. C. M. Perrins who after Dr. Lack's death added supervision of my work to his already heavy work-burden; C. C. Townsend of the Royal Botanic Gardens at Kew who identified a large collection of plants; Dr. A. P. Navai of the Iranian Meteorological Department who supplied meteorological data; P. J. Conder, S. Cramp, Dr. P. R. Grant, Dr. D. A. Scott, Dr. A. Zahavi and Dr. Y. Yom-tov who allowed me to use some of their unpublished data; D. I. M. Wallace who painted plate 1 in his inimitable masterly way; Dr. D. G. Dawson, Dr. E. K. Dunn, L. Schifferli and M.Webber who patiently helped with my statistical problems; Dr. A. W. Diamond, Dr. M. P. L. Fogden, A. J. Gaston, P. A. D. Hollom, Dr. P. J. Jones, Dr. D. Lack, Dr. H. F. Lamprey, Dr. D. H. Morse, Dr. C. M. Perrins and R. P. Prŷs-Jones who read all or parts of earlier drafts of the manuscript and suggested many improvements; D. F. Vincent who checked the references; the staff and students of the Edward Grey Institute for much kindness and help in many ways; my parents for their support and encouragement; and my wife, Rosalie, who helped in a multitude of ways including collecting and identifying arthropods, preparing the final versions of most of the figures, typing the manuscript and gastronomically.

I am also extremely grateful to the British Ornithologists' Union for the award of a generous studentship which supported me during the last year in the field and during the writing-up in Oxford.

CHAPTER II

THE ENVIRONMENT OF S. W. IRAN

GEOGRAPHICAL LIMITS OF THE STUDY:

The study was carried out in the area shown in figure 3 which I refer to as S. W. Iran or S. W. Persia. The limits of the area are shown in more detail in figure 4. It includes all of the province of Fars; most of the province of Persian Gulf and Sea of Oman Ports and Islands; and parts of the provinces of Khuzistan, Isfahan and Kerman (see map inside front cover). The total land area is approximately 404,000 km^2 (cf. The British Isles with an area of c. 313,000 km^2).

TOPOGRAPHY:

S. W. Persia has very varied topography the main features of which are shown in figure 4. The area is traversed from northwest to southeast by the Zagros mountains which separate the coastal plain of the Persian Gulf from the high plateau of central Iran. The coastal plain is rather narrow, mostly between one and 30 km wide, and at its greatest extent between Bushire and Dalaki it is only 70 km in width. It is everywhere between sea level and 150 m above sea level and is largely composed of flat or gently undulating alluvial silts and gravels (plate 16). The Zagros rise steeply either directly out of the sea or from the coastal plain and form a belt of impressive folded mountains roughly 300 km wide. The fold structures in many areas are very regular forming long parallel hogs' backs which are aligned from northwest to southeast. The intervening synclines have been mostly filled in to give flat valley bottoms (plate 4). The hogs' backs are closest together and reach their highest elevations in the northwest where Kuh-i-Dinar rises to 4,404 m above sea level. Towards the southeast the ridges become generally lower and more widely spaced with broader valleys between them. There is also greater dislocation and over-thrusting giving more broken country. The mountain sides in the Zagros

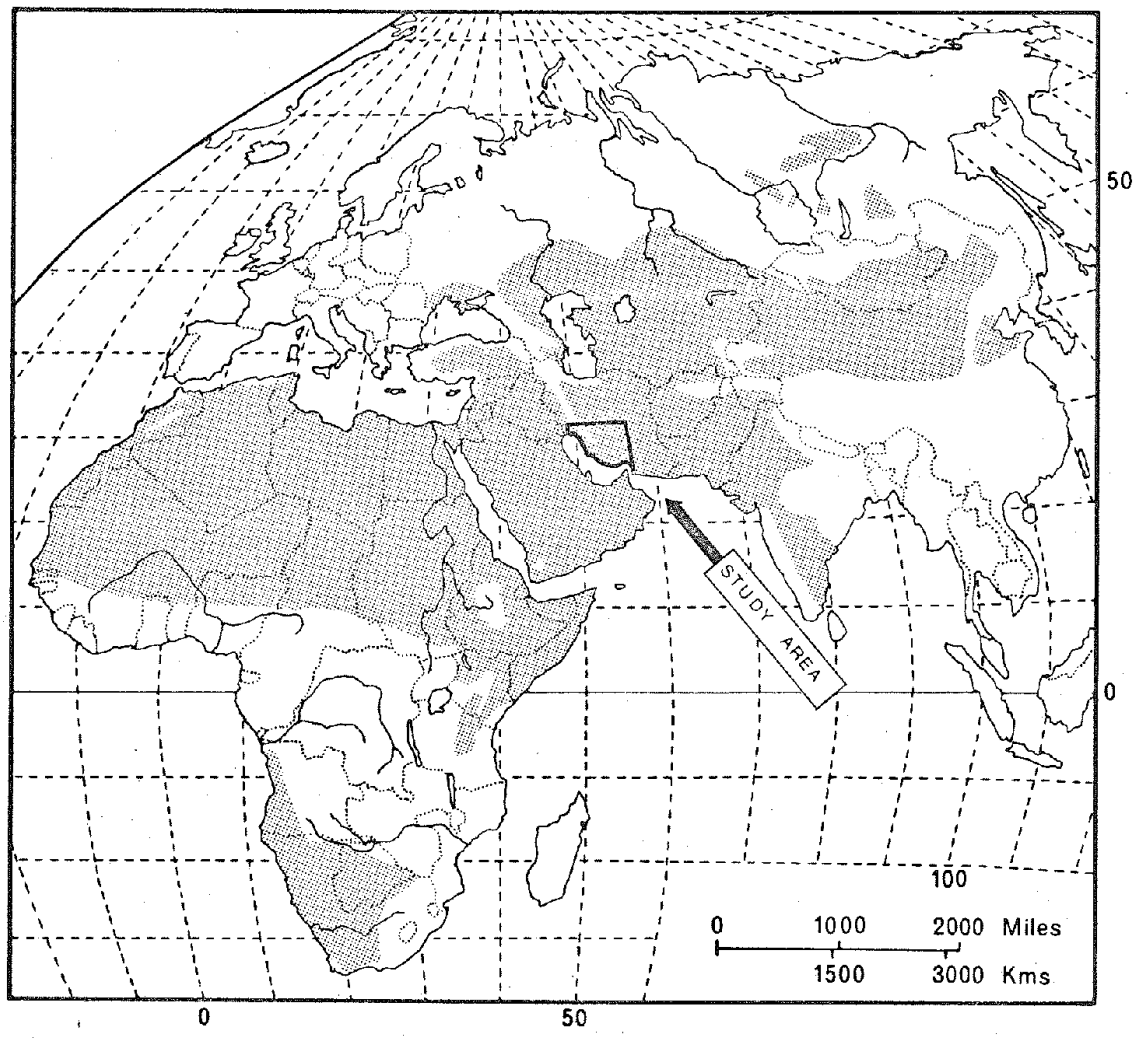
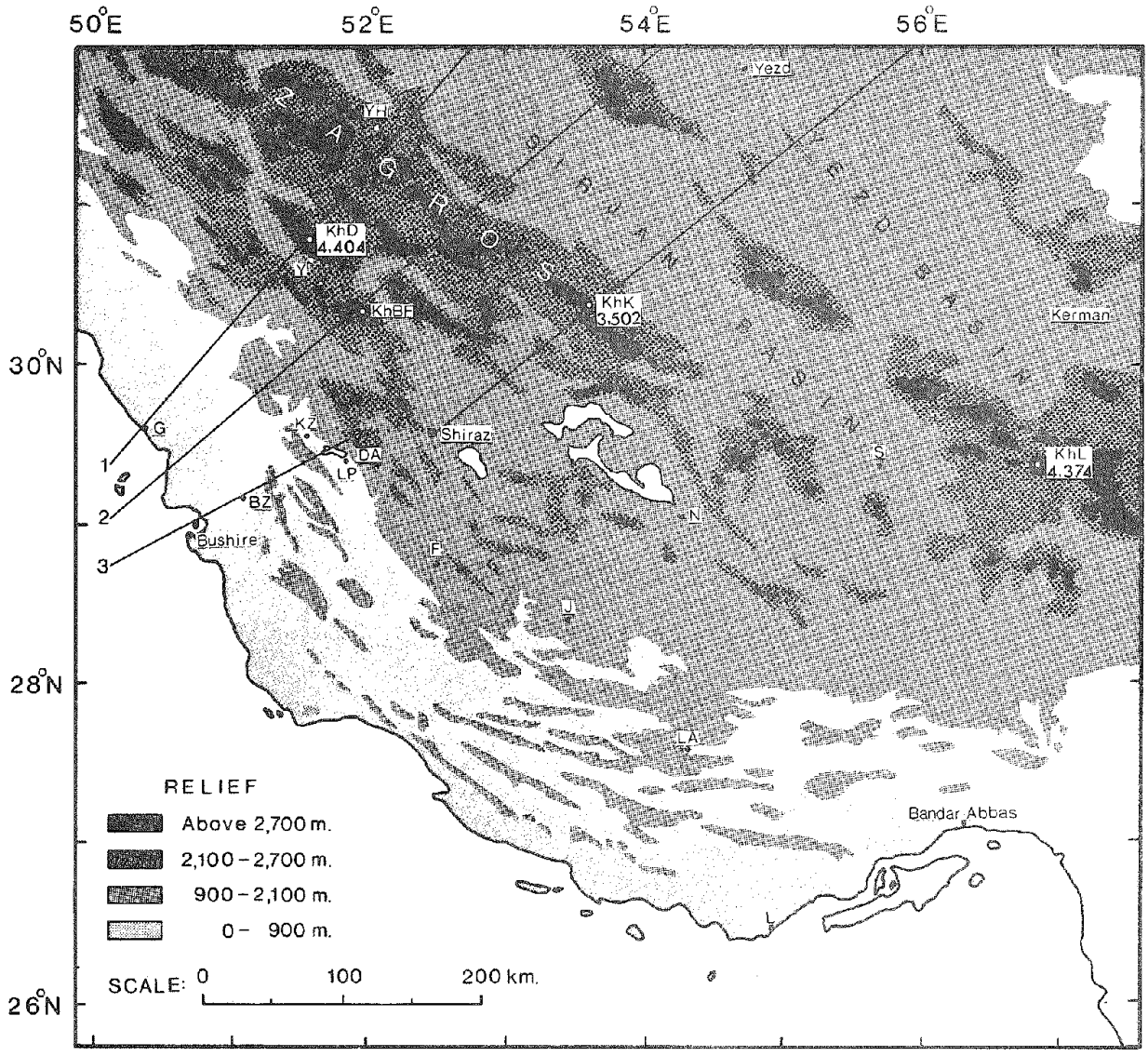
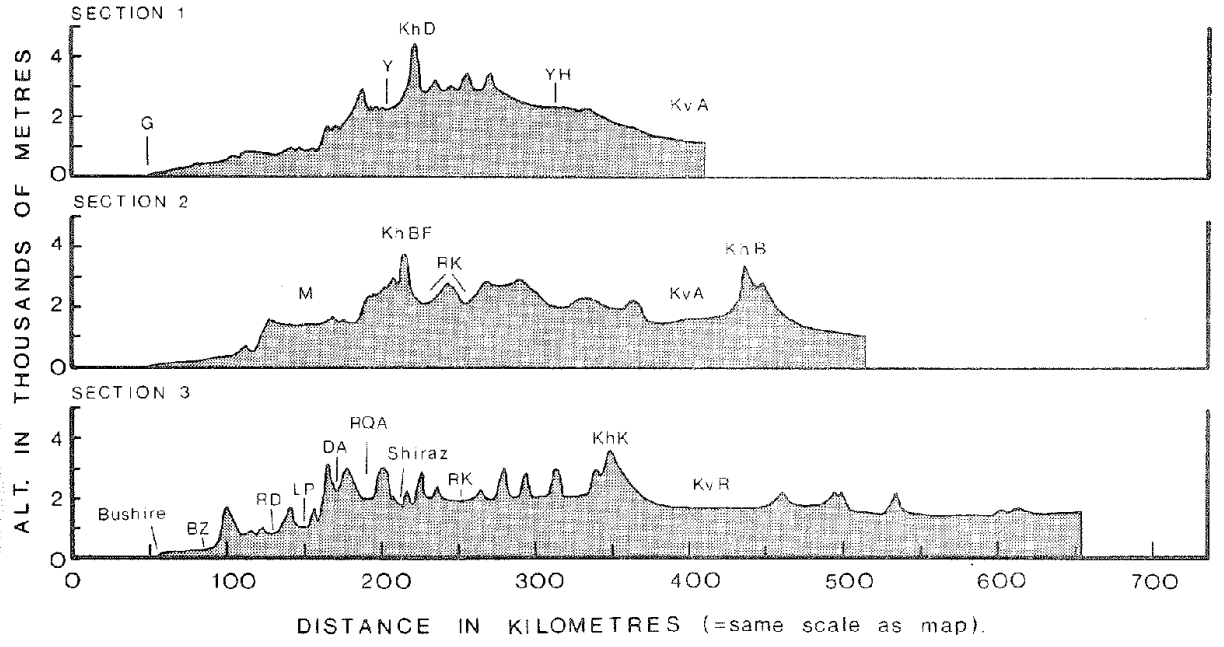


Figure 3 . Map of the Old World showing the distribution of the arid zone and the limits of the study area in S.W.Iran.

KEY

Extremely arid, arid and semiarid areas (Simplified after Meigs 1953).





KEY

TOWNS AND AREAS

BZ – Borazjan
DA – Dasht-i-Arjan
F – Firuzabad
G – Ganaweh
J – Jahrum
KZ – Kazerun
L – Lengeh
LA – Lar
LP – Lake Perishan
N – Niriz
M – Mamasani
S – Sirjan
Y – Yasuch
YH – Yezd-i-Kharst

MOUTAINS (Kuh in Farsi)
(spot heights in metres)

KhB – Kuh-i-Bunkahar
KhBF – Kuh-i-Barm-i-Firuz
KhD – Kuh-i-Dinar
KhK – Kuh-i-Khatun
KhL – Kuh-i-Lalehzar

RIVERS

RQA – R. Qara Aghach
RK – R. Kur
RD – R. Dalaki

SALT WASTES (Kavir in Farsi)

KvA – Kavir-i-Abarghuh
KvR – Kavir-i-Ribat

Figure 4. The topography of S. W. Iran.

are mostly steep and rocky with little soil. The valley bottoms are predominantly of silt usually with dense stones and gravel near the valley sides which decrease in abundance away from the hills.

The rocks in the Zagros are mainly Tertiary and Upper Mesozoic limestones, sandstones, shales, and marls which are predominantly pale brick-red, pale grey or pale brown. They are softest in the south-western foothills where gypsum, rock salt, anhydrite, marl, silt, and sandstones form typical "badlands" (plate 15). The massive hogs' backs of the higher Zagros are mostly hard Asmari (Oligo-Miocene) and Cretaceous limestones.

To the northeast the Zagros give way to a series of inland drainage basins on the Persian plateau. These are separated by low divides or well developed mountain ranges as between the Sirjan and Yezd basins, where Shir Kuh (45 km S. W. of Yezd) reaches 4,075 m above sea level. The basins include vast tracts of flat or gently undulating country mostly between 1,000 and 1,500 m above sea level. The lower parts are occupied by temporary salt lakes, salt slime and mud or dry salt crust depending on the season. These salt wastes or playas are known as kavirs in Farsi.

CLIMATE:

S. W. Persia lies approximately at the centre of the Old World arid zone (fig. 3). However in the Zagros the aridity is somewhat ameliorated by orographic precipitation. This precipitation and the influence on temperature of the varied relief combine to give a wide range of climatic conditions in S. W. Persia.

Until the establishment of the Iranian Meteorological Department in 1956, few meteorological records were kept in S. W. Persia. However since then 60 recording stations have been set up in the area. At 40 of these, records of precipitation have been kept for five or more years and at 27, temperature records for five or more years. These data have

been published in Meteorological Year Books (Iranian Meteorological Department 1956-1968) and form the basis of the following account of climate. I have had to use these raw data since the only published analyses of the climate of S. W. Persia occur in general works on the climate of Iran (e. g. Naval Intelligence Division 1945, Ganji 1968) and are not detailed enough for the present study.

Precipitation:

Precipitation in S. W. Persia is almost entirely confined to the winter and spring falling mainly between late October and the end of April (fig. 5). It is mostly brought by depressions which move eastwards from the Mediterranean. They cross the low-lying northern part of the Arabian peninsula, but retain most of their moisture until they rise over the Zagros. Precipitation in S. W. Persia is greatest over the western highlands of the Zagros which receive over 400 mm (mean annual) and where the highest recorded mean annual precipitation is 575 mm at Emam Ghaiss which has an altitude of 2,400 m above sea level. As the depressions move eastwards they become exhausted of moisture and the eastern rim of the Zagros and the central plateau are in a rain shadow and mostly receive less than 200 mm mean annual precipitation (overlay 1[1]). The amount of precipitation varies widely from year to year, both droughts and flooding being of regular occurrence. In 1970-71, when most of the fieldwork for this study was done, the winter rains were poor (fig. 5) and consequently there was little flush of vegetation in the following spring. Figure 5 illustrates three important features of the rainfall regime in S. W. Persia: 1) its seasonality, 2) its irregularity, and 3) the contrast in amount between a low-lying station on the coast (Bushire), a station in the Zagros (Shiraz) and one in the rain shadow (Kerman).

Temperature:

The strongest influences on actual surface temperatures in

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[1]Overlays are stored in a pocket at the end of this volume, but since these can easily be lost, photocopies of them are bound in with the text.

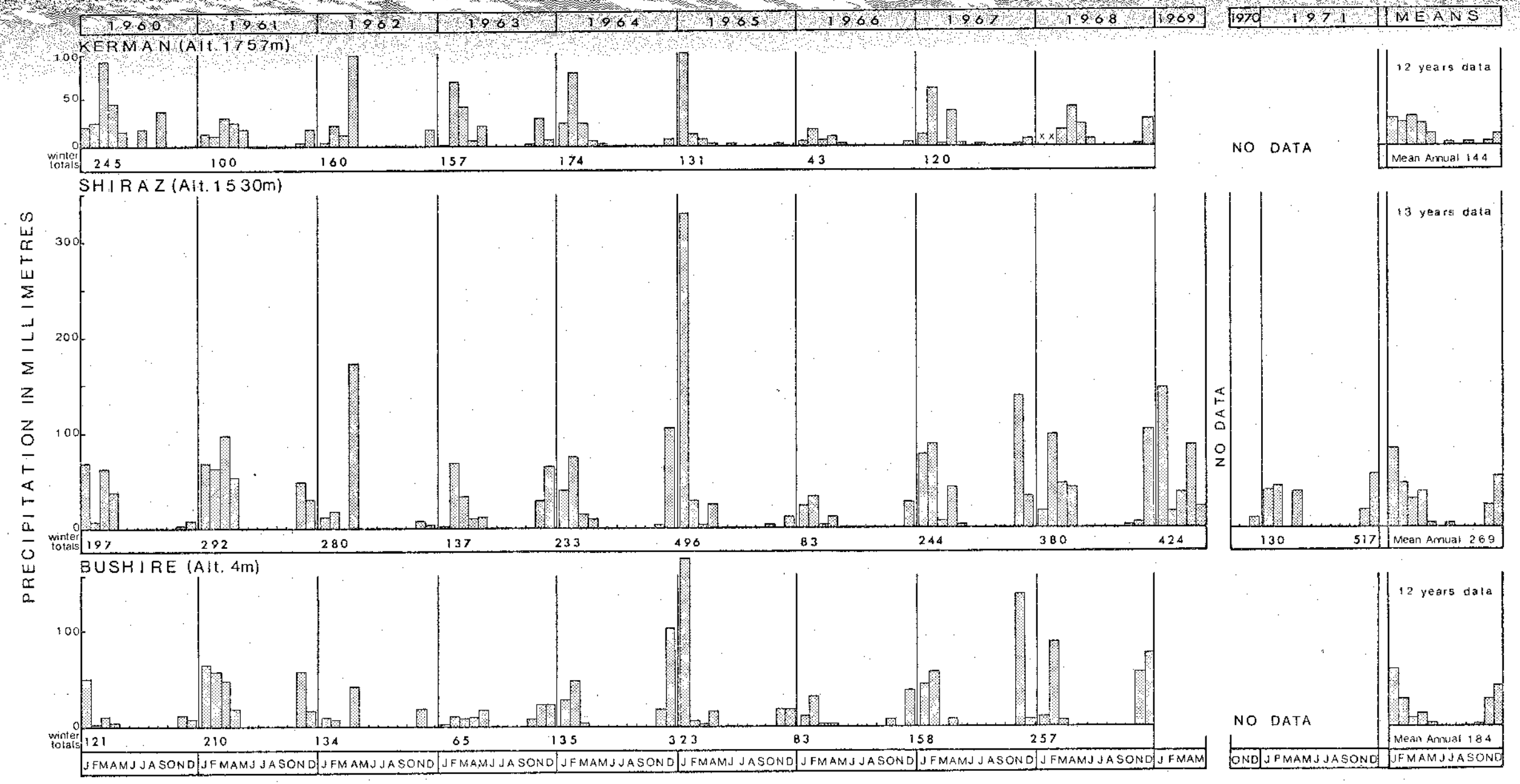
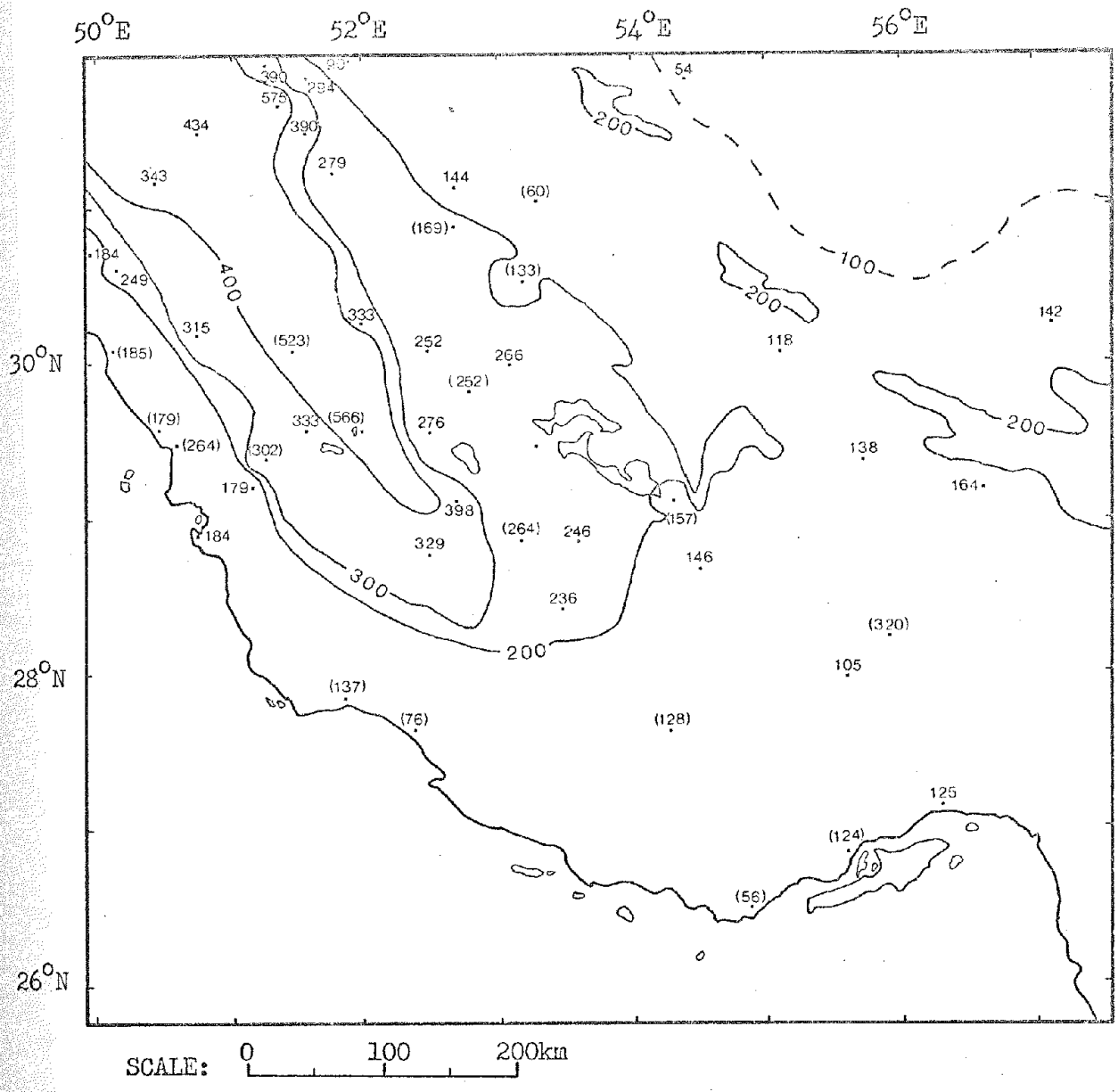


Figure 5. Monthly precipitation at three stations in S.W. Persia.

x = missing values

(Data from Met. Year Books 1956–1968 (Iranian Met. Dept. Tehran) and unpublished records 1969–1971 (Met. Office Shiraz).)

MEAN ANNUAL PRECIPITATION



KEY

127 Mean annual precipitation based on five or more years of data.

(128) Mean annual precipitation based on two-four years of data.

Isohyets drawn with reference to the plotted values and the local relief.

Isohyets with doubtful alignment.

Overlay 1. Mean annual precipitation (millimetres) in S. W. Iran.

(Based on Meteorological Year Books 1956-1968 published by the Iranian Meteorological Department, Tehran.)

S. W. Iran are the seasons and the topography. This is because maritime influence is restricted to a narrow coastal belt by the bulwark of the Zagros and because temperatures are only rarely affected by air masses from elsewhere, as when the Siberian high pressure belt extends over the area in winter bringing with it cold continental air from central Asia. Analyses of the relationships between mean monthly temperatures at various stations in S. W. Iran and altitude showed that in all months a large and significant proportion of the variation in temperature between the stations was explained by the differences in altitude (appendix A). The forms of these relationships are indicated by fitted linear regression lines of mean monthly temperatures on altitude (appendix A). These regression lines can be used to estimate mean monthly temperatures for any locality of known altitude in S. W. Iran and they have been used in this way in the construction of figure 6 in which the annual cycle of temperature in S. W. Iran is summarised. Owing to the lack of maritime influence and the prevalence of clear skies, the mean annual temperature range* is everywhere large (approximately 22°C, cf. Oxford, England, where the mean annual range is 13.3°C), with January the coldest and July the hottest month. For the same reasons the diurnal range of temperature at inland stations is also considerable, being usually 15° - 20°C. Due to the range of altitude there are considerable regional differences in temperature regime. On the coast at Bushire the mean annual range of temperature is 14.3° - 32.6°C, at Shiraz (1,530 m above sea level) 5.9° - 28.2°C and at Mehre Gird (2,600 m above sea level) in the high Zagros 0.8° - 20.1°C. The distributions of mean monthly temperatures in January and July are given in overlays 2 and 3.

BIOCLIMATIC ZONES:

The regional differences in precipitation and temperature in S. W. Iran produce a wide range of climatic conditions which strongly influence the vegetation. I defined the boundaries of the main bio-climatic zones of S. W. Iran (overlay 4) using the classification of Pabot (1967) and applying it to my own data on climate and the

*The annual range of temperature is defined as the difference between the mean temperatures of the warmest and coldest months (Trewartha 1954).

S. W. Iran are the seasons and the topography. This is because maritime influence is restricted to a narrow coastal belt by the bulwark of the Zagros and because temperatures are only rarely affected by air masses from elsewhere, as when the Siberian high pressure belt extends over the area in winter bringing with it cold continental air from central Asia. Analyses of the relationships between mean monthly temperatures at various stations in S. W. Iran and altitude showed that in all months a large and significant proportion of the variation in temperature between the stations was explained by the differences in altitude (appendix A). The forms of these relationships are indicated by fitted linear regression lines of mean monthly temperatures on altitude (appendix A). These regression lines can be used to estimate mean monthly temperatures for any locality of known altitude in S. W. Iran and they have been used in this way in the construction of figure 6 in which the annual cycle of temperature in S. W. Iran is summarised. Owing to the lack of maritime influence and the prevalence of clear skies, the mean annual temperature range* is everywhere large (approximately 22°C, cf. Oxford, England, where the mean annual range is 13.3°C), with January the coldest and July the hottest month. For the same reasons the diurnal range of temperature at inland stations is also considerable, being usually 15° - 20°C. Due to the range of altitude there are considerable regional differences in temperature regime. On the coast at Bushire the mean annual range of temperature is 14.3° - 32.6°C, at Shiraz (1,530 m above sea level) 5.9° - 28.2°C and at Mehre Gird (2,600 m above sea level) in the high Zagros 0.8° - 20.1°C. The distributions of mean monthly temperatures in January and July are given in overlays 2 and 3.

BIOCLIMATIC ZONES:

The regional differences in precipitation and temperature in S. W. Iran produce a wide range of climatic conditions which strongly influence the vegetation. I defined the boundaries of the main bio-climatic zones of S. W. Iran (overlay 4) using the classification of Pabot (1967) and applying it to my own data on climate and the

*The annual range of temperature is defined as the difference between the mean temperatures of the warmest and coldest months (Trewartha 1954).

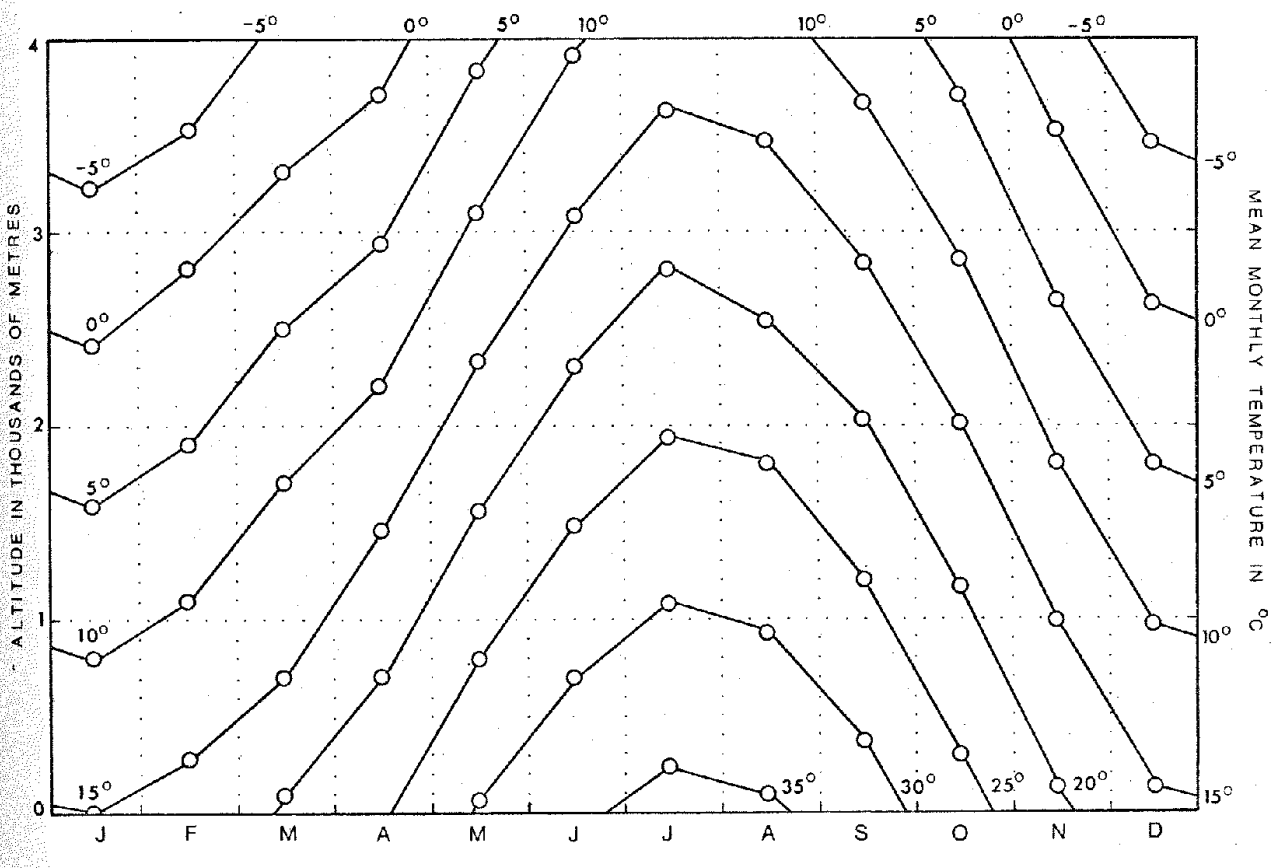
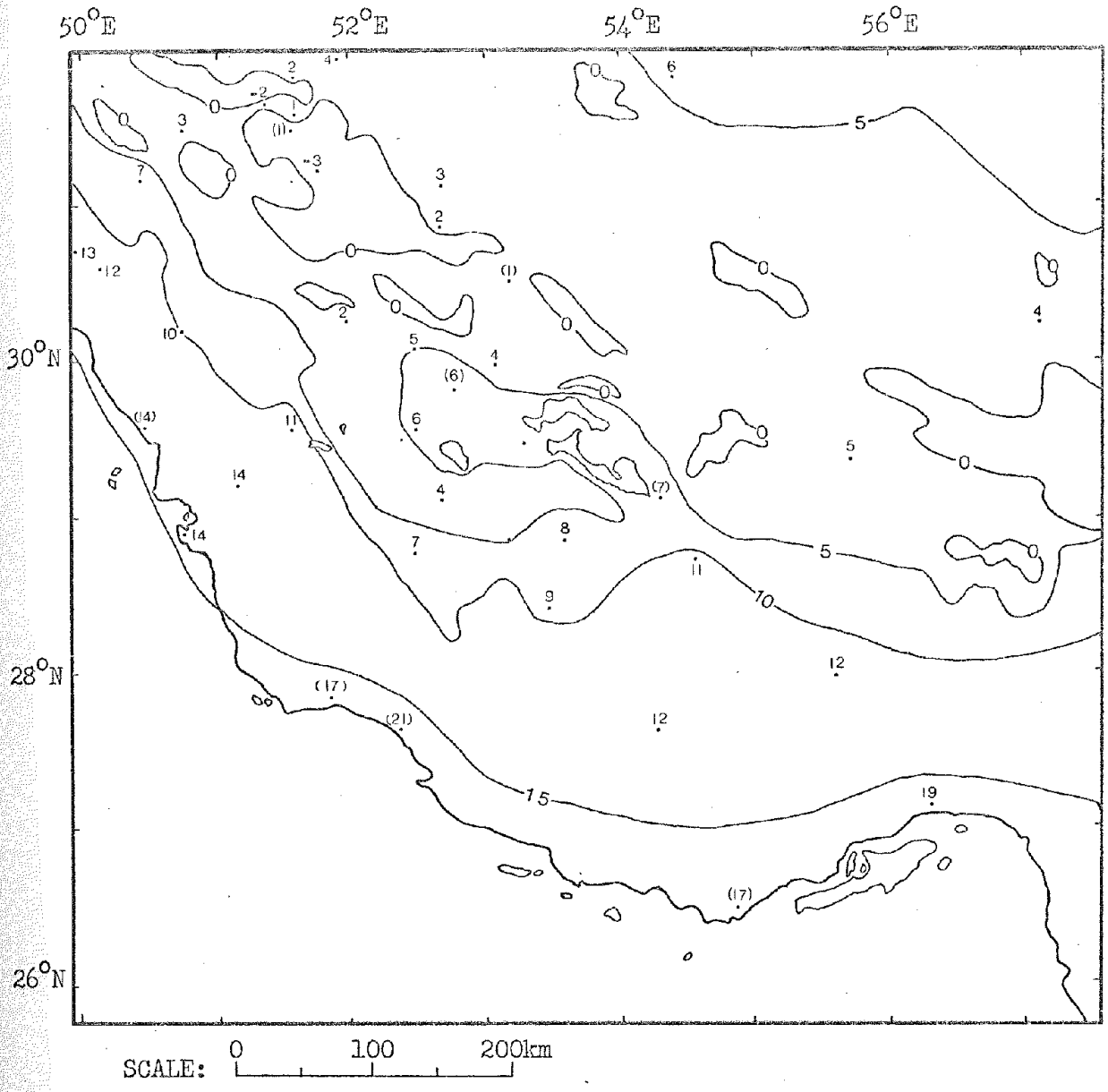


Figure 6. Annual cycle of temperature (°C) in S. W. Iran.

(Based on regression analyses of mean monthly temperature on altitude. See appendix A.)



KEY

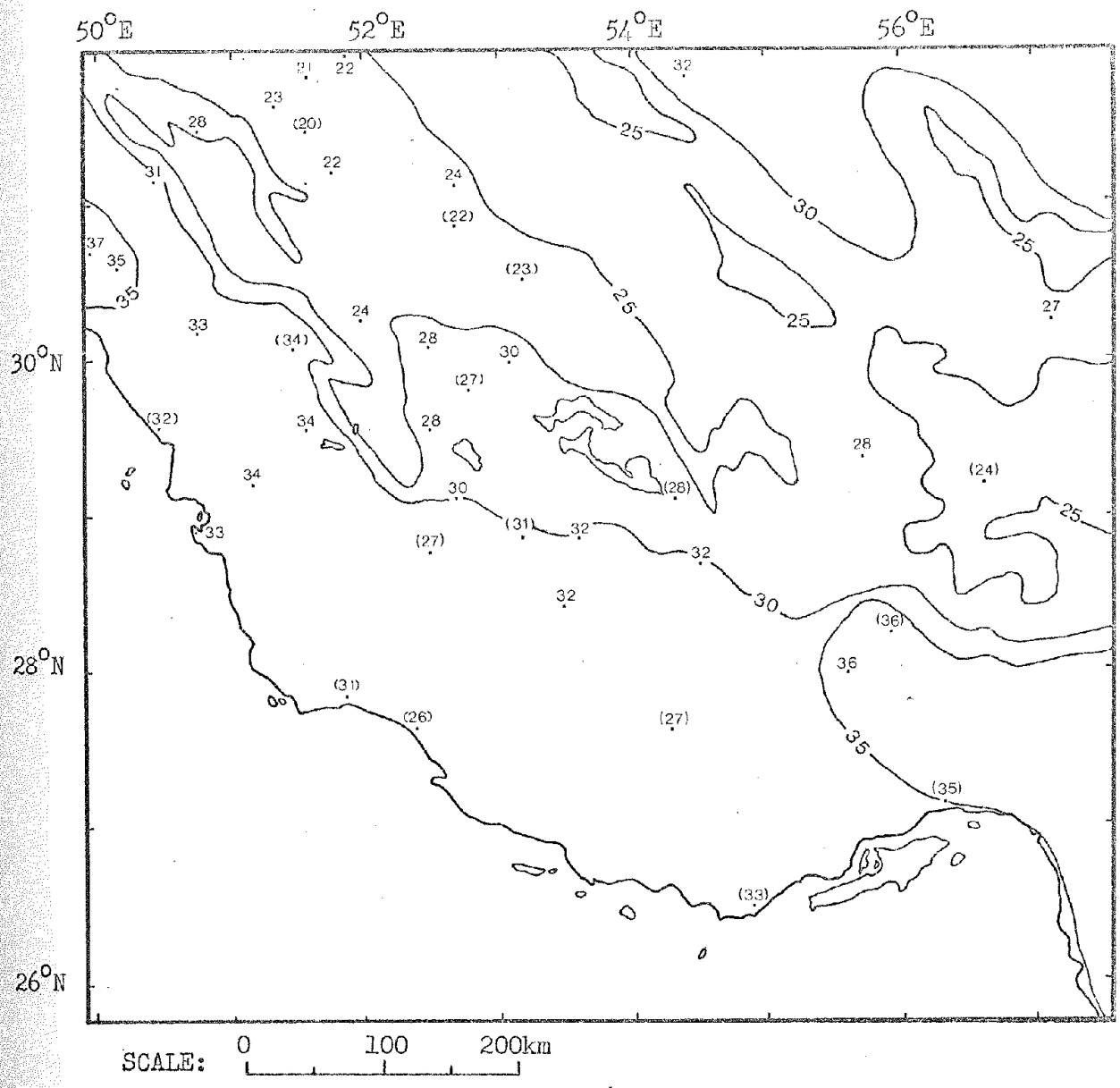
13 Mean monthly temperature based on five or more years' data.

(15) Mean monthly temperature based on two-four years' data.

Isotherms drawn with reference to plotted values and the local relief.

Overlay 2. Mean monthly actual surface temperatures (°C) for January in S. W. Persia.

(Based on Meteorological Year Books 1956-1968 published by the Iranian Meteorological Department, Tehran.)



KEY

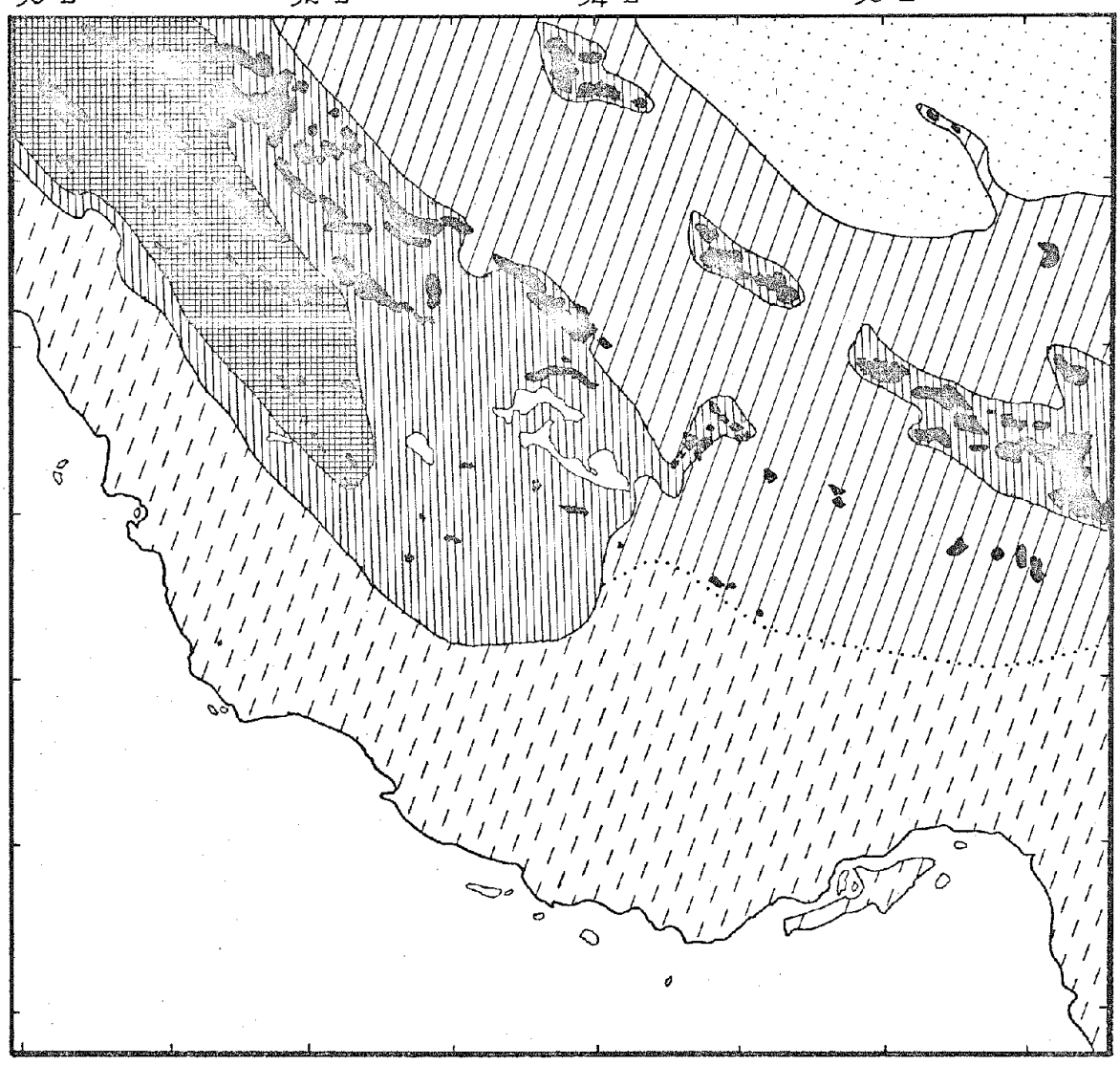
32 Mean monthly temperature based on five or more years' data.

(28) Mean monthly temperature based on two-four years' data.

Isotherms drawn with reference to plotted values and the local relief.

Overlay 3. Mean monthly actual surface temperatures (°C) for July in S. W. Persia.

(Based on Meteorological Year Books 1956-1968 published by the Iranian Meteorological Department, Tehran.)



KEY

- Montane zone (above 2,700m).
- Xerophilous forest (>400mm mean annual precipitation).
- Sub-steppe (200-400mm mean annual precipitation).
- Cold steppe (100-200mm mean annual precipitation) (mean temperature in January <10°C).
- Warm steppe (100-200mm mean annual precipitation) (mean temperature in January >10°C).
- Sub-desert (<100mm mean annual precipitation).

Overlay 4. Bioclimatic zones of S. W. Persia. (For summary of characteristics of each zone see table 2 and for method of delimitation see text pages 22 & 28.)

BIOCLIMATIC ZONE*	APPROXIMATE ALTITUDINAL RANGE (metres)	MAIN VEGETATION TYPES	MEAN ANNUAL PRECIPITATION (mm)	MEAN MONTHLY TEMPS (°C)		CLIMATIC DIVISION**	
				JANUARY	JULY		
MONTANE	Above 2,700	Open stony ground, scree and cliffs with scattered thorn-cushions and spiny shrublets giving way to low density bush communities often dominated by Astragalus spp. or Daphne acuminata towards the lower limits of the zone.	Prob. 600+ in west Prob. 300+ in east	<-2	<20	Sub-humid	
XEROPHILOUS FOREST	800-2,700	Low density oak woodland dominated by Quercus brantii. Now much reduced and replaced by steppe communities.	>400	-2-10	20-30		
SUB-STEPPE	700-2,700	Steppe communities with scattered trees of Pistacia atlantica and bushes of Amygdalus scoparia and Amygdalus eburnea. Now mostly replaced by steppe.	200-400	-2-10	20-30	Semi-arid Sc 13	
STEPPE a) Cold steppe	1,000-2,000	Steppe dominated by Artemisia spp., tragacanthic species such as Astragalus or bushes of Zygophyllum atriplicoides.	100-200	2-10 mostly <5	25-30	Ac 13	Arid
b) Warm steppe	0-1,000	Sparse steppe communities with, in places, scattered trees (mostly Acacia spp. and Ziziphus spp.) or bushes (particularly Ziziphus spp. and Calotropis procera).	100-200	10-20	30-40	Ac 24	
SUB-DESERT	800-2,000	Ground mostly bare, but with scattered shrublets and bushes in favoured localities.	<100	2-10	25-35	Ac 14	

Table 2. Bioclimatic zones of S. W. Persia.

*Categories slightly modified after Pabot (1967).

**Climatic divisions of Meigs (1953) showing rough correspondence with the bioclimatic zones.

S = semi-arid, A = arid, c = winter concentration of rain. The first and second figures denote the mean monthly temperature of the coldest and hottest month respectively. 1 = 0-10°C, 2 = 10-20°C, 3 = 20-30°C, 4 = 30°C.

distribution of selected vegetation types (appendix B). The characteristics of each zone are summarised in table 2. The boundaries thus defined correspond well with the climatic divisions of Köppen (as presented by Trewartha 1954) and Meigs (1953); with the vegetation divisions of Bobek (1951, 1968), UNESCO-FAO (1969) and Zohary (1963); and with the bioclimatic divisions of UNESCO-FAO (1963) and Pabot (1967).

VEGETATION:

In this section I describe the vegetation of each bioclimatic zone, paying special attention to the physiognomy of each vegetation type since habitat selection by birds has been shown to be strongly influenced by the density and structural features of vegetation (e. g. Lack 1933, 1937; MacArthur and MacArthur 1961; Cody 1968, 1974; Wiens 1969 and review by Hildén 1965). The terms used to describe the vegetation are defined below:

Thorn-cushion: Cushion-shaped spiny plant up to 50 cm high.

Shrublet: Woody plant up to 50 cm high which usually branches from the base.

Bush: Woody plant 50 cm - 2 m high which usually branches from the base.

Tree: Woody plant two or more metres tall, usually with central trunk, but sometimes branching from the base.

Steppe: Plant community dominated by shrublets and/or small (<50 cm) herbaceous plants. In S. W. Persia the individual plants are usually widely spaced with bare ground between each.

Bushland: Plant community dominated by bushes often mixed with steppe species and usually of low density with bare ground between each bush.

Wooded steppe: Steppe with scattered trees and usually a few bushes.

Woodland: Plant community dominated by trees, often with an undergrowth of bushes, shrublets and herbaceous plants.

I now consider the vegetation of each bioclimatic zone in turn:

1) Montane Zone:

This zone includes all mountain areas above 2,700 m above sea level. No climatic records have been kept but it is probable that mean monthly temperatures in January are below -2°C and in July less than 20°C. Mean annual precipitation probably exceeds 600 mm in the west and probably 300 mm in the east. This zone is characterised by bare rock faces, screes and stony ground with sparse vegetation dominated by thorn-cushions (including Acantholimon spp.) and spiny shrublets (including Astragalus spp.). During summer in favourable places annuals flourish, including particularly species in the families Cruciferae, Compositae (especially thistles), Labiatae, Euphorbiaceae, and Gramineae (plate 2). Towards the lower limits of the zone bushes, particularly of Astragalus sp., and Daphne acuminata become common and in some places there are scattered trees of Juniperus polycarpos and Lonicera nummularifolia (plate 3).

2) Xerophilous Forest:

Xerophilous forest is found on the western flanks of the Zagros between about 800 m and 2,700 m above sea level where mean annual precipitation exceeds 400 mm. Mean monthly temperatures range between -2°C and 10°C in January and 20° - 30°C in July. The forest is dominated by almost pure stands of the broad-leaved, deciduous Persian Oak (Quercus brantii). The trees are mostly between three and ten metres high and usually widely enough spaced for steppe communities to develop on the open ground between them (plate 5). In some places other tree species occur as well, such as Pistacia atlantica, Acer monspessularium and often there are scattered bushes including Crataegus sp., Amygdalus eburnea, Daphne acuminata and Cotoneaster racemiflora. The ground layer usually includes scattered shrublets and in the spring a crop of herbaceous annuals including particularly species in the families Compositae (especially thistles), Labiatae, Euphorbiaceae, Liliaceae

(especially Fritillaria imperialis), and Gramineae. During the spring the ground in some places becomes completely covered with vegetation (plate 6) but there is always some bare ground, the amount varying particularly with the stoniness of the ground, the rainfall and the grazing pressure.

The oak forests of S. W. Persia have been greatly depleted by man's activities and in many places only scattered trees or stunted secondary growth remains. In other areas the forest has been eliminated leaving bare rocky hills and plains with steppe vegetation and perhaps a few scattered bushes (plate 7).

3) Sub-steppe:

Sub-steppe communities occur where the mean annual precipitation is between 200 - 400 mm and are found in drier places along the lower edge of the oak woods on the western flanks of the Zagros and particularly in the dry leeward areas of the Zagros.

The climatic climax vegetation of the sub-steppe zone is wooded steppe, a steppe community with scattered trees, mostly Pistacia atlantica, and bushes, mostly Amygdalus eburnea and Amygdalus scoparia (Bobek 1968, Pabot 1967) (plate 8). The trees and bushes have largely been removed by man and today can be found only in isolated patches, where often the thorny Amygdalus eburnea predominates (plate 9). The steppe ground layer remains and is now the characteristic vegetation type of the sub-steppe zone. Heavy grazing by domestic sheep and goats has greatly influenced the steppe communities which are now dominated by anti-pastoral species and perennial grasses are relatively rare. There are two major types of steppe community. The first is dominated by relatively unpalatable Artemisia spp., mostly Artemisia herba-alba (plate 11). The second, tragacanthic steppe, is dominated by spiny shrublets such as Astragalus spp., Acantholimon spp., Acanthophyllum spp., Lactuca orientalis, and Noaea mucronata. Often the two types occur in mixed communities. The height of the shrublets varies from a few centimetres to about 50 cm and the distance between them from an

average of about 50 cm to several metres. At most times of year the ground between the shrublets is bare, but in spring there is a flush of herbaceous vegetation which varies in luxuriance with the rainfall and the grazing pressure. In years of high rainfall the surface of the ground may be completely covered over quite large areas for several weeks by a dense sward including particularly species in the families Cruciferae, Compositae (especially thistles), Papaveraceae, Gramineae, and Cyperaceae (especially Carex stenophylla).

On saline ground there are plant communities of similar structure but dominated by halophytic plants. The commonest species are in the family Chenopodiaceae and include the shrublets Halocnemum strobilaceum, Seidlitzia rosmarinus, Salsola spp., Suaeda spp., and various bushes including Haloxylon spp. Bushes and small trees of Tamarix spp. are also common.

4) Steppe:

The steppe zone occupies areas with a mean annual rainfall of between 100 - 200 mm, and is sub-divided on the basis of temperature.

a) Cold Steppe:

Cold steppe conditions are found on the Persian plateau between about 1,000 - 2,000 m above sea level. Mean monthly temperatures in January go down to between 2° - 10°C and over most of the area are below 5°C. Summers are warm with mean monthly temperatures in July varying between 25° - 30°C. In the west of this zone the characteristic vegetation is steppe similar to that found in the sub-steppe zone, but as rainfall diminishes towards the east, gradual changes take place including the following: 1) the density of the communities decreases, 2) more drought-resistant plant species become dominant and 3) pressure on the vegetation from fuel-gathering and grazing becomes less with two results: a) many of the steppe shrublets such as Artemisia spp., which are invariably closely cropped by grazing animals in the sub-steppe zone and the wetter western parts of the cold steppe zone, grow to 30 cm or more in the drier parts

of the cold steppe zone and b) in the latter areas bushes are able to survive and the vegetation is often dominated by them, particularly the xerophytic form Zygophyllum atriplicoides (plate 12). These bushes are generally widely spaced (2 - 10 m apart) with bare ground and scattered shrublets between them. They are mostly about one metre tall, but some reach a height of two metres. They owe their stature to age. I cut sections of branches from several bushes of Zygophyllum atriplicoides, obtained near Sirjan, and although none was more than a metre tall, counts of annual rings revealed that they were all over a hundred years old.

b) Warm Steppe:

Warm steppe conditions are found on the coastal plain and in the foothills of the Zagros below about 1,000 m above sea level. Mean monthly temperatures in winter range from 10° - 20°C which means that there is no period when plant growth is inhibited by low temperatures.* Consequently there is a flush of vegetation as soon as the rains come (which contrasts with the rest of S. W. Iran where mean monthly temperatures fall below 10°C and growth of vegetation is delayed until temperatures rise in the spring). The summers in the warm steppe area are hot, mean monthly temperatures in July ranging from 25° - 30°C. Apart from the growth of short herbaceous vegetation in winter and spring, which may be dense in places, the vegetation of this zone is generally sparse. Usually the ground is bare with only a few scattered shrublets (plates 15 and 16). However in favoured localities there are scattered bushes and trees including particularly Ziziphus spp. (plate 13), Acacia spp. (plate 14), Prosopis spp., and Calotropis procera.

5) Sub-desert:

Sub-desert occurs in areas where the mean annual precipitation

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*Growth of many plants begins at about 10°C (Meigs 1953), and in Iraq, Guest (1966) found that despite sufficient rainfall the growth of vegetation was delayed until the spring in areas with mean January temperatures below 10°C. This seems to apply in S. W. Iran as well.

is less than 100 mm. In S. W. Persia such conditions are found in the Yezd basin and extend eastwards. Vegetation is restricted to favoured places such as dry water courses where scattered shrublets and bushes, particularly Tamarix spp., are found.

IMPACT OF MAN:

S. W. Iran has been inhabited by man since prehistoric times and in considerable densities for more than 3,000 years (Naval Intelligence Division 1945). During this period he has played an important part in molding the present-day landscape particularly through his activities as a cultivator, pastoralist and gatherer of woody fuel.

Cultivation:

Owing to the low precipitation over most of the area and its concentration during the winter months most of the arable farming relies on irrigation. As a result of this and the rocky nature of much of the terrain the proportion of land under cultivation is relatively small (probably between 10 and 20 per cent of the land surface) and is mainly concentrated around scattered villages in alluvial plains and broad valley bottoms. The remainder of the land surface is largely undeveloped and supports the types of vegetation described above.

Grazing and fuel-gathering:

The vegetation, particularly of the wetter more densely populated parts of S. W. Iran, has been greatly modified and severely degraded by the grazing of domestic stock and the gathering of woody vegetation for fuel. Over much of the area trees and bushes remain only in relict patches and steppe communities have become dominated by anti-pastoral species.

THE IMPORTANCE OF GRAZING IN CREATING WHEATEAR HABITAT

From the point of view of wheatear ecology a very important feature of the present vegetation of S. W. Iran is that there is rarely

a continuous ground layer. This allows all the bioclimatic zones to be inhabited by wheatears which require open bare ground on which to feed. The bareness of the ground, at least in the forest, sub-steppe and the wetter parts of the steppe zones, is largely due to over grazing. This has been dramatically demonstrated in an exclosure established by the Iranian Ministry of Agriculture at Dorayesardabeh near Shiraz. After nine years without grazing the surface of the ground has become almost completely covered by a thick perennial layer of mostly herbaceous vegetation dominated by tussock grasses, particularly Bromus tomentellus. Plate 10 shows the area after four years without grazing. The area is now unsuitable for wheatears, and it therefore seems likely that in the absence of grazing by domestic stock there would be much less habitat for wheatears in S. W. Iran.



Plate 2. Montane zone of Kuh-i-Barm-i-Firuz showing vegetation dominated by thorn-cushions. O. oenanthe held breeding territories on the flatter ground and O. xanthoprymna in the gullies and on the valley sides. (c. 2,500 - 3,600 m, June 1971).



Plate 3. Lower limits of the montane zone on Kuh-i-Dinar. The dark trees on the hillsides are Juniperus polycarpos. The bushes in the foreground are mostly Daphne acuminata. O. xanthoprymna was a common breeding bird in this area. (c. 2,700 - 4,000 m, August 1967).



Plate 4. The Dasht-i-Barm in the Zagros between Dasht-i-Arjan and Kazerun showing parallel hogs'backs with intervening plain. The vegetation is sparse oak woodland dominated by Quercus brantii. (c. 900 - 2,500 m, xerophilous forest zone; November 1967).

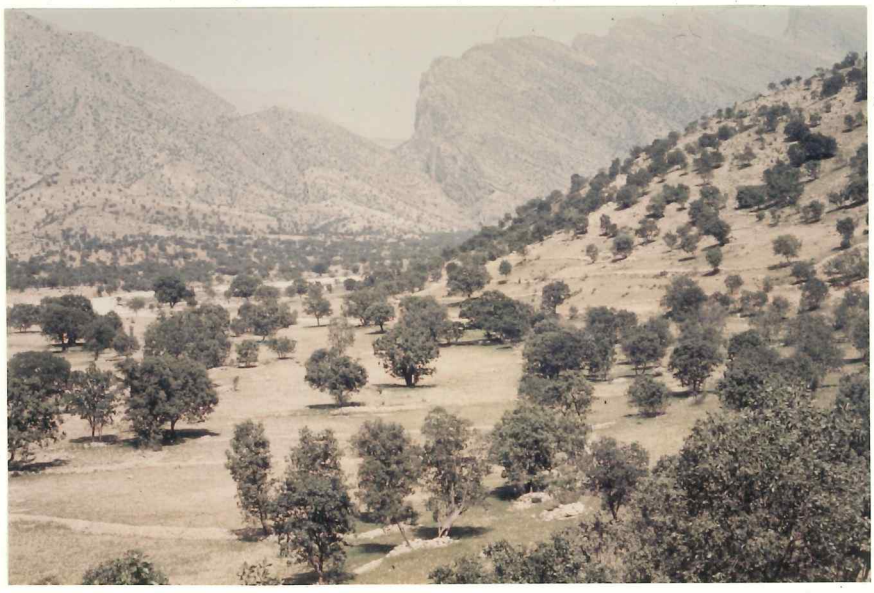


Plate 5. Oak woods dominated by Quercus brantii in the Zagros between Dasht-i-Arjan and Kazerun. This is typical breeding habitat for O. hispanica. (c. 1,600 - 2,500 m, xerophilous forest zone; May 1972).



Plate 6. In the xerophilous forest zone the ground is often completely covered in places by a spring flush of herbaceous vegetation. The plants with the red flowers are Fritillaria imperialis. (c. 2,400 m, May 1968).



Plate 7. The valley of Tang-i-Shul, 50km north of Shiraz, in the xerophilous forest zone which has been denuded of trees. O. finschii, O. lugens, O. isabellina and probably O. hispanica bred in this valley. (c. 2,200 - 2,700 m, May 1968).

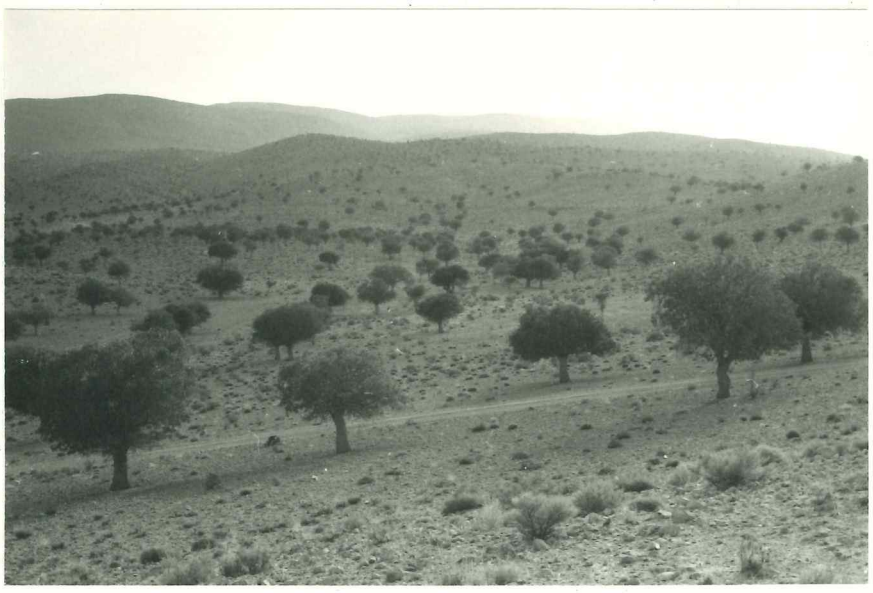


Plate 8. Wooded steppe, a hundred kilometres northeast of Shiraz, with Pistacia atlantica the dominant tree. (c. 2,000 - 2,500 m, sub-steppe zone; July 1971).



Plate 9. Remnants of wooded steppe near Gumoon. All that is left are a few scattered trees of Pistacia atlantica and thorny bushes of Amygdalus eburnea. The rocky hillside and cliffs behind were the habitat of O. alboniger. (c. 1,650 m, sub-steppe zone; February 1971).



Plate 10. Exclosure, near Shiraz, showing the regeneration of herbaceous vegetation dominated by Bromus tomentellus after four years without grazing. (c. 1,600 m, sub-steppe zone; November 1967).

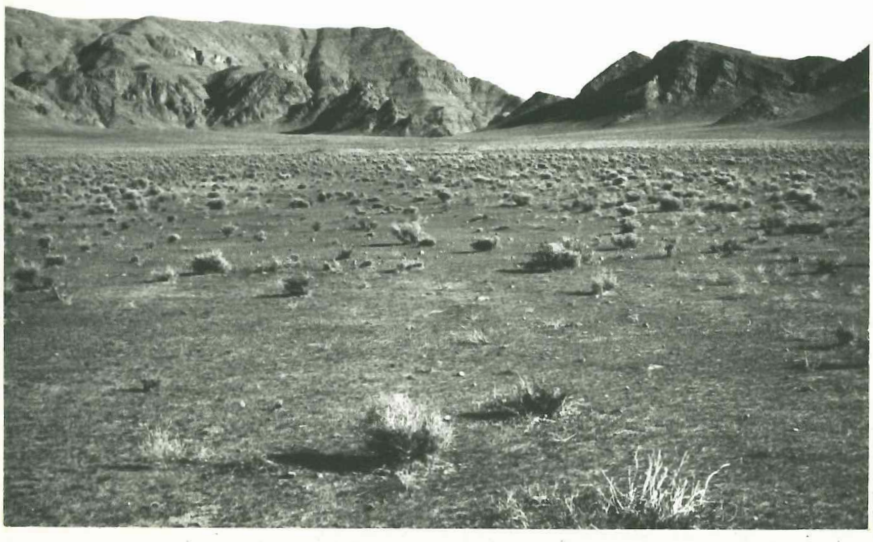


Plate 11. Medium density Artemisia steppe near Niriz, typical habitat of O. isabellina (c. 1,600 m, sub-steppe zone; November 1967).



Plate 12. Bushland in the Sirjan Kavir dominated by Zygophyllum atriplicoides, typical habitat of O. deserti. (c. 1,550 m, cold steppe zone; April 1966).



Plate 13. Medium density steppe with scattered bushes of Ziziphus spina christi, in the warm steppe zone near Firuzabad. (c. 850 m, warm steppe zone; July 1968).

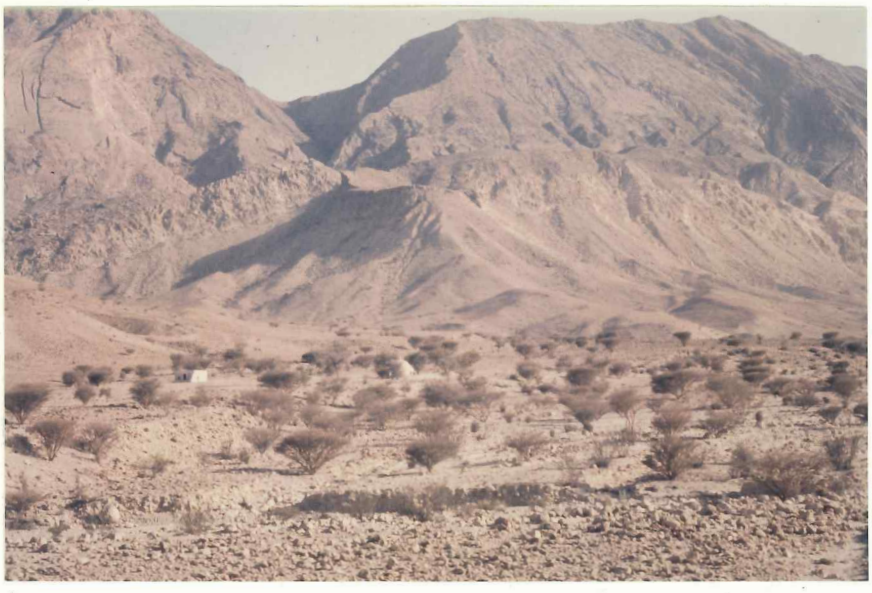


Plate 14. Acacia sp. in the Zagros foothills between Lar and Lengeh. These dry hills are the habitat of O. alboniger. (c. 600 - 1,200 m, warm steppe zone; May 1971).



Plate 15. "Badlands" near Dalaki, which are typical of the southwestern foothills of the Zagros and are the habitat of O. alboniger. (c. 300 - 1,000 m, warm steppe zone; July 1968).



Plate 16. Alluvial coastal plain near Ganaweh with scattered shrublets and bushes (mostly Chenopodiaceae), probably wintering habitat of O. deserti, O. isabellina and O. finschii. (c. 50 m, warm steppe zone; January 1973).

CHAPTER III

FIELDWORK AND METHODS

The fieldwork was done during two periods in Iran:

PERIOD I. SEPTEMBER 1964 - SEPTEMBER 1968: PRELIMINARY STUDIES.

In the first period I collected data about wheatears as part of a survey of the status of all bird species in S. W. Persia, but no special attention was paid to them. The data fall into four categories:

A) Spot surveys:

I made spot surveys throughout S. W. Iran in areas of apparently uniform habitat which I described in a standard way and photographed. Then during a walk of between a few hundred metres and several kilometres I counted all birds and recorded any interesting observations. The information from about 1,200 spot surveys was entered on punch-cards to facilitate rapid extraction of data.

B) Other observations:

For all other birds, such as those seen from a moving car, I noted date, number, locality, altitude, and habitat which I recorded on standard forms.

C) Maharlu census:

To gain more detailed information about seasonal changes and habitat selection I made a regular census near Lake Maharlu, 25 km southeast of Shiraz. This involved a walk of 16 km through various habitats including dry limestone hills, steppe areas with various plant communities, agricultural land, and dry mudflat with scattered, small, salt-tolerant plants. On each occasion I took the same route to ensure comparable coverage. I employed a mapping technique of recording, using a new map for each census on which I plotted the exact position of each bird. In 1967 I made 34 censuses at approximately weekly intervals and in 1968 five during the breeding season.

D) Birds in the hand:

During the four years, I trapped five wheatears of two species for ringing and examination and collected 77 of 11 species. These aided and confirmed field identifications, enabled detailed examination of plumage, provided weights, measurements, gut contents, skeletal material, and data about moult. The skins will be deposited in the Biology Department Museum at Pahlavi University, Shiraz.

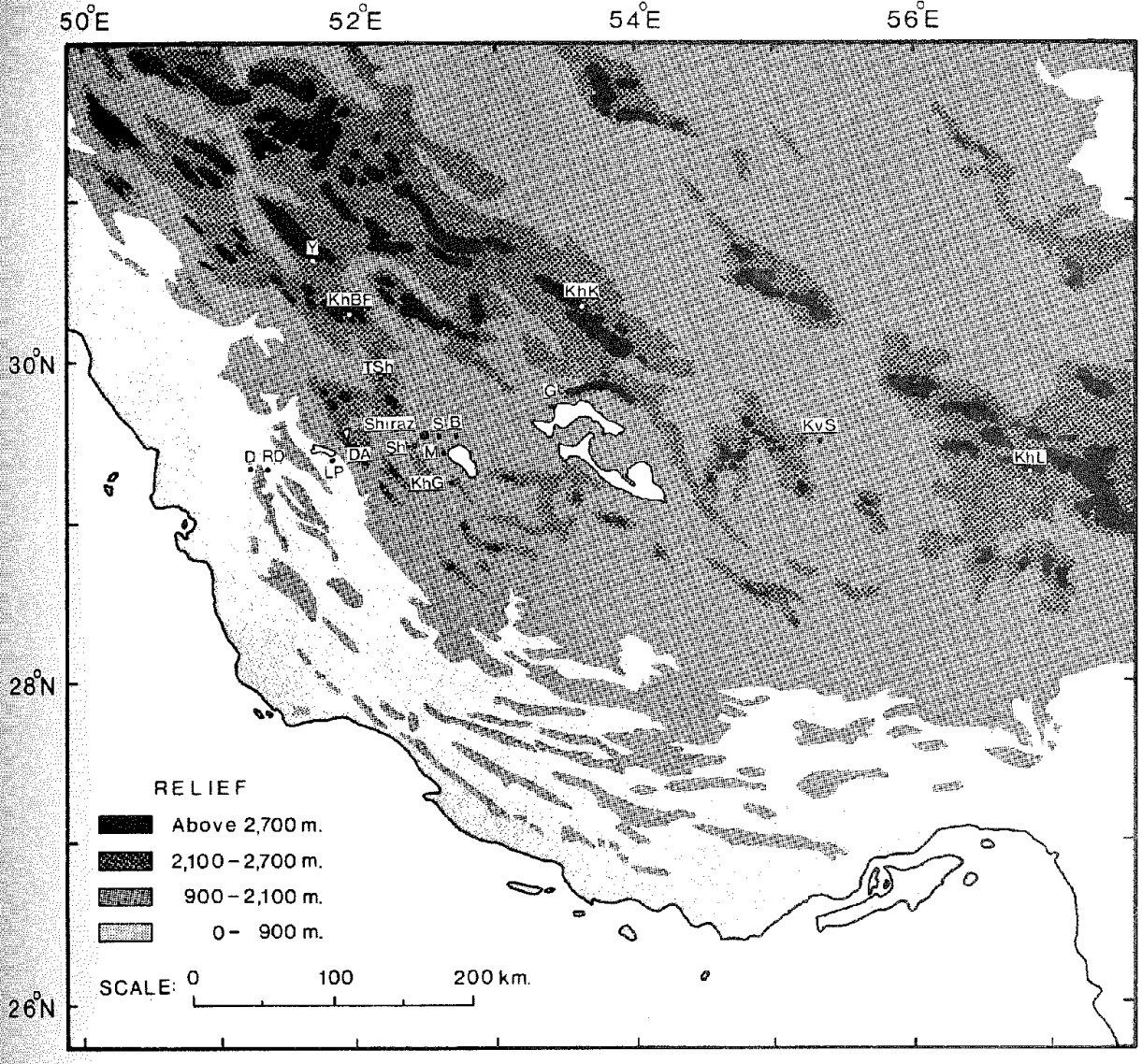
At the end of this period I summarised the status of each species and plotted the locations of all records on maps bearing a 10 km^2 grid. This provided an excellent foundation upon which to build a special study of wheatears.

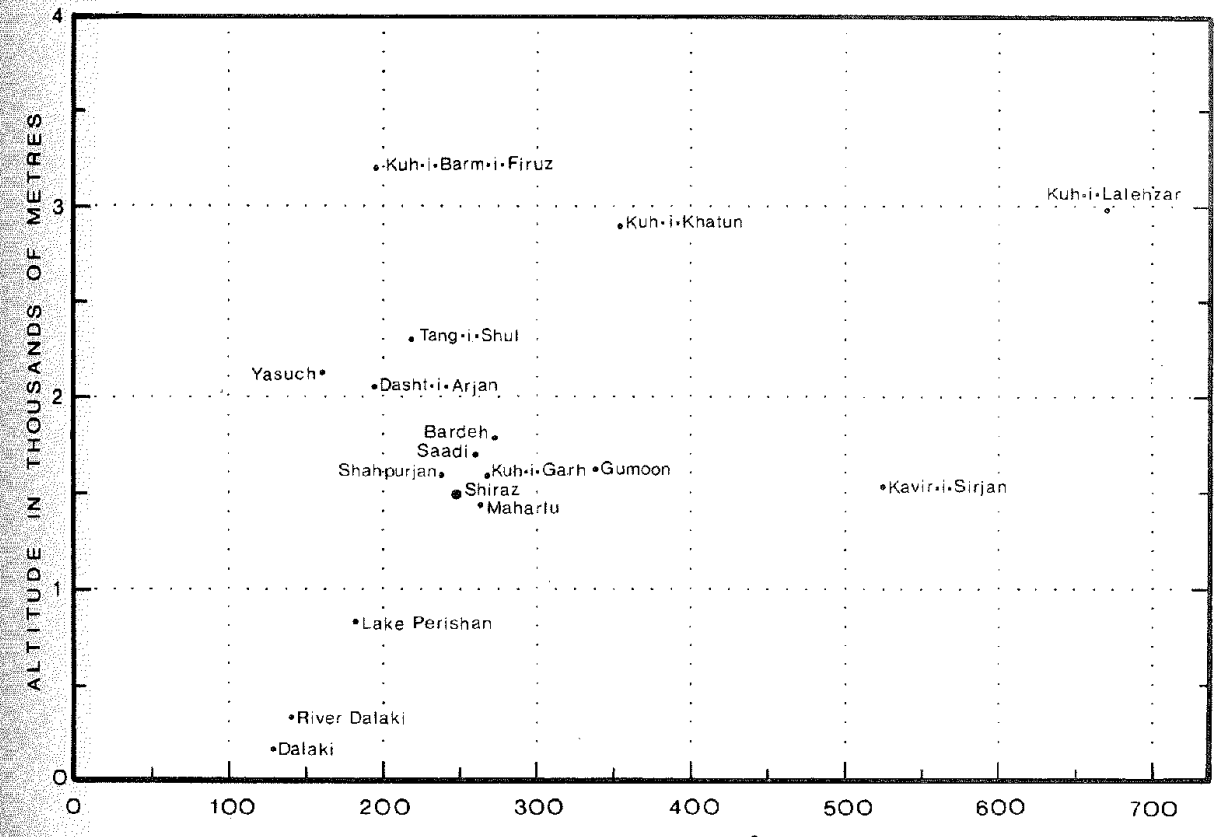
PERIOD II. OCTOBER 1970 - SEPTEMBER 1971, 25 APRIL - 8 MAY 1972 AND 20 - 31 JANUARY 1973: SPECIAL STUDY OF WHEATEARS.

During the second period I spent almost all my time studying wheatears. I continued to make spot surveys and to record all birds in the same way as during the preliminary studies but I paid particular attention to the wheatears. I also continued collecting and added 190 wheatears of 11 species to those already obtained. However I did most of my work in 19 study areas which were chosen to include representative habitats of all the wheatear species and particularly to include places where different combinations of species occurred together.

The locations and altitudes of the study areas are shown in figure 7 and the main features of each, together with a list of wheatears that occur, and my coverage are given in table 3.

The poor roads and the distances between the study areas meant that I could not cover them all equally. I therefore concentrated between half and three-quarters of my time in a core-area in the vicinity of Shiraz, which I worked approximately every other fortnight. In the alternate fortnights I made longer expeditions to the other





KEY

B	–	Bardeh	KhK	–	Kuh-i-Khatun	RD	–	R. Dalaki
D	–	Dalaki	KhL	–	Kuh-i-Lalehzar	S	–	Saadi
DA	–	Dasht-i-Arjan	KvS	–	Kavir-i-Sirjan	Sh	–	Shahpurjan
G	–	Gumoon	LP	–	Lake Perishan	TSh	–	Tang-i-Shul
KhBF	–	Kuh-i-Barm-i-Firuz	M	–	Maharlu	Y	–	Yasuch
KhG	–	Kuh-i-Garh						

Figure 7. Locations and altitudes of the study areas.

STUDY AREAS (in descending altitudinal order)	APPROXIMATE ALTITUDINAL RANGE (metres)	APPROXIMATE AREA (hectares)	APPROXIMATE DISTANCE OF WALK (metres)	WHEATEARS		HABITATS							COVERAGE	
						Structure				Vegetation			Number of visits in each month	Number of days on which observations made
				BREEDING	WINTERING	Cliff	Rocky hillside	Piedmont	Plain	Low density steppe veg.	Zygophyllum bush	Oak woods	J F M A M J J A S O N D	
KUH-I-BARM-I-FIRUZ	3,749 2,700	57	3,000	O, X	nil severe winter	+	+	+	+	+			1 1 2 2	15
KUH-I-LALEHZAR	3,300 2,700		15,000	L, X		+	+	+	+	+			1 1 1	6
KUH-I-KHATUN	3,000 2,800		8,000	X	probably nil in mid-winter	+	+	+	+	+			1 1	4
TANG-I-SHUL	2,500 2,200	39	2,200	F,H,I,L	"	+	+	+	+	+			1 2 1 1 1	13
YASUCH	2,150 2,100		6,000	H	"		+	+	+	+		+	1 1 2	10
DASHT-I-ARJAN	2,100 2,000	39	3,100	H	nil severe winter		+	+	+	+		+	2 2 5 1 1 1 2	24
BARDEH	1,900 1,700		1,600	[F] , I	F, X [A]		[+]	[+]	+	+			2 1 1 2 1 1 1 1 1	14
GUMOON	1,650 1,600		3,500	A, I	A, F, X	+	+	+	+	+			3 1 1 1 2	21
SAADI	1,800 1,600	15	1,300	A,F,L	A	+	+	+		+			2 5 2 1	10
KUH-I-GARH	1,700 1,500	10	1,000	F?,I,L	A, F, X	+	+	+	+	+			1 1 1 3 1	8
SHAHPURJAN	1,700 1,500	21	2,400	A,P,L	A, F, X	+	+	+	+	+			1 2 1 2 1 1 1 3	19
SIRJAN KAVIR	1,550		5,400	D	(D) (F)				+	+	+		1 2 2 2 2	13
MAHARLU CENSUS 1967—1968	1,600 1,450	250	16,000	I, L	A, F, X	+	+	+	+	+			4 4 3 6 4 5 3 2 2 2 3 1	39
MAHARLU VALLEY	1,600 1,450	26	2,800	I, L	A, F, X	+	+	+	+	+			1 1 2 1 1 1	8
MAHARLU NORTH	1,500 1,450	94	5,400	I	F, X		+	+	+	+			5 2 4 3 2 2 2 3 2 2 2 3	65
MAHARLU SOUTH	1,500 1,450	32	2,400	I	A, F, X		+	+	+	+			4 2 3 2 1 1 1 1	17
LAKE PERISHAN	850 800	80	4,400	I?	(D) F,I,X		+	+	+	+			2 1 1 1	10
DALAKI RIVER	350 300	10	1,000	A	A, X	+	+	+	+	(+)			1 1 1 1 1	8
DALAKI	200 150	54	2,700	A	A, X, [I, D] (P,M,F)	+	+	+	+	(+)			1 1 1 1	8

Table 3. List of study areas with details of main features, status of

wheatears and coverage.

KEY

( ) = a few
[ ] = nearby
? = possible but not confirmed
A = O. alboniger
D = O. deserti
F = O. finschii
H = O. hispanica
I = O. isabellina
L = O. lugens
M = O. monacha
O = O. oenanthe
P = O. picata
X = O. xanthoprymna

localities. The Shiraz area was chosen for the main effort because it is the hub of communications in S. W. Iran and because of its central position in relation to the main natural regions. This meant that five species of wheater bred in the core-area and five more within a day's drive.

On visits to study areas I always camped to ensure crack-of-dawn starts and so that meteorological equipment and furled mist-nets could remain out all night without risk of theft. Visits varied from one to four days.

I drew large-scale sketch-maps of all the areas, using a simple compass traverse and triangulation technique. The distances were measured approximately by pacing. On each map I marked the major physical features, land-marks and habitat divisions. The maps were duplicated and a new one used on each occasion.

On each visit to a study area the following procedures were carried out:

A) Census:

As at Maharlu in 1967 and 1968, I followed a standard route and used a mapping technique for recording. During each census I noted on the map the positions of all birds and the positions and details of displays, singing, breeding activity, heat stress, and clashes between wheatears.

B) Mapping territories:

I determined the territorial boundaries of wheatears by marking on the sketch-map where individuals went of their own accord, where they clashed with neighbours, and where they went when driven by me. The driving experiments, a technique used by Hartley (1949), proved a relatively quick method of determining territorial limits since, when chased, wheatears invariably double back at territorial boundaries and cannot be driven off their home-ground. By pursuing birds in every

direction I defined the approximate limits of their territories. The validity of the method was shown by chasing marked individuals on several different days and finding that the areas occupied were in most cases virtually the same.

C) Activity studies:

I watched individual birds continuously for five-minute periods to document quantitatively foraging strategies, feeding stations, feeding rates, types of perch used, and methods of locomotion. A small portable tape-recorder was employed to chronicle the observations which were later transferred onto punch-cards.

D) Trapping:

Birds were caught mostly with mist-nets but also in nets set over the entrances of roost holes. All birds were marked with numbered aluminium rings and combinations of coloured-rings which allowed individual recognition in the field. For each bird the following details were noted: age, sex, measurements, weight, condition of plumage, stage of moult, presence or absence of a brood-patch, and body temperature which was measured orally. A total of 124 wheatears of eight species was handled.

E) Meteorological recordings:

Temperature and relative humidity were recorded continuously by a thermo hygrograph which, for security reasons, had to be situated on the ground under the Land Rover. This was deemed permissable, since the shade under the car was much the same as the shade of rocks and caves which is so important for wheatears. Temperatures in the open were recorded at hourly intervals throughout the day. At first measurements were taken on the ground only, but later readings were also taken at five and ten cm above the ground. These temperatures were measured using unshaded mercury thermometers with bulbs of five mm in diameter. The readings were therefore influenced by the radiation balance of the sensors (Geiger 1966) and the tendency for heat to be conducted along the stems of the thermometers away from the bulbs (Macfadyen 1963).

However the following observations showed that the errors are not large enough to invalidate the method: 1) Under similar conditions thermistors and mercury thermometers invariably gave the same results; 2) sensors sprinkled with a thin layer of dust from the substrate (in the test case fine dry dun-coloured sand similar in colour to much of the ground in S. W. Iran), a method used by Buxton (1924) and Holm and Edney (1973) to eliminate the errors introduced by the difference in radiation balance between the sensors and the substrate, gave temperature readings of 0.25 - 0.5°C lower than similar sensors laid on the surface of the ground in full sunlight; 3) sensors five cm above the ground and shielded from direct sunlight gave readings of 2.75 - 3°C lower than unshielded sensors in similar positions nearby.

Evaporation was monitored hourly throughout the day both in the shade and in the open using piche evaporometers with the filter-papers set at ten cm above the ground which is about wheatear head-height. Subjective notes were made about wind, rain and cloud cover.

F) Sampling invertebrates:

Invertebrates were sampled in three ways to give an indication of food availability.

1) Pitfalls: Plastic coffee cups with about four cm of soapy water in the bottoms were inserted into holes in the ground with the mouths flush with the surface. A line of ten such traps at ten m intervals was set in the same holes on each occasion and left open from dawn until dusk. The arthropod samples were weighed and counts made of the numbers in various size categories and in different taxonomic groups.

2) Sweep-netting: Samples of arthropods from 100 shrublets were taken by holding a sweep-net under each and beating it with a stick three times in quick succession. The samples were treated in the same way as those obtained in the pitfalls.

3) Transects: The occurrence and abundance of arthropods on different slopes at different times of the day were studied using

standard 100 m transects. These were walked at intervals during the day and all the arthropods on open ground within a strip one m wide were counted and roughly classified. On each occasion the ground surface temperature was measured using a mercury thermometer (see section E pp. 45-46).

G) Vegetation description:

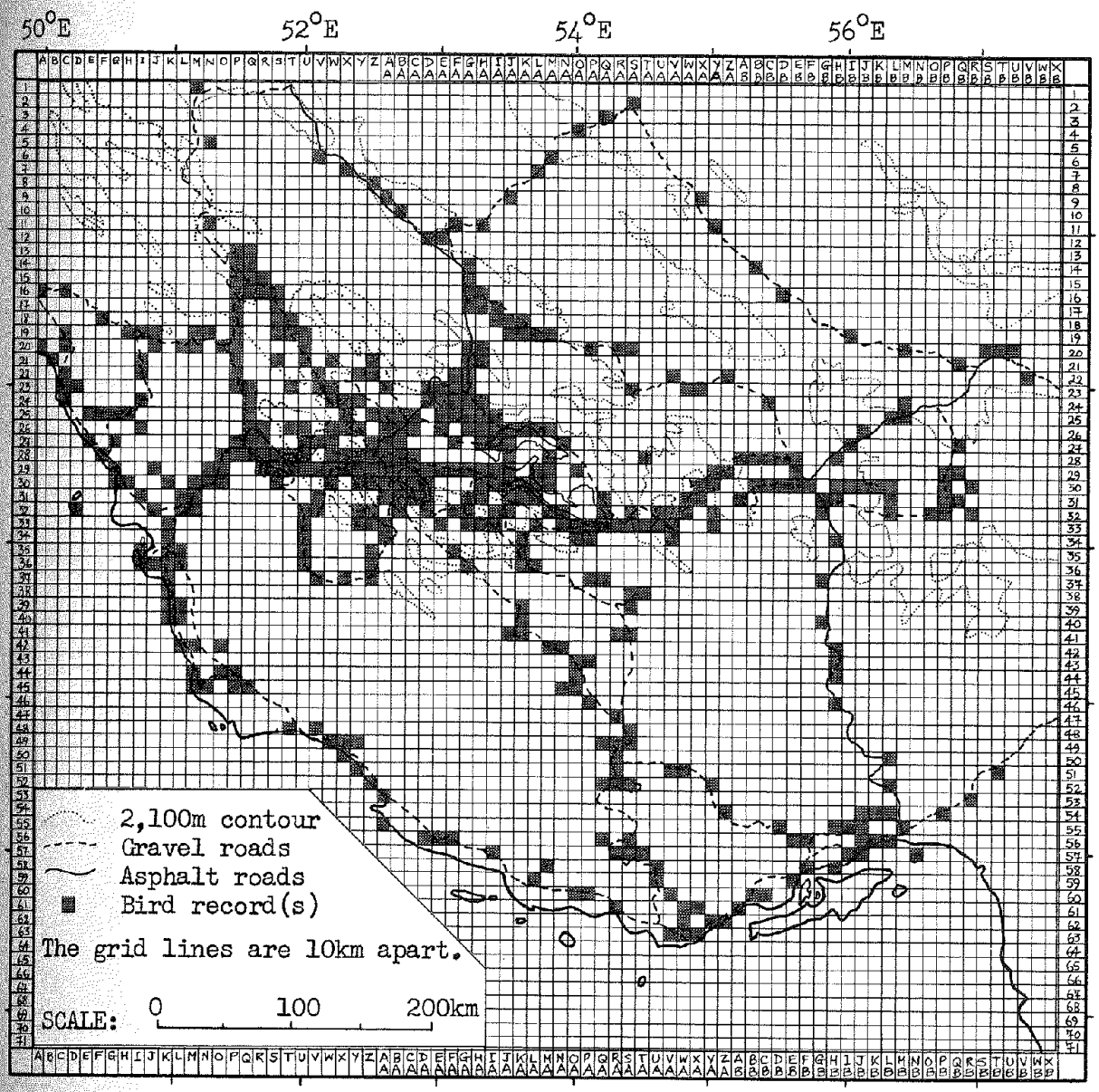
On each visit the condition of the vegetation was noted and details marked on the sketch-map.

COVERAGE:

During my five years in S. W. Persia I did fieldwork on 842 days and explored all the major and secondary roads at least once. The geographical, altitudinal and seasonal coverage is shown in figure 8. Although coverage was patchy both seasonally and geographically, I believe it was sufficient to give a reasonably accurate picture of the distribution and status of each species of wheatear in S. W. Iran as well as a good indication of the range of habitat and climatic conditions in which each occurs. I therefore believe that my data provide an adequate basis for comparing the distributions and habitats of the various species of wheatear, especially since wherever one species was recorded there was equal opportunity for finding any of the other species as well. Hence if one species was found, the absence of another represented a negative record for that species.

STATISTICAL TREATMENT OF RESULTS:

Statistical analyses were carried out with the aid of a Nova 1220 computer using procedures described in text-books on statistics by the following authors: Simpson, Roe and Lewontin 1960; Siegel 1965; Sokal and Rohlf 1969; Langley 1970; Hollander and Wolfe 1973 and Zar 1974.



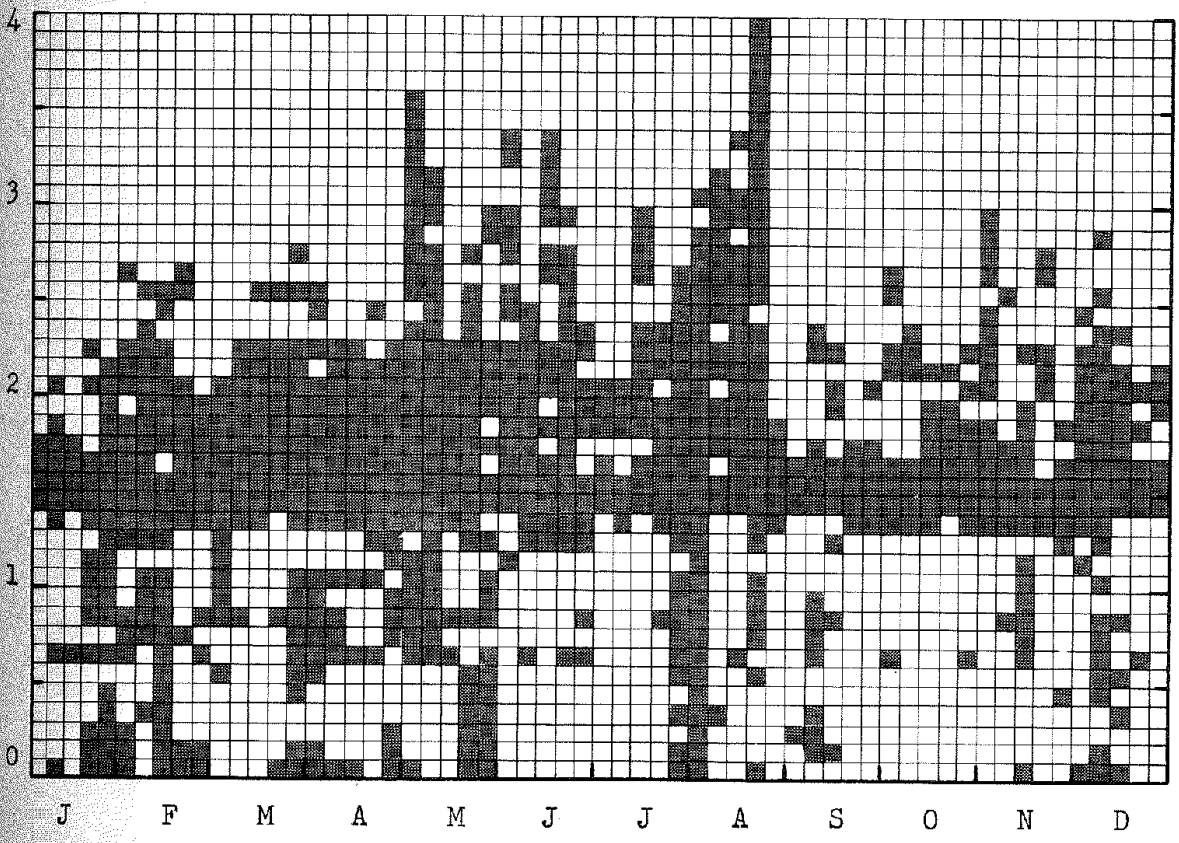


Figure 8. Coverage of the study area as indicated by the geographical, altitudinal and seasonal distribution of bird records. The routes travelled are also shown.

CHAPTER IV

DISTRIBUTION AND STATUS

The aim of this chapter is to summarise the available data on the distribution and status of the various species of wheatear that occur in S. W. Iran.

INTRODUCTORY NOTES:

The information for each species is treated under two headings; first its world range and status and then its distribution and status in S. W. Iran. Outlines and explanatory notes for each section are given below:

A) World range and status.

Under this heading a brief summary of the world status of each species is given together with a map showing its breeding and wintering ranges. This information is included to give perspective to the situation in S. W. Iran.

Maps: Although an effort has been made to make the maps as accurate as possible they must be regarded as only approximate since the distributions of wheatears in many areas are still imperfectly known.

B) Distribution and status in S. W. Iran.

In these sections all available records are summarised and evaluated to establish, as far as possible, the distribution and status of each wheatear species in S. W. Iran. Breeding records are discussed first and then non-breeding records.

1) Breeding records:

Breeding records fall into two categories which are defined below:

DISTRIBUTION AND STATUS - INTRODUCTORY NOTES

a) Breeding proved: Proof of breeding was based on observations of at least one of the categories of evidence listed in table 4.

b) Breeding probable: Breeding was recorded as probable when birds were seen behaving as though they could be breeding, in suitable habitat within the limits of the breeding season of the species as determined below:

Determination of the limits of the breeding season: I defined the breeding season of each species as the period between the date when the earliest pair became established on its territory and the date when the young of the latest pair became independent of their parents. These limits were established for each species as follows: All proven breeding records were assembled. In some cases I had followed the progress of individual pairs and knew the limits of the nesting cycle by observation but in most cases I had made only one or two observations during the cycle. For these, the minimum limits of the nesting cycle were calculated using the schedule given in table 4. For example, if parents were seen carrying food to chicks in the nest, the nesting cycle must have started at least 30 days before and would last at least 15 days longer. I used the beginning of the earliest nesting cycle and the end of the latest to define the minimum limits of the breeding season of each species (fig. 9).

The lengths of the stages in the nesting cycle of wheatears, given in table 4, are based on data reported by Witherby et al. 1938, Dementiev and Gladkov 1968 and personal observations. After nest-building has begun the stages are well-defined and of fairly constant duration. However the length of the first stage, between the establishment of the territory and the end of nest-building, varies and is difficult to measure. To be on the safe side, for the purpose of calculating the limits of the breeding season, I allotted 15 days to this stage, but in many cases it probably lasts longer. For example, colour-ringed O. isabellina established territories at Maharlu North during the first fortnight in

Stage	Evidence	No. of days
1) Establishment of territory and pair-bond.	Much territorial aggression and singing. Sexual displays. Presence of pair in same territory. (Used with discretion)	15
Nest-building.	Adults carrying nesting material.	
2) Laying and incubation.	Bird seen to enter nest-hole without food and remain inside.	15
	Vascularised and edematous brood-patch (used with discretion).[1]	
	Eggs seen.	
3) Nestling period.	Parents carrying food to chicks in nest.	15
	Pulli seen or heard.	
4) Fledgling period.	Fledglings younger than 15 days seen.	15
	Fledgling fed by parents.	

Table 4. Stages in the nesting cycle of wheatears.

[1] Brood-patches of passerines are moulted shortly before incubation begins and quickly become vascularised and edematous. After the chicks hatch the vascularity and edema begin to subside and the skin which has been somewhat stretched becomes wrinkled and scaly, but by the time the young fledge the skin is almost back to normal (Bailey 1952).

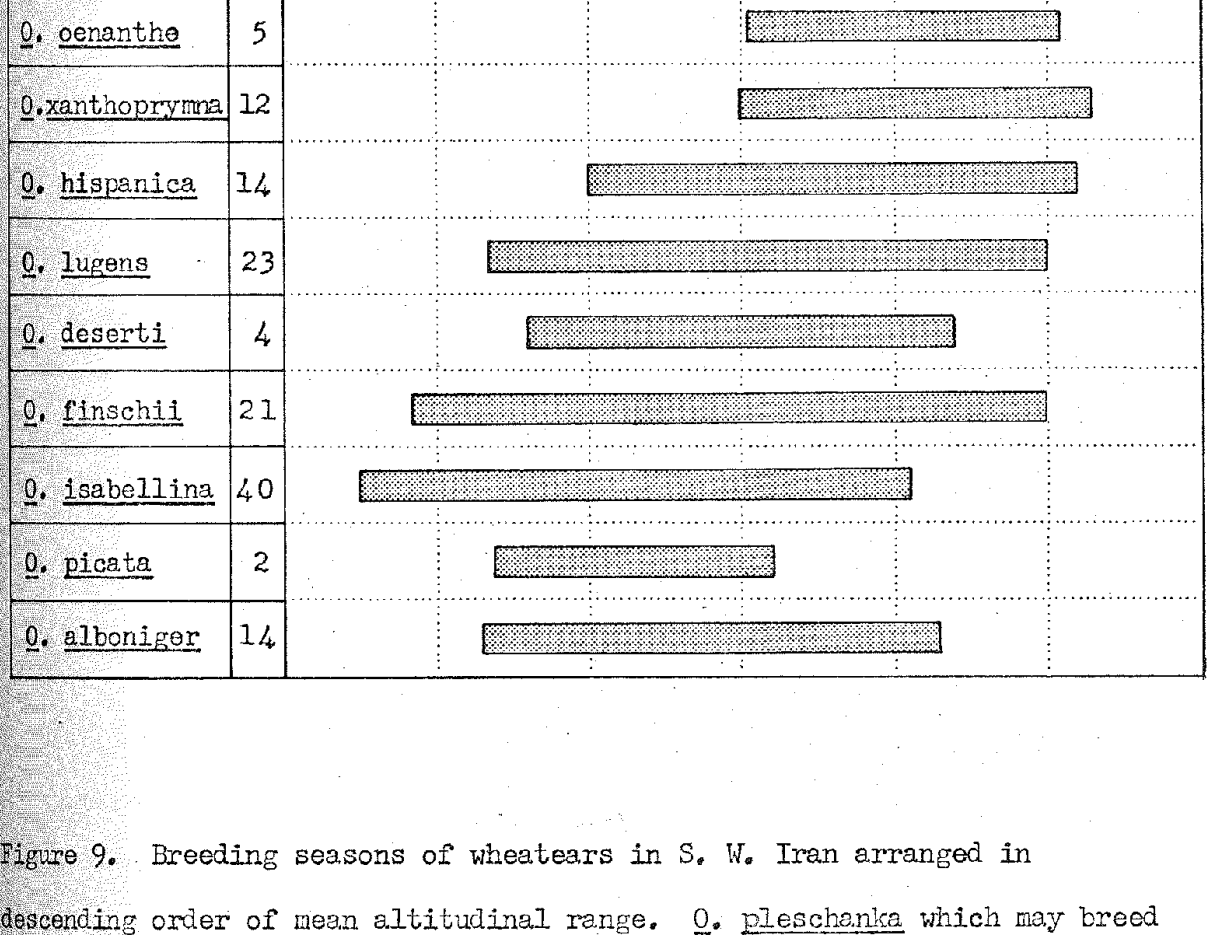


Figure 9. Breeding seasons of wheatears in S. W. Iran arranged in descending order of mean altitudinal range. O. pleschanka which may breed occasionally (pp. 87-91) and O. monacha which probably breeds in small numbers (p. 81) have been omitted from this figure.

(N = number of proved breeding records. For method of calculation of limits of breeding season, see text pp. 50 & 53.)

February but fledglings were not seen until early May.

2) Non-breeding records:

The status of birds which were not breeding or probably not breeding was difficult to determine since there are no readily observed criteria for distinguishing residents, summer visitors, winter visitors, or even migrants which often hold territories for short periods while on passage (Conder 1956, Simmons 1951 and personal observations). Therefore I assembled all the non-breeding records of each species of wheatear and from the distribution and seasonal occurrence of these, together with notes on the behaviour of individual birds, I deduced, as far as possible, the status of each record. The records were allotted to one or a combination of the categories which are defined below:

a) Resident: Birds that remain in the same area throughout the year.

b) Summer visitor: Birds on their breeding grounds which will migrate to winter elsewhere.

c) Winter visitor: Birds on their wintering grounds which will migrate to breed elsewhere.

d) Migrant: Birds on passage and those wandering after the breeding season. All birds seen in places where they were known to stay only a short time were classified as migrants.

In the above analysis the census-data from the study areas were particularly informative since negative records were substantiated and they included cases where the history of particular individuals was known. Individual birds were identified by colour-rings and where apparently identical birds were seen in the same place on several successive occasions they were scored as being probably the same individual. Relevant census results are reported in tables 5, 6, 8, 9, 11, 12, 14, and 15.

DISTRIBUTION AND STATUS - INTRODUCTORY NOTES

Overlay maps showing locations of records:

The locations of all records of wheatears in S. W. Iran are presented on transparent overlay maps with the same scale as the topographic, climatic and bioclimatic maps (fig. 4 and overlays 1-4). This has been done to aid comparisons between distributions by enabling maps to be superimposed. Overlays 5-8 show the locations of all proven and probable breeding records and overlays 9-17 all other records together with notations of status. The overlays are stored in a pocket at the end of this volume, but since they can easily be lost photocopies of overlays 5-17 are bound into the volume at the end of this chapter pp. 102-114.

The overlay maps were prepared by plotting the locations of the records on base maps bearing 10 km^2 grids which have been omitted from the final drafts for clarity. A figure showing the altitudes of the records is attached to each map. The breeding records are plotted against longitude on the same scale as the map while the other records are plotted against date.

Summary maps:

At the end of this chapter three maps are presented which summarise the probable geographical distributions and altitudinal ranges of breeding and wintering wheatears in S. W. Iran (figs. 22-24, pp. 99-101). These distributions are intended to take account of gaps in the coverage and were deduced from the following information: 1) positive and negative records of wheatears in S. W. Iran; 2) the distribution in S. W. Iran of habitat that was probably suitable for each species (i. e. areas with similar terrain, altitudes and bioclimates to those where birds were actually found); and 3) the distributions of the various species in the rest of Iran. Each probable distribution is discussed in the systematic treatment of species.

To facilitate comparisons the summary maps are drawn on the same scale as the overlay maps showing the locations of records.

DISTRIBUTION AND STATUS - O. ALBONIGER

SYSTEMATIC TREATMENT OF SPECIES:

1) O. ALBONIGER (Hume's Wheatear).

World range and status:

The range of O. alboniger is shown in fig. 10. Most birds are resident but some wander after the breeding season and reach southern Iraq and eastern Arabia (Vaurie 1959).

Distribution and status in S. W. Iran:

O. alboniger is present in S. W. Iran throughout the year. It breeds from sea level to about 1,900 m above sea level in the steppe, sub-steppe and deforested parts of the xerophilous forest zones (cf. overlays 4 and 5). I believe the paucity of breeding records from the cold steppe zone is due partly to lack of coverage and partly to the nature of the terrain, which being predominantly rolling plains, is largely unsuitable for this species that usually frequents steep rocky ground. Accordingly I believe that O. alboniger probably breeds in rocky areas throughout the cold steppe zone of S. W. Iran. This view is supported by the widespread occurrence of the species in the cold steppe zone in other parts of Iran and by the evidence of Blanford (1876) who found a female and two recently fledged young near Kerman. It is not known whether O. alboniger occurs in the sub-desert zone of S. W. Iran, but this is probable in view of the observations of D. A. Scott (pers. comm.) who found the species common in June 1973 in the hills along the road from Nain to Tabas which runs through sub-desert country in central Iran. The probable breeding distribution of O. alboniger in S. W. Iran is, therefore, as shown on the summary map (fig. 22).

Comparison of overlays 5 and 9 shows that there is little seasonal change in the geographical and altitudinal distribution of records of O. alboniger in S. W. Iran which suggests that the species is resident. This is supported by the census data from the study areas at Gumoon, Saadi, Shahpurjan, Dalaki, and Dalaki River where O. alboniger was present in both the breeding season and winter and was never found

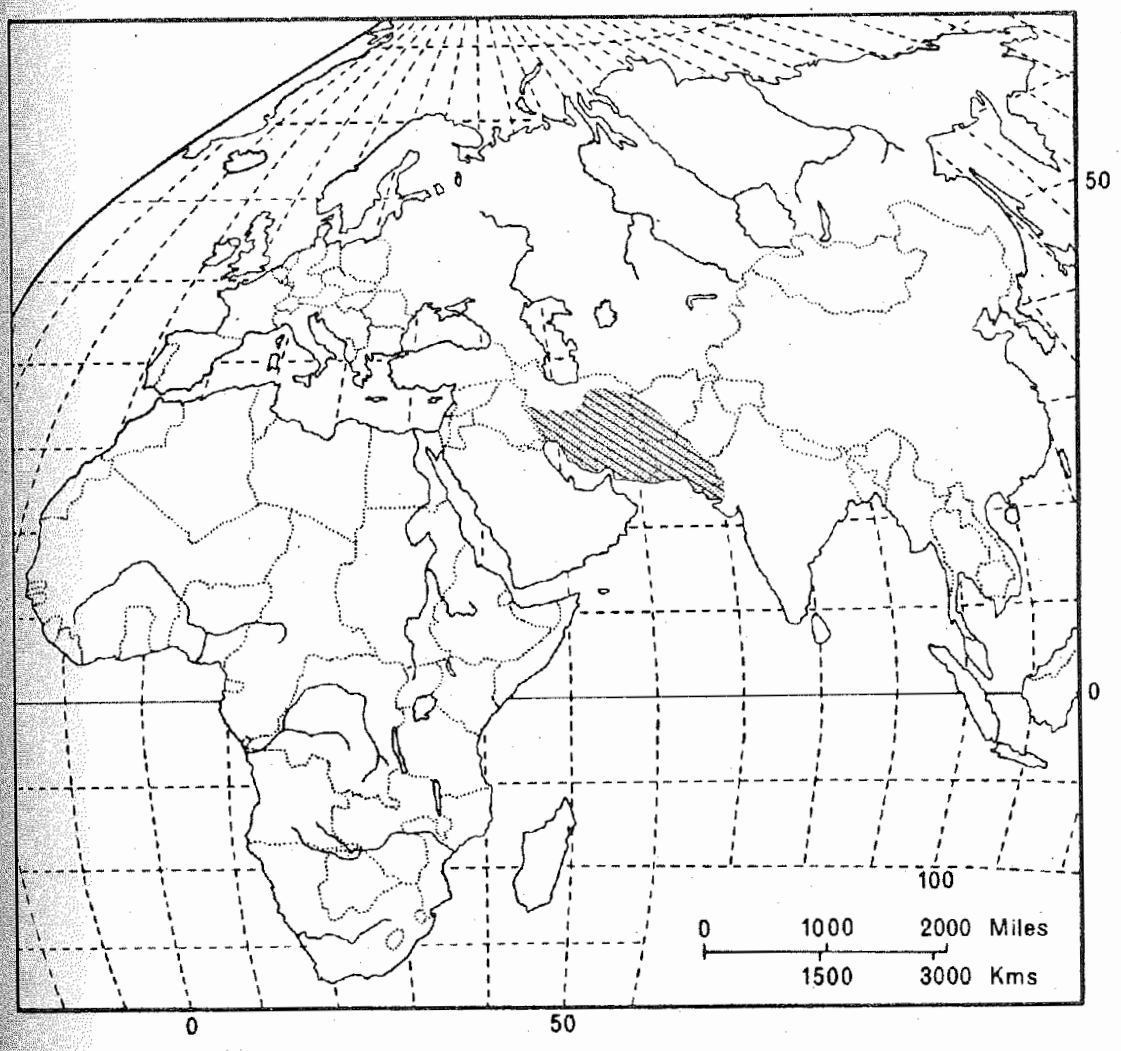


Figure 10. Breeding and wintering ranges of O. alboniger.

(Based on data from: Vaurie 1959, Ripley 1961, Hüe and Etchécopar 1970, and recent observations in Iran by L. Cornwallis and D. A. Scott.)

O. ALBONIGER

STUDY AREAS (Descending alt. order) + INDIVIDUAL BIRDS	OCT 1-15	OCT 16-31	NOV 1-15	NOV 16-30	DEC 1-15	DEC 16-31	JAN 1-15	JAN 16-31	FEB 1-15	FEB 16-29	MAR 1-15	MAR 16-31	APR 1-15	APR 16-30	MAY 1-15	MAY 16-31	JUNE 1-15	JUNE 16-30	JULY 1-15	JULY 16-31	AUG 1-15	AUG 16-31	SEPT 1-15	SEPT 16-30	MAY 1972 1-15
GUMOON					[(2)]	(3)			[3p+1]	5p+3					[(1)]					3	[(6)]				
SAADI	(1)						(1)		(1)			1p+2	6c	1p+1	3p+1							7			
O. alboniger pA												+	+	+	+							-			
KUH-I GARH							5				-	1p	-	-								-			
SHAHPURJAN				(1)	(2)	4		(2)	2		1		1pc		3				5				4		1p+5f
O. alboniger ♂ blue						/			/		/		/c		✓				✓				?		-/+5f
" " ♀ orange p						/			/		/		✓c		✓				-						
" " A						+			+																
" " B															+m				+				+		
MAHARLU CENSUS (Begun January 1967)	1	5	5	2		3	2	4	4	3	1	-	-	-	-	-	-	2	1	4	1	3		4	
O. alboniger A	+	+	+	+		+	+	+	+	+	+	+	-	-	-	-	-	+	-	-	-	+*		+	
" " "							+	+	-	+	-	-	-	-	-	-	-	Ground shared by C + D							
" " B																		+m	-	+	-	+		+	
" " C		+	+	+		-												+	+	+	+	+		+	
" " "																									
" " D	+	+	-	-		-																			
" " "																									
MAHARLU VALLEY							2	3		4	-	-	-		-							-			
O. alboniger A							+	+		+	-	-	-		-							-			
" " B							+	+		-	-	-	-		-							-			
MAHARLU SOUTH						2	2	2	1	2	1	-	-						-			-		2	
O. alboniger A						+	+	+	+	+	+	-	-						-			-		+*	
" " ♀ yellow						/	✓	✓	-	✓	-	-	-						-			-		✓	
DALAKI RIVER								1p+1	[(6)]					1p+2	[(1p+f)]					[(10)]			1p+3		
DALAKI								(1p+1)	1p+5					4pc+4 +2f									7		

Table 5. Standard counts and records of individuals of O. alboniger in study areas in S. W. Persia. Most of the observations were made between 1 October 1970 and 30 September 1971 and are arranged in chronological order.

KEY

( ) = nearby or non-standard count.
[ ] = 1964-1968 (omitted for Maharlu Census 1967-68).
- = negative record.
b = at least one bird nest-building.
c = at least one bird carrying food to chicks.
f = fledgling.
m = moult.
n = nest found.
p = pair.

Individual birds in approximately the same territory on consecutive occasions:

✓ = colour-ringed individual.
/ = apparently identical to and probably the same bird as was later colour-ringed.
+ = apparently identical bird, probably the same individual.
? = O. alboniger present but not seen whether ringed or not.

to be absent (table 5). However I have too few data to determine whether individuals ever remain on the same territory throughout the year.

In contrast to the above observations, the censuses in the dry hills to the south of Lake Maharlu and at Kuh-i-Gahr showed that some O. alboniger undertake seasonal movements (table 5). At these localities O. alboniger was a winter visitor and the studies of individuals suggested that these birds probably held the same territories throughout the winter. Indeed a female O. alboniger, marked with a yellow colour-ring, maintained the same territory at Maharlu South from at least the end of December 1970 until the end of February 1971 and then after an absence of six and a half months she returned to the same territory at the end of September 1971. The origin of these immigrants is unknown, but since I can find no reports in the literature of O. alboniger migrating, it seems likely that these birds had moved only locally during post-breeding dispersal. This view is supported by the fact that the winter visitors begin to arrive at the end of June which is about the time when the young and breeding pairs disperse at the end of the breeding season.

The foregoing evidence shows that the distribution of O. alboniger in winter is similar to its breeding distribution and it has been so drawn on the summary map (fig. 24).

2) O. DESERTI (Desert Wheatear).

World range and status:

The range of O. deserti is shown in fig. 11. Birds that breed in North Africa and N. W. Arabia are mainly sedentary while those that breed in Asia are mostly summer visitors to their breeding grounds (Etchécopar and Hüe 1967, Dementiev and Gladkov 1968).

Distribution and status in S. W. Iran:

O. deserti is present in S. W. Iran throughout the year. It breeds almost entirely within the cold steppe zone from about 1,400 - 2,500 m above sea level (cf. overlays 4 and 8). The breeding range of

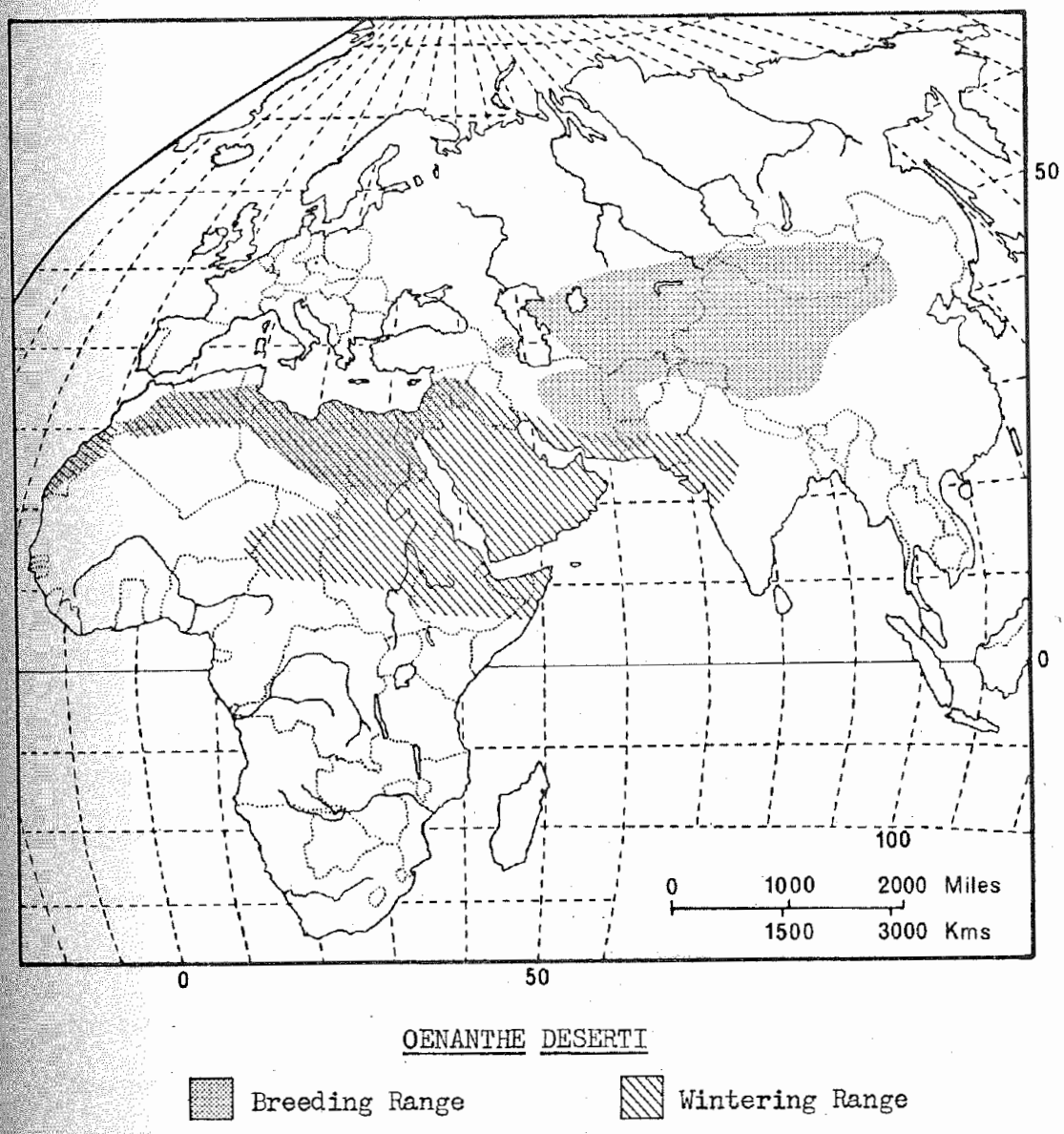


Figure 11. Breeding and wintering ranges of O. deserti.

(Based on data from: Meinertzhagen 1954; Vaurie 1959; Ripley 1961; Etchécopar and Hüe 1967; Dementiev and Gladkov 1968; Stresemann, Portenko and Mauersberger 1971; Moreau 1972; and recent observations in Iran by L. Cornwallis and D. A. Scott.)

the species in the rest of Iran is also largely confined to the cold steppe zone. Consequently the breeding range of O. deserti in S. W. Iran probably coincides closely with the cold steppe zone and it has been so drawn on the summary map (fig. 23). It is not known whether O. deserti breeds in the sub-desert zone.

O. deserti is common on its breeding grounds in S. W. Iran from about mid-March until at least the beginning of October. However by mid-winter it is rare or absent (cf. overlays 8 and 10). None were seen during visits to the breeding grounds in December 1966 or February 1970; only a few solitary birds were seen in December 1970 and one in February 1973. Therefore at least most of the breeding population migrate. Most birds seen on the breeding grounds outside the breeding season were probably summer visitors but I have insufficient data to distinguish them from migrants. The few birds seen in winter may have been residents, migrants or winter visitors. Consequently all records of birds on the breeding grounds outside the breeding season and between mid-March and the end of October were recorded as probably summer visitors/?migrants and the rest as residents/winter visitors/migrants.

Outside the breeding range, in areas above about 800 m above sea level in the western Zagros, O. deserti occurs in small numbers from the beginning of October until mid-December and from mid-January until mid-April (cf. overlays 8 and 10). Casual observations near Shiraz and data from the regular censuses in the study areas at Barm-i-Firuz, Dasht-i-Arjan and near Lake Maharlu showed that most O. deserti in these areas appeared briefly on passage in autumn or spring. However a few set up territories which they probably maintained for up to six weeks. For example, at Maharlu North a female (probably the same bird) occupied a territory from 28 October until 26 November 1970 and at Maharlu during the 1967 census a female (probably the same individual) was seen repeatedly in the same territory from 24 January until 7 March (table 6). I classified these birds as migrants but their actual status is uncertain.

STUDY AREAS (Descending alt. order) + INDIVIDUAL BIRDS	OCT		NOV		DEC		JAN		FEB		MAR		APR		MAY		JUNE		JULY		AUG		SEPT	
	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-30
BARM-I-FIRUZ			2	[-]											[-]			-			[-]			
DASHT-I-ARJAN				3	[-]				-	[-]			[-]	-	-	[-]					-		-	-
BARDEH		4	3		-		-		-			-	-		-						-			
O. deserti ♂A		+	+		-		-		-			-	-		-						-			
O. deserti ♂B		+	+		-		-		-			-	-		-						-			
GUMOON					[(3)]	[-]			[-]	(2)					[-]					-		[-]		
SIRJAN KAVIR					1 [(-)]				(-)			[(6)]	[(4)]	[(7)]	[(4p+9 +2f)]		[(7)]							
MAHARLU CENSUS (Begun January 1967)	1	3	3	-		-	-	2	2	3	3	1	3	-	-	-	-	-	-	-	-	-		-
O. deserti ♀A								+	+	+	+			-	-	-	-	-	-	-	-	-		-
O. deserti ♂B										+	+			-	-	-	-	-	-	-	-	-		-
MAHARLU NORTH	-	1	1	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-		-	1	-	1
O. deserti ♀A		+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
LAKE PERISHAN				2				1								-							1	
DALAKI									(3)					-									2	

Table 6. Standard counts and records of individuals of O. deserti in study areas in S. W. Persia. Most of the observations were made between 1 October 1970 and 30 September 1971 and are arranged in chronological order.

KEY

( ) = nearby or non-standard count. [ ] = 1964-68 (omitted for Maharlu 1967). - = negative record. f = fledgling. p = pair.

Individual birds in approximately the same territory on consecutive occasions: + = apparently identical bird, probably the same individual.

The autumn birds may have been attempting to winter but were forced to leave for some reason or they may have been spending part of the winter at Maharlu before moving to other wintering grounds. The birds which arrived at the end of January may have been forced out of wintering grounds elsewhere and have been taking refuge for the rest of the winter. As a result of the above evidence all O. deserti of unconfirmed status which were seen off the breeding grounds of the species and in areas above 800 m above sea level were recorded as migrants except five seen in the Niriz Basin in December and January which could have been winter visitors and were recorded as migrants/winter visitors (overlay 10).

In the coastal lowlands and Zagros foothills below about 800 m above sea level, O. deserti occurs from mid-September until mid-December and from mid-January until the end of March (overlay 10). The status of these birds is uncertain since no observations have been made in this area between mid-December and mid-January and data from censuses and ringing are too few to provide any clues. Some are probably wintering since O. deserti winters in Mesopotamia (Allouse 1953), on the island of Fao at the head of the Persian Gulf (Sharpe1886), on Bahrain (Rogers and Gallagher 1973), and in Oman and the Trucial States (Stanford 1973). It also probably winters in lowland Khuzistan where between 7 and 9 January 1972, D. A. Scott (pers. comm.) saw 21 O. deserti on a drive of about 300 km, and where between 13 and 21 January 1973 I saw 30 O. deserti on a drive of 1,490 km. However if it does winter in the lowlands of S. W. Iran, only small numbers are involved since in late January and early February I found the species uncommon. Thus between 21-24 January 1973, I drove 685 km on the coastal plain through habitat which was mostly suitable for O. deserti and saw only 20 birds and between 30 January and 1 February 1971 I drove 80 km through similar country near Dalaki and located only five birds. The only other record in January was of one bird at Lake Perishan in 1971. Of these birds, all those that I studied in detail (10 out of 26) were holding territories and were probably wintering. However since migrants begin to appear in upland areas of S. W. Iran in

mid-January, the birds in the lowlands could have been migrants.

Later in February (20-24 1971), D. A. Scott (pers. comm.) drove over a similar route to the one taken by me in the journeys described above and found O. deserti rather more numerous that I did. His and my results from roughly the same areas are given in table 7.

AREA	21-24 Jan 1973 L. C.	30 Jan-1 Feb 1971 L. C.	20-24 Feb 1971 D. A. S.
Hendijan[1] - Bandar Deylam (106 km)	6	Not covered	16
Bandar Rig - Bushire (100 km)	0	5	20
Bushire - Mand River (120 km)	7	Not covered	25+

Table 7. Numbers of O. deserti seen in three areas on the coastal plain of S. W. Iran.

The differences between my 1973 figures and those of Scott in 1971 could have been due to differences in the sizes of the wintering populations in the two years but I think this is unlikely since my 1971 and 1973 counts were similar. I therefore believe that some of Scott's birds were migrants.

As a result of the above evidence, all birds of unconfirmed status seen below 800 m above sea level in January and early February were recorded as probably winter visitors/?migrants and those between mid-February and the end of March as probably spring migrants/?winter visitors. I am uncertain of the status of the birds seen in the autumn and they were recorded as winter visitors/migrants (overlay 10).

The probable wintering distribution of O. deserti in S. W. Iran has been drawn to include all areas in the hot steppe zone below 800 m above sea level (summary map fig. 24).

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[1]Hendijan is in Khuzistan 106 km W. N. W. of Bandar Deylam.

DISTRIBUTION AND STATUS - O. FINSCHII

3) O. FINSCHII (Finsch's Wheatear).

World range and status:

The range of O. finschii is shown in fig. 12. Most populations are partly migratory (Vaurie 1959, Dementiev and Gladkov 1968).

Distribution and status in S. W. Iran:

O. finschii is present in S. W. Iran throughout the year but is most numerous and widespread during the winter (cf. overlays 6 and 11). It breeds between about 1,600 and 2,500 m above sea level mainly in the wetter parts of the sub-steppe zone, but also in eastern deforested parts of the xerophilous forest zone (cf. overlays 4 and 6). Within this rather restricted area O. finschii was found breeding in relatively few localities but in some of these it was quite common. The distribution of records shown on overlay 6 probably gives a reasonable indication of the breeding distribution of O. finschii in S. W. Iran since the species is conspicuous and not easily overlooked and since their distribution fits in well with the breeding distribution of O. finschii in the rest of Iran (fig. 12). The probable breeding distribution of O. finschii in S. W. Iran is, therefore, as shown on the summary map (fig. 23).

After the breeding season the young disperse. The adults separate and thereafter are found holding solitary territories.

The status of the O. finschii that breed in S. W. Iran is uncertain since few have been marked and after the breeding season they are indistinguishable from migrants and winter visitors. However some are probably resident and others summer visitors. The evidence for this is briefly reviewed below:

At Tang-i-Shul in 1971, where O. finschii bred quite commonly, some adults, mostly males, lingered on their breeding territories until the beginning of September (table 8). They probably remain at least into November, as ten were seen there on 5 November 1970, but these were not

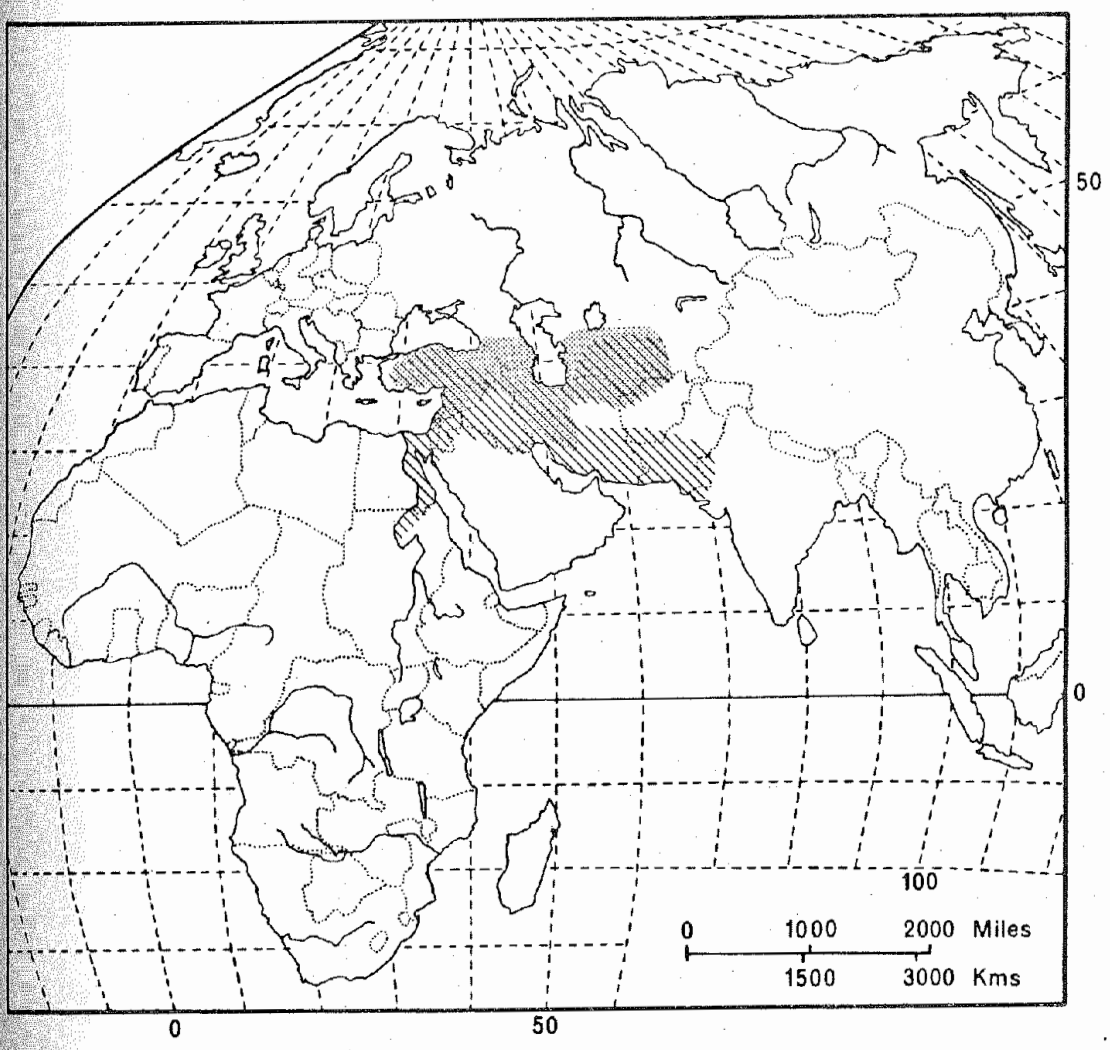


Figure 12. Breeding and wintering ranges of O. finschii.

(Based on data from: Vaurie 1959; Ripley 1961; Dementiev and Gladkov 1968; Hüe and Etchécopar 1970; Stresemann, Portenko and Mauersberger 1971; and recent observations in Iran by L. Cornwallis and D. A. Scott.)

O. FINSCHII

STUDY AREAS (Descending alt. order) + INDIVIDUAL BIRDS	OCT 1-15	OCT 16-31	NOV 1-15	NOV 16-30	DEC 1-15	DEC 16-31	JAN 1-15	JAN 16-31	FEB 1-15	FEB 16-29	MAR 1-15	MAR 16-31	APR 1-15	APR 16-30	MAY 1-15	MAY 16-31	JUNE 1-15	JUNE 16-30	JULY 1-15	JULY 16-31	AUG 1-15	AUG 16-31	SEPT 1-15	SEPT 16-30	MAY 1972 1-15	JAN 1973 16-30
TANG-I-SHUL			10											4p+5 bc			3p+3 cm+7f						10		2p+4 nc	
O. finschii ♂ yellow/red pA														√n			√+2f						√		√	
" " ♀ pA														-			+						-		-	
" " ♂														+			+cf						+			
" " ♀ red pB														√			√						-		√n*	
" " ♂														+			++f						-			
" " ♀ pC														+			-						+			
" " ♂														+			++f						+			
" " ♀ pD														-			-						-			
" " ♂														+			+m+f						+			
" " ♀ pE														+b			+m						-			
BARDEH		2	9		4		5		7			-	-		-						-					
GUMOON					[1]	[2]			[2]	1					[-]					-		[-]				
SAADI												-	1pc	1p	-							1			2p+3+3f	
KUH-I-GARH							5				-			-	1	1						-				
SIRJAN KAVIR					[4]				(4)			[-]	[-]	[-]	[-]		-									
MAHARLU CENSUS (Begun January 1967)	12	12	12	8		11	11	14	14	12	1	-	2	-	-	-	-	-	-	-	-	2		8		
MAHARLU NORTH		15	13	15	13	20	22	21	19	19	6	-	-	-	-	-	-	-	-		-	-	4	10	-	(4)
O. finschii ♂ red		√	√	√	√	√	√	√	√	√	√	-	-	-	-	-	-	-	-		-	-	-	√	-	
" " ♂ blue		√	√	√	√	√	√	√	√	√	-	-	-	-	-	-	-	-	-		-	-	-	-	-	
" " ♂ yellow right		-	-	-	-	√	√	√	√	√	√	-	-	-	-	-	-	-	-		-	-	-	-	-	
" " ♂ orange		/	/	/	/	√	√	√**																		
" " ♂ pink/white		/	/	/	/	√	√	√	√	√	-	-	-	-	-	-	-	-	-		-	-	√	√	-	√
" " ♂ red/blue		/	/	/	/	/	/	√	√	√	-	-	-	-	-	-	-	-	-		-	-	√	√	-	
" " ♂ red/metal		/	/	/	/	/	/	/	√	√	√	-	-	-	-	-	-	-	-		-	-	-	-	-	
LAKE PERISHAN				10		10									-	-				[-]			1			7
O. finschii ♂ green				√		√									-	-							-			√
" " ♂ yellow left				√		√									-	-							-			√

Table 8. Standard counts and records of individuals of O. finschii in study areas in S. W. Persia. Most of the observations were made between 1 October 1970 and 30 September 1971 and are arranged in chronological order.

KEY

( ) = nearby or non-standard count.
[ ] = 1964-1968 (omitted for Maharlu 1967-68).
- = negative record.
b = at least one bird nest-building.
c = at least one bird carrying food to chicks.
f = fledgling.
m = moult.
n = nest found.
p = pair.

Individual birds in approximately the same territory on consecutive occasions:

√ = colour-ringed individual.
/ = apparently identical to and probably the same bird as was later colour-ringed.
+ = apparently identical bird, probably the same individual.

*O. finschii ♀ red in territory 150m from one held in spring 1971.

**Killed by Kestrel, Falco tinnunculus.

***In addition to the colour-ringed birds, reported in the table, which held winter territories at Maharlu North and Lake Perishan, unringed birds, assumed to be the same individuals were seen repeatedly in the same territories during the winter as follows: Bardeh 5, Maharlu Census 1967 12, Maharlu North 13, Maharlu South 3, and Perishan 4.

ringed and they could have been winter visitors. However I think it unlikely that O. finschii winters at Tang-i-Shul since at an altitude of 2,200 m above sea level the winters are probably too severe. I therefore believe that O. finschii is a summer visitor to Tang-i-Shul and probably to all its breeding localities above about 2,000 m above sea level. At lower altitudes some O. finschii may be resident since at two localities near Shiraz the species was recorded wintering, breeding and in mid-August before the winter visitors arrive. I have no proof that the same individuals were present during each period, but it seems likely and in which case these birds were resident.

In most of my study areas and over much of S. W. Iran O. finschii is a common winter visitor (table 8, overlay 11). It occurs widely from sea level to about 1,900 m above sea level in the steppe, sub-steppe and deforested parts of the xerophilous forest zones. The probable winter distribution of O. finschii in S. W. Iran has, therefore, been drawn to include all areas below 1,900 m above sea level in these bioclimatic zones (summary map fig. 24). It is not known whether O. finschii occurs in the sub-desert zone in winter.

Most O. finschii that are winter visitors to S. W. Iran arrive between the end of August and the end of October and stay until the beginning of March. During this period they maintain individual territories. At Maharlu North and Lake Perishan studies of nine colour-ringed males showed that these birds remained in the same territories throughout the 1970-71 winter and that three of the seven at Maharlu North returned to exactly the same territories in September 1971. In January 1973 the two colour-ringed birds at Lake Perishan and one of those at Maharlu North were located holding the same territories as in the winter of 1970-71 (table 8). Additional evidence of winter territoriality was obtained during the Maharlu census of 1967 and during 1970-71 from the study areas at Bardeh, Maharlu North, Maharlu South, and Lake Perishan where apparently identical unringed birds were repeatedly seen in the same territories throughout

the winter and were probably the same individuals. The origin of the winter visitors is unknown. Some may have bred in S. W. Iran but the relative abundance in winter suggests that most are immigrants from further north.

In the wintering population of O. finschii in S. W. Iran, males outnumber females. Of 40 casual observations during the 1970-71 winter, 87.5 per cent were males and 12.5 per cent were females. These results could have been biassed by the more conspicuous plumage of males (plate 1, p. 2). However out of 74 territorial birds observed during the same period in the study areas, where females were unlikely to have been overlooked despite their more cryptic plumage, 81 per cent were males and 19 per cent were females. In both samples males were significantly more numerous than females (chi-squared test, $p<0.001$).

I cannot find any information about the sex ratio in the wintering populations of O. finschii in other areas but, in view of the general tendency in birds for females to migrate further than males (Nice 1937, Lack 1944b, Newton 1972), it seems likely that most female O. finschii winter further south than the males. The reasons why, in some species, the sexes differ in their wintering distributions are uncertain but Lack (1954 and 1968), discussing partial migration, suggested that competition for food might be the factor that determines whether a bird migrates or not and argued that the reason why more females than males migrate is that males generally occupy a higher place than females in the pecking order. I have some evidence which suggests that the predominance of male O. finschii in S. W. Iran in winter may be explained in a similar way. This evidence will be briefly reviewed below:

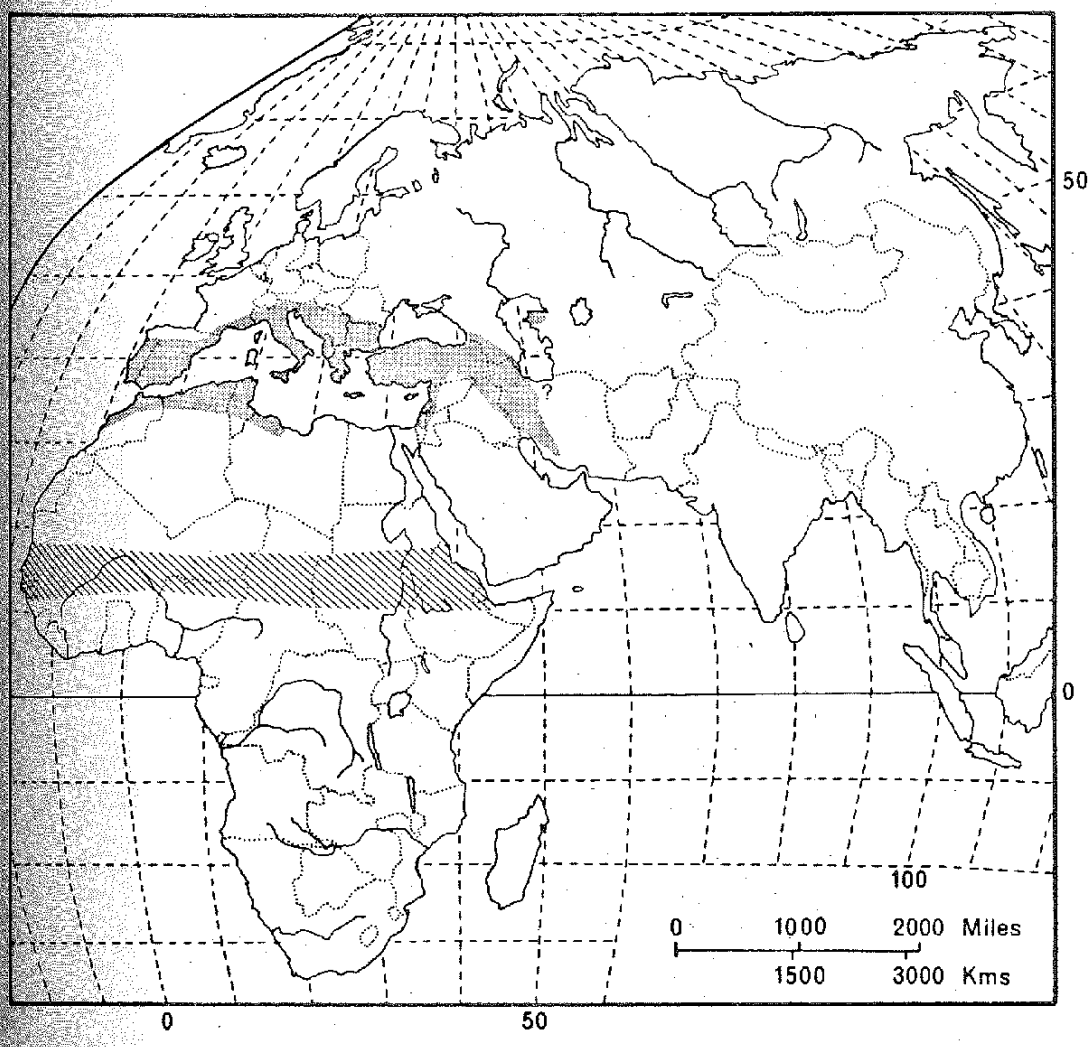
In S. W. Iran in winter male and female O. finschii defend separate territories. The function of these territories is uncertain but the facts that: 1) they are vacated at the end of winter, 2) they are used for feeding and 3) all other wheatears are excluded from them, suggest that the territorial behaviour may have food value (see discussion

of winter territory in Lack 1954). Hence the ability to procure a good territory probably has strong survival value. In S. W. Iran males are probably socially dominant to females which enables them to occupy better territories than females. My evidence for this is as follows: 1) In two instances involving different birds I observed a female O. finschii trespass on the territory of a male and in both cases the female was attacked by the male and rapidly retreated. 2) Of five pairs of O. finschii that bred at Tang-i-Shul in the spring of 1971, four males and only one female remained on their breeding territories in the following September (table 8). The reason for this is not known but it is possible that the females were driven off by the males. 3) At Maharlu North during the 1970-71 winter the four territories held by female O. finschii (fig.59, p.291) were in poorer habitat, from the point of view of cover and availability of arthropod food (p.174), and were established later than the territories of most males. It is not known why the females established their territories later than the males but it is possible that they had been ousted from better areas by males. 4) At Maharlu North O. finschii $♀F_3$ (fig. 59,p.291) was present on the same ground on 25 November and 16 December but was absent on 23 December after which the area was included in the territory of an adjacent male. The reason for the disappearance of this bird is unknown but it is possible that she was ousted by the adjacent male. Although no definite conclusions can be drawn from these observations, they support the hypothesis that the unequal sex ratio in the wintering population of O. finschii in S. W. Iran is due to competitive exclusion of females by males.

4) O. HISPANICA (Black-eared Wheatear)

World range and status:

The range of O. hispanica is shown in fig. 13. It is migratory wintering in Africa south of the Sahara.



OENANTHE HISPANICA

Breeding Range Wintering Range

Figure 13. Breeding and wintering ranges of O. hispanica.

(Based on data from: Grote 1939, Vaurie 1959, Voous 1960, Moreau 1972, and recent observations in Iran by L. Cornwallis and D. A. Scott.)

DISTRIBUTION AND STATUS - O. HISPANICA/O. ISABELLINA

Distribution and status in S. W. Iran:

O. hispanica is a summer visitor to S. W. Iran, where it is a common breeding bird in the xerophilous forest zone on the western flanks of the Zagros between about 1,600 and 2,700 m above sea level (cf. overlays 4 and 7). In view of this evidence and the distribution of O. hispanica in the rest of Iran (fig. 13) its breeding distribution in S. W. Iran probably coincides roughly with the xerophilous forest zone, and has been so drawn on the summary map (fig. 22). O. hispanica arrives in S. W. Iran during early April and is present within the breeding range until mid-September.

Like other species of wheatear, O. hispanica is invariably territorial and some, at least, probably remain on the same territory during most of their stay in S. W. Iran. My evidence for this is that a male colour-ringed as a breeding bird at Dasht-i-Arjan in May 1971 was still holding the same territory on 17 August. However his mate had departed. Some O. hispanica occupy the same territories in successive years. Thus two colour-ringed males whose territories were plotted in August 1971 were back on approximately the same ground in May 1972.

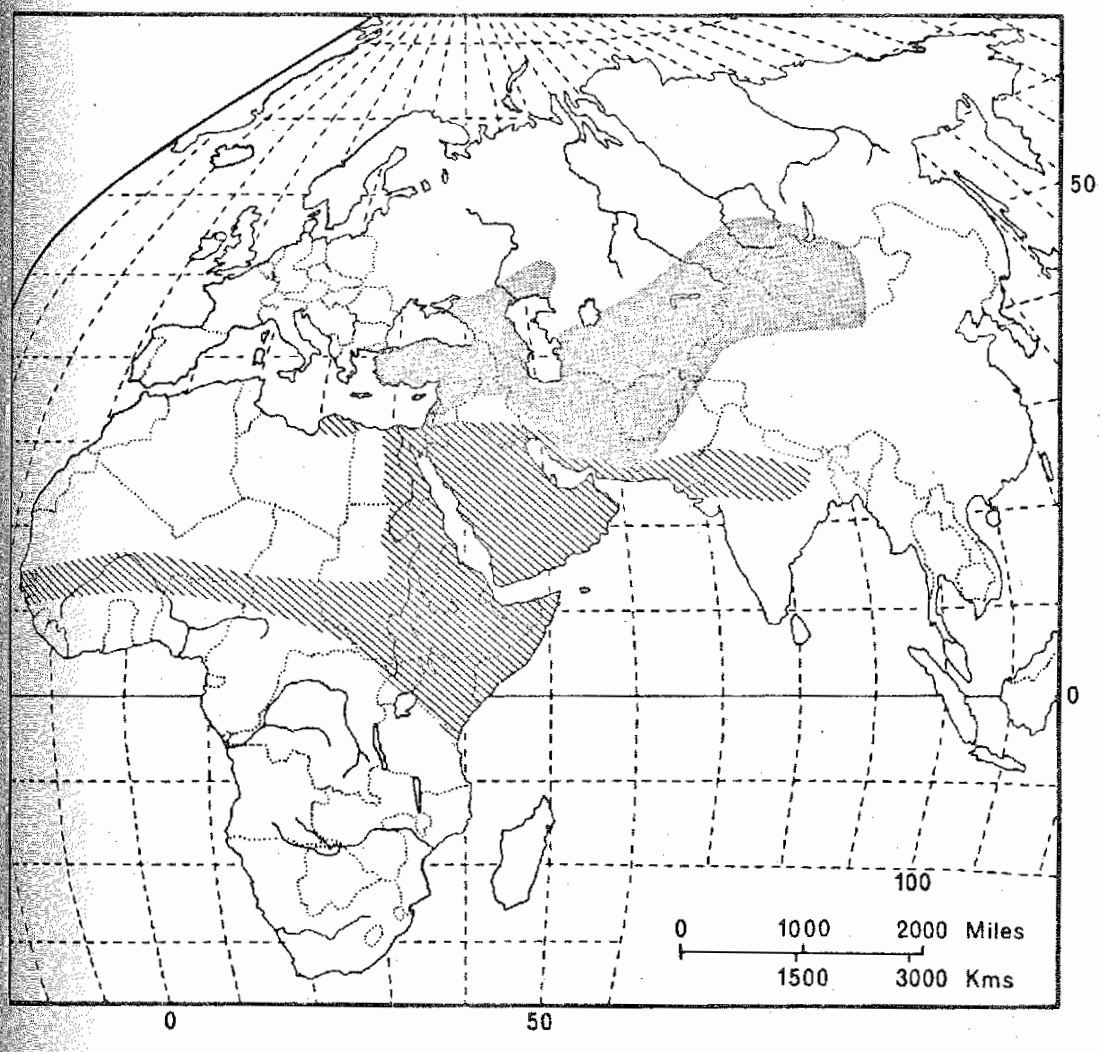
5) O. ISABELLINA (Isabelline Wheatear).

World range and status:

O. isabellina is a summer visitor to most of its breeding range which together with its wintering range is given in fig. 14.

Distribution and status in S. W. Iran:

In S. W. Iran O. isabellina is a common and widespread summer visitor to the sub-steppe zone where it breeds mostly between 1,400 and 2,200 m above sea level, but some may breed as low as 800 m above sea level (cf. overlays 4 and 8). My records suggest that it does not breed in the steppe zone except perhaps in a few places at the edges of irrigated farmland. I have therefore drawn the probable breeding distribution of O. isabellina in S. W. Iran to coincide with the distribution of the sub-steppe zone (summary map fig. 23).



OENANTHE ISABELLINA

Breeding Range Wintering Range

Figure 14. Breeding and wintering ranges of O. isabellina.

(Based on data from: Grote 1937; Meinertzhagen 1954; Vaurie 1959; Ripley 1961; Etchécopar and Hüe 1967; Dementiev and Gladkov 1968; Hüe and Etchécopar 1970; Stresemann, Portenko and Mauersberger 1971; and recent observations in Iran by L. Cornwallis and D. A. Scott.)

DISTRIBUTION AND STATUS - O. ISABELLINA

O. isabellina is abundant within its breeding range in S. W. Iran from the beginning of February until mid-November (overlays 8, 12 and 13). Breeding begins in mid-February and continues until the end of May. As soon as the young are independent they disperse and the adult members of the pairs separate. Consequently after the end of June only solitary O. isabellina are seen which means that migrants are difficult to distinguish from summer visitors. However some indication of how long the summer visitors stay and of the main migration period is given by the results of the regular censuses and studies of colour-ringed birds. For example, at Maharlu North the central part of the study area was occupied completely by eight pairs of O. isabellina during the second half of February (table 9). The territories were mapped as soon as they were established and by 7 May, 14 of the 16 birds had been colour-ringed. This enabled me to follow what happened to these breeding birds and to identify newcomers to the central area (scored as "unknown birds" in table 9). After the breeding season the young and most of the females left the area while the majority of the males remained on their breeding territories until the end of August. During July and August only a few unknown birds were seen, but in September most were newcomers, presumably migrants. Thus on 7 September nine out of 11 were unknown and on 22 September five out of six. O. isabellina was recorded at Maharlu until mid-November and probably most birds seen after the beginning of September were on passage. At Dasht-i-Arjan, where O. isabellina does not breed, migrants were seen from mid-August until the end of November. As a result of this evidence, birds of unconfirmed status seen on the breeding grounds outside the breeding season were recorded as probably summer visitors/?migrants if they were seen before 1 September and as probably migrants/?summer visitors if they were seen on or after 1 September (overlays 12 and 13).

The winter quarters of O. isabellina which breed in S. W. Iran are unknown, but a ringing recovery shows that some leave Iran. A female O. isabellina which bred in May 1971 near Shiraz was recovered by Prince Faisel Bin Jassem Althani at Doha in Qatar on 27 January 1972. The Shiraz birds arrive back on their breeding ground during mid-February. Therefore

STUDY AREAS (Descending alt. order) + INDIVIDUAL BIRDS		OCT		NOV		DEC		JAN		FEB		MAR		APR		MAY		JUNE		JULY		AUG		SEPT		MAY 1972
		1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-30	1-15
BARM-I-FIRUZ				2	[-]											[-]			[-]			[-]				
TANG-I-SHUL				1											6p+2c	[(2)]			1m					4		4
DASHT-I-ARJAN					2	[-]				-	[-]				-	-	[-]							51*	35		-
BARDEH			7	-		-		-		2			2p+5	5		4p+4+5f						16				
MAHARLU CENSUS (Begun January 1967)		13	12	11	3		-	-	-	1	7p+10	8p+20	5p+9	5p+10 b	2p+9 c 7p+8 +9f	6p+4 c 4p+19 c	3p+8	2p+16	2p+9 +4f 3p+23 +1f	7	9	9	21		20	
MAHARLU NORTH			13	2	-	-	-	-	-	3	10p+8	15p+11	13p+11	10p+21	9p+12	14p+18	13p+7	2p+14	13	18		16	13	19	14	6p+15
Central area known birds:-																										
♂ blue/red ♀ unringed	pA			-	-	-	-	-	-	/	✓	✓	-	-	√c	-	√2fm	-	-	-		-	-	-	-	-
				-	-	-	-	-	-	+	+	+	-	-	+c	+	+	+m	-	+		-	+	-	-	
♂ orange/orange ♀ green/red	pB			-	-	-	-	-	-	√	√	√	-	-	-	√c	√	-	-	-		-	-	-	-	√c
				-	-	-	-	-	-	/	√	√	-	-	-	√c	√	-	-	-		-	-	-	-	♀uc
♂ white/orange ♀ white/purple	pC			-	-	-	-	-	-	/	/	√	√	-	-	√c	√	√m	-	-		✓	✓	-	-	-
				-	-	-	-	-	-	/	/	-	-	-	-	√i	√	-	-	-		-	✓**	-	-	-
♂ red/white ♀ white/red	pD			-	-	-	-	-	-	/	/	√	-	√n	√c	√2f	-	-	-	-		-	-	-	-	√c
				-	-	-	-	-	-	/	/	√	-	√n	√c	√	-	-	-	-		-	-	-	-	√c***
♂ white/blue ♀ purple/purple	pE			-	-	-	-	-	-	/	/	√	-	√	√c	√f	✓	-	✓			-	✓	-	-	-
				-	-	-	-	-	-	/	/	√	-	√n	√i	√2f	-	-	-			-	-	-	-	
♂ green/green ♀ unringed	pF			-	-	-	-	-	-	✓	✓	√	✓	-	-	√c	√f	-	✓	-		✓	✓	✓	✓	✓
				-	-	-	-	-	-	+	+	+	+	-	+c	+	+	-	+	-		-	+	-	-	
♂ blue/blue ♀ purple/white	pG			-	-	-	-	-	/	✓	✓	√	√	√	√c	-	√m	✓	√m		✓	✓	✓	-	-	✓
				-	-	-	-	-		Y†	Y†	/	/	/	√c	√2f	√m	-	-	-		-	-	-	-	♀u
♂ red/white/red ♀ green/white	pH			-	-	-	-	-	-	/	/	/	/	√	√c	√	-	-	-			-	✓	✓	-	-
				-	-	-	-	-	-	/	/	/	√	√i	√c	√	√	√	-	-		✓	-	-	-	-
Total seen of the 16 known birds breeding in central area of Maharlu North				-	-	-	-	-	1	8p	8p	7p+1	3p+1	5p	7p+1	7p+1	1p+4	4	3		4+1f	8+1f	2	1	6p+1††	
Unknown birds seen in central area (= surplus unringed + birds ringed but not seen again.)				-	-	-	-	-	2	5	3	4	3	2	3	2	1	-	2		1	2	9	5		
LAKE PERISHAN				5				5							1p+5					[1]			14			
DALAKI								(8)	(12)						(2)								1			

Table 9. Standard counts and records of individuals of O. isabellina in study areas in S. W. Persia. Most of the observations were made between 1 October 1970 and 30 September 1971 and are arranged in chronological order.

KEY

( ) = nearby or non-standard count.
[ ] = 1964-1968 (omitted for Maharlu Census 1967-68).
- = negative record.
b = at least one bird nest-building.
c = at least one bird carrying food to chicks.
f = fledgling.
i = incubation patch.
m = moult.
n = nest found.
p = pair.
u = unringed.

Individual birds in approximately the same territory on consecutive occasions:

✓ = colour-ringed individual.
/ = apparently identical to and probably the same bird as was later colour-ringed.
+ = apparently identical bird, probably the same individual.

*Six of these were colour-ringed but none of them was seen again.

**About 100m from breeding territory.

***Pairs D and E held adjacent territories in 1971. In May 1972 ♂ white/blue and ♀ white/red were missing and ♀ purple/purple had moved and become mated to ♂ red/white.

†♂ blue/blue was mated to ♀ yellow/yellow at the beginning of the season but she disappeared and was replaced by ♀ purple/white.

the one killed at Doha could have been wintering there or it could have been on passage returning from further south.

In the spring, summer visitors return to their breeding grounds at about the same time as passage migration begins. Consequently migrants were only distinguished on the breeding grounds in a few localities where positive evidence of their status was obtained. All other records of O. isabellina within the breeding range in spring were classified as probably summer visitors/?migrants (overlay 12).

In parts of S. W. Iran outside its breeding range, O. isabellina occurs as a migrant in areas above about 800 m above sea level. Below this altitude, on the western flanks of the Zagros and on the coastal plain, it occurs in small numbers from the end of July until mid-November and from mid-January until the end of April (overlays 8, 12 and 13). The status of these birds is uncertain since this area has not been well studied and has not been covered at all in December and early January. Some were probably migrants but others may well have been wintering since O. isabellina winters in Mesopotamia (Allouse 1953), on the island of Fao at the head of the Persian Gulf (Sharpe1886), on Bahrain (Rogers and Gallagher 1973), and is one of the commonest wintering wheatears throughout Arabia (Meinertzhagen 1954). It also probably winters in small numbers in lowland Khuzistan as D. A. Scott (pers. comm.) saw eight between Ahwaz and Susangerd (about 55 km) on 9 January 1972 and I saw 11 O. isabellina between 13 and 21 January 1973 on a drive of about 1,490 km. However if it winters in lowland parts of S. W. Iran, it does so only in small numbers since in late January and early February I found the species scarce. Thus from 21-24 January 1973, I drove 685 km on the coastal plain which is mostly suitable habitat for O. isabellina and saw only 16 birds and between 30 January and 1 February 1971 I drove 80 km over similar terrain near Dalaki and saw only seven birds. The only other records in January were of five birds near Lake Perishan in 1971 and one at the same place in 1973. Of these birds, all the ones I studied in detail (19 out of 29) were vigorously defending territories and were probably wintering. However since,

in the Zagros at least, O. isabellina appears on its breeding grounds in early February, they could have been migrants.

Later in February O. isabellina probably occurs on passage in quite large numbers in lowland areas of S. W. Iran. The evidence for this is that, in contrast to my observations reported above, D. A. Scott (pers. comm.) found O. isabellina "very numerous" when he drove over a similar route to mine between 20 and 24 February 1971. His and my results from roughly the same areas are given in table 10.

AREA	21-24 Jan 1973 L. C.	30 Jan-1 Feb 1971 L. C.	20-24 Feb 1971 D. A. S.
Hendijan[1] - Bandar Deylam (106 km)	9	Not covered	100+
Bandar Rig - Bushire (100 km)	1	7	Very numerous
Bushire - Mukhdan, nr. R. Mand (120 km)	2	Not covered	12

Table 10. Numbers of O. isabellina seen in three areas on the coastal plain of S. W. Iran.

The differences between my 1973 figures and those of Scott in 1971 could have been due to differences in size of the wintering population in the two years but this is unlikely since my 1971 and 1973 counts were similar. I therefore believe that Scott's birds were probably mostly migrants.

As a result of the above evidence, all birds of unconfirmed status seen off the breeding grounds in January and early February were recorded as probably winter visitors/?migrants and those from mid-February until May as probably spring migrants/?winter visitors. I am uncertain of the status of the birds seen in autumn and they were recorded as winter visitors/migrants. Records of probable winter visitors and summer visitors

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[1]Hendijan is in Khuzistan 106 km W. N. W. of Bandar Deylam.

outside the breeding season are plotted on overlay 12 and migrants on overlay 13. The probable wintering range of O. isabellina in S. W. Iran, based on the above evidence, is given on the summary map (fig. 24).

6) O. LUGENS (Mourning Wheatear).

World range and status:

The breeding and wintering ranges of O. lugens are given in fig. 15. Over much of its range it is resident or wanders after the breeding season (Vaurie 1959). However O. lugens persica which breeds in southern Iran migrates to winter in Arabia (Meinertzhagen 1954).

Distribution and status in S. W. Iran:

O. lugens is a summer visitor to S. W. Iran where it breeds widely in the sub-steppe zone between 1,500 and 2,700 m above sea level (cf. overlays 4 and 7). It was also found breeding on the edge of the cold steppe zone in the dry hills to the east of Niriz and on the flanks of Kuh-i-Lalehzar, but owing to lack of coverage in suitable habitat it is not known whether the species breeds widely in this zone or if it extends into the sub-desert zone. However in view of the facts that O. lugens probably breeds in the cold steppe zone in northern Iran (Passburg 1959, Erard and Etchécopar 1970[1]) and breeds in some very arid areas in other parts of its range (Meinertzhagen 1954, Brosset 1961, Etchécopar and Hüe 1967[2]), it probably breeds in mountainous areas in the cold steppe zone of S. W. Iran and may extend into the sub-desert zone. The probable breeding range of O. lugens in S. W. Iran is, therefore, as shown on the summary map (fig. 22).

---

[1] In northern Iran in the cold steppe zone Passburg (1959) found O. lugens fairly common in early April in rocky country south of Qum and Erard and Etchécopar (1970) found a pair on 9 April 1967 established on the steep rocky banks of a river to the west of Robat Karim which lies a few kilometres southwest of Tehran.

[2] Outside Iran O. lugens breeds in several areas which, like the steppe and sub-desert zones of S. W. Iran, were classified by Meigs (1953) as having arid climates, for example in southern Arabia (Meinertzhagen 1954), Sinai and Egypt east of the Nile (Etchécopar and Hüe 1967) and in south-eastern Morocco in areas with less than 100 mm mean annual precipitation (Brosset 1961).

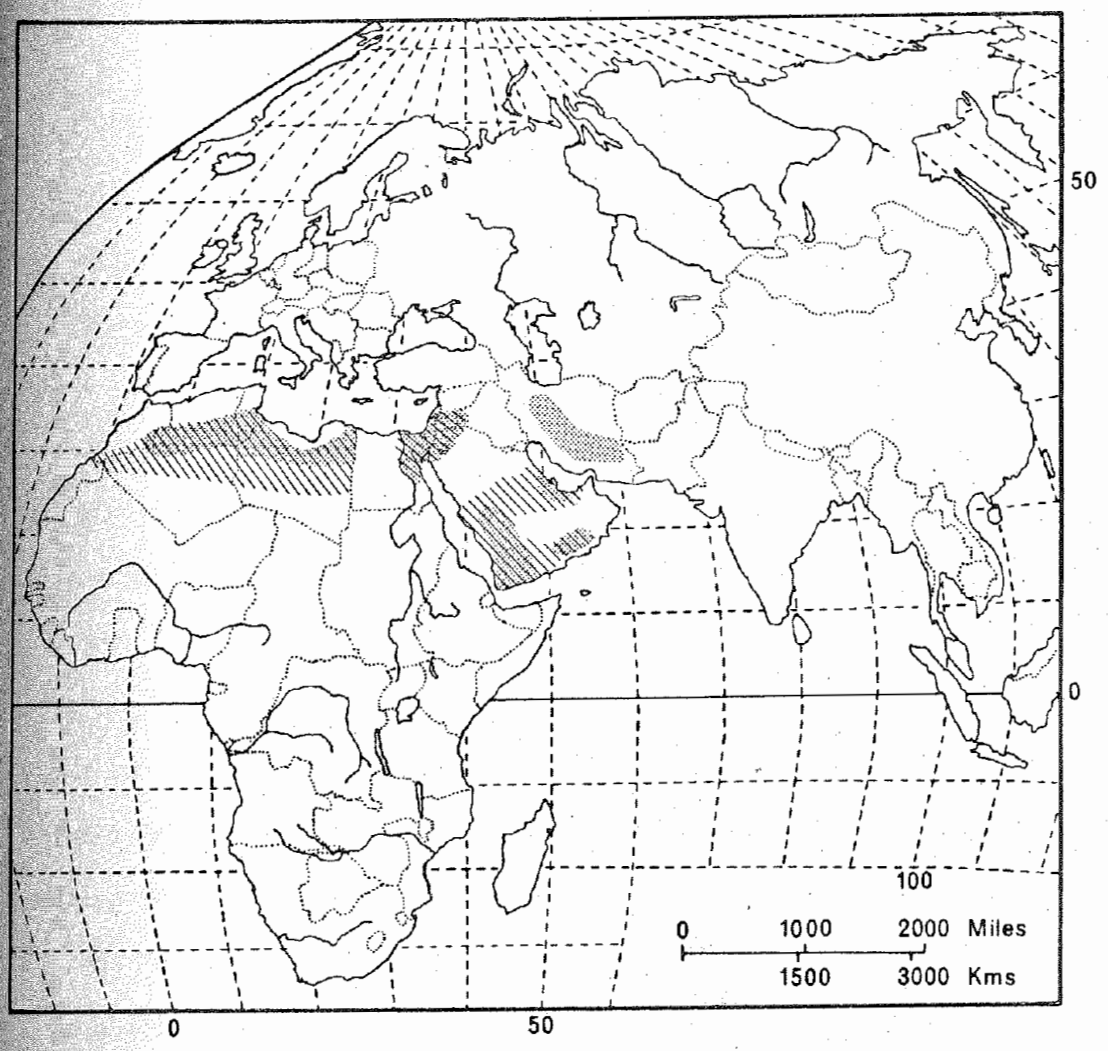


Figure 15. Breeding and wintering ranges of O. lugens.

(Based on data from: Meinertzhagen 1954, Vaurie 1959, Etchécopar and Hüe 1967, Hüe and Etchécopar 1970, and recent observations in Iran by L. Cornwallis and D. A. Scott.)

DISTRIBUTION AND STATUS - O. LUGENS

When the young are independent they disperse, the adult members of the pair separate and after the end of June only solitary birds are seen. I made two observations which I think suggest that break-up of the family groups is brought about by one adult driving the others out of the communal territory. The dominant adult is probably the male but unless the two birds can be compared, and the female seen to be browner than the male, separation of the sexes in the field is uncertain. The first of these observations was made in the study area at Saadi on 13 May 1971. An adult O. lugens was found in its territory with three free-flying young. Suddenly the adult began to chase one of the young birds as if trying to drive it out of the territory. The chase continued relentlessly for two minutes. The second observation was made in the study area at Kuh-i-Gahr on 19 May 1971. I found three free-flying young O. lugens being fed regularly by a drab female and occasionally by a bright male. I watched this family for half an hour during which the male persisted in chasing the female mercilessly around the territory. There is no evidence that O. lugens is double-brooded in S. W. Iran so I think the chasing was aggressive and not courtship, especially as the female, while fleeing, uttered shrill thrrr thrrr thrrr notes which I interpreted as stress calls.

Outside the breeding season O. lugens occurs in small numbers within the breeding range until mid-November. It then disappears until mid-February when it returns to breed (overlay 14). Some of the birds which stay in S. W. Iran after the breeding season probably remain on their breeding territories since at Saadi and Tang-i-Shul breeding territories were occupied by solitary individuals until the end of August and the beginning of September respectively (table 11).

In autumn a few O. lugens were found holding territories in places where they had not bred and where they did not subsequently winter (table 11). They may have been birds which had bred nearby and moved only short distances or migrants pausing while on passage. In either event their presence in the areas concerned was short-lived and they were classified

STUDY AREAS (Descending alt. order) + INDIVIDUAL BIRDS	OCT		NOV		DEC		JAN		FEB		MAR		APR		MAY		JUNE		JUL		AUG		SEPT		MAY 1972
	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-30	1-15
TANG-I-SHUL			2											2pn			1pc+5+4f						6		3
♂ p 1			+														+c						+		
♀ p 1			+														+c						+		
♂ p 2			+											+			-						+*		
♀ p 2			+											+			-						+		
♂ p 3			-											+			+						+		+
♀ p 3			-											+			+f						+*		+
BARDEH		1	2		-		-		-			-	-		-						-				
O. lugens A		+	+		-		-		-			-	-		-						-				
SAADI												3p	1pn+3	1	1p+2+4f							1			1
♂ p 1												+	+	+	+f							+			+
♀ p 1												+	+												
KUH-I-GARH							-				2			3pbc+5	1c	2pf+1						-			
SHAHPURJAN			-		-	-	-	-	-		3p	2p+1	1p		1				-				-		1pc+2
MAHARLU CENSUS (Begun January 1967)	-	1	-	-		-	-	-	1	2	1p+2	1	1p+1	2 3bc	1 -	1	-	- 1+2f	-	-	-	-	-	1	
MAHARLU VALLEY							-	-		-	3p+3	4	1pn+3		1pc							-			
MAHARLU SOUTH						-	-	-	-	-	1	-	-						-			-		-	
DALAKI									1					-									-		

Table 11. Standard counts and records of individuals of O. lugens in study areas in S. W. Persia. Most of the observations were made between 1 October 1970 and 30 September 1971 and are arranged in chronological order.

KEY

( ) = nearby or non-standard count.
[ ] = 1964-1968 (omitted for Maharlu Census 1967-68).
\+ = apparently identical bird, probably the same individual, in approximately the same territory on consecutive occasions.
* = two birds in different parts of a territory that was occupied by a pair but no evidence that paired.

b = at least one bird nest-building.
c = at least one bird carrying food to chicks.
f = fledgling.
p = pair.
n = nest found.

as migrants. Similarly, birds which appeared for short periods in spring were classified as migrants.

O. lugens has been recorded three times during February on the coastal plain of the Persian Gulf (overlay 14). These birds could have been wintering, but since the population that breeds in S. W. Iran begins to return during February they could equally have been on passage. O. lugens is a winter visitor to Bahrain where it is found from October to March (Rogers and Gallagher 1973). It would not therefore be surprising to find it wintering in the coastal lowlands of S. W. Iran. However I did not see the species during a journey of 765 km through the area in January 1973 and if it does winter there it must be in very small numbers.

7) O. MONACHA (Hooded Wheatear).

World range and status:

The range of O. monacha is shown in fig. 16. It is mainly resident but some wander after the breeding season (Vaurie 1959).

Distribution and status in S. W. Iran:

In S. W. Iran O. monacha is probably resident in small numbers in the most desolate and arid parts of the hills bordering the Persian Gulf. I did not spend much time in these areas and found O. monacha on only four occasions, three times in winter and once in the breeding season. The latter record, on 25 May 1967, was of five males along eight km of track through "badlands" about 80 km southeast of Bushire (overlay 6). The three winter records were as follows: 1) a male on 30 January 1971 in barren marl and gypsum hills in the Dalaki study area, 2) a female on 31 January 1971 in a dry wadi cut into a desolate alluvial plain near Dilbar on the coastal plain of the Persian Gulf and 3) a male near Bandar Deylam on 22 January 1973 in an area of small rounded marl hills and deeply incised wadis with a smattering of small plants. The only other O. monacha that I encountered in S. W. Iran was a male on 12 December 1966 in an area of scattered tamarisk bushes on the shore of Lake Tashk near

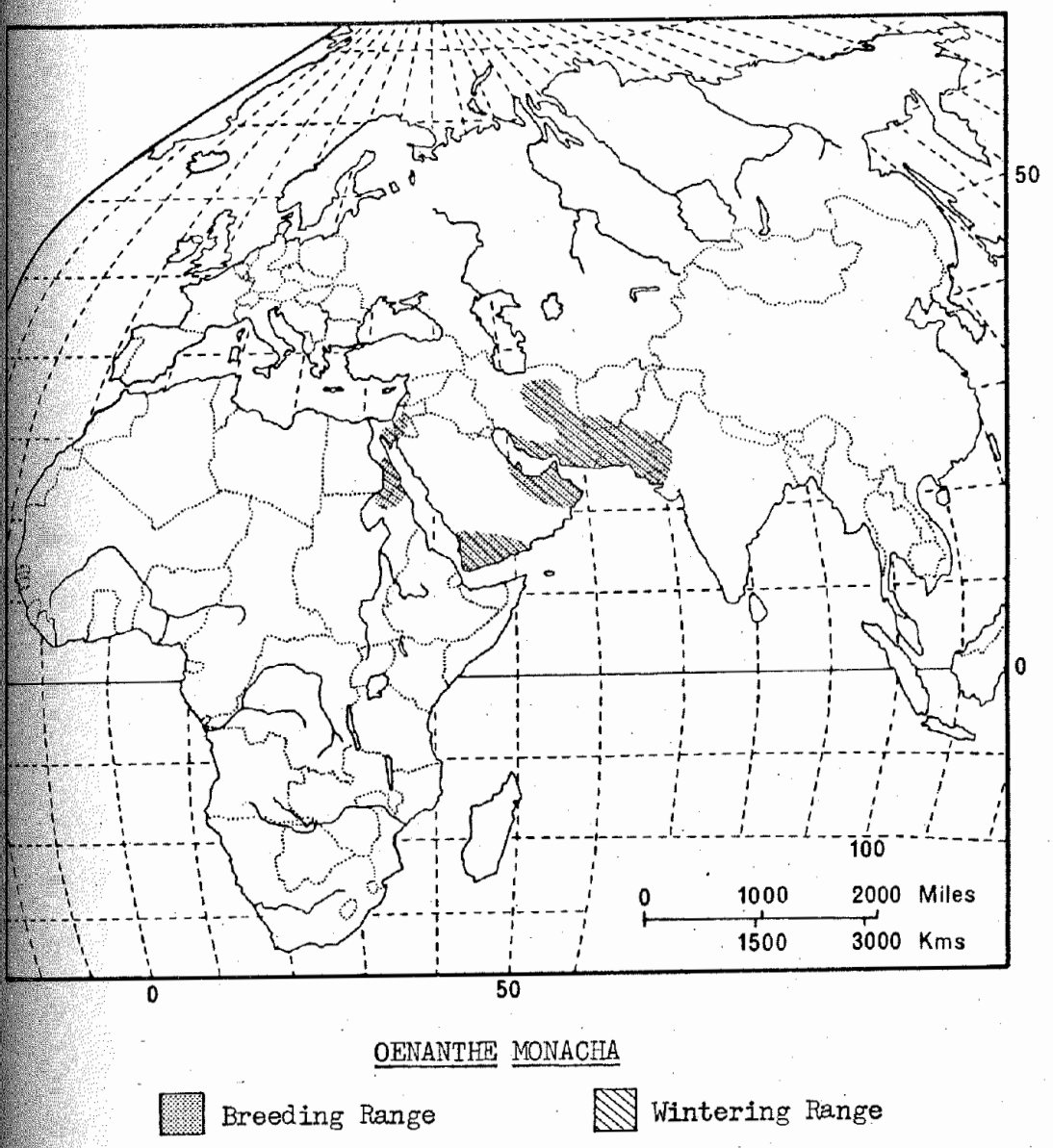


Figure 16. Breeding and wintering ranges of O. monacha.

(Based on data from: Meinertzhagen 1954, Vaurie 1959, Ripley 1961, Etchécopar and Hüe 1967, Hüe and Etchécopar 1970, and recent observations in Iran by L. Cornwallis and D. A. Scott.)

the Gumoon study area. The origin and status of this bird are unknown but since O. monacha probably breeds in the arid interior of Iran it may have been a straggler from there.

8) O. OENANTHE (Wheatear).

World range and status:

The breeding and wintering ranges of O. oenanthe are given in fig. 17. Over most of its breeding range it is migratory but is probably resident in north Africa (Vaurie 1959).

Distribution and status in S. W. Iran:

O. oenanthe is a summer visitor to S. W. Iran where it breeds largely in the montane zone above 2,700 m above sea level, but has been recorded probably breeding as low as 2,500 m above sea level (overlay 8). The probable breeding distribution in S. W. Iran has, therefore, been drawn to include all land above 2,500 m above sea level (summary map fig. 23). It is present on the breeding grounds from the end of March until at least the end of August.

In the rest of S. W. Iran, O. oenanthe occurs on passage when it is widespread in small numbers in spring but rare in autumn. Stopovers are usually brief and I have no evidence of this species establishing territories while on passage (overlay 15 and table 12).

9) O. PICATA (Eastern Pied Wheatear).

World range and status:

The range of O. picata is given in fig. 18. The species is mainly migratory but some southern breeding populations are partly resident (Dementiev and Gladkov 1968, Ali and Ripley 1973).

Distribution and status in S. W. Iran:

In S. W. Iran O. picata breeds in very small numbers between about 450 and 2,400 m above sea level in the xerophilous forest, sub-steppe and steppe zones (cf. overlays 4 and 6). The only pair about which I have any

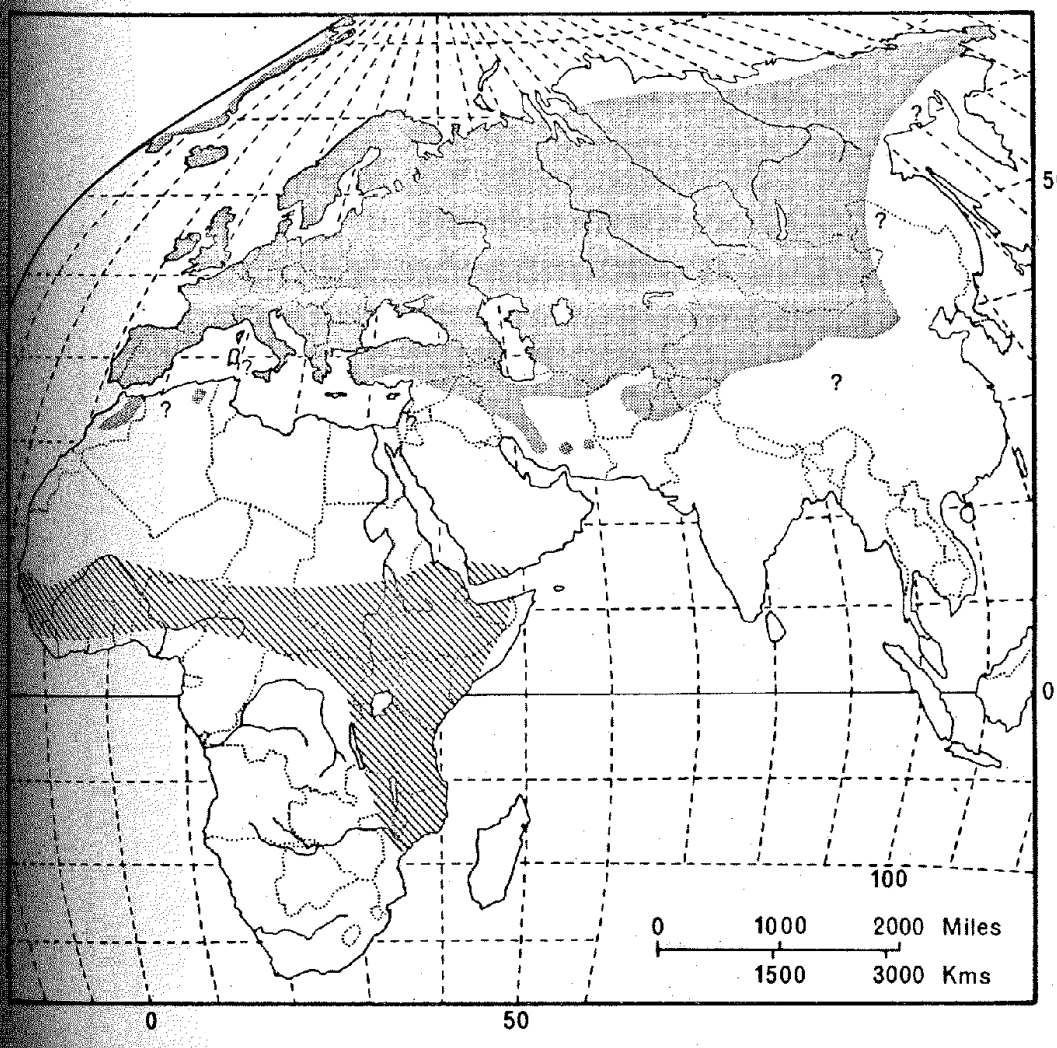


Figure 17. The breeding range (omitting western Greenland, north-eastern Canada and Alaska) and the wintering range of O. oenanthe.

(Based on data from: Meinertzhagen 1954, Vaurie 1959, Voous 1960, Etchécopar and Hüe 1967, Dementiev and Gladkov 1968, Hüe and Etchécopar 1970, Moreau 1972, and recent observations in Iran by L. Cornwallis and D. A. Scott.)

STUDY AREAS (Descending alt. order)	OCT		NOV		DEC		JAN		FEB		MAR		APR		MAY		JUNE		JULY		AUG		SEPT		MAY 1972
	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-30	1-15
BARM-I-FIRUZ			-	-											[11]			(6pc+10 +6f)			[3]				
DASHT-I-ARJAN				-	[-]				-	[-]			[-]	-	-	[-]						1	-	-	-
BARDEH		-	-		-		-		-			-	1		-						-				
SHAHPURJAN				-	-	-	[-]	[-]	-		1		-		-				-				-		1
MAHARLU CENSUS (Begun January 1967)	-	-	-	-		-	-	-	-	-	-		3	2	16		-	-	-	-	-	-	-	-	
MAHARLU VALLEY							-	-		-	-	-	12		-							-			
DALAKI								-	-					1									-		

Table 12. Standard counts of O. oenanthe in study areas in S. W. Persia. Most of the observations were made between 1 October 1970 and 30 September 1971 and are arranged in chronological order.

KEY

( ) = nearby or non-standard count.
[ ] = 1964-1968 (omitted for Maharlu 1967-68).
- = negative record.
c = at least one bird carrying food to chicks.
f = fledgling.
p = pair.

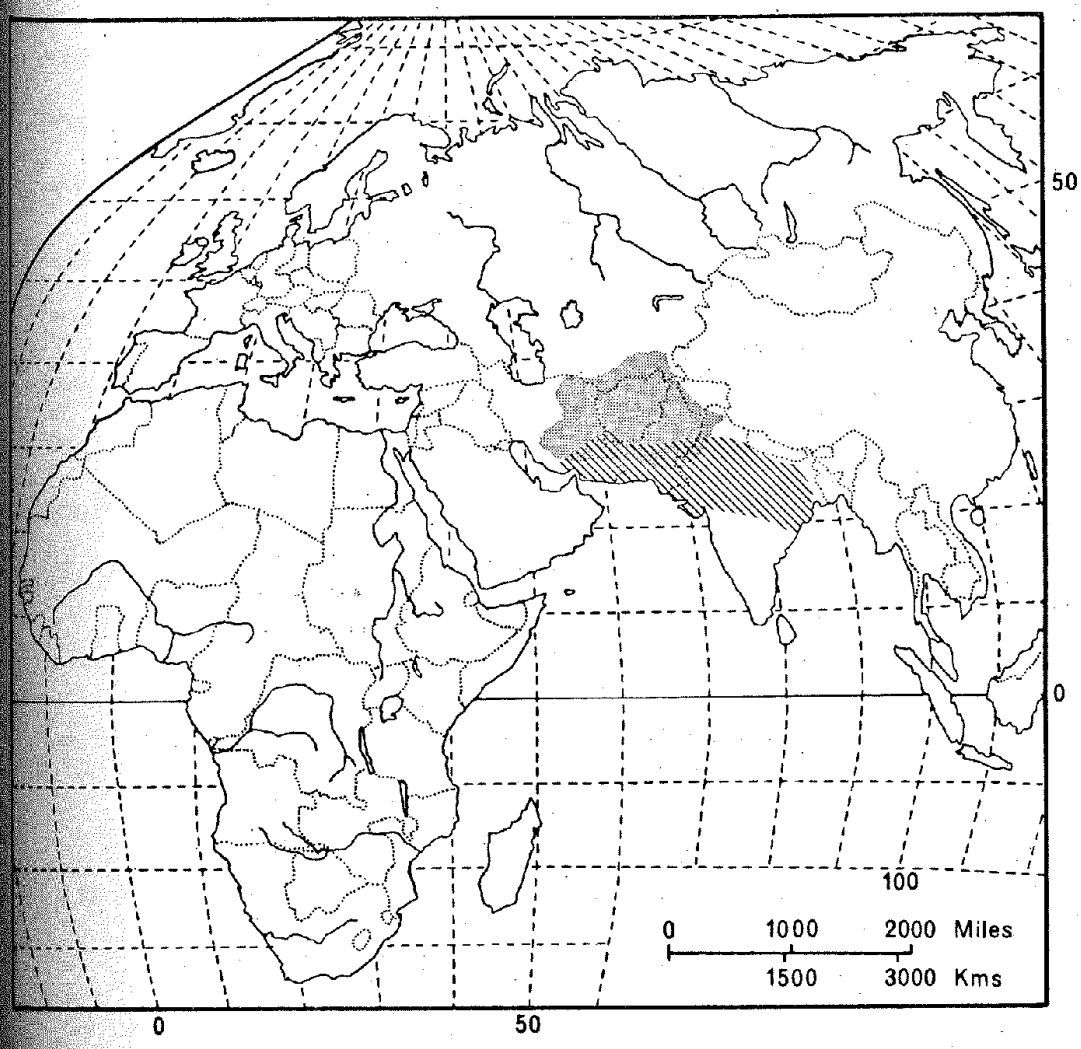


Figure 18. Breeding and wintering ranges of O. picata.

(Based on data from: Vaurie 1959, Ripley 1961, Dementiev and Gladkov 1968, Hue and Etchécopar 1970, and recent observations in Iran by L. Cornwallis and R. A. Scott.)

detailed information is one which bred in the Shahpurjan study area in 1971. Having been absent all winter, the pair arrived during late February or early March and had established a territory by 15 March. Both parents were feeding flying young on 11 May but on my next visit, on 14 July, I could find only the male, which was colour-ringed. By 1-2 September he also had disappeared. The members of this pair were summer visitors to their breeding ground but a few which occurred in winter may have been residents or winter visitors. Winter records of O. picata in S. W. Iran are listed in table 13.

Date	No/Sex	Locality	Altitude	Habitat
12 Nov 1970	2♂	Near Lake Maharlu	1,500 m	Steep, stony, rocky, hillside and adjacent area of dry farmland.
23 Jan 1973	1♂	Near Mukhdan, coastal plain of Persian Gulf	20 m	On hedge bordering palm garden on alluvial plain.
26 Jan 1973	1♂	Between Dasht-i-Arjan and Kazerun	1,200 m	On pistachio tree on plain adjacent to steep rocky hillside.
26 Jan 1971	1♂	Near Kazerun	800 m	Near mud wall across dry farmland.
1 Feb 1971	1♀	Near Dalaki	100 m	Stony piedmont.

Table 13. Winter records of O. picata in S. W. Iran.

10) O. PLESCHANKA (Pied Wheatear).

World range and status:

The breeding and wintering ranges of O. pleschanka are given in fig. 19. The species is migratory.

Distribution and status in S. W. Iran:

In S. W. Iran O. pleschanka occurs chiefly on passage when it is common and widespread in both spring and autumn (overlay 16). In addition there are a few records which suggest that breeding may occasionally occur or be attempted. These records are listed below:

1) Koelz obtained a specimen on 29 March near Niriz which he

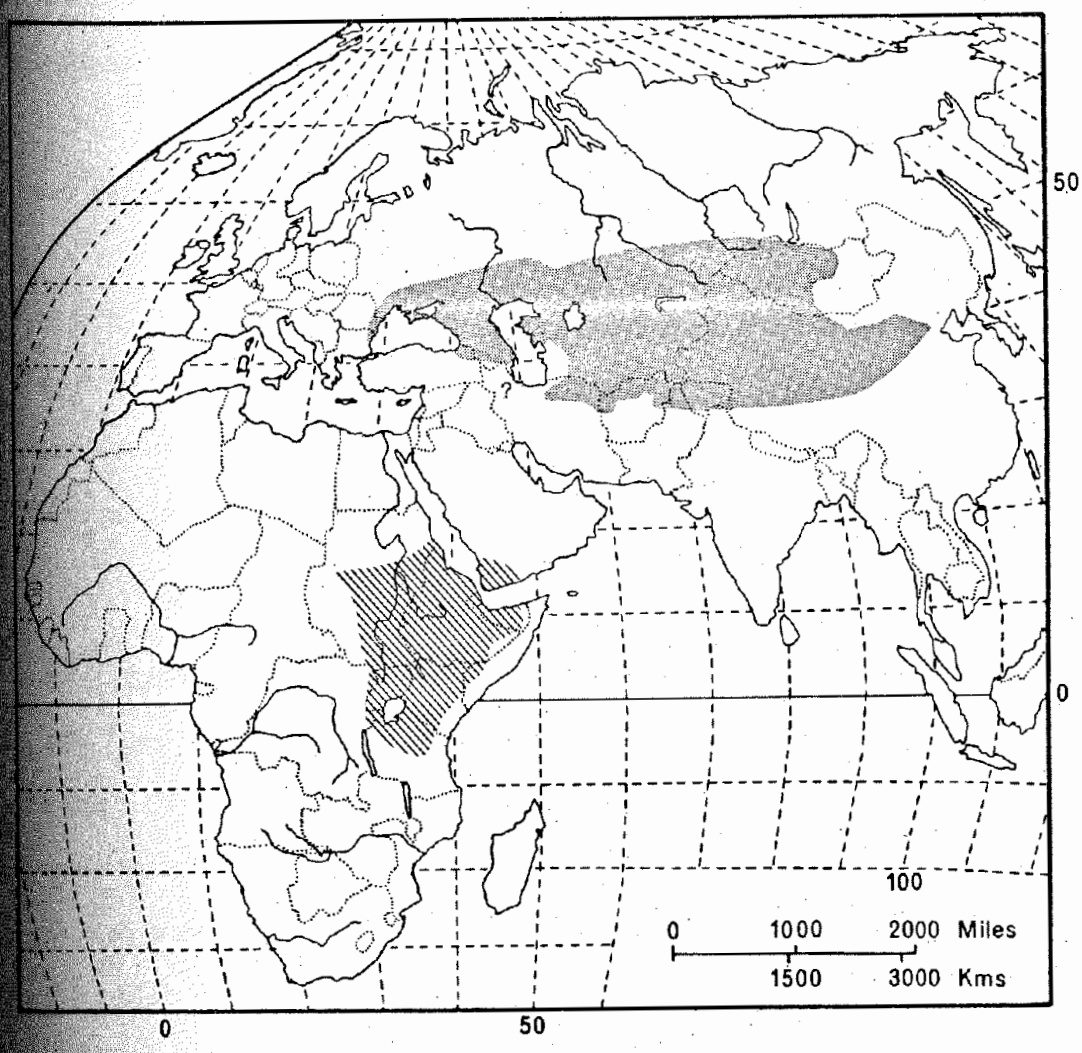


Figure 19. Breeding and wintering ranges of O. pleschanka.

(Based on data from: Grote 1937, Meinertzhagen 1954, Vaurie 1959, Vaous 1960, Ripley 1961, Etchécopar and Hüe 1967, Dementiev and Gladkov 1968, Hüe and Etchécopar 1970, Moreau 1972, and recent observations in Iran by L. Cornwallis and D. A. Scott.)

labelled as "laying" (Vaurie 1949).

2) Erard and Etchécopar (1970) reported a male carrying food near Persepolis on 18 April 1967.

3) I found four pairs of O. pleschanka established on territories in rocky valleys in the hills west of Lake Maharlu during April 1967 and April 1971. They were behaving as though they were going to breed and may have attempted to do so but were evidently unsuccessful since by the beginning of May they had all disappeared (table 14).

Vaurie (1949) reported that the breeding ranges of O. pleschanka and O. hispanica overlap in S. W. Iran. However my observations (cf. overlays 7 and 16) do not support this view and I believe Vaurie's evidence for overlap can be interpreted differently. Vaurie based his conclusion on data from three localities where he alleged that both species were breeding or were taken during the breeding season. The data from these three localities will be examined below:

1) Dasht-i-Arjan: At Dasht-i-Arjan Koelz collected an O. hispanica between 8 and 10 April and an O. pleschanka on 9 April. He gave no proof that these birds were breeding but Vaurie implied from the dates that both were on their breeding grounds. I found O. hispanica a common breeding bird at Dasht-i-Arjan from the beginning of April until the beginning of July and so I agree that Koelz's specimen of O. hispanica could have been breeding. However I suggest that his specimen of O. pleschanka could have been a migrant since I found that passage of this species continues throughout April.

2) Shiraz: Blanford (1876) reported specimens of single males of O. hispanica and O. pleschanka which were obtained at Shiraz during June but he gave no indication that these birds were breeding. Vaurie quoted these records and implied from the dates that the birds were on their breeding grounds. I regard this as insufficient evidence that the two species overlap in breeding range even if the specimens were identified correctly, which is open to question in view of the confusion in wheatear taxonomy which prevailed at that time. Indeed Vaurie himself apparently

STUDY AREAS (Descending alt. order) + INDIVIDUAL BIRDS	OCT		NOV		DEC		JAN		FEB		MAR		APR		MAY		JUNE		JULY		AUG		SEPT		MAY 1972
	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-30	1-15
BARM-I-FIRUZ			12												[-]			-			[-]				
DASHT-I-ARJAN				13	[-]				-	[-]			[1*]	-	-	[-]						-		7	-
BARDEH		2	-		-		-		-			1	-		-						-				
SAADI												2	-	-	-							14			
SHAHPURJAN				[-]	-	-	[-]	[-]	-		(2)		5		-				-			-			-
MAHARLU CENSUS (Begun January 1967)	-	-	-	-		-	-	-	-	1	2	2	2p+3	1p+6 1	1 -		-	- -	-	-	-	-		-	
♂ pA	-	-	-	-		-	-	-	-	-	-	-	+	+	-		-	-	-	-	-	-		-	
♀ pA	-	-	-	-		-	-	-	-	-	-	-	+	-	-		-	-	-	-	-	-		-	
♂ pB	-	-	-	-		-	-	-	-	-	-	-	+	+	-		-	-	-	-	-	-		-	
♀ pB	-	-	-	-		-	-	-	-	-	-	-	+	-	-		-	-	-	-	-	-		-	
♂ pC	-	-	-	-		-	-	-	-	-	-	-	+	+	-		-	-	-	-	-	-		-	
♀ pC	-	-	-	-		-	-	-	-	-	-	-	-	+	-		-	-	-	-	-	-		-	
MAHARLU NORTH	-	2	1	-	-	-	-	-	-	-	2	3	3	-	1	-	-	-	-	-	-	-	1	-	-
O. pleschanka ♀A	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MAHARLU VALLEY							-	-		-	-	1	1p+26		1							-			

Table 14. Standard counts and records of individuals of O. pleschanka in study areas in S. W. Persia. Most of the observations were made between 1 October 1970 and 30 September 1971 and are arranged in chronological order.

KEY

( ) = nearby or non-standard count. [ ] = 1964-1968 (omitted for Maharlu Census 1967-68). + = apparently identical bird, probably the same individual, in approximately the same territory on consecutive occasions. p = pair. * = Vaurie 1949.

acknowledged this difficulty by appending a query to Blanford's record of O. pleschanka.

3) Niriz: On 29 March when Koelz collected the laying female O. pleschanka mentioned above he also obtained an O. hispanica of unspecified status which, from the date, Vaurie regarded as a breeding bird. My observations suggest that this record is early and very far east for O. hispanica to be breeding. Alternatively it could have been a vagrant.

I therefore dispute Vaurie's contention (loc. cit.) that there is overlap in the breeding ranges of O. hispanica and O. pleschanka in S. W. Iran.

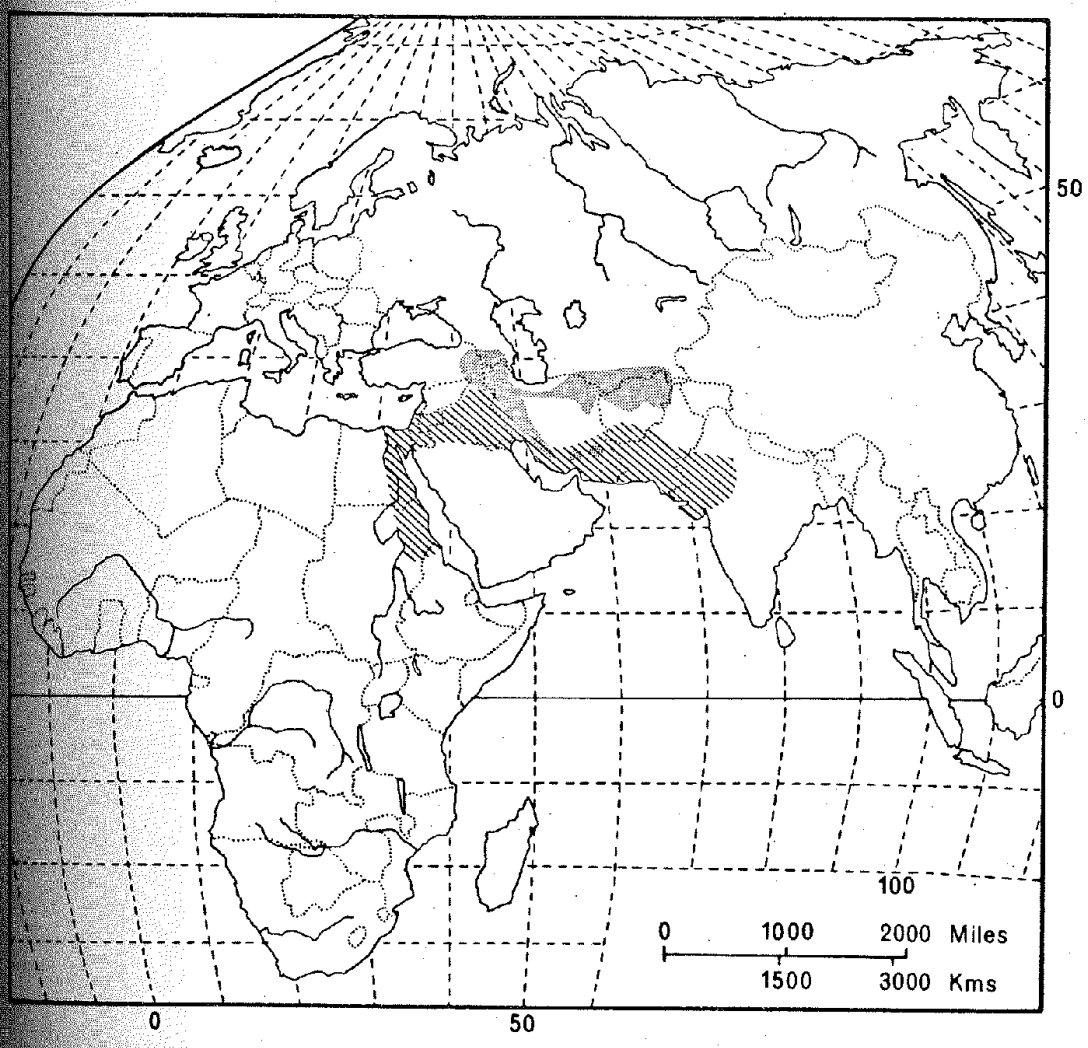
11) O. XANTHOPRYMNA (Red-tailed Wheatear).

World range and status:

The breeding and wintering ranges of O. xanthoprymna are given in fig. 20. The species is migratory but some southern populations may move only altitudinally (Dementiev and Gladkov 1968).

Distribution and status in S. W. Iran:

In S. W. Iran O. xanthoprymna probably breeds in all mountainous country above about 2,500 m above sea level since I found it a common breeding bird in all such areas that I visited (overlay 5). The probable breeding distribution of the species in S. W. Iran has been drawn accordingly (summary map fig. 22). After the breeding season it was found holding individual territories within the breeding range until the beginning of November (overlay 17). The status of these birds is uncertain but they were probably members of the breeding population. On visits to the montane zone in late November and early December O. xanthoprymna was absent, even from localities where it was known to breed. Hence the S. W. Iranian breeding population of O. xanthoprymna is migratory, but it is not known whether these birds simply move to lower altitudes in S. W. Iran to winter or whether they migrate further south.



OENANTHE XANTHOPRYMNA

Breeding Range Wintering Range

Figure 20. Breeding and wintering ranges of O. xanthoprymna.

(Based on data from: Meinertzhagen 1954, Vaurie 1959, Ripley 1961, Etchécopar and Hüe 1967, Dementiev and Gladkov 1968, Hüe and Etchécopar 1970, and recent observations in Iran by L. Cornwallis and D. A. Scott.)

STUDY AREAS (Descending alt. order) + INDIVIDUAL BIRDS	OCT 1-15	OCT 16-31	NOV 1-15	NOV 16-30	DEC 1-15	DEC 16-31	JAN 1-15	JAN 16-31	FEB 1-15	FEB 16-29	MAR 1-15	MAR 16-31	APR 1-15	APR 16-30	MAY 1-15	MAY 16-31	JUNE 1-15	JUNE 16-30	JULY 1-15	JULY 16-31	AUG 1-15	AUG 16-31	SEPT 1-15	SEPT 16-30	MAY 1972 1-15
BARM-I-FIRUZ			2	[(-)]											[(6p+2)]			2p+7c+8f				[(27)]			
KUH-I-KHATUN					-															11+3f					
TANG-I-SHUL			(1)											-	-		-	-					-		-
DASHT-I-ARJAN				-	[-]				-	[-]			[-]	-	-	[-]					-			1	-
BARDEH		-	-		1		1		-			-	-		-						-				
GUMOON					[(1)]	[3]			[6]	4					[-]					-		[-]			
SAADI												2	-	-	-							-			
KUH-I-GAHR							1				3			-	-	-						-			
SHAHPURJAN				[-]	(1)	6			2		8		-		-				-				-		-
O. xanthoprymna A						+			-		+		-		-				-				-		-
" " B						+			+		+		-		-				-				-		-
" " C						+			+		+		-		-				-				-		-
" " D					+	+			-		+		-		-				-				-		-
MAHARLU CENSUS (Begun January 1967)	2	4	5	4		5	2	7	3	3	6		1	-	-	-	-	-	-	-	-	-		1	
O. xanthoprymna A	-	+*	+	-			+	+	+	+	+		-	-	-	-	-	-	-	-	-	-		-	
" " B	±	±	±	=		+		+	+	+	+		-	-	-	-	-	-	-	-	-	-		+*	
" " C	±	±	±	±		+		+	+	+	+		-	-	-	-	-	-	-	-	-	-		+*	
" " D	-	+*	+	+		+		+		+	+		-	-	-	-	-	-	-	-	-	-		-	
" " E	-	-	-	+		-	+	+		+	+		-	-	-	-	-	-	-	-	-	-		-	
MAHARLU NORTH		7	4	3	3	3	1	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-
O. xanthoprymna red		/	✓	✓	✓	✓	✓	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-
" " A		+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	
" " B		+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	
MAHARLU SOUTH						2	9	1	-	-	1	-	-						-			-		1	
O. xanthoprymna red/yellow							/	✓	-	-	-	-	-						-			-		-	
MAHARLU VALLEY							(1)	(1)		(1)	3	2	-		-							-			
O. xanthoprymna A							+	+		+	+	+	-		-							-			
LAKE PERISHAN				1				1								-							-		
DALAKI									2					-									-		

Table 15. Standard counts and records of individuals of O. xanthoprymna in study areas in S. W. Persia. Most of the observations were made between 1 October 1970 and 30 September 1971 and are arranged in chronological order.

KEY

( ) = nearby or non-standard count.
[ ] = 1964-1968 (omitted for Maharlu Census 1967-68).
- = negative record.
c = at least one bird carrying food to chicks.
f = fledgling.
p = pair.
* = in same territory but no evidence that same bird as in previous winter.

Individual birds in approximately the same territory on consecutive occasions:

✓ = colour-ringed individual.
/ = apparently identical to and probably the same bird as was later colour-ringed.
+ = apparently identical bird, probably the same individual.

DISTRIBUTION AND STATUS - O. XANTHOPRYMNA

In other parts of S. W. Iran O. xanthoprymna is a winter visitor. Thus from mid-September until the end of March it is common and widespread from sea level to 2,100 m above sea level in lower deforested parts of the xerophilous forest zone, and in the sub-steppe and warm steppe zones (overlay 17, table 15). Coverage was insufficient to establish categorically whether or not O. xanthoprymna winters in the cold steppe zone. However in view of the following evidence, if it does occur it can be only in small numbers: 1) I did not record O. xanthoprymna during the studies outlined in table 16; and 2) O. xanthoprymna has not been reported wintering in the cold steppe zone in other parts of Iran. The sub-desert zone was not visited in winter and it is not known whether O. xanthoprymna occurs there, but this seems unlikely considering the status of the species in the cold steppe zone where temperatures are similar but precipitation and hence probably food is more abundant than in the sub-desert zone.

Date	No. days	Distance covered (km)	Notes
December 1966	2	c. 100	Included walks in both plains and hills.
February 1970	1	c. 280	"
December 1970	5	c. 340	"
February 1973	1	c. 280	"

Table 16. Winter coverage in the cold steppe zone of S. W. Iran. No O. xanthoprymna were recorded.

As a result of the above evidence the probable winter distribution of O. xanthoprymna in S. W. Iran was drawn to include all areas between sea level and 2,100 m above sea level in the xerophilous forest, sub-steppe and warm steppe zones (summary map fig. 24).

The origin of the O. xanthoprymna that winter in S. W. Iran is not known. Some may be birds that bred in the high Zagros within S. W. Iran but since O. xanthoprymna is more abundant in S. W. Iran in winter than in the breeding season many must be immigrants from further north.

In S. W. Iran in winter O. xanthoprymna is invariably solitary

and territorial. Colour-ringed and apparently identical birds which were probably the same individuals were recorded regularly in the same territories in several study areas (table 15). The evidence from the Maharlu census 1967 and the Shahpurjan study area suggests that some birds may maintain the same territory throughout the winter. However at Maharlu North and South all the O. xanthoprymna disappeared during January 1971. This could have been due to mortality or midwinter movement.

Migrants were distinguished in a few localities where O. xanthoprymna neither breeds nor winters and in the census areas at Maharlu North and Shahpurjan where larger counts were made in autumn and spring respectively than during the winter. Any other migrants went undetected due to the difficulty of distinguishing them from winter visitors. However I doubt whether O. xanthoprymna is a common migrant in S. W. Iran since so few transients were detected in the study areas.

SUMMARY:

In this section the status and distribution of wheatears in S. W. Iran are summarised diagrammatically. Table 17 summarises the status of the various species; fig. 21 their seasonal occurrence; table 18 the bioclimatic zones in which each occurs; and figs. 22-24 summarise their probable geographical distributions and altitudinal ranges (for explanation of figs. 22-24 see p. 54). In addition pictorial representations of the typical habitats of the various species, based on data presented in Chapter V, are given in figs. 22-24.

WHEATEAR SPECIES	SUMMER VISITOR	RESIDENT	WINTER VISITOR	MIGRATION	
				SPRING	AUTUMN
O. alboniger		+			
O. deserti	+	(+)?	(+)?	(+)	(+)
O. finschii	+	(+)?	+		
O. hispanica	+				
O. isabellina	+		(+)?	+	+
O. lugens	+			(+)	(+)
O. monacha		(+)?			
O. oenanthe	+			+	(+)
O. picata	(+)	(+)?	(+)?		
O. pleschanka	(+)?			+	+
O. xanthoprymna	+		+	(+)	(+)
TOTALS: 11	7 + (1) + (+)?	1 + (4)?	2 + (3)?	3 + (3)	2 + (4)

Table 17. Summary of status of wheatears in S. W. Iran

KEY

\+ = common in suitable localities

( ) = small numbers

? = unconfirmed

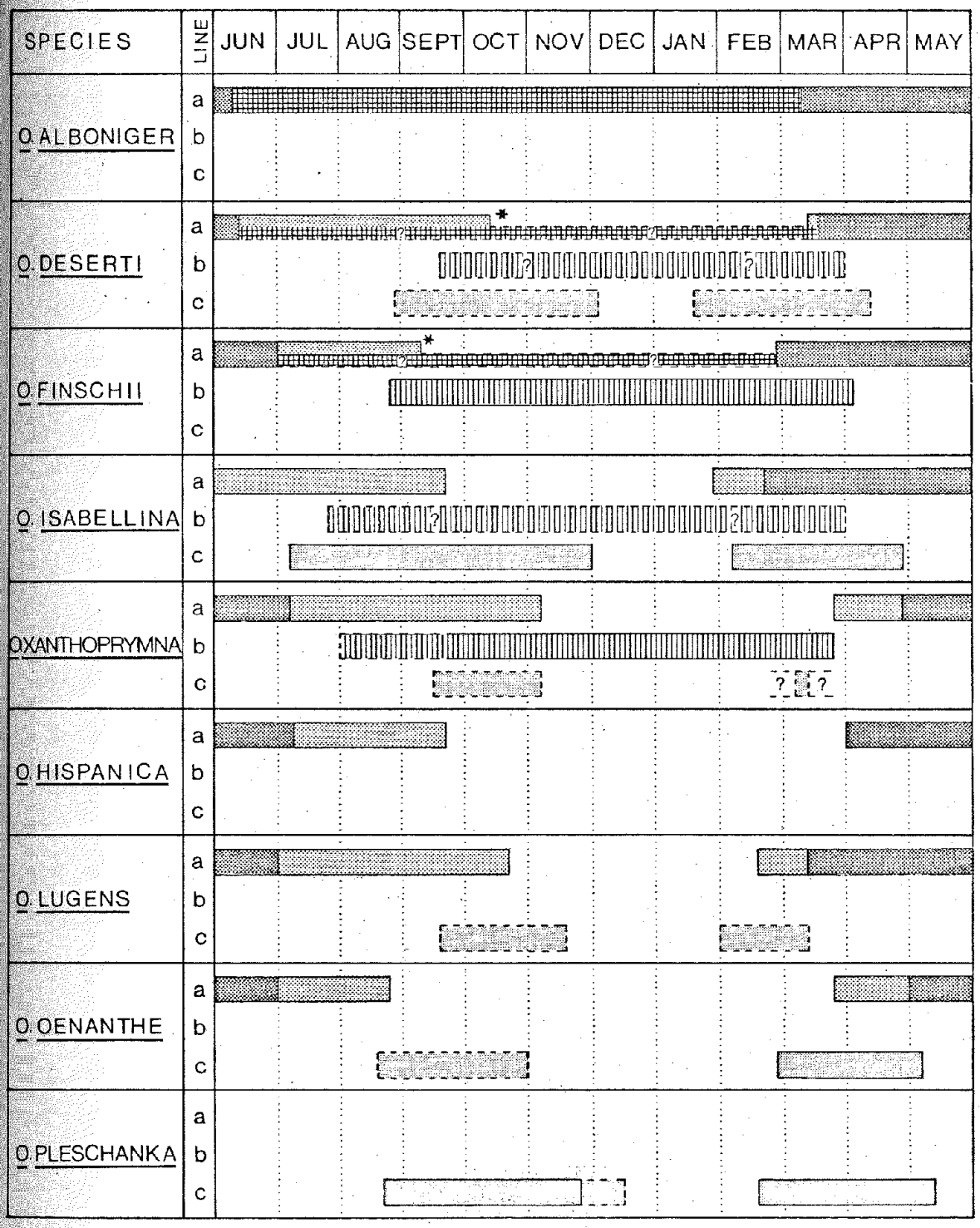


Figure 21. Seasonal occurrence of wheatears in S. W. Persia emphasising status outside the breeding season. Residents and winter visitors are listed first in alphabetical order followed by summer visitors and migrants. (N. B. O. monacha and O. picata are rare and have been omitted from the figure.)

KEY

For each species:

Line a) shows: = residents outside the breeding season.
= summer visitors outside the breeding season.
= breeding birds.

Line b) shows: = winter visitors.

Line c) shows: = migrants.

= common in suitable localities. = small numbers.

? = status unconfirmed.

* The breeding populations of O. finschii and O. deserti may be partially resident.

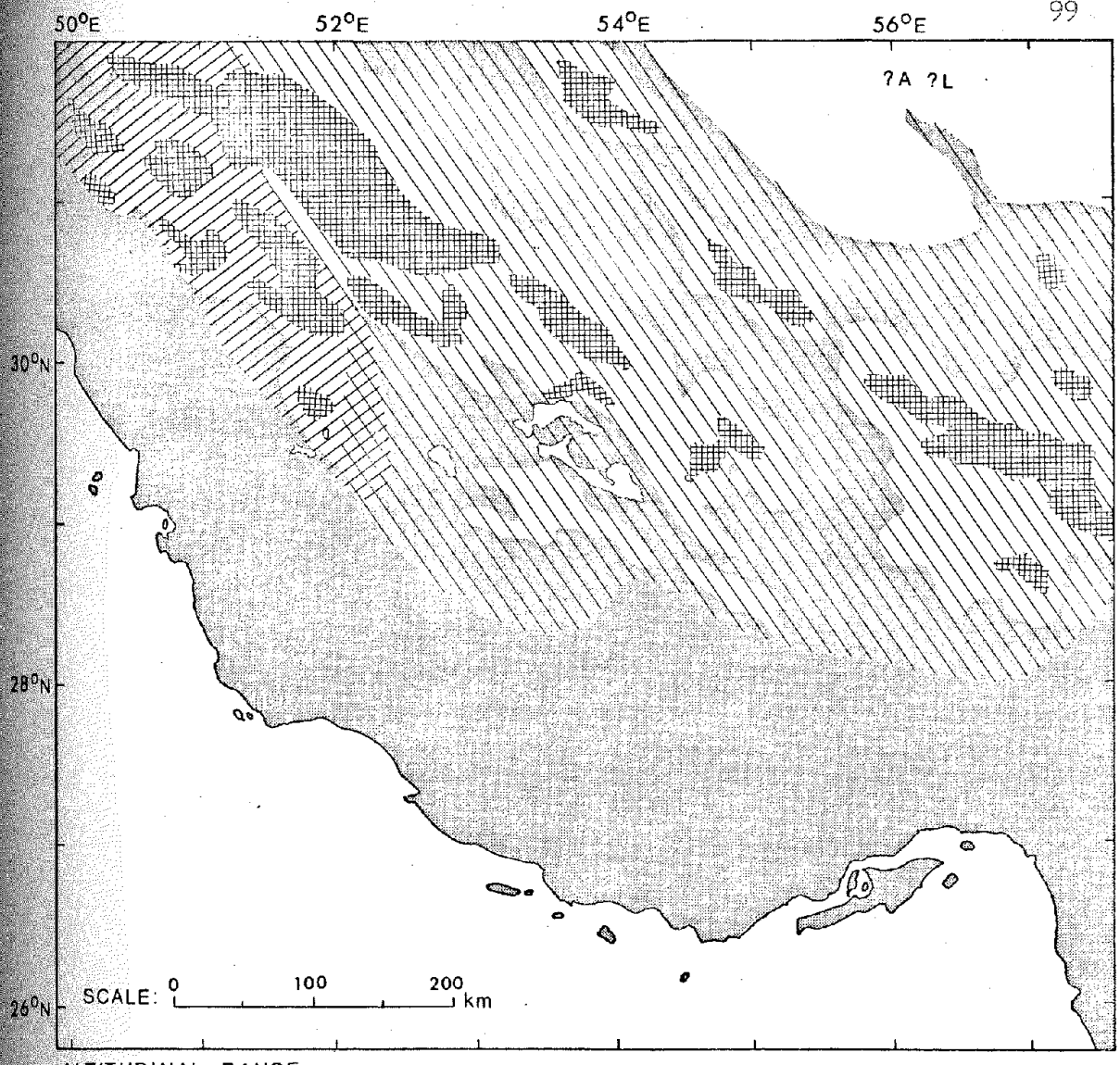
	WHEATEAR SPECIES	BIOCLIMATIC ZONE * MONTANE	XEROPHILOUS FOREST	SUB-STEPPE	COLD STEPPE	WARM STEPPE
BREEDING SEASON	O. oenanthe	+				
	O. xanthoprymna	+				
	O. hispanica		+			
	O. finschii		(+)d	+		
	O. isabellina		(+)d	+	(+)	
	O. pleschanka			(+)?		
	O. lugens		(+)d	+	+?	
	O. deserti				+	
	O. picata		(+)d	(+)	(+)	(+)
	O. alboniger		(+)d	+	+?	+
	O. monacha					(+)
WINTER	O. alboniger			+	+?	+
	O. finschii			+	+	+
	O. xanthoprymna			+		+
	O. deserti					(+)
	O. isabellina					(+)

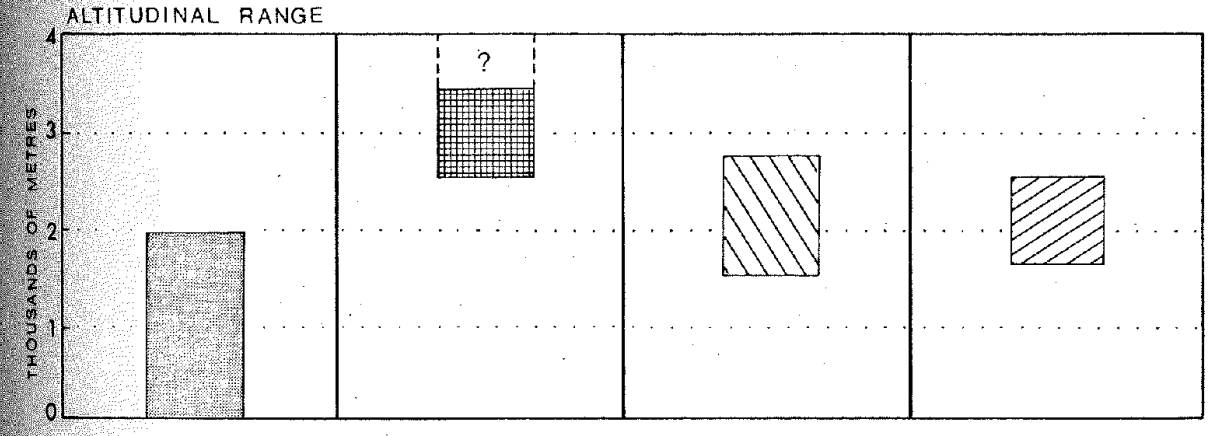
Table 18. Occurrence of wheatears in the bioclimatic zones of S.W.Iran.

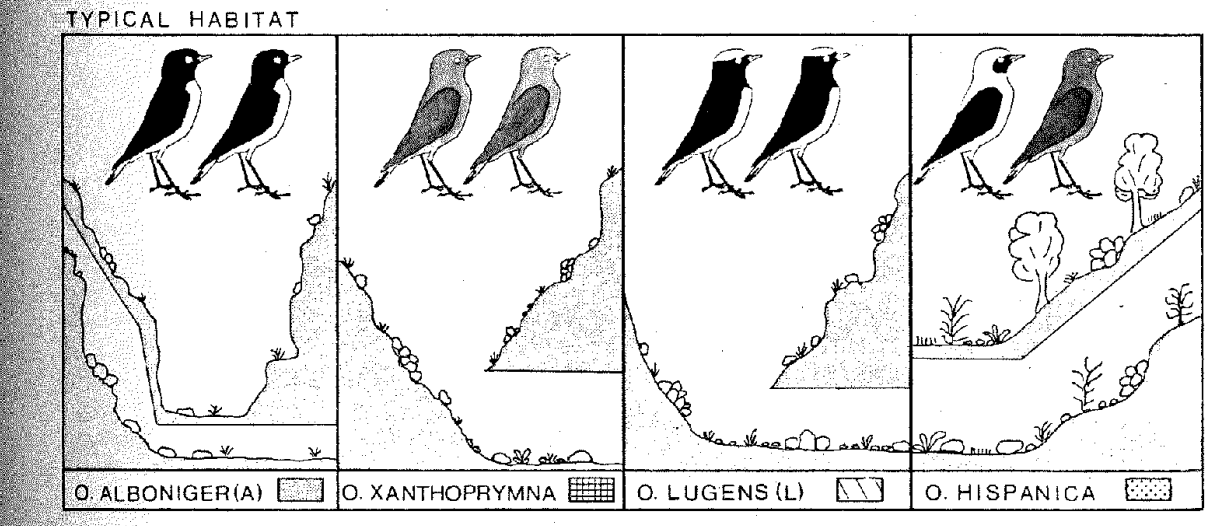
KEY

+ = widespread and common in suitable localities.
(+) = small numbers usually on edge of zone.
d = deforested areas.
? = unconfirmed.

*See pp. 22 and 28; table 2 p. 27 and overlay 4, p. 26.



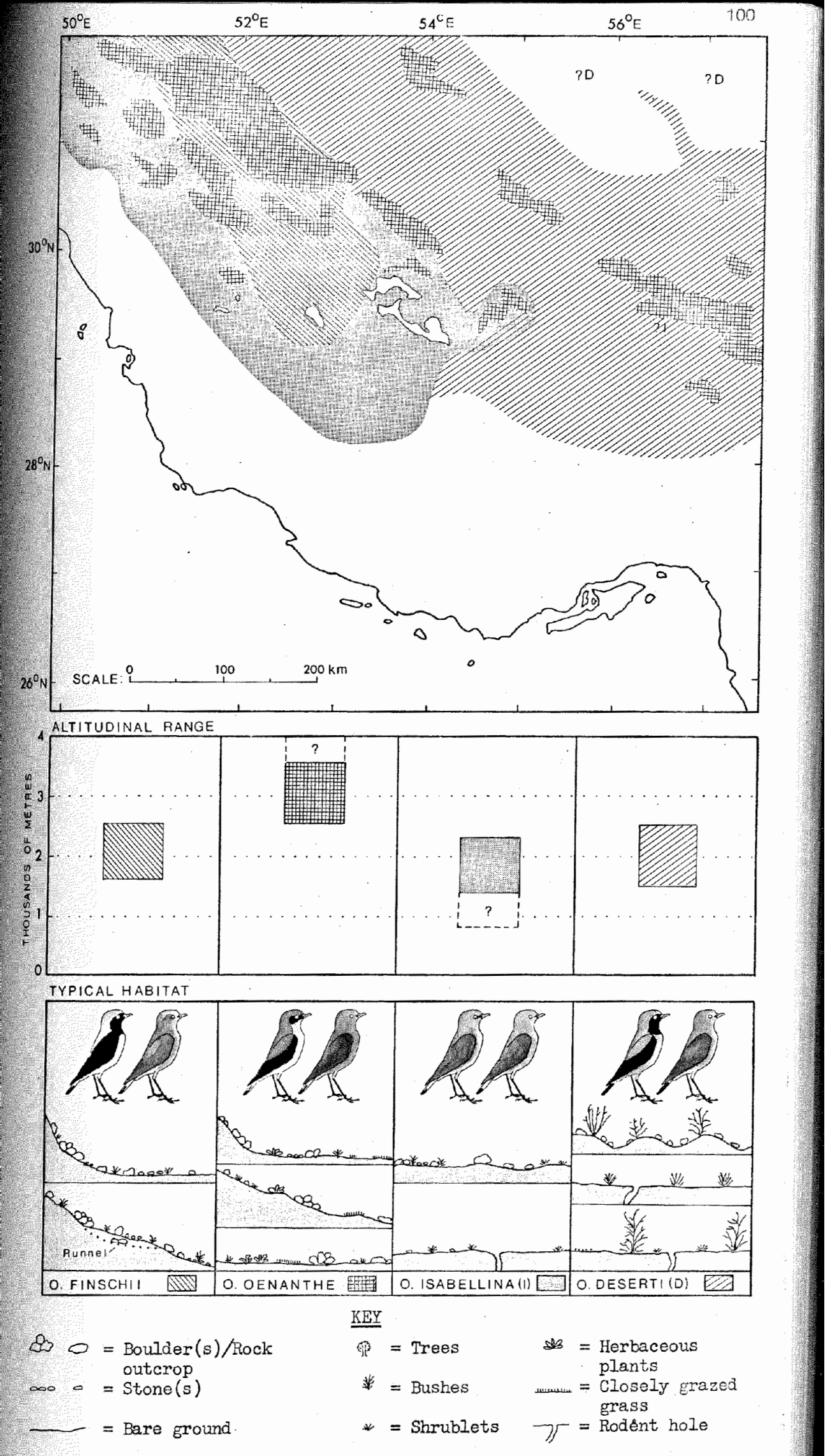




KEY

= Boulder(s)/Rock outcrop
= Stone(s)
= Bare ground
= Trees
= Bushes
= Shrublets
= Herbaceous plants
= Closely grazed grass
= Rodent hole

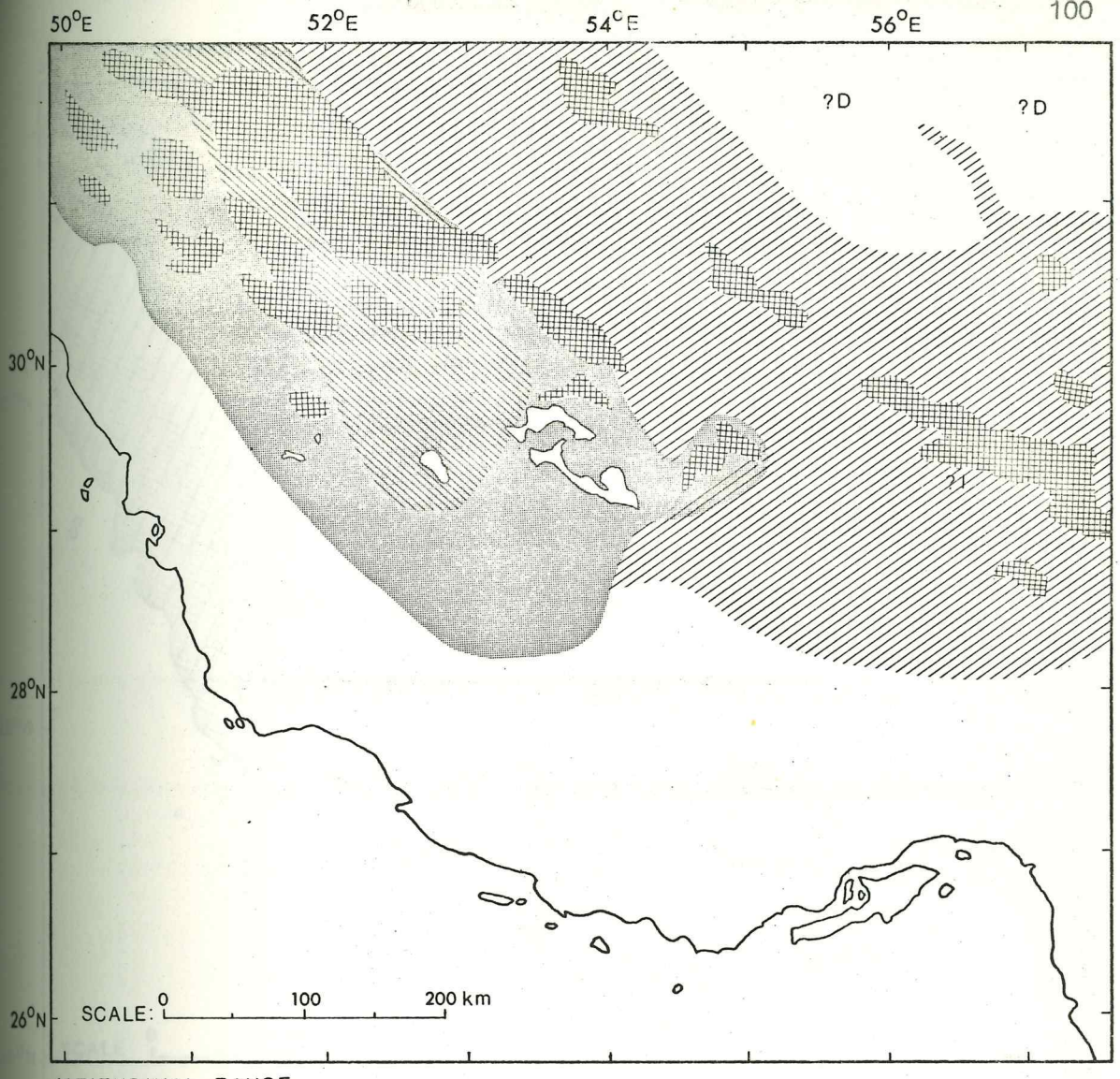
Figure 22. Probable distributions, altitudinal ranges and typical habitats of wheatears breeding in mountainous country in S. W. Persia. (Based on records reported on overlays 5 and 7; on map of bio-climatic zones, overlay 4; and habitat sections of chapter V.)

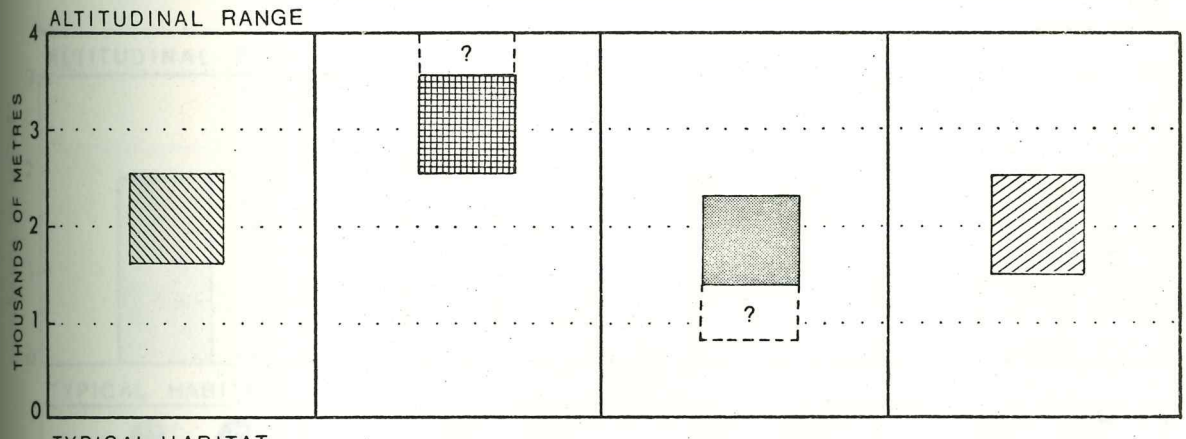


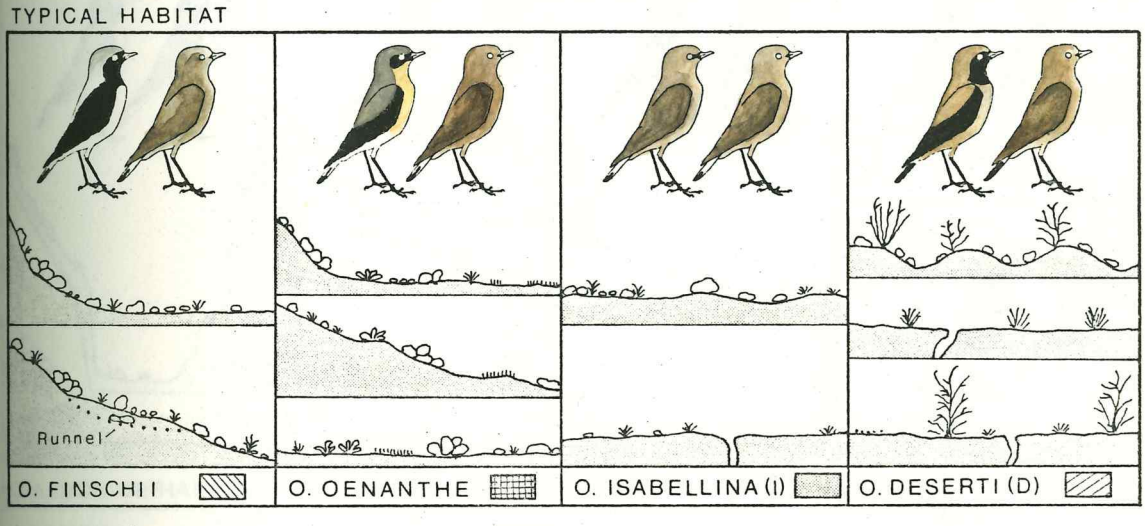
KEY

= Boulder(s)/Rock outcrop
= Stone(s)
= Bare ground
= Trees
= Bushes
= Shrublets
= Herbaceous plants
= Closely grazed grass
= Rodent hole

Figure 23. Probable distributions, altitudinal ranges and typical habitats of wheatears breeding on flatter ground in S. W. Persia. (Based on records reported on overlays 6 and 8; on map of bio-climatic zones, overlay 4; and habitat sections of chapter V.)



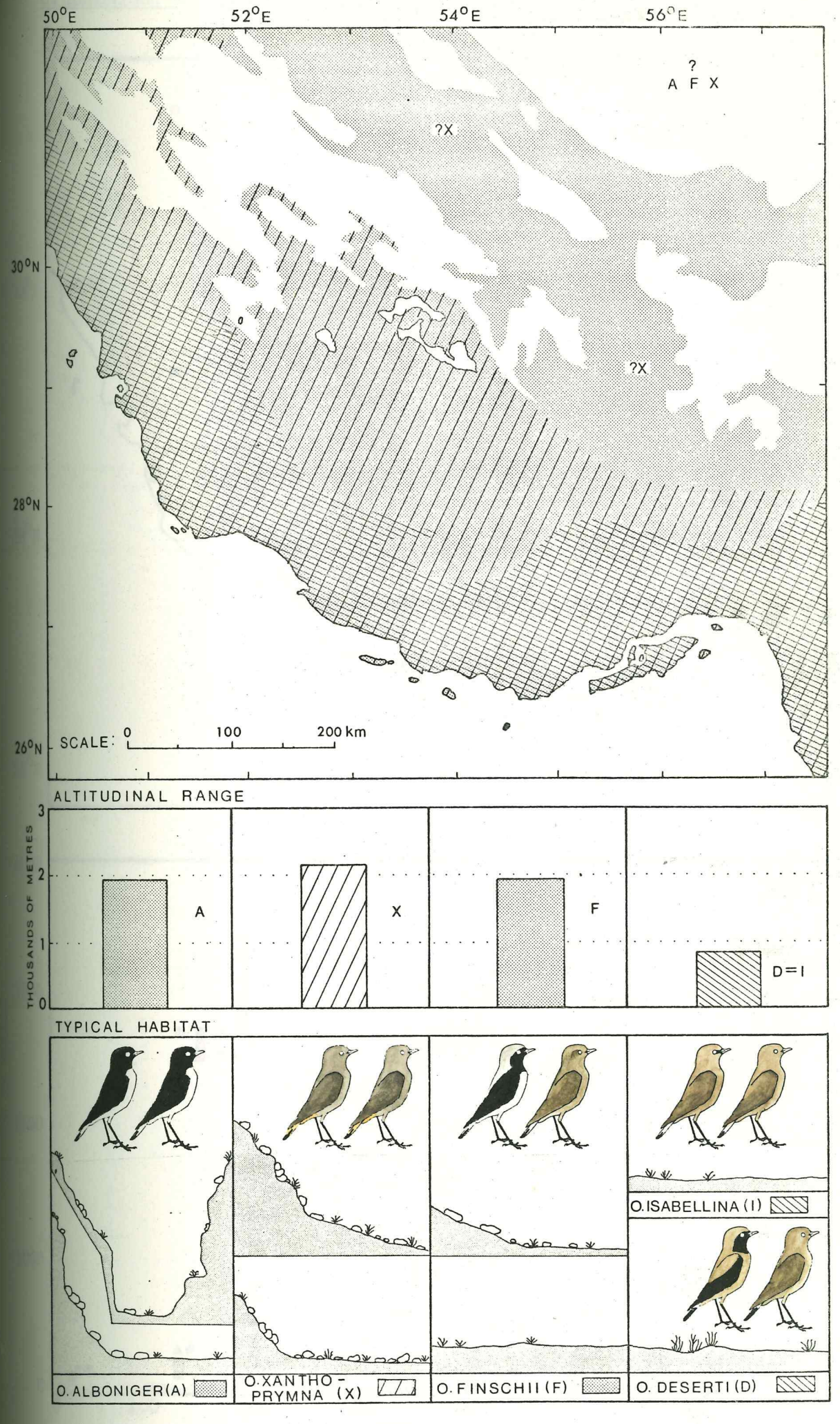




KEY

= Boulder(s)/Rock outcrop
= Stone(s)
= Bare ground
= Trees
= Bushes
= Shrublets
= Herbaceous plants
= Closely grazed grass
= Rodent hole

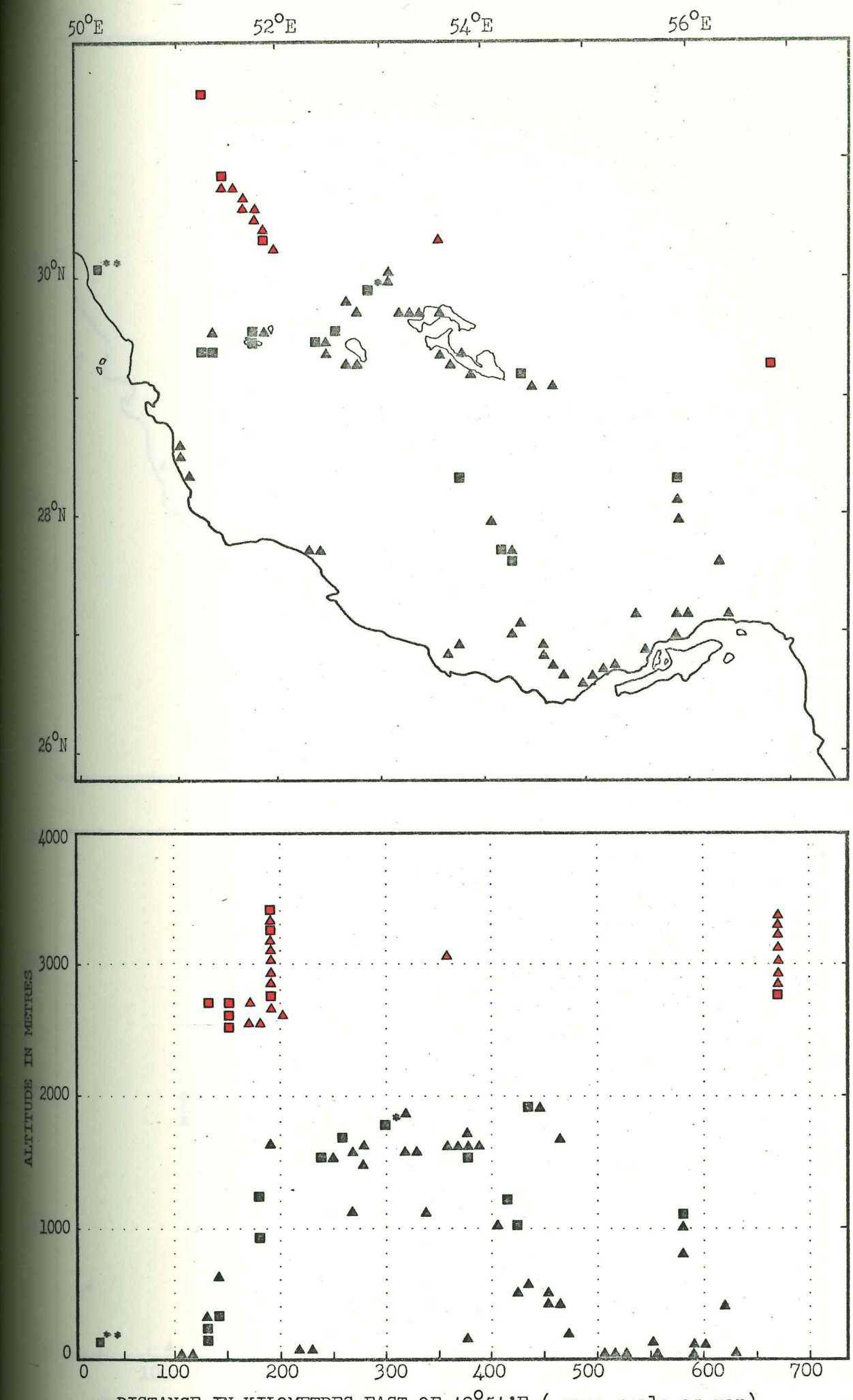
Figure 23. Probable distributions, altitudinal ranges and typical habitats of wheatears breeding on flatter ground in S. W. Persia. (Based on records reported on overlays 6 and 8; on map of bio-climatic zones, overlay 4; and habitat sections of chapter V.)



KEY

= Boulder(s)/Rock outcrop
= Stone(s)
= Bare ground
= Trees
= Bushes
= Shrublets
= Herbaceous plants
= Closely grazed grass
= Rodent hole

Figure 24. Probable distributions, altitudinal ranges and typical habitats of five species of wheatear that winter in S. W. Persia. (Based on records reported on overlays 9-12 and 17; on map of bio-climatic zones, overlay 4; and habitat sections of chapter V.)



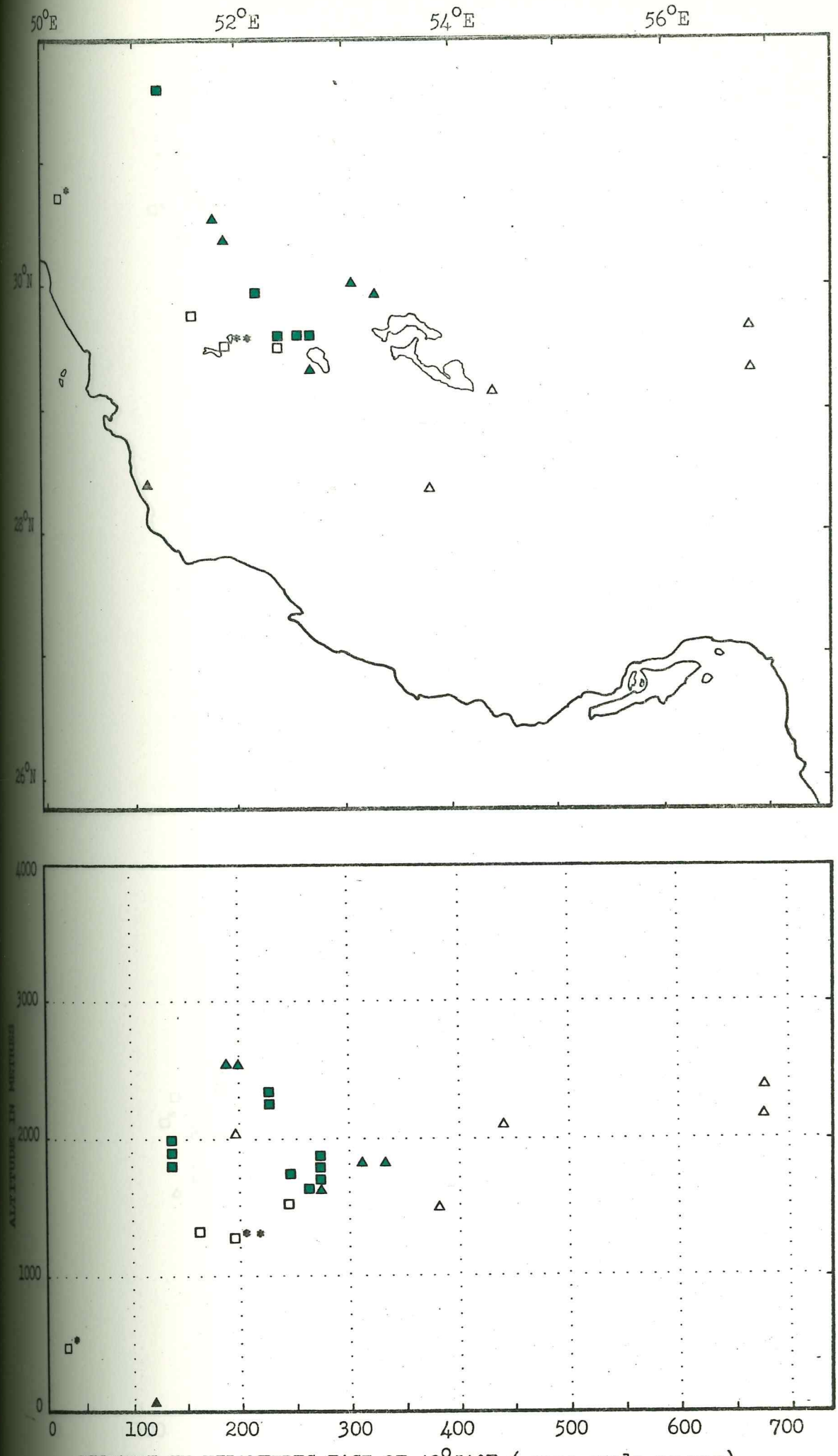
Overlay 5. Altitudinal and geographical distribution of breeding localities in S. W. Persia of O. alboniger and O. xanthoprymna.

Breeding records: Proven Probable

O. alboniger

O. xanthoprymna

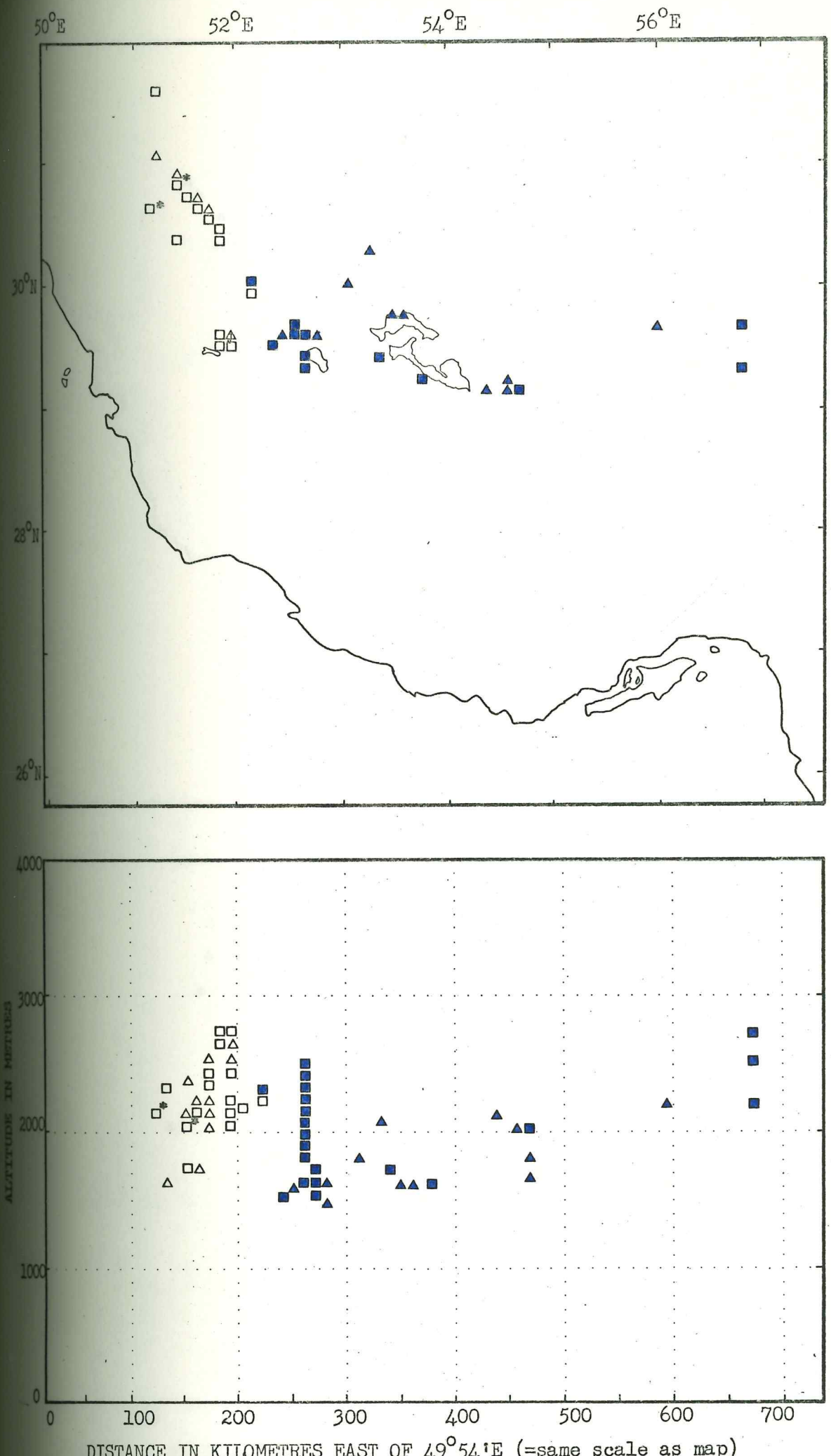
*Erard and Etchécopar 1970. ** D. A. Scott pers. comm.



Overlay 6. Altitudinal and geographical distribution of breeding localities in S. W. Persia of O. finschii, O. monacha and O. picata.

Breeding records:	Proven	Probable	
	■	▲	O. finschii
	■	▲	O. monacha
	□	△	O. picata

*S. Cramp pers. comm. **D. A. Scott pers. comm.



Overlay 7. Altitudinal and geographical distribution of breeding localities in S. W. Persia of O. hispanica and O. lugens.

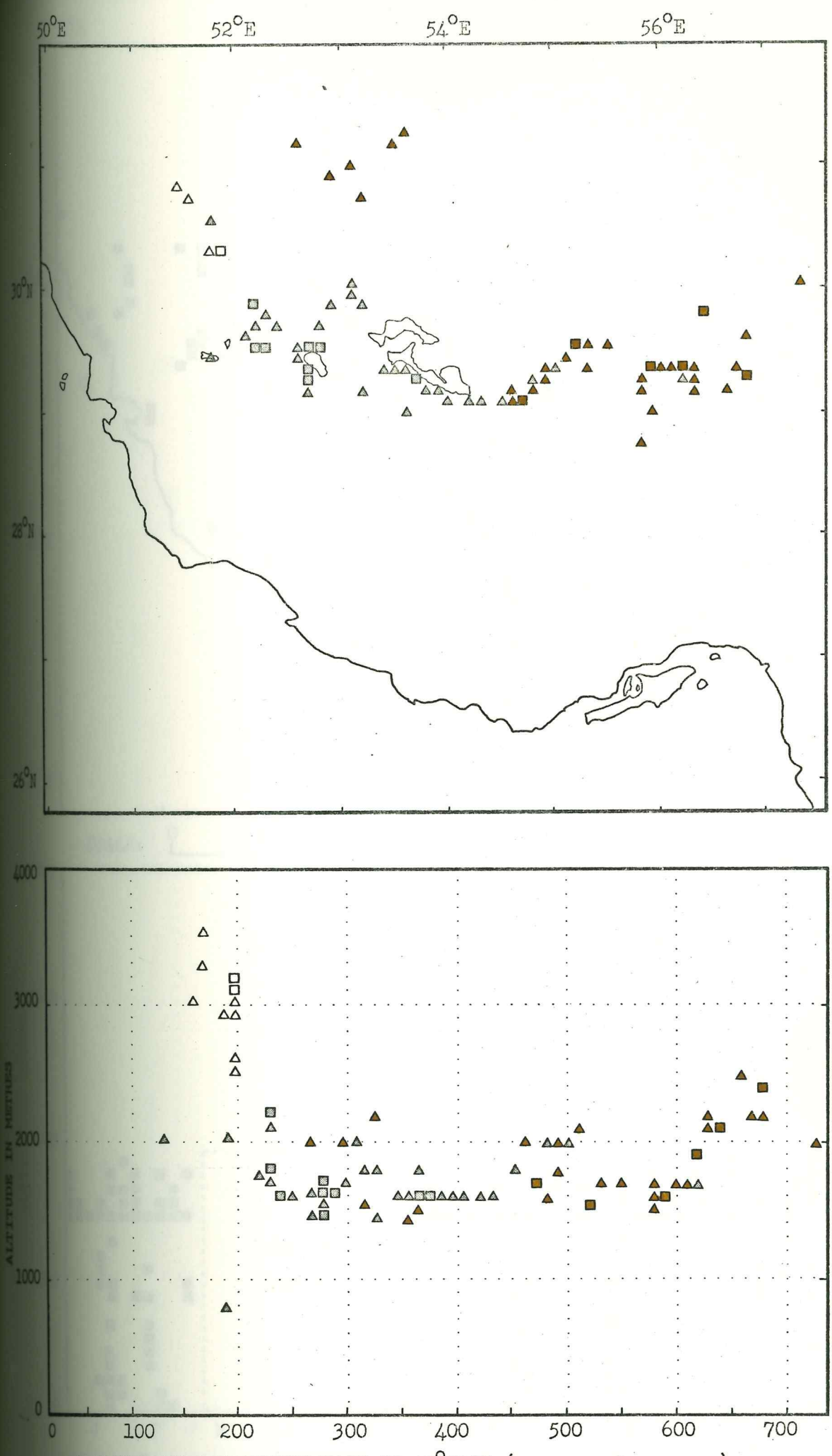
Breeding records: Proven □ ■ Probable △ ▲

O. hispanica

O. lugens

*Witherby 1903.

N.B. Where the two species bred in the same locality the symbols are placed side by side.

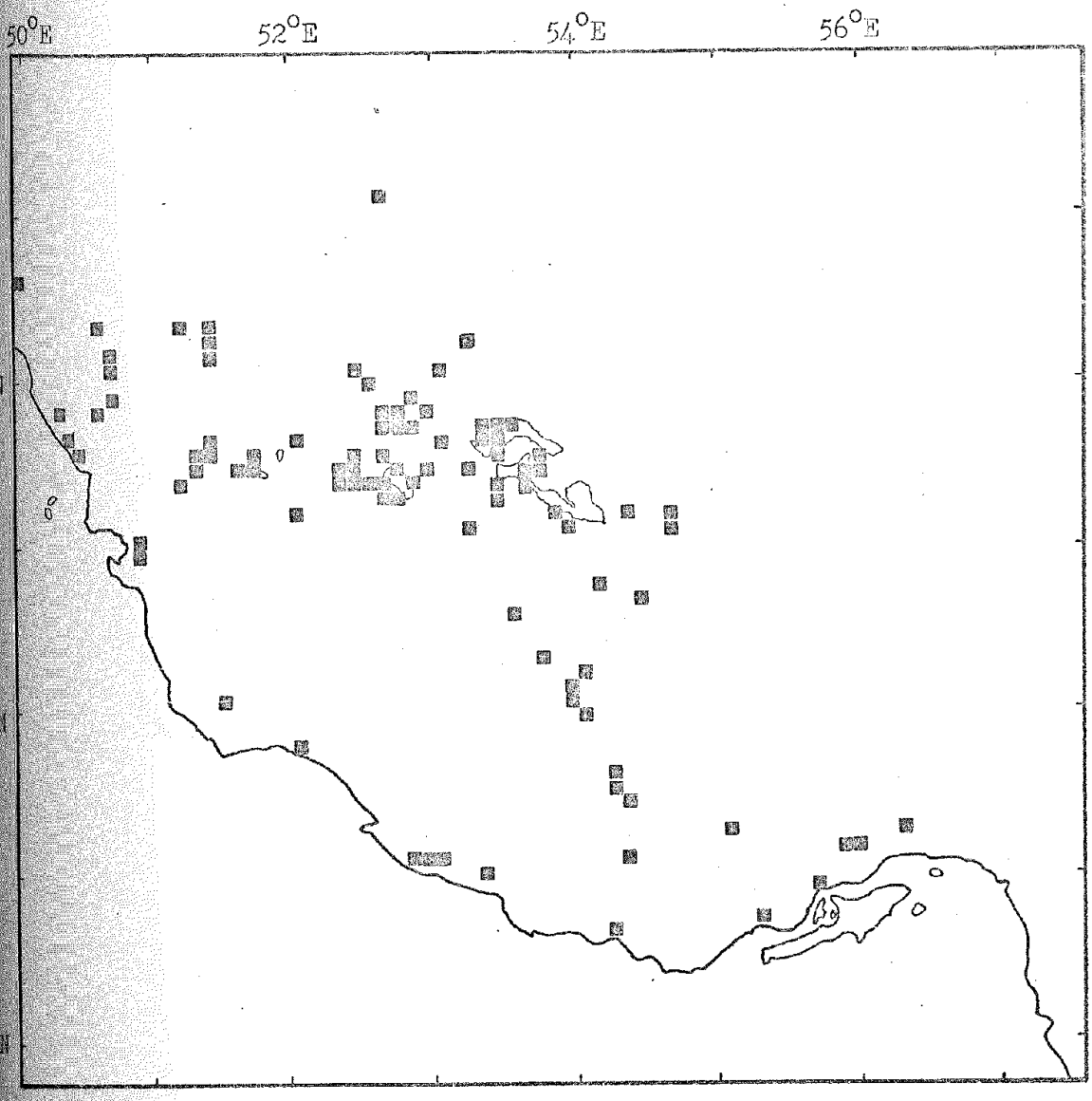


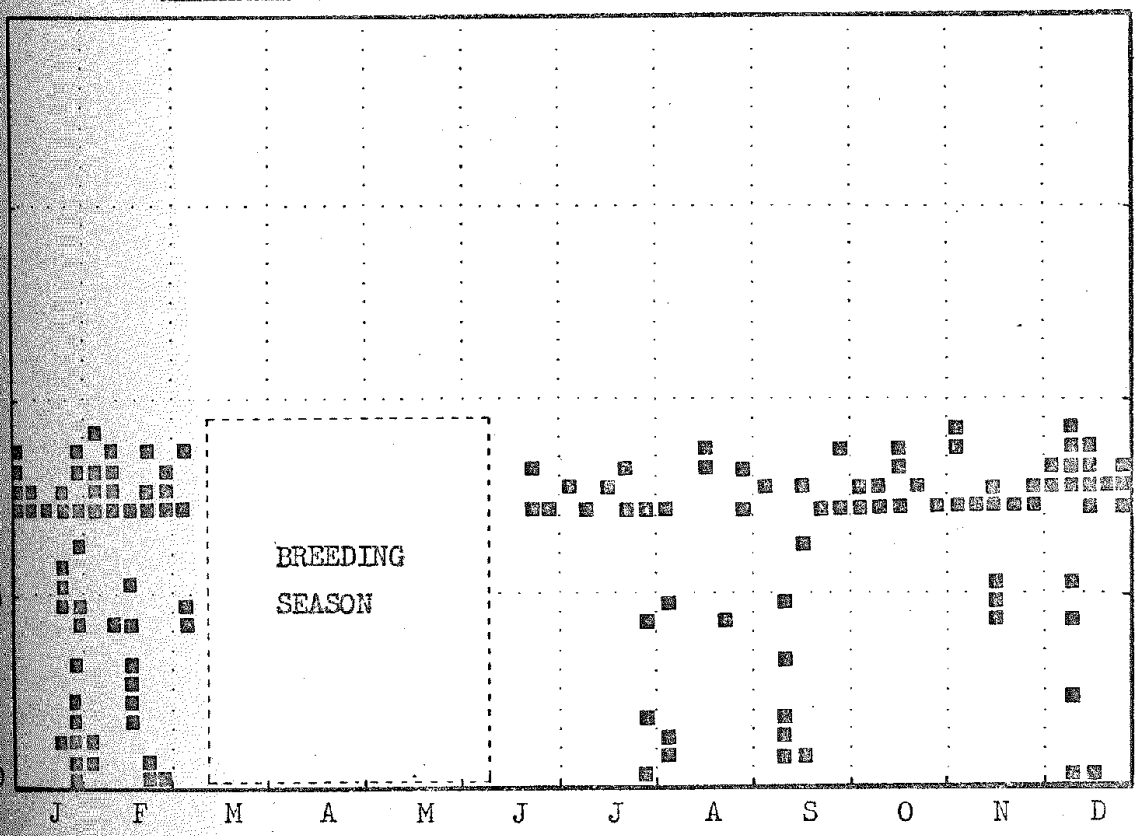
Overlay 8. Altitudinal and geographical distribution of breeding localities in S. W. Persia of wheatears inhabiting flat ground.

Breeding records: Proven Probable

■ ▲ O. deserti
▣ ▲ O. isabellina
□ △ O. oenanthe

N. B. Where more than one species bred in the same locality the symbols are placed side by side.

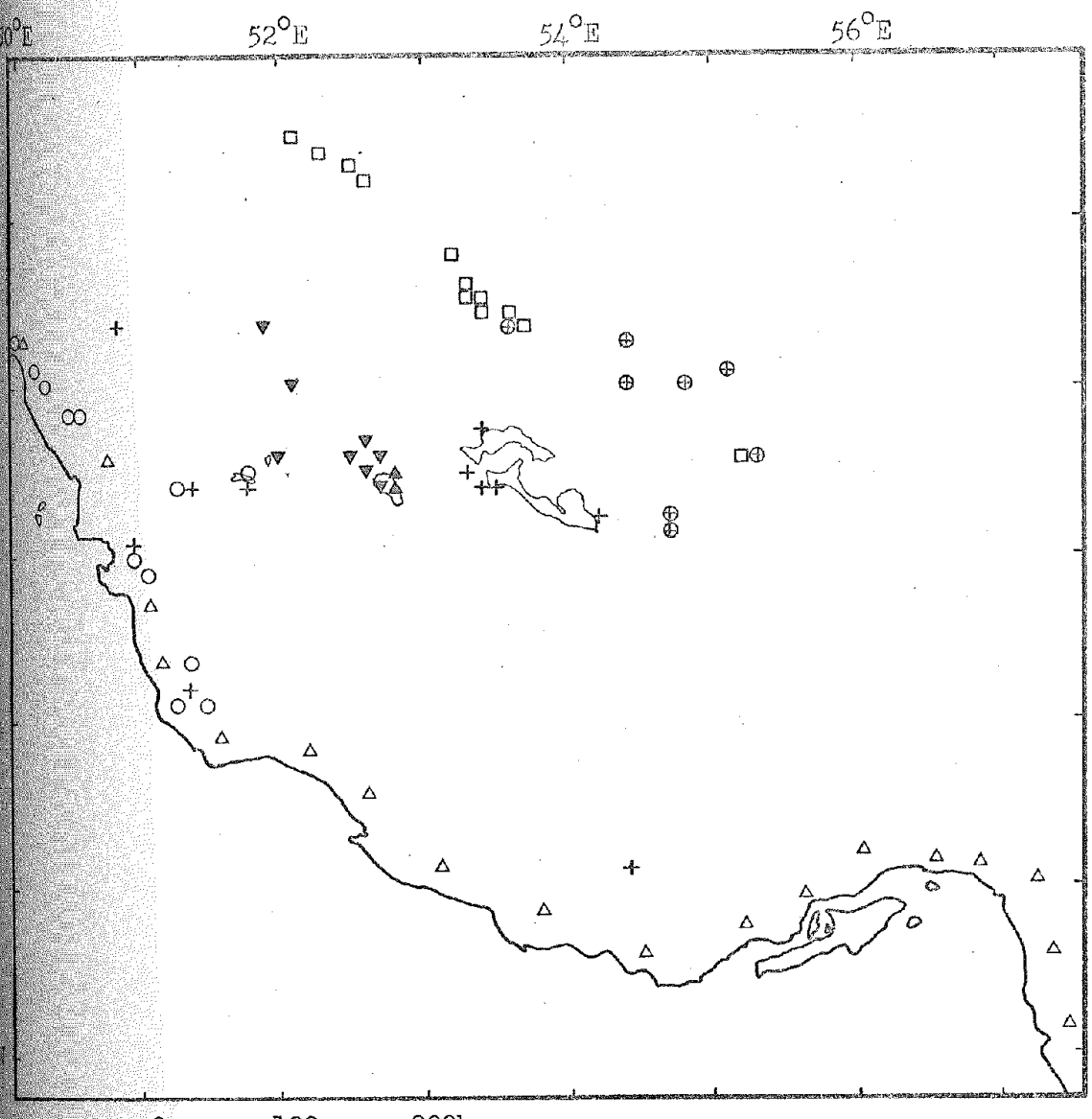


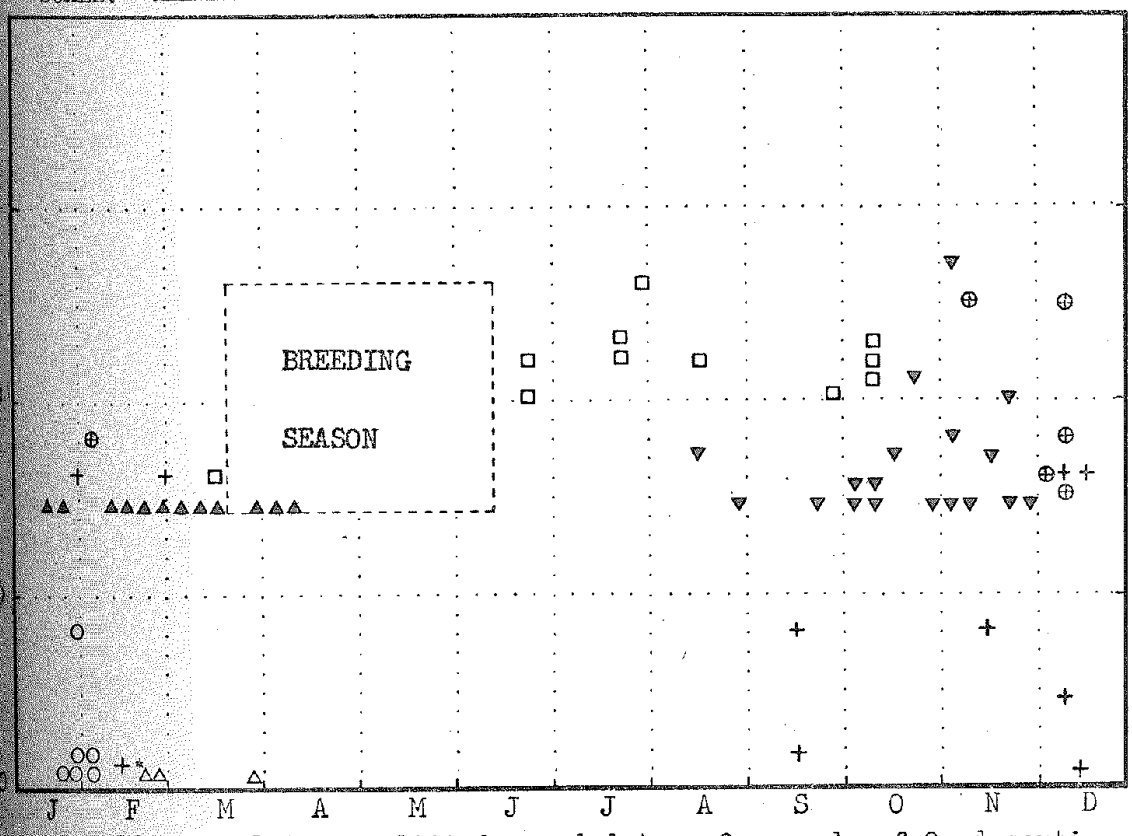


Overlay 9. Localities, altitudes and dates of records of O. alboniger in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

■ resident.

N. B. Eight of the above records were contributed by D. A. Scott.

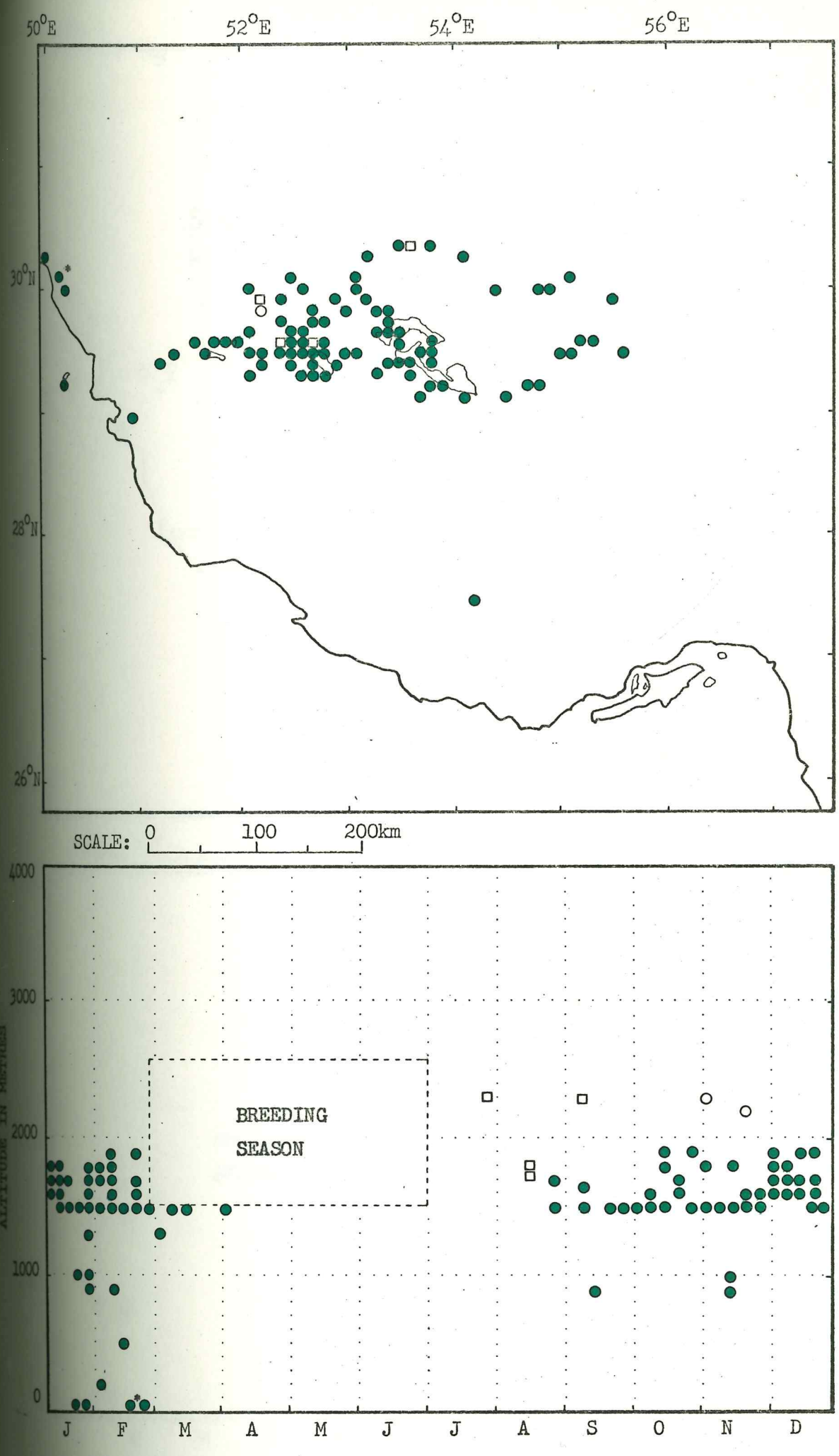




Overlay 10. Localities, altitudes and dates of records of O. deserti in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

- □ probably summer visitor/?migrant.
- O probably winter visitor/?migrant.
- + winter visitor/migrant.
- ⊕ winter visitor/resident/migrant.
- ▲ spring migrant.
- △ probably spring migrant/? winter visitor.
- ▼ autumn migrant.

*The records of probable spring migrants in February on the coastal plain were contributed by D. A. Scott.

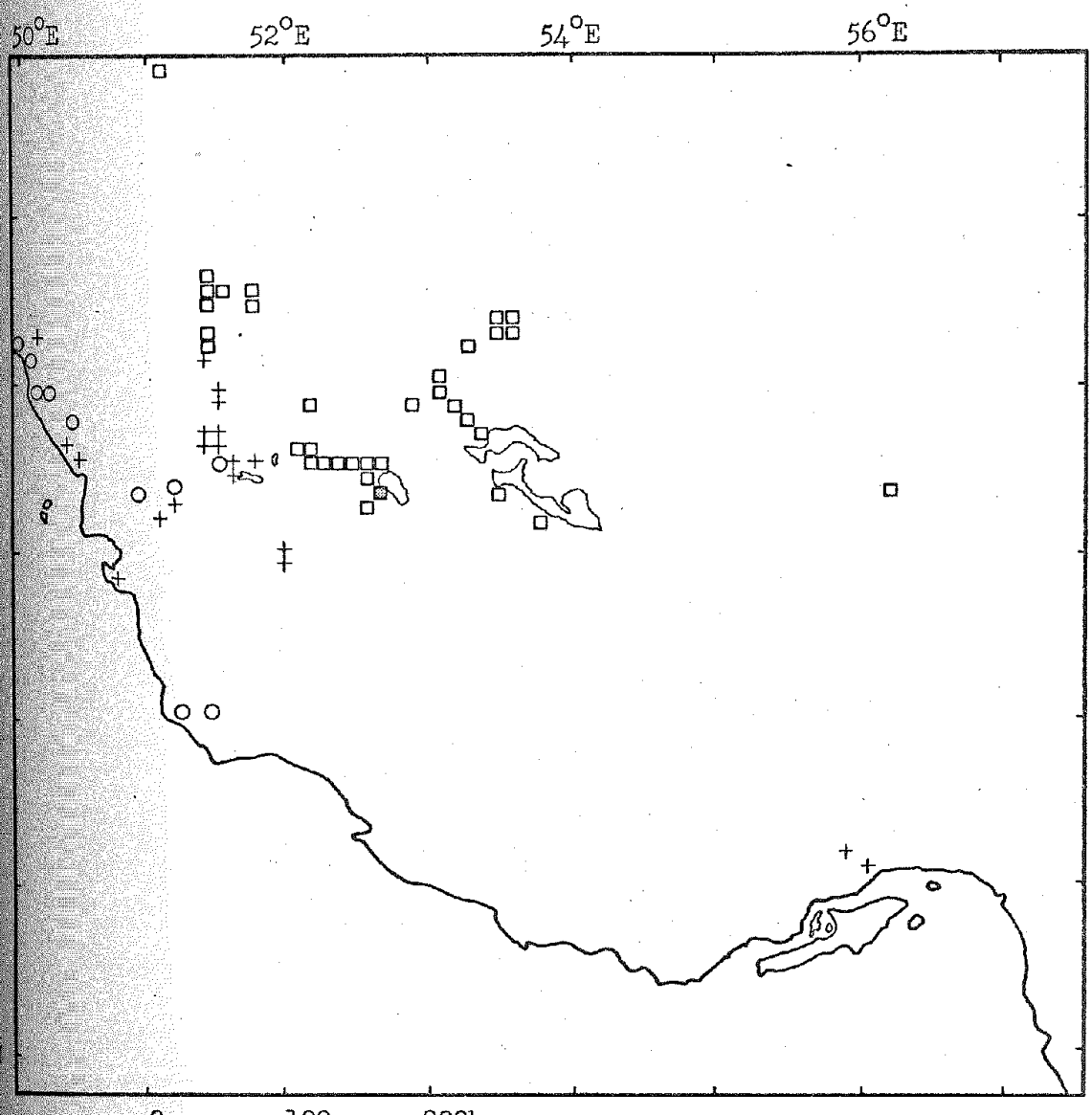


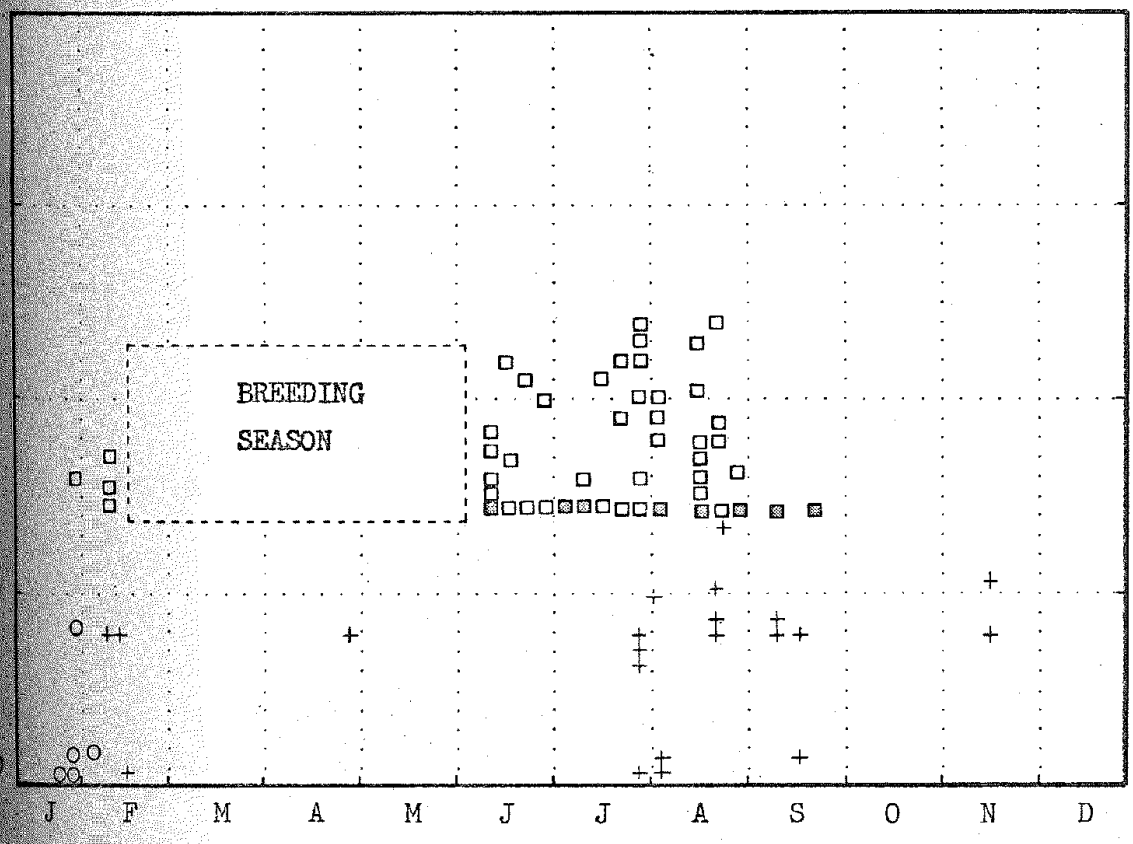
Overlay 11. Localities, altitudes and dates of records of O. finschii in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

□ summer visitor/resident. ○ summer visitor/resident/winter visitor.

● winter visitor (probably includes a few residents and migrants).

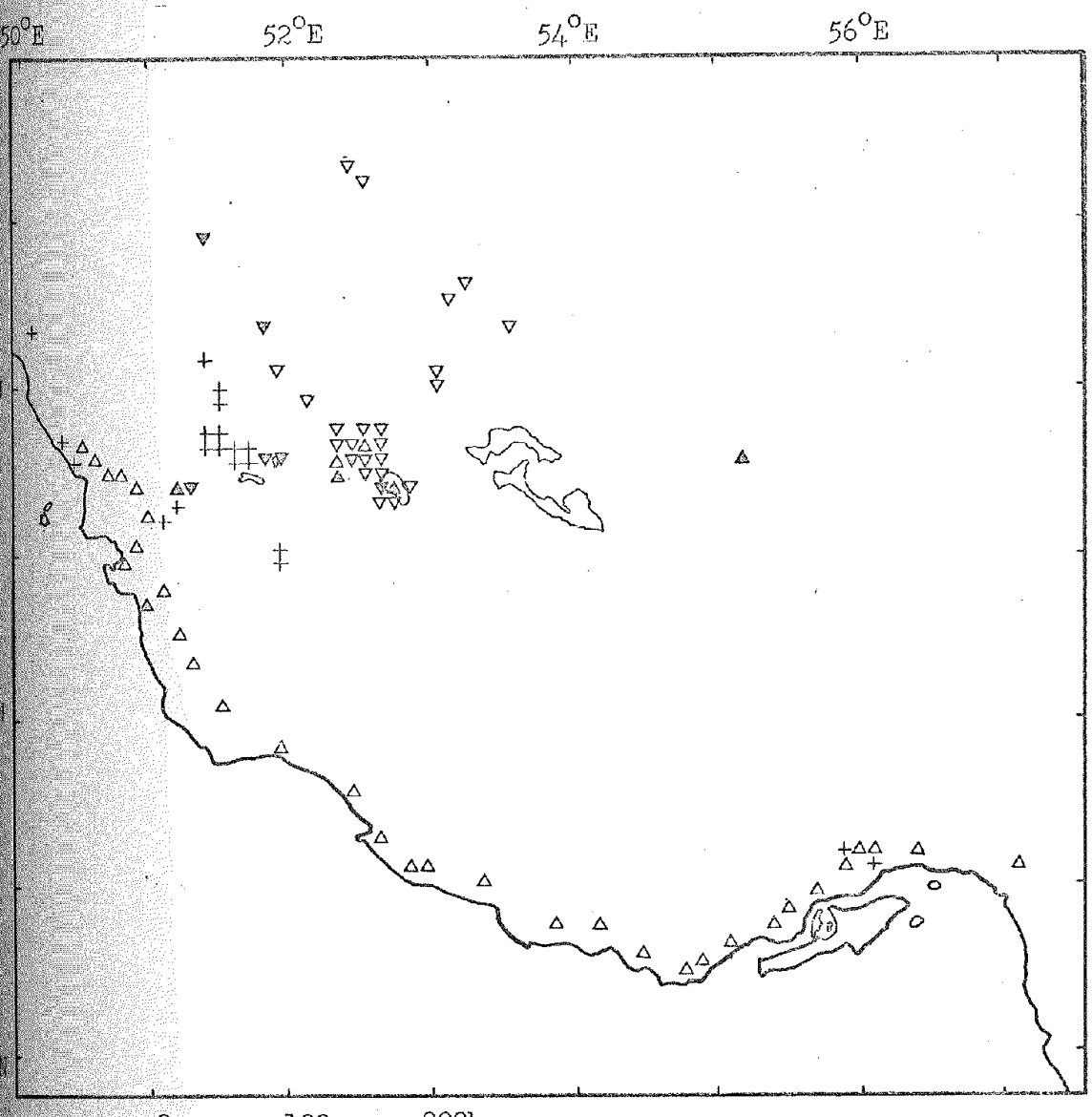
*D. A. Scott pers. comm.

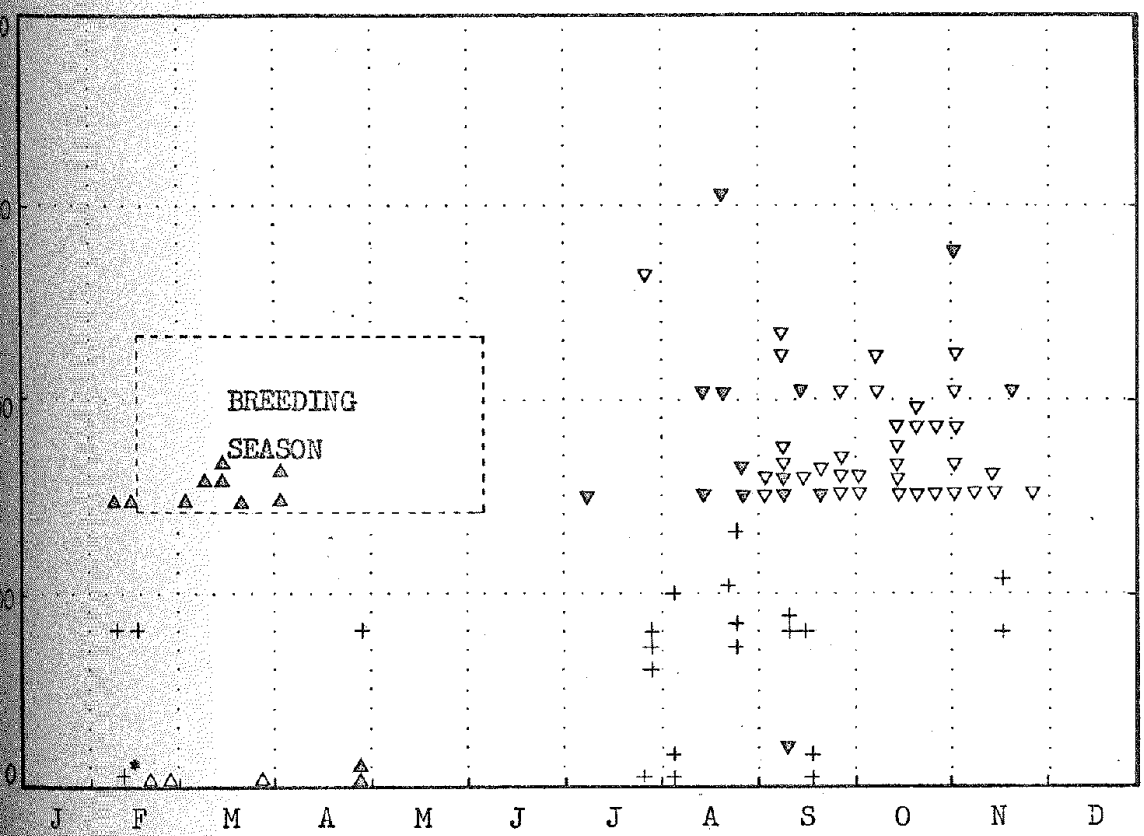




Overlay 12. O. isabellina: localities, altitudes and dates of records in S. W. Persia of winter visitors and of summer visitors outside the breeding season.

■ summer visitor. ◉ winter visitor.
□ probably summer visitor/?migrant. ○ probably winter visitor/?migrant.
+ winter visitor/migrant.

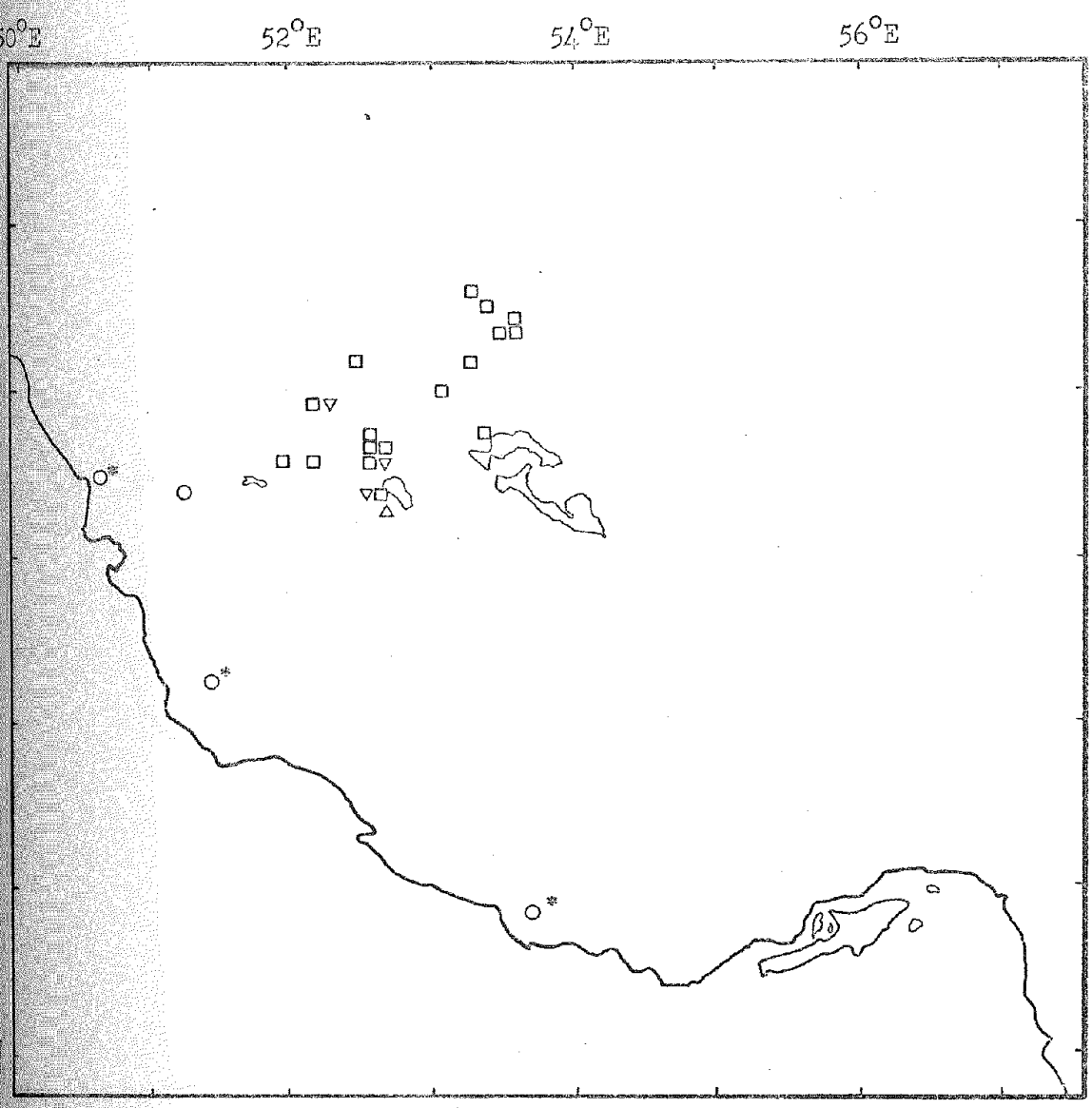


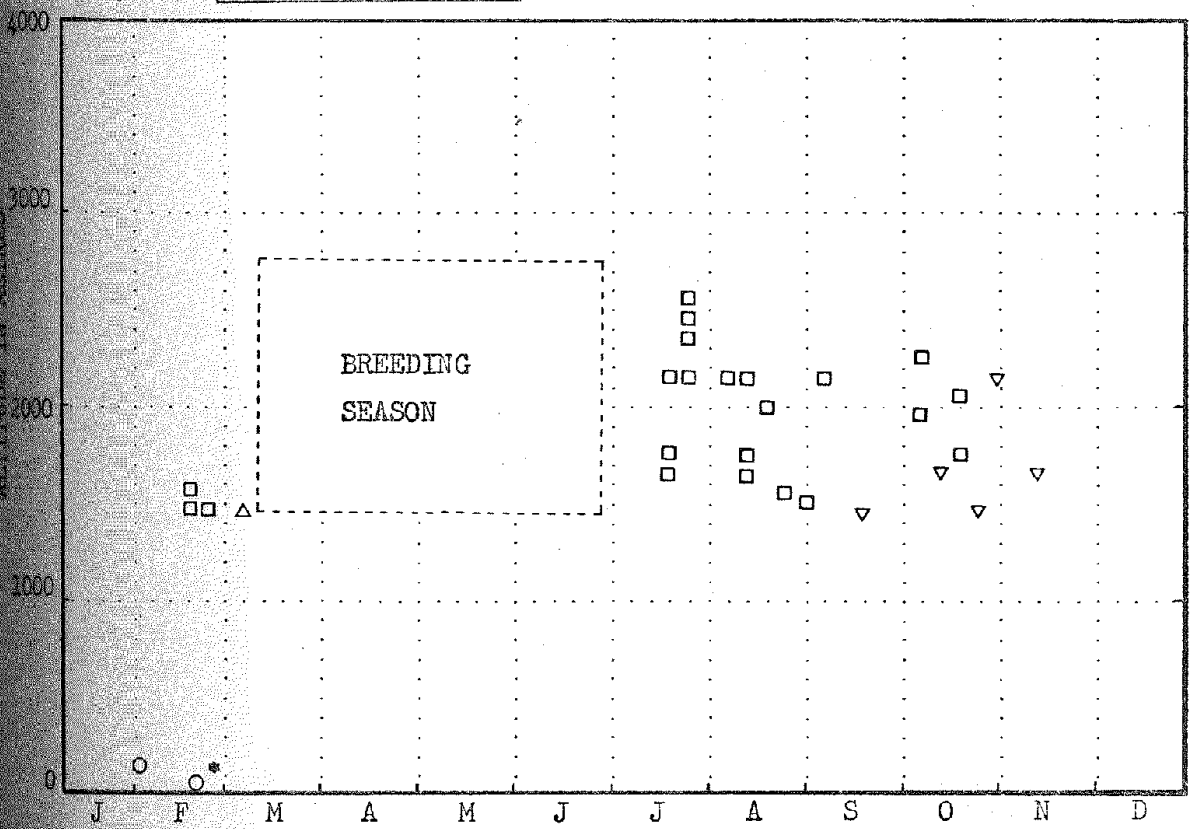


Overlay 13. Localities, altitudes and dates of records of migrant O. isabellina in S. W. Persia.

▲ spring migrant. △ probably spring migrant/?winter visitor.
▼ autumn migrant. ▽ probably autumn migrant/?summer visitor.
+ migrant/?winter visitor.

*The records of probable spring migrants in February on the coastal plain were contributed by D. A. Scott.



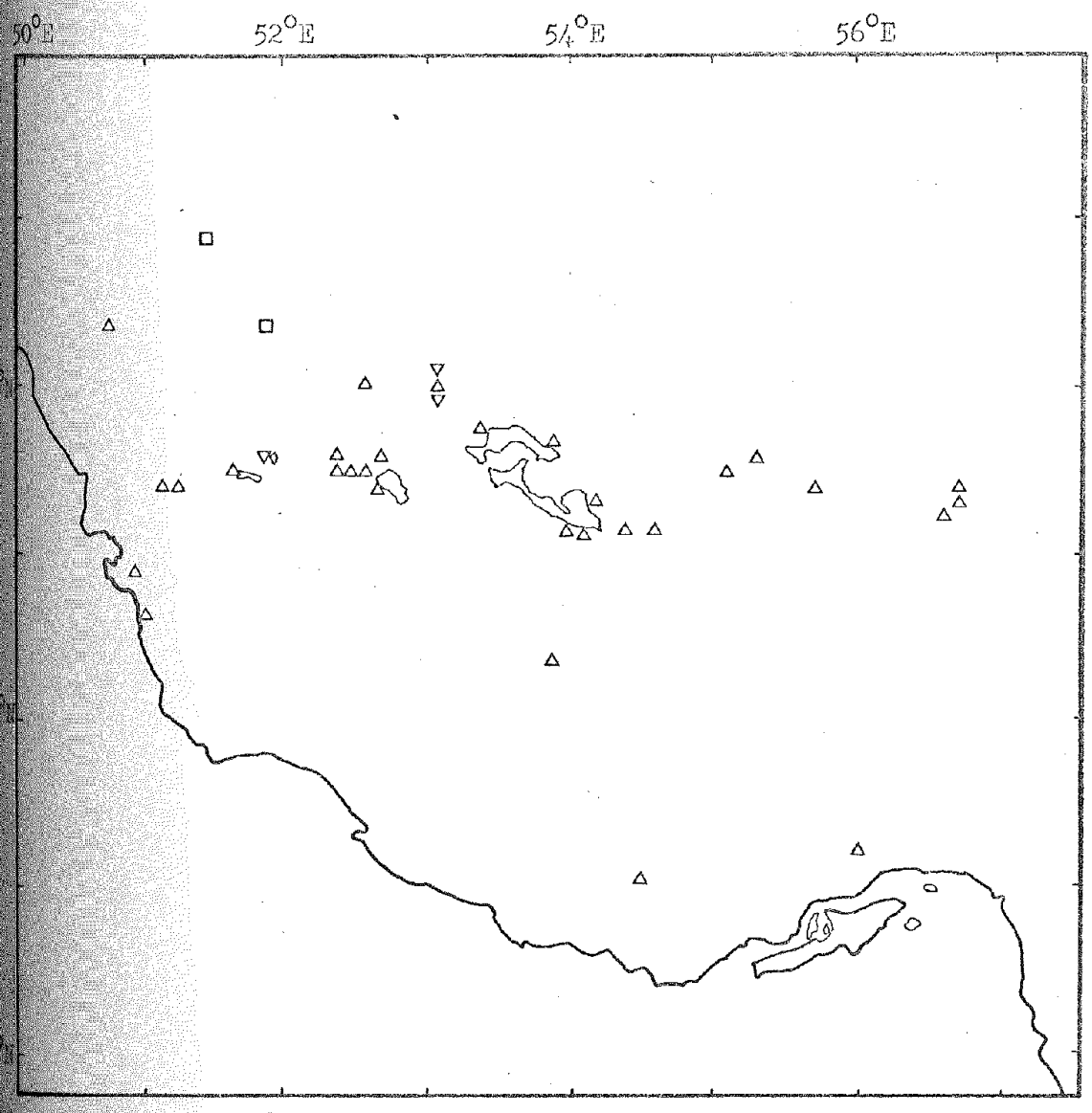


Overlay 14. Localities, altitudes and dates of records of O. lugens in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

□ summer visitor. ○ winter visitor/migrant.

△ spring migrant. ▽ autumn migrant.

*D. A. Scott pers. comm.



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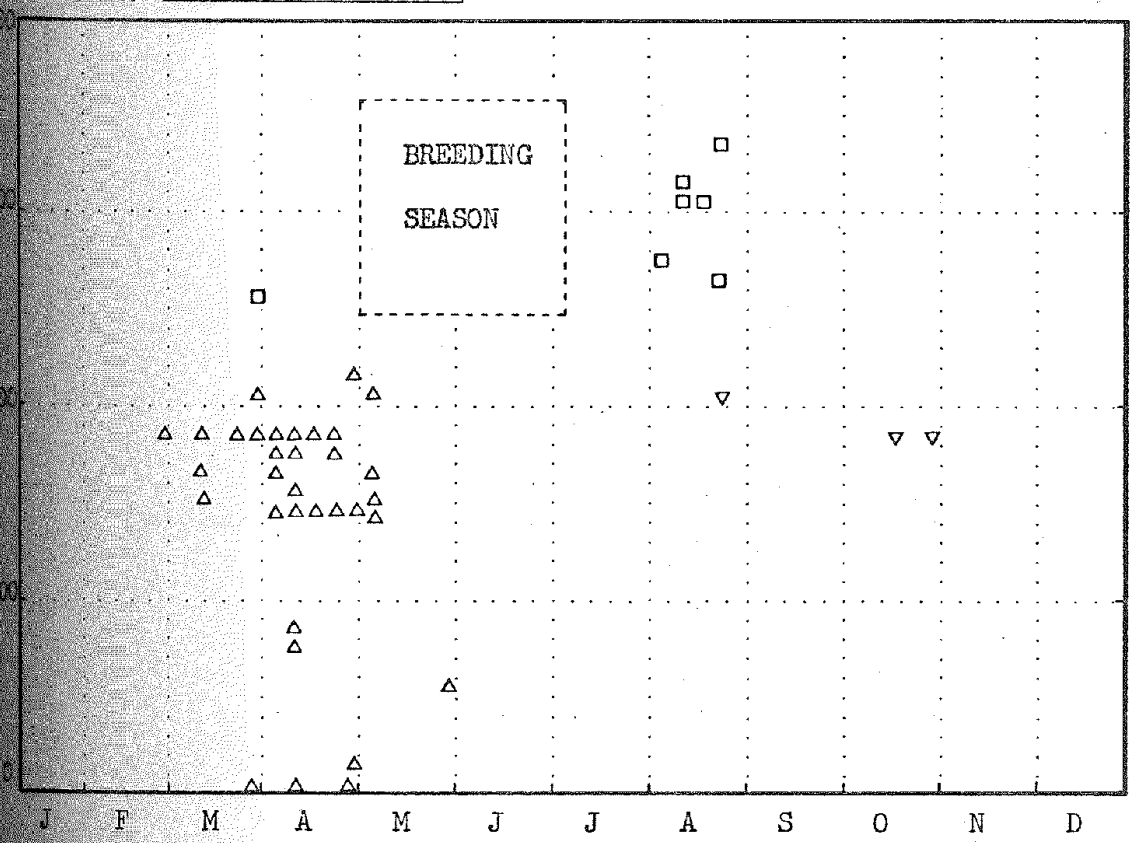
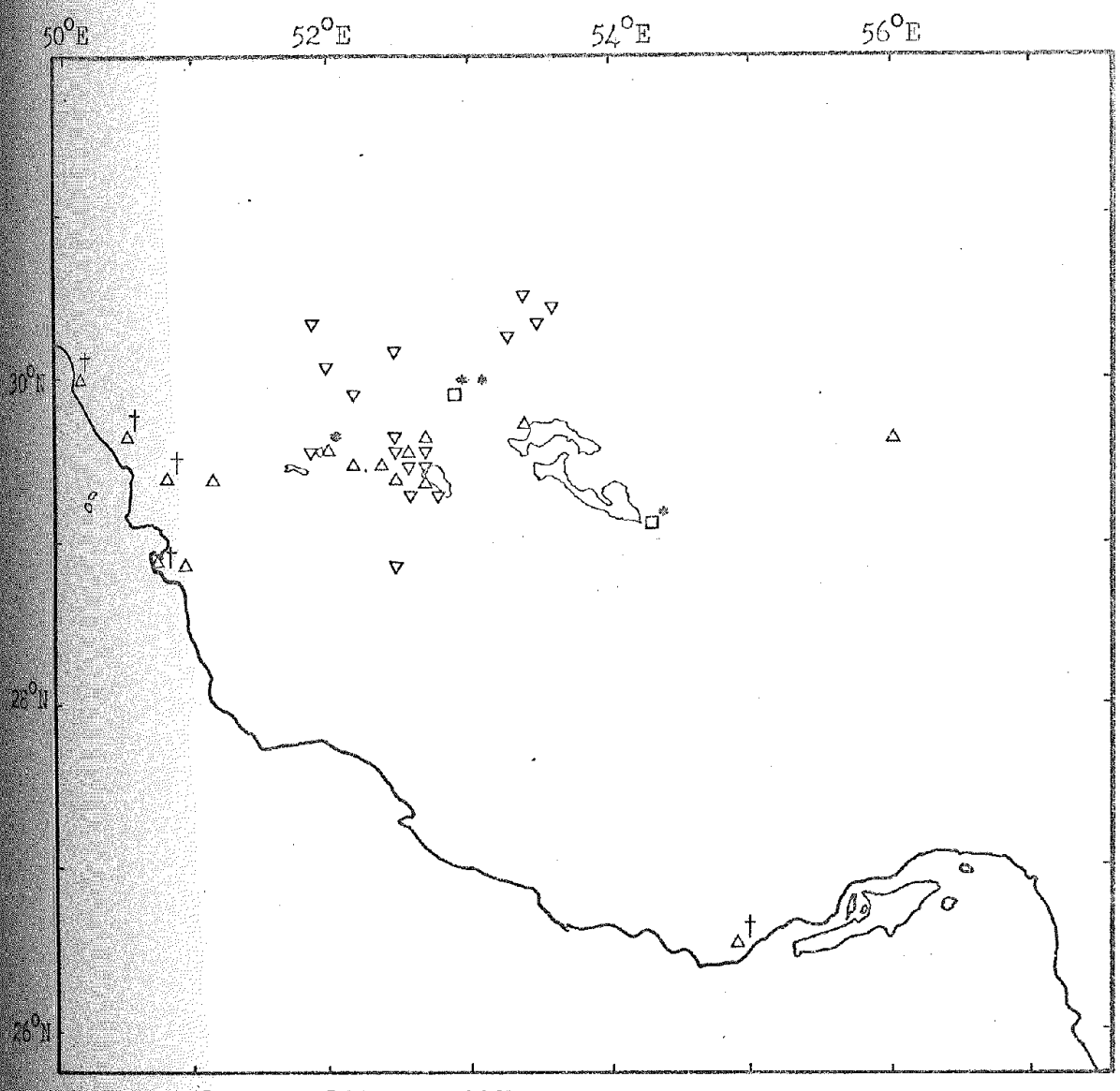
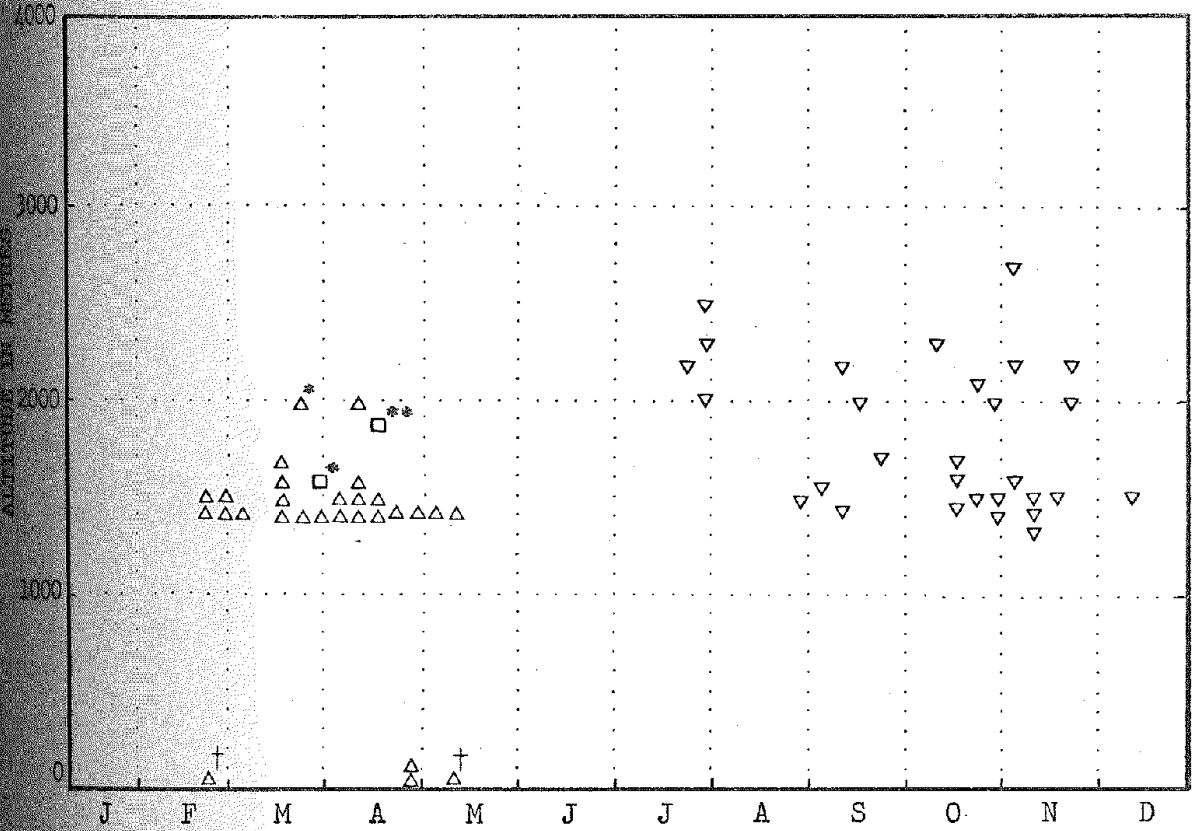


Overlay 15. Localities, altitudes and dates of records of O. oenanthe in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

□ summer visitor. △ spring migrant. ▽ autumn migrant.





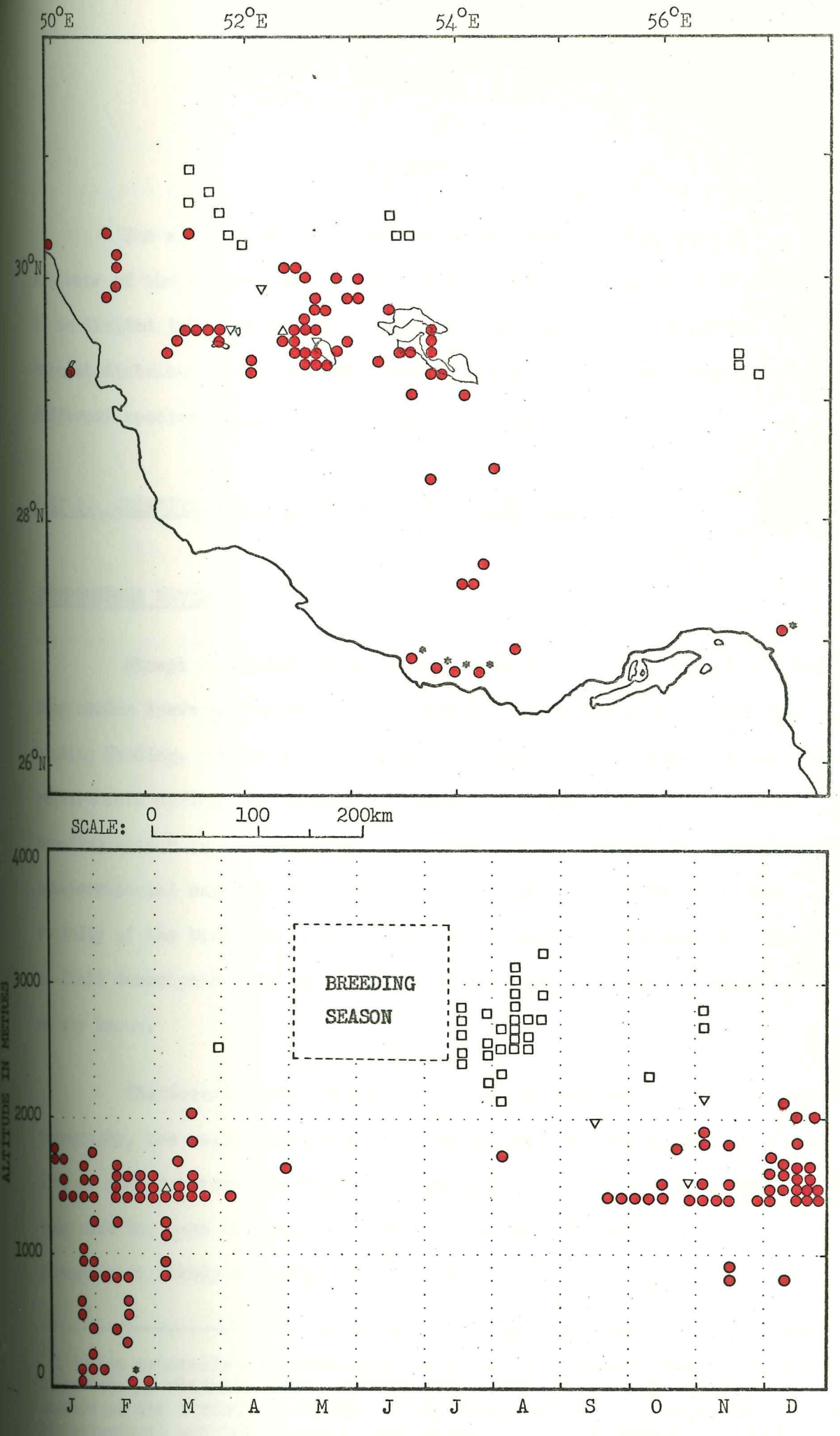
Overlay 16. Localities, altitudes and dates of records of O. pleschanka in S. W. Persia.

△ spring migrant. □ breeding. ▽ autumn migrant.

*Vaurie 1949.

**Erard and Etchécopar 1970.

†D. A. Scott pers. comm.



Overlay 17. Localities, altitudes and dates of records of O. xanthoprymna in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

□ summer visitor. ● winter visitor.

△ spring migrant. ▽ autumn migrant.

*D. A. Scott pers. comm.

CHAPTER V

HABITAT

The aims of this chapter are to describe and discuss the habitats of the various species of wheatear that occur in S. W. Iran. It is divided into two parts: In the first a quantitative analysis of habitat distribution is presented and in the second the habitats of the different species are discussed systematically.

PART I. QUANTITATIVE ANALYSES OF HABITAT DISTRIBUTION:

INTRODUCTORY NOTES:

Except on migration wheatears invariably hold territories which they seldom leave and where they perform all their daily activities including feeding. Hence their territories must meet all their habitat requirements during the periods of tenure which are often as long as a breeding season or wintering period. Consequently, except in the case of non-territorial migrants for which descriptions of the habitat in the vicinity of the birds were made, analyses of wheatear habitats were based on field descriptions of territories the extents of which were approximately known.

The descriptions of wheatear habitats were made in terms of the topography, the vegetation, the stone-cover and the density and distribution of rock-outcrops and boulders. These features were chosen because they were the most obvious variables in the habitats and those which were thought most likely to influence habitat selection.[1] For each variable

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[1] It is now generally accepted that two sorts of factors influence habitat selection: a) ultimate factors which affect the survival and reproductive success of the birds, for example food, cover and requirements imposed by the structural and behavioural characteristics of the species concerned; and b) proximate factors (or psychological factors) such as the presence of a song-post or the general look of the habitat which do not necessarily have direct biological significance but serve as cues by which birds recognise favourable habitat (Lack 1933, 1937 and 1944a; Hildén 1965; Orians 1971).

HABITAT - QUANTITATIVE ANALYSIS

several mutually exclusive categories were defined which could be readily distinguished in the field and which covered all the conditions likely to be encountered (these categories are used in figs. 26-29). The habitat in each territory (or in the vicinity of non-territorial migrants) was then described by scoring the appropriate category of each of the four main variables. These variables are discussed below and categories and terms which are not self-explanatory are defined:

1) Topography:

The main topographical features of wheatear habitat are illustrated in fig. 25. Most of the terms used are self-explanatory but those that are not are defined below:

Steep hillside: A hillside with an average angle of slope of 25° or more above horizontal. Angles of slope were measured with a clinometer or estimated by eye.

Gentle slope: A slope of less than 25° above horizontal.

Piedmont: Gentle slope between the foot of a cliff or steep hillside and an adjacent plain.

Shallow runnel: A predominantly dry water course of one to two metres deep, usually cut into a gently sloping hillside or piedmont and with steep stony sides and boulders in the bottom.

The features of the topography that were thought likely to be important for wheatears were: the slope of the ground; the presence or absence of cliffs and runnels; and whether the area in question was in or included a valley or valleys. These features were considered important to wheatears for the following reasons: a) all may serve as cues in habitat selection; b) all affect the amount of shade which under some circumstances is important in thermoregulation; c) cliffs and runnels usually provide cover and nest-sites; d) slope influences angles of insolation which influence ground temperatures and hence thermoregulation by birds;

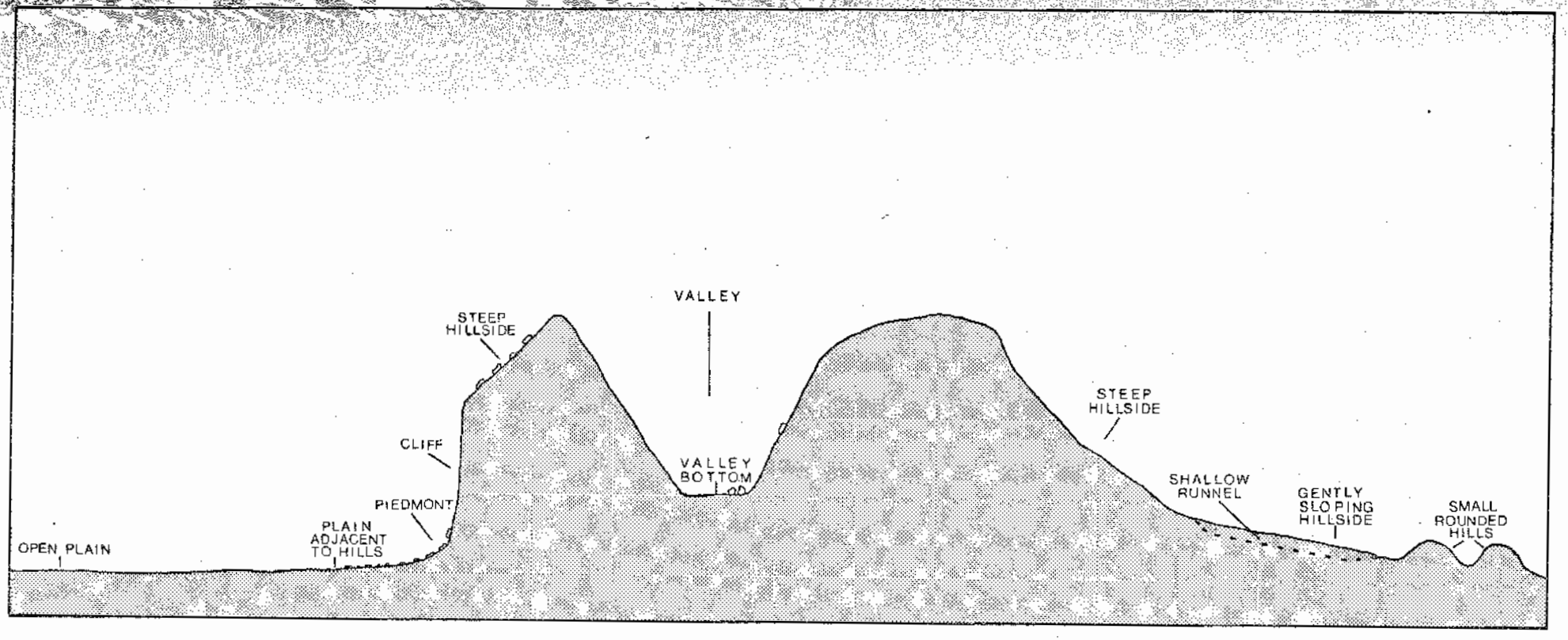

Figure 25. Topographical features of wheatear habitat.

e) slope affects the mode of locomotion used by birds and f) slope is correlated with the amount of arthropod prey available on open ground (see pp. 174-175 where evidence is discussed which suggests that on average higher densities of potential arthropod prey for wheatears occur on piedmonts and in valley bottoms than on plains and more on plains than on steep stony hillsides). The topography of wheatear habitats was therefore described in terms of these features (figs. 26-29). The categories used are self-explanatory.

2) Vegetation:

The vegetation of S. W. Iran was described in outline in chapter II (pp. 29-33) and the terms used in the description were defined on p. 28. Features of the vegetation that were considered important for wheatears were its density, patchiness and physiognomy. These features are probably important to wheatears for the following reasons: 1) They influence the amount of shade cast by plants; 2) the density and patchiness of the ground vegetation affects the ease with which birds can use pedal locomotion, and locate and capture arthropod prey on the surface of the ground; and 3) the stature, strength and structure of plants determine their value as elevated perches which are used by wheatears as song-posts, as observation points during hunting and in avoiding high temperatures at ground level. The vegetation in wheatear habitat was therefore described in terms of these features (figs. 26-29). Four categories of ground-vegetation ($\leqslant$ 50 cm high) were distinguished:

a) Sparse or very short: Closely grazed, lawn-like, herbaceous vegetation and/or widely scattered shrublets and/or small herbaceous plants covering less than 25 per cent of the ground surface (e. g. parts of plates 16 and 19).

b) Patchy: sparse or very short + medium density: Patches of a) and c) (e. g. plates 2, 8, 12, 16, 19, and 21).

c) Medium density: Scattered shrublets and/or herbaceous plants covering between 25-75 per cent of the ground surface with bare areas between most of the plants (e. g. plates 7, 9, 11, 13, 17, 18, 23, and 25).

d) Patchy: medium density + dense: Patches of c) and areas with dense ground-vegetation which was defined as covering more than 75 per cent of the ground surface (e. g. plates 3, 6, 10, 20, 22, 24, 26, and 27).

Each wheatear territory was alotted to one of the above categories after judging the density and patchiness of the ground-vegetation by eye. In addition the presence of bushes and/or trees was recorded.

3) Stone-cover:

Stones were defined as pieces of rock 2-20 cm in diameter. Stones are probably important to wheatears in the following ways: They provide elevated perches; local shade and where they are dense they present, especially in bright sunlight, variegated backgrounds against which the black and white species of wheatear can be extremely cryptic. Dense stones also hinder pedal progress and probably render arthropod prey on the ground difficult to locate and catch. Three categories of stone-cover were distinguished (figs. 26-29):

a) None or sparse: Less than 50 per cent of the ground covered by stones (e. g. plates 11, 12, 16, 20, and 24).

b) Patchy: none or sparse + dense: Patches of a) and c) (e. g. plates 2, 8, 13, 17, 19, 22, and 27).

c) Dense: 50 per cent or more of the ground covered by stones (e. g. plates 7, 9, 18, 23, and 25).

The density and patchiness of stone-cover were estimated by eye.

4) Rock-outcrops and boulders:

Rock-outcrops varied in size, but were often several m high and were frequently jagged and cracked. Boulders were defined as blocks of detached rock of more than 20 cm in diameter. These features are probably important to wheatears in the following ways: They provide shade, elevated perches and often nest-sites and cover where birds can escape from predators and adverse weather. The four categories used are self-explanatory (figs. 26-29).

HABITAT - QUANTITATIVE ANALYSIS/O. ALBONIGER

RESULTS:

The results of the quantitative analyses of wheatear habitats are summarised in figs. 26-29. Breeding habitats, habitats of wheatears on their breeding grounds outside the breeding season, wintering habitats, and habitats of migrants are treated separately. Throughout, the number of positive scores for each category of the four main habitat variables was expressed as a percentage of the total number of territories studied.

Comparisons of the habitat distributions of the various species of wheatear are made in chapter VII.

PART II. SYSTEMATIC TREATMENT OF SPECIES:

INTRODUCTORY NOTES:

The objectives of this section are first to describe the habitats of the various species of wheatear that occur in S. W. Iran and second to discuss features of these habitats which may be important in habitat selection. Two criteria were used for considering that a habitat feature may be important in habitat selection: a) Correlations between the occurrence of a species and a habitat feature (a technique which has been widely used, for example, by Lack 1933, 1939; Lack and Venables 1939; Lack and Lack 1951; Turček 1957; and MacArthur and MacArthur 1961); and b) the use of habitat features by birds during such essential activities as foraging, thermoregulation, nesting, roosting, avoiding adverse weather, and escaping from predators.

1) O. ALBONIGER (Hume's Wheatear).

Breeding habitat in S. W. Iran:

Forty-nine breeding territories of O. alboniger were studied in S. W. Iran and a quantitative analysis of the characteristics of these is given in fig. 26. O. alboniger is a bird of mountainous country and although it is often seen foraging on relatively flat ground it is seldom seen far from steep, usually rocky, boulder-strewn hillsides or cliffs.

KEY



Territories including runnels

Territories in or including valleys

Territories including cliffs



Scattered trees

Scattered trees and bu

Scattered bushes

N. B. Values of less than five per cent are not shown.

A =	O. alboniger	X =	O. xanthoprymna	O =	O. oenanthe
P =	O. picata	H =	O. hispanica	I =	O. isabellin
L =	O. lugens	F =	O. finschii	D =	O. deserti

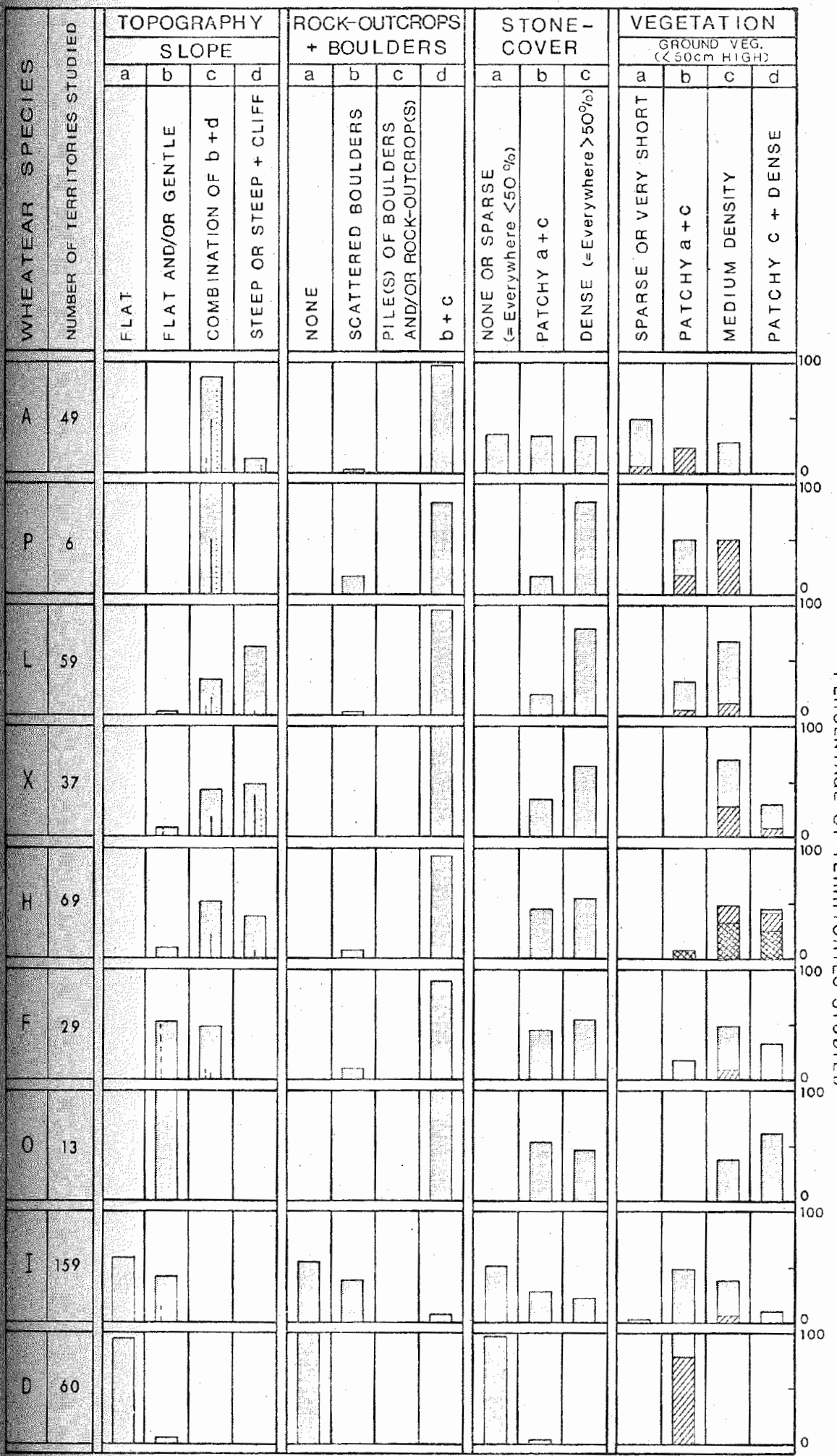

Figure 26. Habitat of wheatears breeding, or probably breeding, in S. W. Iran. The species are arranged according to the steepness of their habitats with those found on hillsides and cliffs at the top and those found on plains at the bottom. For key see opposite, and for method of analysis and definitions of terms see pp. 115-120. (N. B. O. monacha is rare and has been omitted for lack of data.)

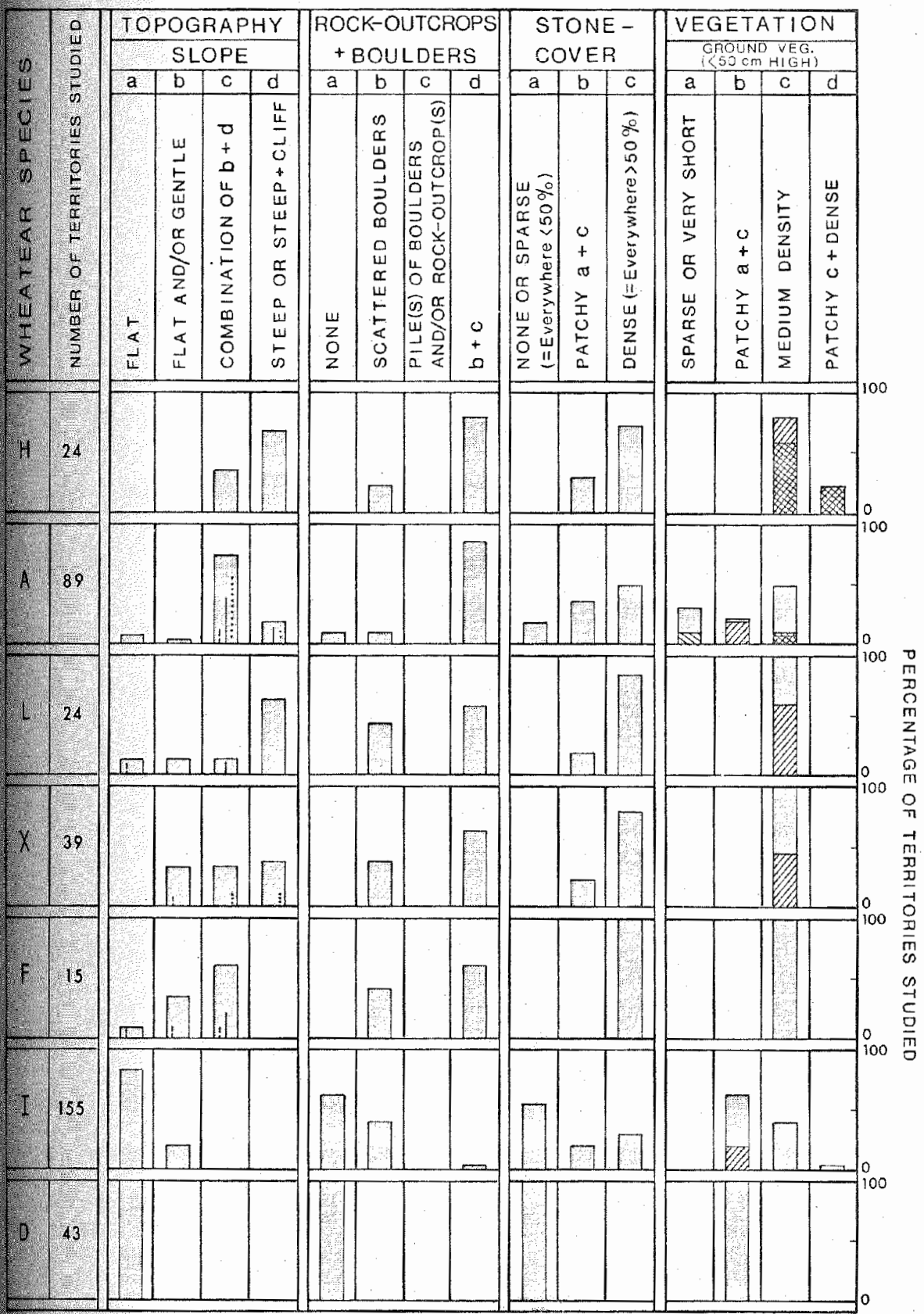

Figure 27. Habitat of wheatears on their breeding grounds, or probably on their breeding grounds, in S. W. Iran outside the breeding season. The species are arranged according to the steepness of their habitats with those found on hillsides and cliffs at the top and those found on plains at the bottom. For method of analysis and definitions of terms see pp. 115-120. (N. B. O. monacha, O. picata and O. oenanthe have been omitted for lack of data.)

KEY

Territories including runnels
Territories in or including valleys
Territories including cliffs

Scattered trees
Scattered trees and bushes
Scattered bushes

N. B. Values of less than five per cent are not shown.

H = O. hispanica L = O. lugens F = O. finschii D = O. deserti
A = O. alboniger X = O. xanthoprymna I = O. isabellina

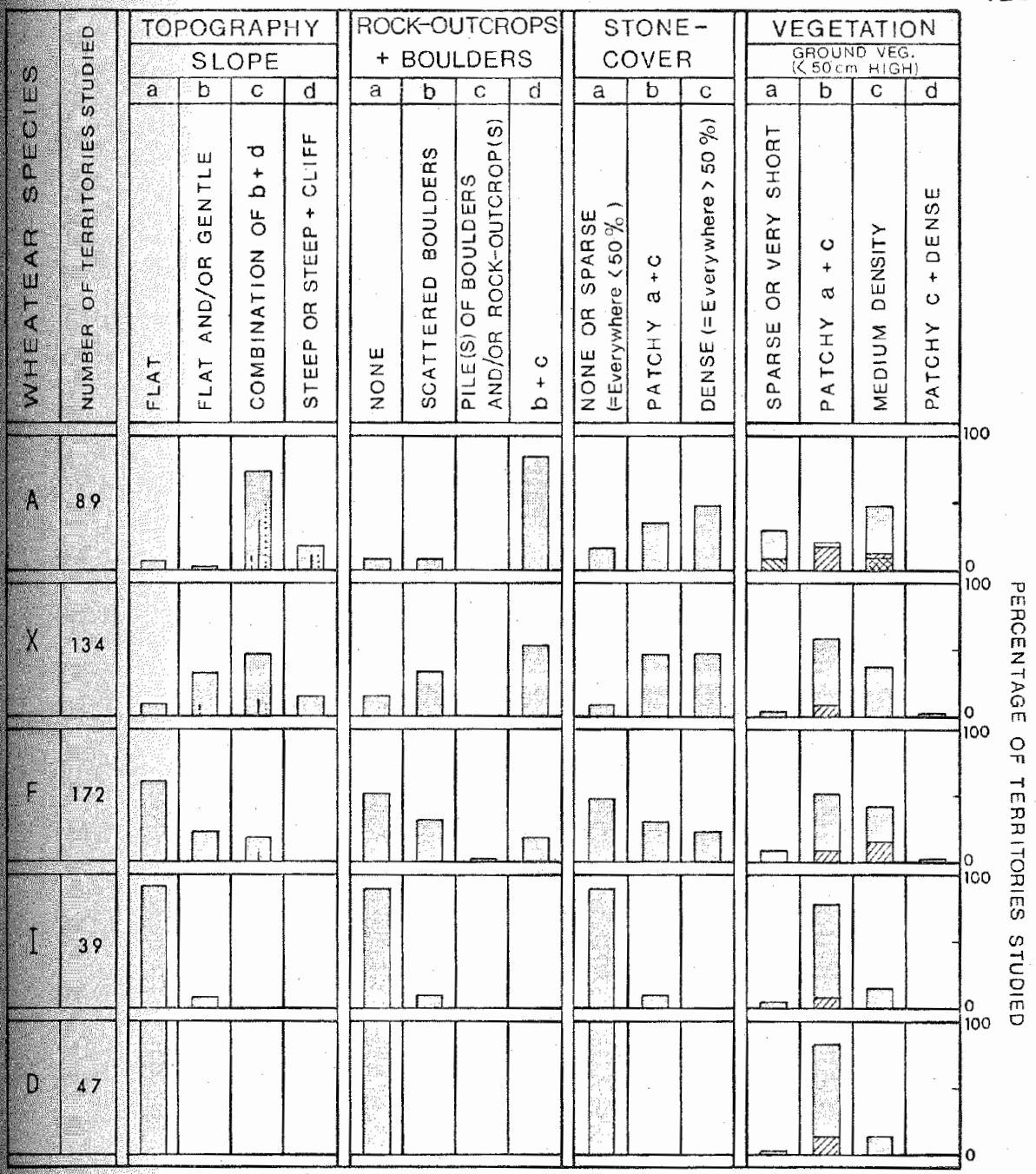

Figure 28. Habitat of wheatears wintering, or probably wintering, in S. W. Iran. The species are arranged according to the steepness of their habitats with those found on hillsides and cliffs at the top and those found on plains at the bottom. For method of analysis and definitions of terms see pp.115-120. (N. B. O. monacha and O. picata are rare and have been omitted for lack of data.)

KEY

Territories including runnels
Territories in or including valleys
Territories including cliffs

Scattered trees
Scattered trees and bushes
Scattered bushes

N. B. Values of less than five per cent are not shown.

A = O. alboniger
X = O. xanthoprymna
F = O. finschii
I = O. isabellina
D = O. deserti

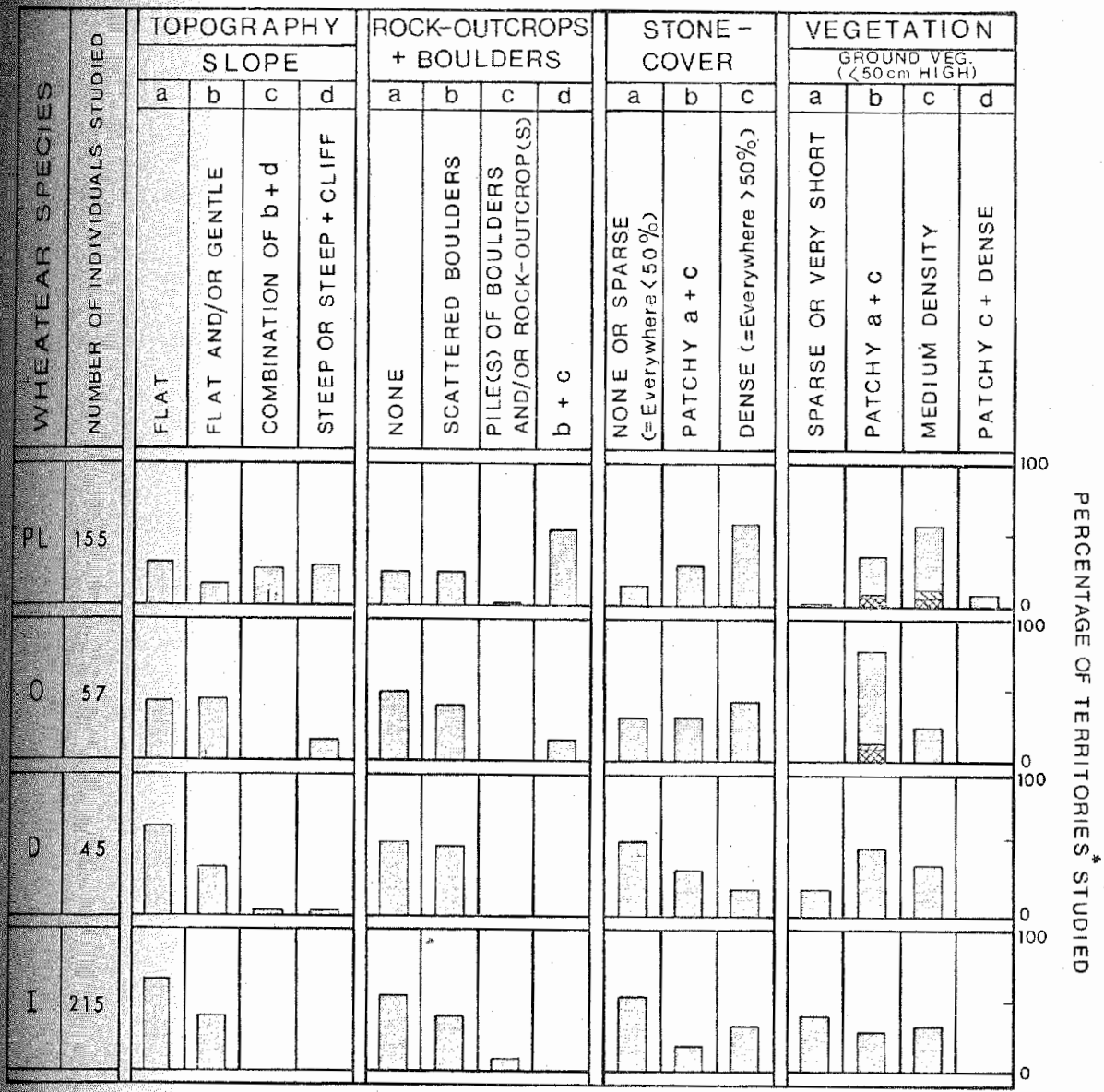

Figure 29. Habitat of migrant and probably migrant wheatears in S. W. Iran. The species are arranged according to the steepness of their habitats with those found on hillsides and cliffs at the top and those found on plains at the bottom. For method of analysis and definitions of terms see pp. 115–120. (N. B. Species that were rarely detected on passage have been omitted.)

KEY

Territories* including runnels
Territories* in or including valleys
Territories* including cliffs

Scattered trees
Scattered trees and bushes
Scattered bushes

N. B. Values of less than five per cent are not shown.

PL = O. pleschanka
O = O. oenanthe
D = O. deserti
I = O. isabellina

*or ground in the vicinity of non-territorial birds.

HABITAT - O. ALBONIGER

It is particularly common where ranges of hills outcrop from plains, and in valleys and ravines in the warm steppe zone. Plates 14 and 15 and figs. 44,p.223 and 46,p.225 give photographic impressions of the type of country.

The nature of the ground surface and the amount of vegetation varied within and between territories. In some territories, particularly those in marl badland country, the ground was predominantly stoneless silt or marl while in others stones and gravel covered most of the ground. However most territories included both stony and relatively stone-free areas. Vegetation was never dense. A few territories included oak woodland but the vegetation in most varied from medium density steppe communities in the sub-steppe zone to widely scattered steppe plants in the warm steppe zone.

Habitat features which may be important in habitat selection:

a) Bare ground: O. alboniger feeds mainly on bare ground (fig. 39, p. 181) which is therefore probably an important factor in habitat selection.

b) Steep rocky hillsides and/or cliffs: All the territories of O. alboniger that I studied included steep rocky hillsides and/or broken cliffs which therefore may be proximate factors in habitat selection. These features may also be ultimate factors in habitat selection since they were used by the birds during several important activities. For example they were used as sources of local shade, as song-posts, as perches during periods of inactivity, and rocks and boulders on rocky hillsides were used as vantage points from which birds launched feeding attacks. Rocky features are probably also important for the following reasons: They provide, especially in bright sunlight, variegated dark and light backgrounds against which these black and white birds can be extremely cryptic; they provide refuges from predators and adverse weather which are probably particularly important for the young; and they provide roost-holes and nest-sites. Hue and Etchécopar (1970) stated that O. alboniger always nests in rock crevices and never in mammal burrows. My observations of two nests and eight broods of newly fledged young are consistent with this view.

HABITAT - O. ALBONIGER

c) Flat or gently sloping ground: Eighty-six per cent of the territories of O. alboniger that I studied included some flat or gently sloping ground, such as a strip of plain adjacent to a rocky hillside, an area of piedmont or a valley bottom (fig. 26) and in the remaining 14 per cent of territories that were high up on steep rocky hillsides, far away from plains or valley bottoms, there were generally local patches of ground that were less steep. These flatter areas were important feeding grounds, probably because prey was more abundant (pp. 174-175) and easier to catch than on the steeper rockier ground. Hence flat or gently sloping ground may be an ultimate factor in habitat selection.

d) Shaded feeding grounds: Territories of O. alboniger in the lower, hotter parts of S. W. Iran invariably included hills and gorges of such configurations that they provided general shade in some part of each territory throughout most of the day. Birds were often seen feeding in these shaded areas which may be important for habitat selection in areas where high temperatures in open sunlight restrict the availability of arthropod prey (see pp. 170 and 173 and appendix D) and create problems of thermoregulation for these largely black birds.

Non-breeding habitat in S. W. Iran:

Eighty-nine territories of O. alboniger were studied outside the breeding season and a quantitative analysis of the characteristics of these is given in fig. 27. Eighty-two per cent of these territories were similar to breeding territories and included steep rocky hillsides and/or cliffs. However seven territories of non-breeding O. alboniger were found in more open country. Three of these were on rocky piedmonts or gently sloping hillsides in winter which perhaps reflects the fact that shade is of less importance during cooler weather. The other four were on the coastal plain of the Persian Gulf, about one km from the nearest hills, in an area with scattered acacia trees, during a period of extremely hot weather at the end of June 1971. These birds spent most of their time either sitting in the lower branches of acacias where they were in the shade and exposed to a cool sea breeze or feeding on the ground in the shade of the trees where insects were numerous.

HABITAT - O. ALBONIGER/O. DESERTI

Habitat outside S. W. Iran:

In eastern Iran in the provinces of Khurasan and Baluchistan O. alboniger occurs in rugged, rocky terrain similar to that in which it is found in S. W. Iran (Erard and Etchécopar 1970 and personal observations). It also occurs in similar habitat in Iraq (Meinertzhagen 1954) and in Sind (Ticehurst 1922).

2) O. DESERTI (Desert Wheatear).

Breeding habitat in S. W. Iran:

Sixty breeding territories of O. deserti were studied in S. W. Iran and a quantitative analysis of the characteristics of these is given in fig. 26. All these territories were in vast, open, sometimes gently undulating plains. The substrate was typically stoneless silt or gravel but in two territories there were patches where stones covered more than 50 per cent of the ground surface. The vegetation in all these territories included a ground layer of steppe species which varied in density from patches where plants were sparse to patches where they covered between 25 and 50 per cent of the ground surface. In addition in 78 per cent of the territories studied there were scattered bushes, mainly of Zygophyllum atriplicoides. In territories that lacked bushes there were always some shrublets of more than 30 cm high. A typical example of the breeding habitat of O. deserti is illustrated in plate 12.

Habitat features which may be important in habitat selection:

a) Bare ground: O. deserti feeds mainly on bare ground (fig. 39, p.181) which is therefore probably an important factor in habitat selection.

b) Bushes and/or shrublets: All the territories of O. deserti that I studied in S. W. Iran included scattered bushes and/or shrublets and the lives of the birds were so closely associated with them that they are probably important factors in habitat selection. The most obvious ways in which bushes and shrublets are used by O. deserti will be briefly discussed below:

HABITAT - O. DESERTI

i) Perches: O. deserti is very often seen perching on vegetation and in the flat country where it is usually found such elevated perches are probably important in the following ways: 1) in territorial defence by allowing territory owners to see and be seen by rivals; 2) in escape from predators by providing look-out posts from which predators can be spotted from a distance and in providing hiding places; 3) in thermoregulation during hot periods by providing elevated perches where temperatures are lower than on the ground surface; 4) in feeding by providing watch-posts from which large areas of ground can be scanned for arthropod prey. I believe the latter point may be particularly important since O. deserti is found in the steppe zone where arthropods are relatively scarce (p. 173).

ii) Nest-sites: The only report of a nest of O. deserti in S. W. Iran, that I can find, was of one found by Blanford (1876) "...in a small hollow by the side of a bush in a plain covered with scattered low vegetation". In other areas O. deserti nests in holes in the ground, such as rodent burrows, or under or at the bases of bushes (Whitaker 1905, Witherby et al. 1938, Dementiev and Gladkov 1968, Johns 1970). In the territories of O. deserti that I studied in S. W. Iran rodent holes were very local and it seems likely that bushes provided most of the nest-sites.

iii) Shade: Bushes and shrublets provided local sources of shade in which O. deserti were often seen during hot periods.

Outside the breeding season O. deserti that were seen on the breeding grounds were invariably in similar habitat to that occupied during breeding (fig. 27). Indeed many of these birds were probably members of the breeding population lingering on their breeding territories prior to migration. The reason why O. deserti was not recorded in bush-land during this period is that no bushland areas were visited.

Breeding habitat outside S. W. Iran:

Outside S. W. Iran O. deserti breeds in steppe and desert-edge conditions similar to those in which it breeds in S. W. Iran. For example, in Morocco, as in S. W. Iran, it breeds only in areas with a mean annual

precipitation of less than 200 mm (Brosset 1961). However outside S. W. Iran O. deserti occurs in a wider range of habitats than within S. W. Iran. Thus, as well as breeding in open flat alluvial plains, it also breeds in sandy areas; in broken stony or even rocky country and in the Pamirs O. deserti oreophila is found in rocky defiles and high mountain passes. As in S. W. Iran there is usually a sprinkling of dwarf shrubs and other small desert plants (Whitaker 1905, Bannerman 1927, Witherby et al. 1938, Dementiev and Gladkov 1968).

Habitat in winter in S. W. Iran:

O. deserti has not been proved to winter in S. W. Iran but probably does in the lower parts of the hot steppe zone (pp. 62-63). Forty-seven territories of O. deserti that were probably wintering were studied and a quantitative analysis of the characteristics of these is given in fig. 28. These territories were all on the flat alluvial coastal plain of the Persian Gulf and were invariably in places where there were scattered bushes and/or fairly tall (30-50 cm) shrublets and/or herbaceous plants. A photographic impression of the type of ground is given in plate 16.

Habitat in winter outside S. W. Iran:

The wintering habitat of O. deserti outside S. W. Iran appears to be generally similar to that occupied by the species in S. W. Iran but in East Africa it is also found in open acacia country (Ticehurst 1922, Ticehurst et al. 1922, Ali 1945, Archer and Godman 1961, Smith 1971, Moreau 1972).

Habitat of migrants in S. W. Iran:

The habitats in the territories or in the vicinity of 45 migrant O. deserti were studied and a quantitative analysis of the characteristics of these is given in fig. 29. Most of these birds were in open plains with steppe vegetation which varied in density from sparse to medium, but a few were seen on dry farmland and steep hillsides.

HABITAT - O. FINSCHII

3) O. FINSCHII (Finsch's Wheatear).

Breeding habitat in S. W. Iran:

Twenty-nine breeding territories of O. finschii were studied in S. W. Iran and a quantitative analysis of the characteristics of these is given in fig. 26. Fifty-two per cent of these territories were on bare, open, gently sloping hillsides or piedmonts which were invariably broken by dry runnels and/or clumps of boulders (e. g. plate 17). The remaining 48 per cent of territories were at the bases of hillsides and included both steep boulder-strewn or rocky areas as well as some open gently sloping or flat ground (e. g. the lower slopes of the hills in plates 7 & 18; figs. 45 & 46, pp. 224-225).

In most of the breeding territories of O. finschii that I studied the ground was predominantly stony, but the density of stones varied both within and between territories. However most territories included areas, particularly on the flatter ground, which were relatively free of stones and where the birds were often seen feeding. The vegetation in these territories consisted mainly of low-growing steppe communities. The density of the plants varied but only in patches covered more than 75 per cent of the ground surface so that usually there was bare ground between the plants.

Habitat features which may be important in habitat selection:

Although the breeding territories of O. finschii that I studied in S. W. Iran varied they all included bare ground, boulder-strewn and rocky areas and gently sloping or flat areas which therefore may be proximate factors in habitat selection. These features may also be ultimate factors in habitat selection since they were used by the birds during several important activities which will be reviewed below.

a) Bare ground: O. finschii feeds mainly on bare ground (fig. 39, p. 181).

b) Boulder-strewn and rocky areas: These features were important in providing song-posts; watch-posts which were used during feeding; local shade; and nest-sites. Twelve nests of O. finschii were found during

this study and all were in boulder-strewn or rocky areas. Ten were in holes under boulders and two were in crevices in rocks. These sites appear to be typical of the species (Hüe and Etchécopar 1970) although on the Mangishlak Peninsula on the eastern coast of the Caspian Sea some nest in rodent burrows or cracks in dry clay (Mitropolskii 1968). Boulder-strewn and rocky ground is probably also important in providing shelter, particularly for the young, from predators and bad weather. It also provides a variegated dark and light background against which these birds can be extremely cryptic.

c) Gently sloping or flat areas: Birds were frequently seen feeding in these areas which were often relatively stone-free and where prey was probably more available (pp. 174-175) and easier to catch than on steeper stonier ground.

O. finschii that were seen on their breeding grounds outside the breeding season were mainly in the same or similar habitat to that occupied during the breeding season (fig. 27).

Breeding habitat outside S. W. Iran:

I can find little detailed information about the breeding habitat of O. finschii outside S. W. Iran but reports that I have seen suggest that it is broadly similar to the habitat of the species in S. W. Iran. Thus, Benson (1970) stated that in Lebanon O. finschii is found chiefly on steep stony slopes and rocky mountain ravines. In Anatolia, Wadley (1951) found it confined to rocky hillsides, preferring small, narrow, steep-sided rocky valleys and in the Ala Dagh Mountains, in south central Turkey, Gaston (1968) found O. finschii on bare rocky slopes or on large boulder screes. On the Mangishlak Peninsula, on the east coast of the Caspian Sea, Mitropolskii (1968) found the species breeding in rocky foothills but also in plains where it nested in rodent holes.

Habitat in winter in S. W. Iran:

One-hundred-and-seventy-two winter territories of O. finschii were studied in S. W. Iran and a quantitative analysis of the characteristics of these is given in fig. 28. Forty per cent of these were on gently

sloping hillsides or at the bases of steep rocky hillsides; that is ground similar to that occupied during the breeding season. However 60 per cent of the winter territories of O. finschii that I studied were on plains often far from any hills. The ground surface in the winter territories of O. finschii varied from stoneless silt with a few scattered low-growing xerophytic plants (e. g. plate 16) to ground with more, but seldom dense, stones, boulders and steppe vegetation (e. g. plates 17 and 19).

The reason why O. finschii occurs on boulder-free plains in winter in S. W. Iran but not in the breeding season is uncertain, but several explanations may be suggested: 1) The breeding grounds of the O. finschii that winter in S. W. Iran are not known and it is possible that birds that winter in plains also breed in plains. 2) In the breeding season O. finschii may be restricted to hillsides and foothills by competition from O. isabellina which occupies the plains, but I think this is unlikely since O. finschii is socially dominant to O. isabellina (pp.253-254). 3) The presence of rocks and boulders may be of critical importance only during the breeding season and hotter parts of the year when shade, song-posts, nest-sites, and shelter for the young from predators and adverse weather are needed. I think the latter seems the most plausible explanation.

Habitat in winter outside S. W. Iran:

The only description, that I can find, of the winter habitat of O. finschii outside S. W. Iran is by Ticehurst (1926) who found the species on bare plains and at the bases of stony hillsides in Pakistani Baluchistan.

4) O. HISPANICA (Black-eared Wheatear).

Breeding habitat in S. W. Iran:

Sixty-nine breeding territories of O. hispanica were studied in S. W. Iran and a quantitative analysis of the characteristics of these is given in fig. 26. These territories varied considerably: ten per cent were on gently sloping hillsides or in valley bottoms; 39 per cent were confined to steep, stony, rocky hillsides; while the remaining 51 per cent included both steep and gently sloping ground (the type of terrain is illustrated in plates 5, 6, 20 - 22). Most territories included piles

of boulders and/or rock outcrops which were often associated with shallow re-entrants such as the one shown in plate 22. The ground surface in the majority of territories was predominantly stony. In some, stone-cover was patchy but in a few there were virtually no stones. The vegetation in the breeding territories of O. hispanica tended to be richer than in the breeding territories of other species of wheatear in S. W. Iran. All were in the xerophilous forest zone and most were in areas of light woodland which was mainly dominated by oak but sometimes by other species such as pistachio, almond or juniper. Some territories were totally wooded; some included clearings or straddled the edge of woodland; while others, which were probably in deforested areas, had only scattered bushes and perhaps an occasional solitary tree. The trees were generally small (3-10 m high) and widely spaced with the intervening ground occupied by scattered bushes, shrublets, grasses, other herbaceous plants, and patches of bare ground. The density of the low-growing ground vegetation varied with the nature of the substrate (fertility, stoniness, slope, etc.), the amount of grazing and the season. It was most dense in spring when, in response to rising temperatures and the relatively high precipitation (>400 mm mean annual which falls mainly in winter and spring) the ground surfaces in the breeding territories of O. hispanica were often largely covered with a rich flush of herbaceous vegetation (plates 6 and 20). However there were always bare patches which became progressively larger during the ensuing drought.

The majority of breeding territories of O. hispanica that I studied were in undeveloped country but a few were in areas with poor cultivation where there were scattered bushes, boulders and piles of stones.

Habitat features which may be important in habitat selection:

Although the breeding territories of O. hispanica that I studied in S. W. Iran varied, all had features in common which were important in the lives of the birds and which may influence habitat selection. These features will be discussed below:

HABITAT - O. HISPANICA

a) Bare ground: O. hispanica feeds mainly on bare ground (fig. 39, p. 181) which is therefore probably an ultimate factor in habitat selection.

b) Cover and nest-sites: All territories included bushes and/or rock outcrops and/or piles of stones or boulders which provided cover, particularly for the young, from adverse weather and predators. In addition these features provided holes and crevices which are used as nest-sites, but they are not essential for this purpose since O. hispanica also nests in such sites as hollows under stones, holes in banks or recesses in the ground sheltered by tussocks of grass or other plants (Whitaker 1905, Witherby et al. 1938). During the present study, four nests of O. hispanica were found. One was at the bottom of a small hole, about 10 cm deep, in the side of a large rock in a boulder-strewn valley bottom; one was out of sight in a hole in an earth bank and two were on rocky hillsides, one deep in a pile of boulders and the other easily visible in a shallow recess under a stone.

c) Elevated perches: These were very numerous in the territories of O. hispanica and included rocks, boulders, large stones, trees, bushes, and other vegetation. Some, usually taller trees or bushes, were used as song-posts and all types of perch, including quite slender plants, were used extensively by the birds as vantage points from which to locate and launch aerial attacks on arthropod prey which was caught mainly on bare ground. This technique enables the birds to survey wide areas of ground with little expenditure of energy and to hunt unhindered by rough terrain or dense ground vegetation. I believe this feeding strategy, and hence the availability of elevated perches, is important in allowing O. hispanica to inhabit areas where the ground is difficult for a small bird to traverse on foot and/or where there is relatively little and often only scattered patches of bare ground where they can feed; for example, areas which are steep and/or stony and/or subject to spring flushes of herbaceous vegetation which cover most of the surface of the ground (see pp. 264-265 for further discussion of this topic).

HABITAT - O. HISPANICA

Some direct evidence that piles of stones can be an important feature in the breeding habitat of O. hispanica was provided by Hoffmann (1958) who reported that in the Crau, a vast flat plain covered with dense stones and scattered boulders in the Rhône Delta in southern France, the species increased after piles of stones were erected, as obstacles to aeroplanes, during the German occupation. Hoffmann noted that the piles of stones provided perches and nest-sites for the birds.

Outside the breeding season O. hispanica was found on the same or similar ground to that on which it bred (fig. 27).

Breeding habitat outside S. W. Iran:

The breeding habitat of O. hispanica outside S. W. Iran has been described by many authors and appears to be generally similar to that occupied by the species in S. W. Iran. Thus in Tunisia it is a "...bush-loving bird, and evinces a partiality for open, undulating country, where a scrub or dwarf vegetation flourishes, apparently avoiding the more rocky and barren districts frequented by O. oenanthe. ...it generally breeds on a low hillside, or on broken rugged ground, where it places its nest under a rock, or tussock..." (Whitaker 1905). In southern Turkey it is found in lightly wooded hilly country (Hollom 1955) and in Anatolia is addicted to well-cultivated valleys with vineyards and orchards surrounded by stone walls (Wadley 1951). Witherby et al. (1938) described the breeding habitat of O. hispanica as "...chiefly dry rocky or stony and barren places, and arid pastures and vineyards or rough cultivation where stone walls or other suitable nesting sites exist".

In S. W. Iran the breeding range of O. hispanica is confined to areas with a Mediterranean climate.[1] This is largely true of the range of the species outside S. W. Iran but in Morocco its range extends into drier country as far as the 200 mm (mean annual precipitation) isohyet (Brosset 1961) and in Iraq it breeds in the irrigated farmlands at Habbaniya on the

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[1] The Mediterranean climatic type is characterised by a mean annual precipitation of 380-635 mm, mostly concentrated in winter, which usually supports a good flush of ground vegetation in spring (Trewartha 1954, Polunin and Huxley 1965).

Tigris (Chapman and McGeoch 1956) which lies in the sub-desert zone and has a mean annual precipitation of 119 mm (Guest 1966).

Habitat in winter outside S. W. Iran:

In winter in Africa along the southern edge of the Sahara, O. hispanica occurs in acacia steppe or open thorn-bush country (Witherby et al. 1938, Moreau 1972) and in Eritrea in clearings at the edge of woodland, in parks, gardens and acacia country (Smith 1951, 1971).

5) O. ISABELLINA (Isabelline Wheatear).

Breeding habitat in S. W. Iran:

One-hundred-and-fifty-nine breeding territories of O. isabellina were studied and a quantitative analysis of the characteristics of these is given in fig. 26. Most of these territories were on vast open, sometimes gently rolling, plains while a small proportion were on gently sloping piedmonts. Plates 11 and 19 and fig. 45, p. 224 show the type of terrain. The ground surface in the majority of territories was predominantly silt with perhaps a few scattered stones; in some there were patches of dense stones and in a few, stones were dense throughout. The vegetation invariably consisted of steppe communities which varied in density from a few widely spaced dwarf plants to relatively dense steppe where the average distance between shrublets was only about one metre. The ground between the shrublets was bare during most of the year but in spring there was usually a flush of herbaceous plants which varied in density. However in all the territories that I studied, a considerable proportion of the ground was always either bare or had only scattered or very low-growing herbaceous plants which did not prevent the birds from moving about freely on foot.

Most breeding territories of O. isabellina that I studied were in undeveloped steppe but a few were on the edge of cultivation or on abandoned fields.

Habitat features which may be important in habitat selection:

The territories of O. isabellina that I studied in S. W. Iran had several features in common which were important in the lives of the

birds and which may influence habitat selection. These will be discussed below:

a) Open, level, bare ground: O. isabellina forages mainly by making rapid dashes over the ground after prey (fig. 39, p. 181), a strategy that is probably only effective on relatively bare ground. The species is morphologically well-adapted for this foraging technique by virtue of its stature and relatively long legs but by the same tokens and other factors, such as its heavy weight and high wing loading (pp.267-282), it is ill-adapted for the perch, flight and pounce foraging technique which is usually used by wheatears on rough, rocky or steep ground. The presence of open, bare ground is probably therefore an important factor in habitat selection by O. isabellina.

b) Perches: O. isabellina perches relatively little on elevated objects (fig. 39, p. 181) probably partly because it is ill-adapted to use flimsy perches (pp. 267-282) and partly because there are often rather few suitably sturdy perches available. However, especially during hot weather, O. isabellina is frequently seen perching on such stable objects as boulders, clods and firm vegetation. Although these perches undoubtedly serve as look-out posts from which to locate prey their prime importance to the birds is probably in providing resting places that are at lower temperatures than the surface of the ground. This view is supported by frequent observations during hot weather of O. isabellina panting with an open gape even while sitting on elevated perches. I therefore believe that a few sturdy elevated perches may be an important element in the habitat of O. isabellina, especially at lower altitudes where overheating is more of a problem.

c) Shade: Some form of shade, provided for example by vegetation, boulders or holes in the ground, is probably an important ingredient of the habitat of O. isabellina.

d) Nest-sites: Thirty-four nests of O. isabellina were found during this study. One was in a low stone wall in poor farmland and the rest were in the burrows of rodents, mostly Meriones libycus. These sites

are typical of the species but there are reports that the birds sometimes excavate their own holes (Witherby et al. 1938 citing work by Przewalski, Dementiev and Gladkov 1968). It is therefore questionable whether ready-made nest-holes are an essential element in the breeding habitat of this species. However this is probably the case in S. W. Iran since the ground is usually dry and hard and I doubt whether there are many places where O. isabellina could excavate its own burrows from scratch. An indication that numbers of O. isabellina may sometimes be limited locally by a lack of nest-sites was provided by Babaev (1967)[1] who showed a correlation between the numbers of O. isabellina counted on ten-kilometre transects and the numbers of rodent colonies per hectare in an area in the Kara Kum desert of Turkestan. However Babaev did not establish a causal relationship between the number of O. isabellina and the number of rodent colonies and it is possible that both were limited by some other factor.

Habitat of non-breeding birds in S. W. Iran:

The habitat of summer visitors outside the breeding season, migrants and probable winter visitors was similar to that of breeding birds (figs. 27-29 and plate 16).

Habitat outside S. W. Iran:

Outside S. W. Iran both on its breeding grounds and in winter quarters O. isabellina occurs in habitat similar to that in which it is found in S. W. Iran (Ticehurst 1922, Ticehurst et al. 1922, Baker 1924, Grote 1937, Witherby et al. 1938, Ali 1945, Moreau 1972). However in the Caucasus its preferred breeding habitat was considered to be stonefields and scree (Dementiev and Gladkov 1968 citing work by Satunin 1907 and Sotrinskii 1915).

6) O. LUGENS (Mourning Wheatear).

Breeding habitat in S. W. Iran:

Fifty-nine breeding territories of O. lugens were studied in

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[1] Only an English review of this Russian paper was seen - Bird Banding 39:142 (1968).

S. W. Iran and a quantitative analysis of the characteristics of these is given in fig. 26. Sixty-three per cent of these territories were confined to steep, rocky, boulder-strewn hillsides; 34 per cent also included more gently sloping areas of piedmont, valley bottom or plain; and two territories (3%) were on gently sloping hillsides. The type of ground is illustrated in plates 7 and 23 and figs. 44-46, pp. 223-225. In all the territories that I studied the ground surfaces were predominantly stony and strewn with boulders. In addition in most there were broken rock-outcrops and/or piles of boulders. The vegetation consisted of medium density steppe communities often with patches where plants were sparse. Occasionally there were scattered bushes.

Habitat features which may be important in habitat selection:

The breeding territories of O. lugens that I studied in S. W. Iran had a number of features in common which may influence habitat selection. These features will be briefly discussed below:

a) Bare ground: O. lugens feeds mainly on bare ground (fig. 39, p.181) which is therefore probably an important factor in habitat selection.

b) Stony ground: The substrate in the territories of O. lugens was predominantly stony and this may be important to the birds because it provides a background against which their black and white plumage can be extremely cryptic (this topic is discussed further on p. 261).

c) Boulders and rock-outcrops: The breeding territories of O. lugens all included scattered, and usually also piles of, boulders and/or rock-outcrops. These features were used by the birds in a number of ways; for example, as song-posts and as vantage points from which to locate and launch attacks on prey. They also provide local shade, nest-sites and cover, particularly for the young, from predators and adverse weather. Twelve nests of O. lugens were found during this study. Five were in crevices in rock-outcrops, three were in holes under piles of boulders, three were under isolated boulders and one was in a hole in a stone wall at the side of a road. All these nests were out of sight deep inside holes, the entrances of which were built up with barricades

of small pebbles. These sites are typical for the species although it also nests in holes in banks (Whitaker 1905, Jourdain 1915, Hüe and Etchécopar 1970).

Habitat on the breeding grounds in S. W. Iran outside the breeding season:

Outside the breeding season O. lugens occurs in small numbers within the breeding range until mid-November (p.79). During this period 24 territories of the species were studied and a quantitative analysis of the characteristics of these is given in fig. 27. Seventy-six per cent of these territories included steep hillsides and were on the same or similar ground to that on which the species bred but 26 per cent were on flat ground or included a combination of flat and gently sloping ground which was stony, boulder-strewn and supported medium density steppe vegetation and often scattered bushes. O. lugens was seldom found far from steep rocky hillsides during the breeding season and its occupation of plains and gently sloping ground outside the breeding season may be a reflection of any of the following factors: 1) The presence of steep rocky hillsides with rock outcrops and boulder falls may be of crucial importance only during the breeding season and hotter parts of the year when shade, song-posts, nest-sites, and cover for the young are needed. 2) O. lugens may be prevented from occupying plains during the breeding season by competition from breeding O. isabellina which by the autumn are present in smaller numbers. However this is unlikely as O. lugens is probably socially dominant to O. isabellina (pp.253-4). 3) Food supplies on some rocky hillsides may become critically low during the autumn, which is at the end of the dry season, but be better on the adjacent plains (pp. 174-175).

Breeding habitat outside S. W. Iran:

Little detailed information has been published on the breeding habitat of O. lugens outside S. W. Iran, but it appears to be generally similar to that in which it is found in S. W. Iran. Thus in Morocco it occurs locally along the desert edge in areas with a mean annual precipitation of less than 100 mm (Brosset 1961). In Tunisia "...it frequents

the most barren and desolate spots choosing for preference the neighbourhood of marl cliffs and gravel hillocks" (Whitaker 1905).

Elsewhere in North Africa and the Levant it has been reported inhabiting desolate rocky gorges, ravines, wadis, and hillsides (Rothschild and Hartert 1912, Hartley 1949, Smith 1951, Benson 1970).

Winter habitat:

The only reports, that I can find, of the wintering habitat of O. lugens are from Morocco (Smith 1965) and Egypt (Hartley 1949) where it was in habitat similar to that in which it breeds.

7) O. MONACHA (Hooded Wheatear).

Habitat in S. W. Iran:

Little is known about the habitat of O. monacha in S. W. Iran but it is probably confined to dry, desolate wadis and badlands with little vegetation in the hot lowlands bordering the Persian Gulf (see p. 81 for details of records).

Habitat outside S. W. Iran:

The habitat of O. monacha outside S. W. Iran has been described by a number of authors (e. g. Tristram 1867, Dresser 1871-1881, Blanford 1876, Ticehurst 1926, Meinertzhagen 1930 and 1954, Etchécopar and Hüe 1967, Erard and Etchécopar 1970) and it appears throughout its range to be a bird of hot, dry, barren badlands, hills, wadis and plains. Thus Meinertzhagen (1930), describing the habitat of O. monacha in Egypt, wrote as follows: "A bird of most desolate wadis, never approaching cultivation or habitations. Even the proximity of a bush or patch of green herbage seems distasteful. Prefers steep-sided to open wadis". In Persian Baluchistan Blanford (1876) found O. monacha in equally barren country and commented that "...of all the Saxicolae [Oenanthe spp.], none are more thoroughly desert birds; I only met with it in the dreariest of plains and hills, and its favourite resort appeared to be the sandhills on the Makran coast". My own observations of O. monacha in Persian Baluchistan corroborate these descriptions.

HABITAT - O. OENANTHE

8) O. OENANTHE (Wheatear).

Breeding habitat in S. W. Iran:

Thirteen breeding territories of O. oenanthe were studied in S. W. Iran and a quantitative analysis of the characteristics of these is given in fig. 26. Six of these territories were on the edge of the flood plain of a small lake. They included two main elements: a) areas of flat, closely-grazed turf, with scattered and patches of thistles, where the birds were seen foraging; and b) adjacent rocky areas at the feet of the surrounding hills where the nests were probably sited and the chicks of two pairs were seen (plate 24). The remaining seven territories were in stony mountainous terrain and included the bases of hillsides and adjacent flatter areas (plate 25). The vegetation in these territories was patchy. All included some areas where the ground was largely bare, with perhaps a few scattered shrublets while in other parts there were open communities of thorn-cushions and other low-growing tragacanthic plants or dense carpets of thistles or other herbaceous vegetation.

Habitat features which may be important in habitat selection:

Since only 13 breeding territories of O. oenanthe were studied in S. W. Iran, no more than tentative suggestions can be made regarding features which may be important in habitat selection. Nevertheless all these territories had some elements in common which may influence habitat selection. These included:

a) Broken rock outcrops and/or piles of boulders: These were used by the birds as song-posts, nest-sites and cover. However elsewhere in its range, the breeding habitat of O. oenanthe includes flat featureless areas where it nests in holes in the ground, under stones, in old walls, drain-pipes, old tins, kettles, etc. (Witherby et al. 1938). It is therefore likely that rock outcrops or piles of boulders are only of crucial importance where no other nest-sites are available.

b) Flat or gently sloping areas with little or no vegetation: The birds were frequently seen feeding in these areas. Such relatively level feeding grounds may be an important feature in the habitat selection

of O. oenanthe since throughout its range it generally occurs in areas of low relief. Indeed the only report in the literature that I have seen of O. oenanthe breeding on steep hillsides was by Baxter and Rintoul (1953) who found the species plentiful on cliff faces in Argyll, Scotland. However these authors commented that this was in a year when the species was exceptionally abundant and it is possible that intraspecific competition had led the birds to occupy marginal habitat. Furthermore this report did not eliminate the possibility that the territories also included flatter areas as was the case in 12 territories of O. oenanthe that I studied on steep hillsides in Snowdonia, Wales. In these territories the average gradient was steep but the ground was uneven so that some parts were relatively level.

Breeding habitat outside S. W. Iran:

Outside S. W. Iran O. oenanthe breeds in a wide variety of situations which provide open, bare, relatively level feeding areas together with nest-sites (for nest-sites see p. 142). Thus, provided there are nest-sites, it breeds in such areas as bare hillsides, closely grazed pasture, recently burned heather moors, actively worked peat bogs, sand dunes, coastal shingle, open sandy areas in pine forests, and in tundra where it haunts sandy poorly vegetated rises (Witherby et al. 1938, Axell 1954, Dementiev and Gladkov 1968).

In the northern parts of its range O. oenanthe breeds from sea level often to the tops of the mountains. Thus in Greenland it breeds from sea level to 550 m above sea level (Nicholson 1930) and in the British Isles from sea level to 1,200 m above sea level (Bannerman 1954). In the south of its range it is almost entirely montane and its altitudinal distributions in various areas are listed below as examples:

Albania	Above 762 m	(Ticehurst and Whistler 1932).
Mount Parnassus, Greece	1,200 - 2,400 m	(Dresser 1871-1881).
Tadzhikistan, U. S. S. R.	1,800 - 3,500 m	(Dementiev and Gladkov 1968).
Atlas Mountains, Morocco	1,500 - 3,000 m	(Brosset 1961).
Aures Mountains, Algeria	1,600 - 2,000 m	(Rothschild and Hartert 1912).
S. W. Iran	Above 2,500 m	(Present study).

However on some Aegean islands O. oenanthe breeds down to sea level (Wettstein 1938, Stresemann 1950, Watson 1964).

HABITAT - O. OENANTHE/O. PICATA

Habitat of migrants in S. W. Iran:

Migrant O. oenanthe were recorded in all bioclimatic zones where they were most often seen on bare open plains and sometimes on piedmonts or steep rocky hillsides with scanty steppe vegetation (fig. 29).

Winter habitat:

O. oenanthe winters in Africa south of the Sahara where it occurs from sea level to 3,100 m above sea level mainly in the steppe and savanna belts, the driest zones along the southern edge of the desert being largely avoided. It is usually found on open or lightly wooded plains or areas of low relief where there is bare ground or very short grass. It is especially fond of areas which have been recently burnt (Bannerman 1936, Elgood et al. 1966, Moreau 1972).

9) O. PICATA (Eastern Pied Wheatear).

Breeding habitat in S. W. Iran:

O. picata is rare in S. W. Iran and only six breeding territories were studied. A quantitative analysis of the characteristics of these is given in fig. 26. All these territories included a combination of steep and gently sloping ground. Three were in steep sided valleys and included areas of gently sloping valley bottom and the other three included sections of steep hillside together with areas of adjacent gently sloping piedmont. The ground in all these territories was predominantly stony with scattered, and piles of, boulders and usually also rock outcrops. The vegetation consisted mainly of medium density steppe communities often with patches where plants were sparse. In four of the territories there were also scattered bushes.

Breeding habitat outside S. W. Iran:

Outside S. W. Iran O. picata breeds in hilly and broken country with scanty vegetation or in rough cultivation where it frequents particularly small valleys, wadis and the lower slopes of hillsides which are usually stony and boulder-strewn. Thus in Afghanistan Paludan (1959) found O. picata on desolate, stony, boulder-strewn slopes; in rocky

canyons and also in cultivated areas in the bottoms of valleys. In Khurasan, the northeastern province of Iran, Erard and Etchécopar (1970) found O. picata very numerous especially in valleys where the bottom-land and the lower slopes of the sides supported cereal cultivation interspersed with small banks and low stone walls which gave way on the steeper valley sides above to uneven stony ground with a thin growth of grass. In Persian Baluchistan, the southeastern province of Iran, in April 1972 I found O. picata locally common between about 1,100 m and 2,300 m above sea level in a variety of habitats which will be discussed below:

1) A pair and three males were found, spaced out and probably holding territories, along a V-shaped valley with steep sides and open gently sloping areas in the bottom. The ground was predominantly stony and there were scattered boulders and broken rock outcrops. The vegetation consisted of medium density steppe communities with bare ground between the shrublets and scattered almond bushes.

2) Two pairs were found nesting in stone walls bordering small terraced fields on a gently sloping hillside. The fields supported young, green cereal crops but about a quarter of the ground was bare.

3) One pair was found nesting in a stone wall in a territory that included a road; an area of steep, largely stoneless hillside with medium density steppe vegetation and an adjacent tract of valley bottom with small fields of young cereals and patches of bare ground.

4) Five pairs, including one which was nest-building, were found in wide, shallow V-shaped wadis cut through open undulating or gently sloping country. The ground in both the wadis and the surrounding areas was boulder-strewn, predominantly stony and supported scanty steppe vegetation and scattered bushes, mostly of Zygophyllum sp.

5) Three, probably territorial, males were found spaced out along a wadi similar to the ones described in division 4) above but there were no bushes.

HABITAT - O. PICATA

6) Two males and a female, which were probably on breeding territories, were found in wadis similar to those described in division 4) above but the ground was virtually stone and boulder-free and instead was capped with gravel.

7) Two pairs, a lone female, and a lone male were found in wadis with flat bottoms and steep sides which were cut through undulating stony steppe. The beds of these wadis were largely bare with a few scattered stones, boulders, bushes and dwarf palms (Nannorhops richiana). The nest of one of the pairs was built in a hole approximately four m from the floor and about half way up the vertical side of a wadi.

In Persian Baluchistan O. picata was frequently seen sitting on elevated perches from which it often darted to the ground after prey. These perches included boulders, rock outcrops, bushes and even quite slender vegetation such as the ungrazed twigs of artemisia upon which it sat with facility. This habit and ability may be an important factor in enabling this species to locate and attack prey in both cultivated areas where bare feeding ground tends to be patchy and in very dry country where food is probably scarce at most times of year. These points have been discussed more fully in the treatments of O. deserti, p. 128 and O. hispanica, p. 134.

Habitat in winter in S. W. Iran:

All available information on the winter habitat of O. picata in S. W. Iran is presented in table 13, p. 87.

Winter habitat outside S. W. Iran:

The only reports of the winter habitat of O. picata that I can find are from Sind and N. W. India where it occurs in low hills; broken, stony, hummocky country; open semi-desert; thin scrub jungle; areas with dry cultivation and often in the neighbourhood of human habitations and cattle folds where no doubt insects are particularly abundant (Ticehurst 1922, Whistler 1935, Ali 1945).

HABITAT - O. PLESCHANKA

10) O. PLESCHANKA (Pied Wheatear).

Habitat of migrants in S. W. Iran:

The habitat in the territories or in the vicinity of 155 migrant O. pleschanka was studied in S. W. Iran and a quantitative analysis of the characteristics of these areas is given in fig. 29. O. pleschanka occurred in a variety of habitats: Twenty-nine per cent were high up on steep rocky hillsides; nine per cent were in or near the bottoms of steep-sided rocky valleys; 16 per cent were at the bases of steep rocky hillsides and/or on adjacent areas of piedmont or plain; 15 per cent were on gently sloping stony hillsides; and 30 per cent were on open plains. Most of these birds were on stony boulder-strewn ground with medium density steppe vegetation which often had patches where plants were less dense; some were on stoneless alluvial plains with sparse steppe vegetation while a few were in orchards or lightly wooded country.

Breeding habitat:

O. pleschanka breeds in a fairly wide range of habitats including: rough hilly country where it is found in rocky valleys or on stony boulder-strewn slopes; and open steppe, often far from mountains, wherever the ground is broken, for example by clay cliffs, erosion gullies or rock outcrops. It generally occurs in areas with scanty vegetation but also in places with scattered bushes and sometimes in lightly wooded or cultivated country (Grote 1937, Witherby et al. 1938, Shnitnikov 1949, Dementiev and Gladkov 1968). Thus in northern Khurasan, N. E. Iran, Erard and Etchécopar (1970) found O. pleschanka common particularly in vast, undulating steppe with short but fairly dense grass on pebbly ground and with here and there an outcrop of rocks. They also found several pairs in poorer steppe where there were a few scattered bushes. They noted that the species occurred only in areas where the mean annual precipitation is greater than 300 mm. In contrast to these observations by Erard and Etchécopar, D. A. Scott (pers. comm.) found O. pleschanka breeding in small numbers between about 1,700 m and 2,000 m above sea level in fairly lush valleys on the southern slopes of the Elburz Mountains near Semnan in northern Iran. The situations in which he found these birds will be briefly summarised below:

HABITAT - O. PLESCHANKA

1) Two pairs, accompanied by broods of fledglings, and four single birds were seen among scattered bushes and juniper trees in a relatively flat area along the edge of a stream in the bottom of a narrow valley bordered by crags and rocky juniper-clad slopes. Nearby a male and two young were found in a narrow tributary gully with a stream in the bottom and steep rocky sides with scattered bushes and juniper trees.

2) A pair and three lone females were seen near villages in areas of mixed cultivation, with gardens, poplar groves, springs and streams in the bottoms of fairly narrow valleys with rocky sides.

3) Four pairs, each with broods of fledglings, were found in wide valleys bordered by steep rocky hillsides with scattered bushes and juniper trees. The bottom-land supported a lush vegetation of grasses, thistles and other herbaceous plants which in places covered 90 per cent of the ground. The birds were all seen in the vicinity of rocks and stone walls in the valley bottom, but were never far from the valley sides.

Commenting on the habits of O. pleschanka in these Elburz valleys, Scott noted that the birds frequently perched on walls, piles of stones, thistles, and low bushes; and fed on the ground, usually in stony areas with fairly dense vegetation.

Habitat in winter:

In winter in E. Africa and S. W. Arabia O. pleschanka occurs chiefly between 1,200 m and 2,000 m above sea level in the following habitats: rocky, often scrub-clad hillsides; dry open plains where it shows a preference for bushy ground; wadis cut through open country; areas of dry cultivation especially where there are thorn hedges, animal enclosures or human settlements; and in gardens in towns (Grote 1937, Witherby et al. 1938, Archer and Godman 1961, Smith 1971, Moreau 1972).

HABITAT - O. XANTHOPRYMNA

11) O. XANTHOPRYMNA (Red-tailed Wheatear).

Breeding habitat in S. W. Iran:

Thirty-seven breeding territories of O. xanthoprymna were studied in S. W. Iran and a quantitative analysis of the characteristics of these is given in fig. 26. Forty-nine per cent of these territories were restricted to steep, stony, boulder-strewn hillsides; 43 per cent also included more gently sloping areas of piedmont, plain or valley bottom while eight per cent were on gently sloping hillsides. The type of terrain is illustrated in plates 2, 3, 26, and 27. The ground surface in all these territories was predominantly stony and there were always scattered boulders and broken rock outcrops and/or piles of boulders. The vegetation consisted chiefly of montane, usually tragacanthic, shrublets which usually grew widely-spaced with bare ground between them. In spring these communities were augmented by a flush of herbaceous vegetation, including particularly thistles, spurges and mints, which in patches completely obscured the ground. In a few territories there were scattered bushes and in two several stunted trees.

Habitat features which may be important in habitat selection:

The breeding territories of O. xanthoprymna that I studied in S. W. Iran had a number of features in common that were important in the lives of the birds and which may influence habitat selection. These will be briefly discussed below:

a) Boulders and rock outcrops: These features were used by the birds as song-posts and as vantage points from which to locate and launch attacks on arthropod prey on the ground. This feeding strategy which relies on the presence of elevated perches may be important in enabling O. xanthoprymna to feed on steep and stony areas where location of prey from ground level and its pursuit on foot are difficult.

Boulders and rock-outcrops also provide nest-sites and cover from adverse weather and predators which is probably especially important for the young. O.xanthoprymna nests in narrow fissures in rocks, in stone piles and

under boulders (Baker 1933, Dementiev and Gladkov 1968). The only nest found during this study was under a boulder on a steep scree.

b) Feeding areas: The feeding ecology of O. xanthoprymna on its breeding grounds was not studied in detail but casual observations suggested that, as in winter (fig. 39, p. 181) most prey was caught on patches of bare ground which are therefore probably an important ingredient of the habitat of the species.

In territories that included tracts of gently sloping ground such as valley bottom or piedmont (51 per cent of those studied) the birds seemed to favour these flatter areas for foraging and parents were frequently seen taking food from these areas to chicks on nearby hillsides. The remaining territories were high up on steep rocky hillsides and lacked large gently sloping areas but it is possible that they included local patches of flatter ground. Further research is required to determine whether gently sloping feeding areas are an essential component of the habitat of O. xanthoprymna or whether the birds can feed equally well on steep rocky ground.

O. xanthoprymna that occurred on the breeding grounds of the species in S. W. Iran outside the breeding season and which were probably members of the breeding population were found on the same or similar ground to that on which the species bred (fig. 27).

Breeding habitat outside S. W. Iran:

I can find little detailed information on the breeding habitat of O. xanthoprymna outside S. W. Iran. However in the following areas it appears to occupy similar steep rocky hillsides and valleys to those frequented in S. W. Iran: the southern slopes of the Elburz Mountains near Semnan in northern Iran (D. A. Scott pers. comm.); Kuh-i-Taftan in Persian Baluchistan (pers. obs.); Soviet Union (Dementiev and Gladkov 1968); Afghanistan (Paludan 1959); and northern Pakistan (Ali and Ripley 1973).

Habitat in winter in S. W. Iran:

One-hundred-and-thirty-four winter territories of O. xanthoprymna

were studied in S. W. Iran and a quantitative analysis of the characteristics of these is given in fig. 28. Fifteen per cent of these were confined to steep boulder-strewn hillsides; 46 per cent were at the bases of hillsides and included gently sloping or flat ground as well as areas of steep, rocky, boulder-strewn hillside; 31 per cent were on gently sloping hillsides or included a combination of flat and gently sloping ground which was usually stony, boulder-strewn and often broken by dry runnels; and eight per cent were on open, stoneless, boulder-free plains. The vegetation in these winter territories of O. xanthoprymna usually consisted of medium density steppe communities often with patches where plants were sparse. Occasionally there were also scattered bushes.

Comparison of the habitat distribution of O. xanthoprymna in winter with that in the breeding season (cf. figs. 26 and 28) shows: a) that only 15 per cent of winter territories compared with 49 per cent of breeding territories were confined to steep rocky hillsides; b) that 85 per cent of winter territories compared with 51 per cent of breeding territories included flat or gently sloping ground; and c) that 39 per cent of winter territories compared with only eight per cent of breeding territories were confined to flat or gently sloping ground. These differences may be a reflection of the following factors: 1) In winter arthropod prey is probably critically short on many steep rocky hillsides but more is probably available on gently sloping piedmonts, valley bottoms and on plains (pp.174-175); 2) Boulder-strewn rocky hillsides are probably only of crucial importance during the breeding season when song-posts, nest-sites and cover for the young from predators and adverse weather are needed.

Habitat in winter outside S. W. Iran:

The wintering habitat of O. xanthoprymna outside S. W. Iran appears to be similar to that occupied in S. W. Iran. Thus in Pakistan and N. W. India it "...affects semi-desert, flat, stony and sandy land with sparse Capparis and other xerophytic bushes, and sand dunes on the edge of desert; has a marked preference for the foot of rocky hillsides" (Ali and Ripley 1973). In northern Eritrea it winters in rocky hills with light acacia cover (Smith 1971).

HABITAT - SUMMARIES

SUMMARIES OF HABITAT FEATURES WHICH MAY BE IMPORTANT IN HABITAT SELECTION:

Features which may be important in the selection of breeding and wintering habitats by wheatears in S. W. Iran are summarised in tables 19 and 20 respectively. In addition visual impressions of the typical habitats of the various species are given in figs. 22-24, pp. 99-101.

WHEATEAR SPECIES	HABITAT FEATURES														
	Steep, rocky hillside and/or cliff	Pile of boulders or rock outcrop in flat or gently sloping ground	Flat or gently sloping ground		Bare feeding ground		Elevated perches		Shade		Background		Nest-sites/Roosting places		
			Large areas	Small patches	Large areas	Small patches	Stones and/or boulders	Vegetation	General	Local	Variegated light and shade	Uniform dun	Rock crevices, holes under boulders, etc.	Rodent holes	Bushes, shrublets, tussocks, etc.
O. alboniger	+		+	+	+	+	+		+ in hot areas	+	+		+		
O. deserti			+		+			+		+		+		+	+
O. finschii	+	+	+		+	+	+			+	+		+		
O. hispanica	+	(+)	(+)	(+)	+	+	+	+		+	+		+		(+)
O. isabellina			+		+		+ a few	+ a few		+		+	(+)	+	
O. lugens	+	(+)	(+)	(+)	+	+	+			+	+		+		
O. oenanthe	(+)	+	+	+	+	+	+			+	+		+	(+)	(+)
O. xanthoprymna	+	(+)	+	+	+	+	+			+	+		+		

Table 19. Summary of habitat features which may be important in the selection of breeding habitats by wheatears in S. W. Iran. (O. monacha and O. picata have been omitted for lack of data).

+ = probably always or often important (+) = may be sometimes important

WHEATEAR SPECIES	HABITAT FEATURES														
	Steep, rocky hillside and/or cliff	Pile of boulders or rock outcrop in flat or gently sloping ground	Flat or gently sloping ground		Bare feeding ground		Elevated perches		Shade		Background		Roosting places		
			Large areas	Small patches	Large areas	Small patches	Stones and/or boulders	Vegetation	General	Local	Variegated light and shade	Uniform dun	Rock crevices, holes under boulders, etc.	Rodent holes	Bushes, shrublets, tussocks, etc.
O. alboniger	+		+	+	+	+	+	(+)		+	+		+	(+)	
O. deserti			+		+			+		+		+		+	+
O. finschii			+		+	+				+	(+)		+	+	(+)
O. isabellina			+		+					+		+		+	(+)
O. xanthoprymna	(+)	+	+	+	+	+	+			+	(+)		+	+	(+)

Table 20. Summary of habitat features which may be important in the selection of wintering habitats by wheatears in S. W. Iran. (O. monacha and O. picata have been omitted for lack of data).

+ = probably always or often important (+) = may be sometimes important

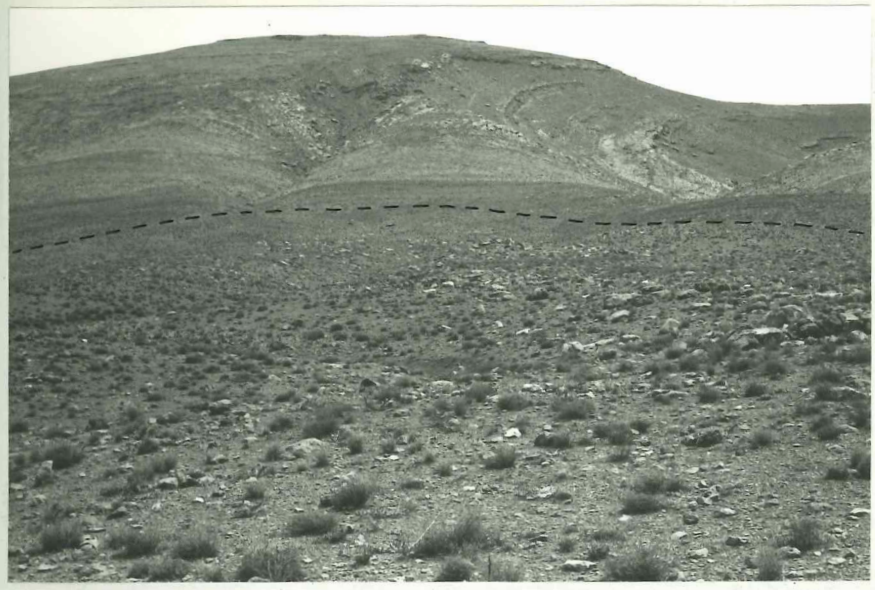

Plate 17. Gently sloping steppe (area below broken line) near the Bardeh study area where O. finschii both bred and wintered. (c. 1,750 m, sub-steppe zone; April 1971).



Plate 18. Breeding territory (area below broken line) of O. finschii in the Tang-i-Shul study area. (c. 2,250 m, xerophilous forest zone; June 1971).



Plate 19. Part of the Maharlu North study area where O. isabellina bred and O. finschii wintered on the flatter ground (see fig. 59, p. 291) (c. 1,450 m, sub-steppe zone; March 1971).



Plate 20. Breeding habitat of O. hispanica in the Yasuch study area in May 1967. Note the dense herbaceous ground layer and numerous elevated perches. (c. 2,100 m, xerophilous forest zone).

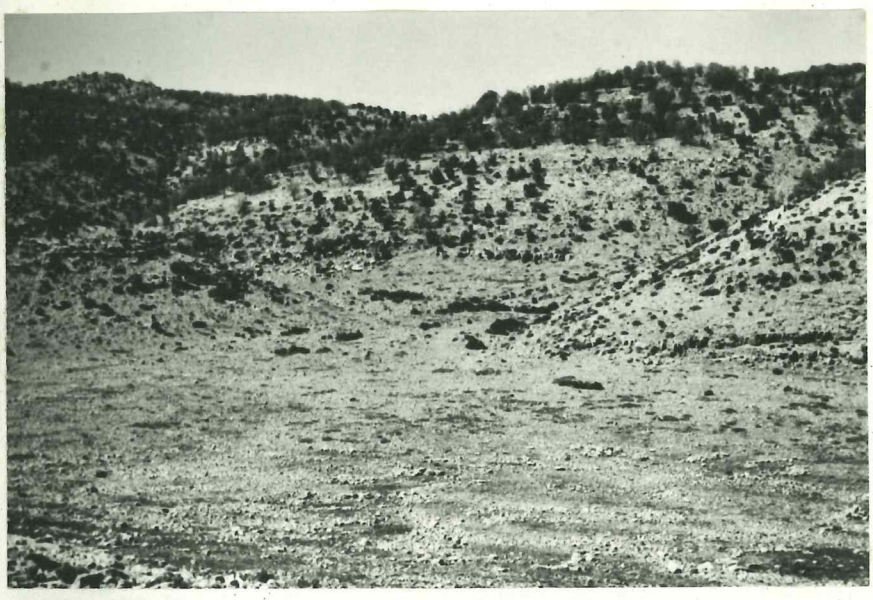

Plate 21. Breeding habitat of O. hispanica in the Dasht-i-Arjan study area in May 1972. Note the rocky boulder-strewn terrain. (c. 2,000 m, xerophilous forest zone).



Plate 22. Breeding habitat of O. hispanica in a deforested area near Kakun in the Zagros. (c. 2,600 m, xerophilous forest zone; June 1971).

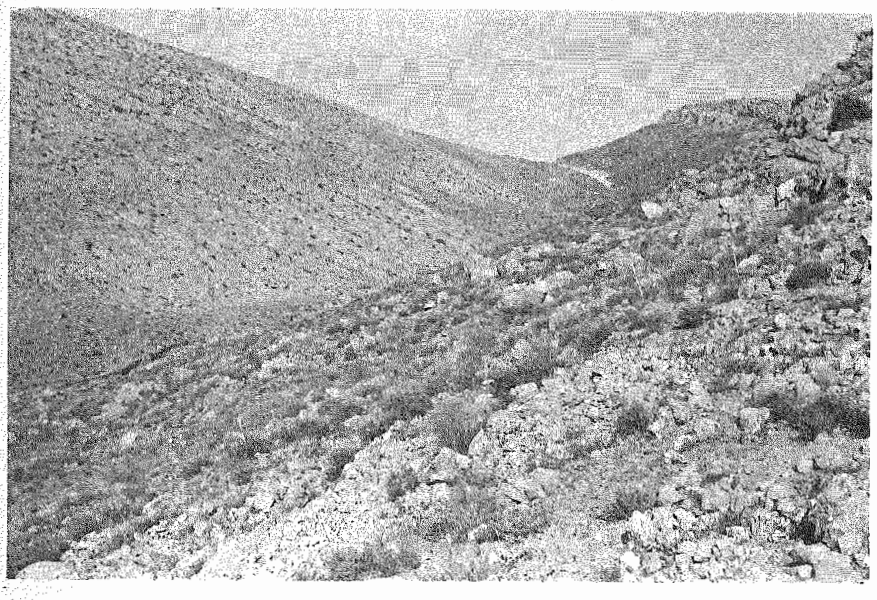

Plate 23. Breeding habitat of O. lugens in the Maharlu Valley study area near Shiraz. (c. 1,500 m, sub-steppe zone; April 1968).

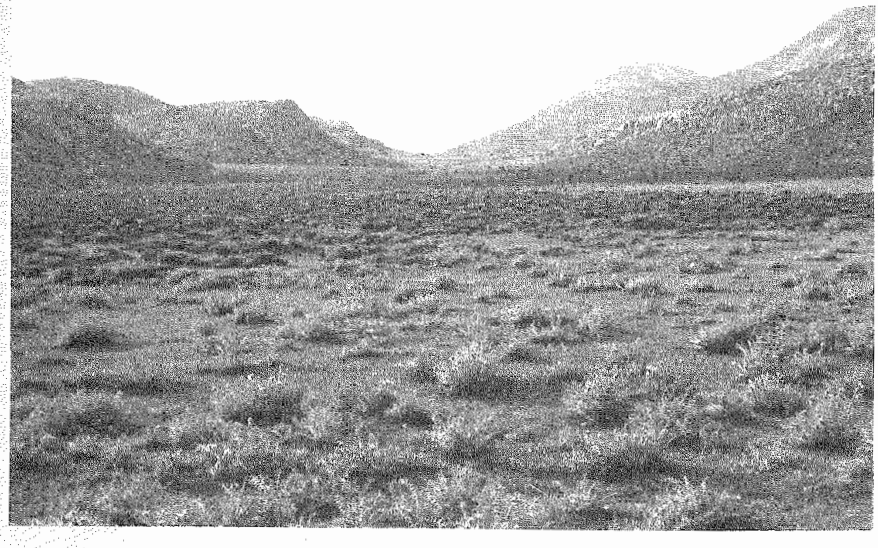

Plate 24. Breeding habitat of O. oenanthe on Kuh-i-Barm-i-Firuz in the high Zagros. (c. 3,100 m, montane zone; June 1971). All of six territories found in this area included the base of a rocky hillside and an adjacent tract of plain.

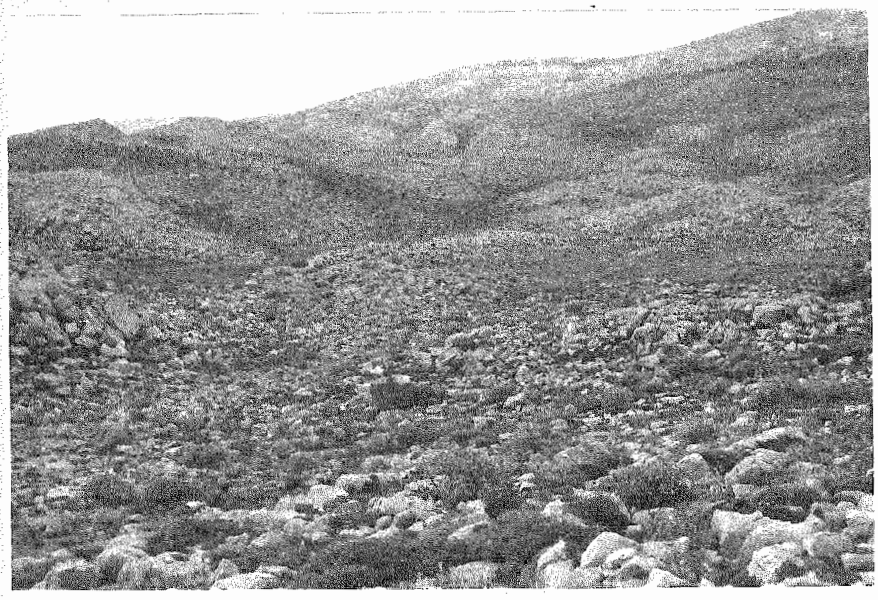

Plate 25. Breeding habitat of O. oenanthe on Kuh-i-Barm-i-Firuz in the high Zagros. (c. 3,000 m, montane zone; June 1971).

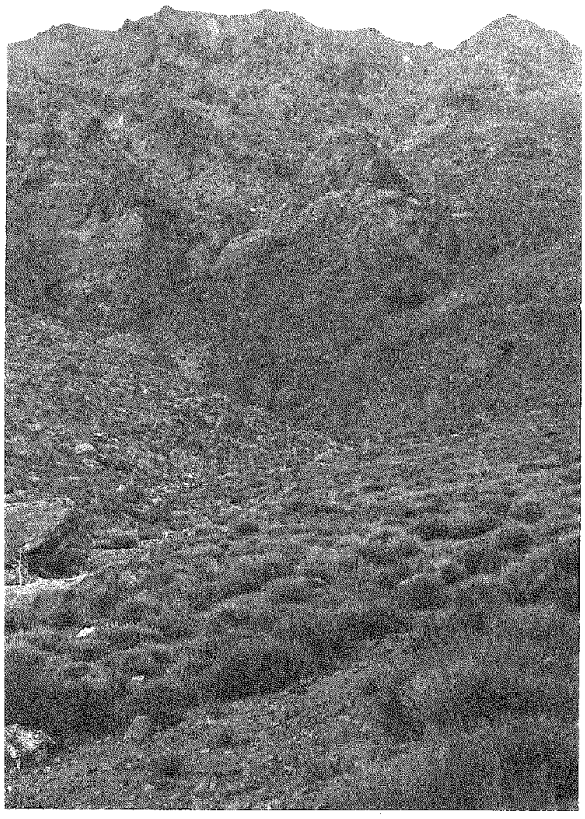

Plate 26. Breeding habitat of O. xanthoprymna on Kuh-i-Lalehzar. (c. 2,700 - 3,300 m, montane zone; June 1971).

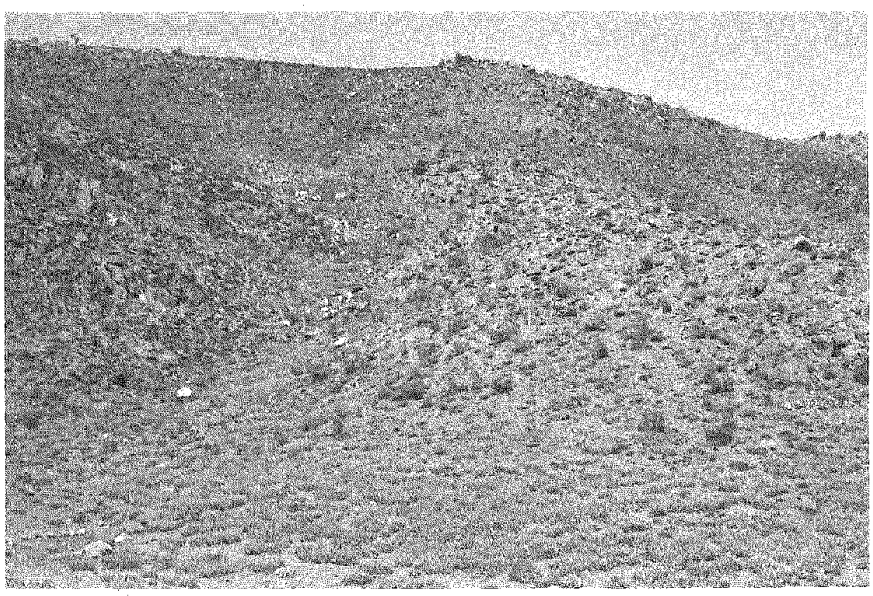

Plate 27. Breeding habitat of O. xanthoprymna near Kakun in the Zagros. (c. 2,700 - 2,800 m, montane zone; June 1971).

CHAPTER VI

FEEDING ECOLOGY

INTRODUCTION:

The feeding ecology of wheatears in S. W. Iran was studied in some detail and with particular emphasis on interspecific comparisons. This was done for three main reasons: 1) For its intrinsic interest since little has been published especially on the comparative aspects of the subject; 2) because a knowledge of the feeding ecology of wheatears was considered fundamental to understanding many aspects of their biology, including the timing of events in their annual cycles, interspecific relationships, habitat selection, distribution and morphology; and 3) the studies could be carried out with particular advantage since wheatears live in open habitats where they can be easily watched while foraging and feed in places where food supply can be relatively easily monitored.

The chapter is divided into three parts: Food supply, foraging and diet.

PART I. FOOD SUPPLY:

Wheatears eat mainly arthropods, particularly worker ants (Formicidae) and beetles (Coleoptera) (tables 22-32, fig. 43). The majority of these are caught on bare ground but some, particularly caterpillars during the breeding season, are picked off low-growing vegetation and a few are dug out of the ground, prized from under stones or caught in the air flycatcher-fashion (fig. 39 and casual observations). To document the supply of arthropod prey that was available to wheatears an attempt was made to measure diurnal, seasonal, regional and inter-habitat variations in the abundance, size distribution and taxonomic composition of arthropods in places where wheatears were known to do most of their feeding, namely on bare ground and on

vegetation that could be reached by birds standing on bare ground. To these ends three methods were employed: pitfall trapping and 100 m transects on bare ground, and sweep-net sampling from vegetation (see pp. 46-47 for procedures). In all samples arthropods of less than two mm in length were disregarded since such small animals, if they are taken at all by wheatears, probably account for only an insignificant proportion of their diets (see p. 204 for discussion of this point). The results of the studies of wheatear food supply are presented below:

1) DIURNAL VARIATIONS IN FOOD SUPPLY:

Diurnal variation in the abundance of arthropods that were available on bare ground to wheatears was investigated a) as background for the study of foraging patterns of wheatears and b) to give a measure of seasonal changes in the number of daylight hours that arthropods were available at different densities (fig. 35). Observations, using the 100 m transect method, were made widely in the sub-steppe zone on plains, piedmonts, steep stony hillsides and in valley bottoms all with heavily grazed steppe vegetation. The 100 m transect method is well suited for sampling arthropods on bare ground and the results which are presented in figs. 30-32 probably give a fair indication of numbers that were present on the ground that was covered. However as a basis for making generalisations about diurnal patterns of arthropod availability, these results must be treated with caution as the sample sizes in the various time periods are small and because, largely owing to the nature of the data, no statistically significant differences in arthropod abundance at different time of day could be demonstrated.* Nevertheless the

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*The difficulties in the statistical treatment of these data may be summarised as follows: 1) Many of the samples include a high proportion of zeros and therefore the data are not normally distributed. Hence a non-parametric method for comparing the samples had to be employed. 2) Since comparisons were suggested by inspection of the data an *a posteriori* test had to be used and as sample sizes differed the only appropriate one that I could find was Dunn's multiple comparison test (Hollander and Wolfe 1973) which is very conservative when large numbers of possible comparisons are involved.

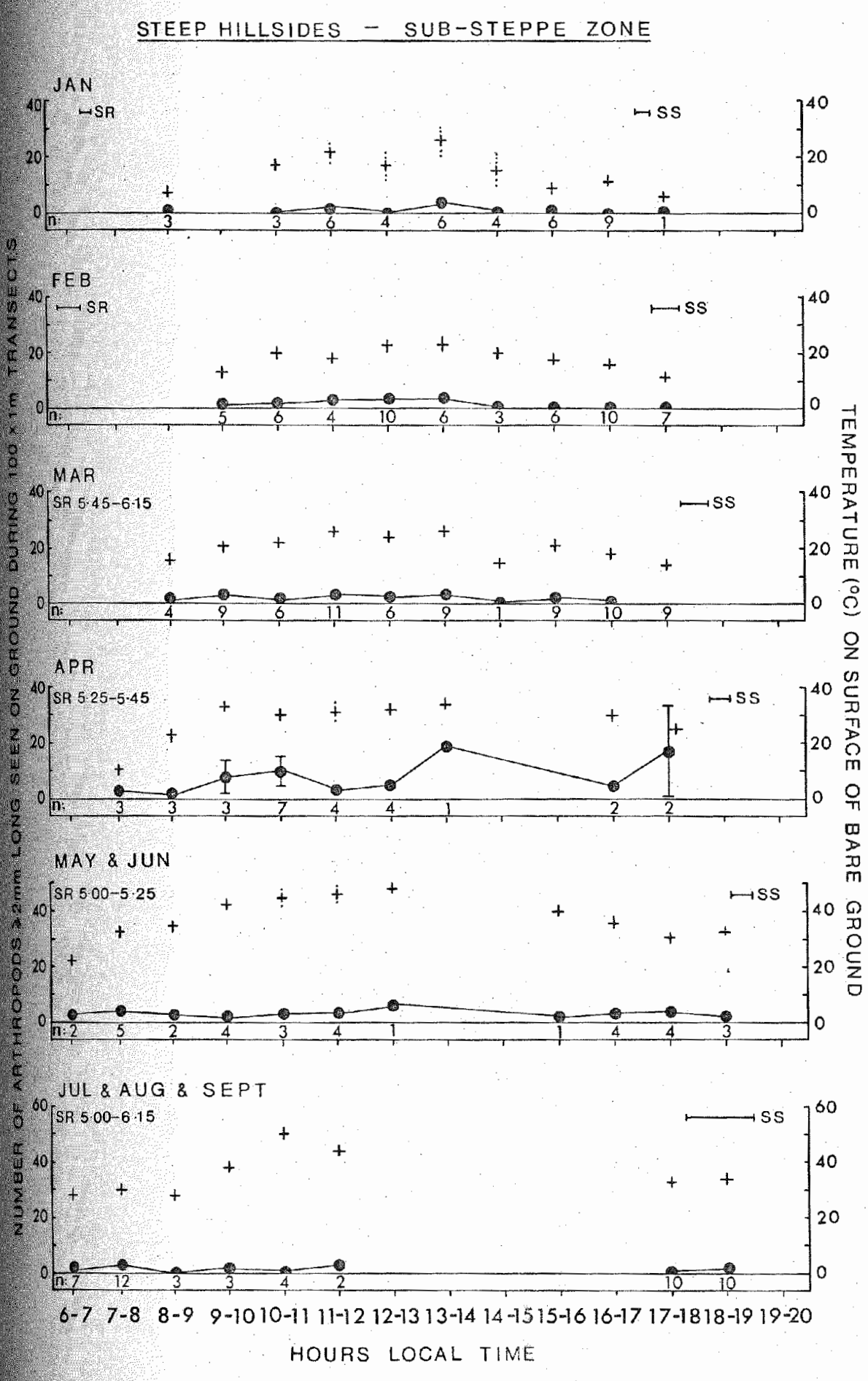

Fig. 30. Numbers of arthropods ≥2mm long seen on the ground during 100 x 1m transects at various times of day during different months on steep stony hillsides with heavily grazed steppe vegetation in the sub-steppe zone of S. W. Iran.

KEY

The data are presented as means ± one standard error where this is greater than two.
● arthropods, + temperature °C, n number of transects, SR sunrise, SS sunset.

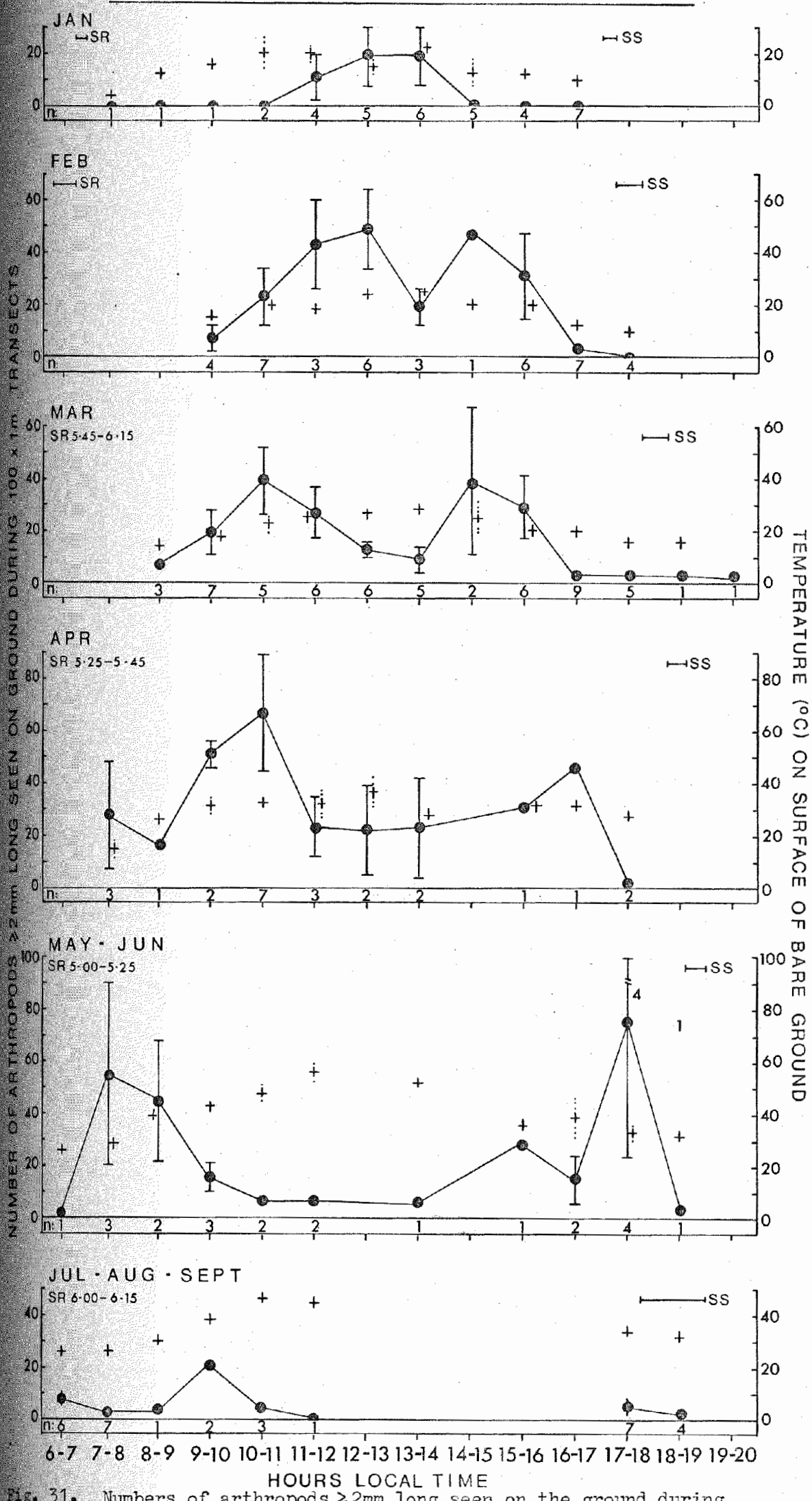

Fig. 31. Numbers of arthropods ≥2mm long seen on the ground during 100 x 1m transects at various times of day during different months on piedmonts and in valley bottoms with heavily grazed steppe vegetation in the sub-steppe zone of S. W. Iran.

KEY

The data are presented as means ± one standard error where this is greater than two.

• arthropods, + temperature °C, n number of transects, SR sunrise, SS sunset.

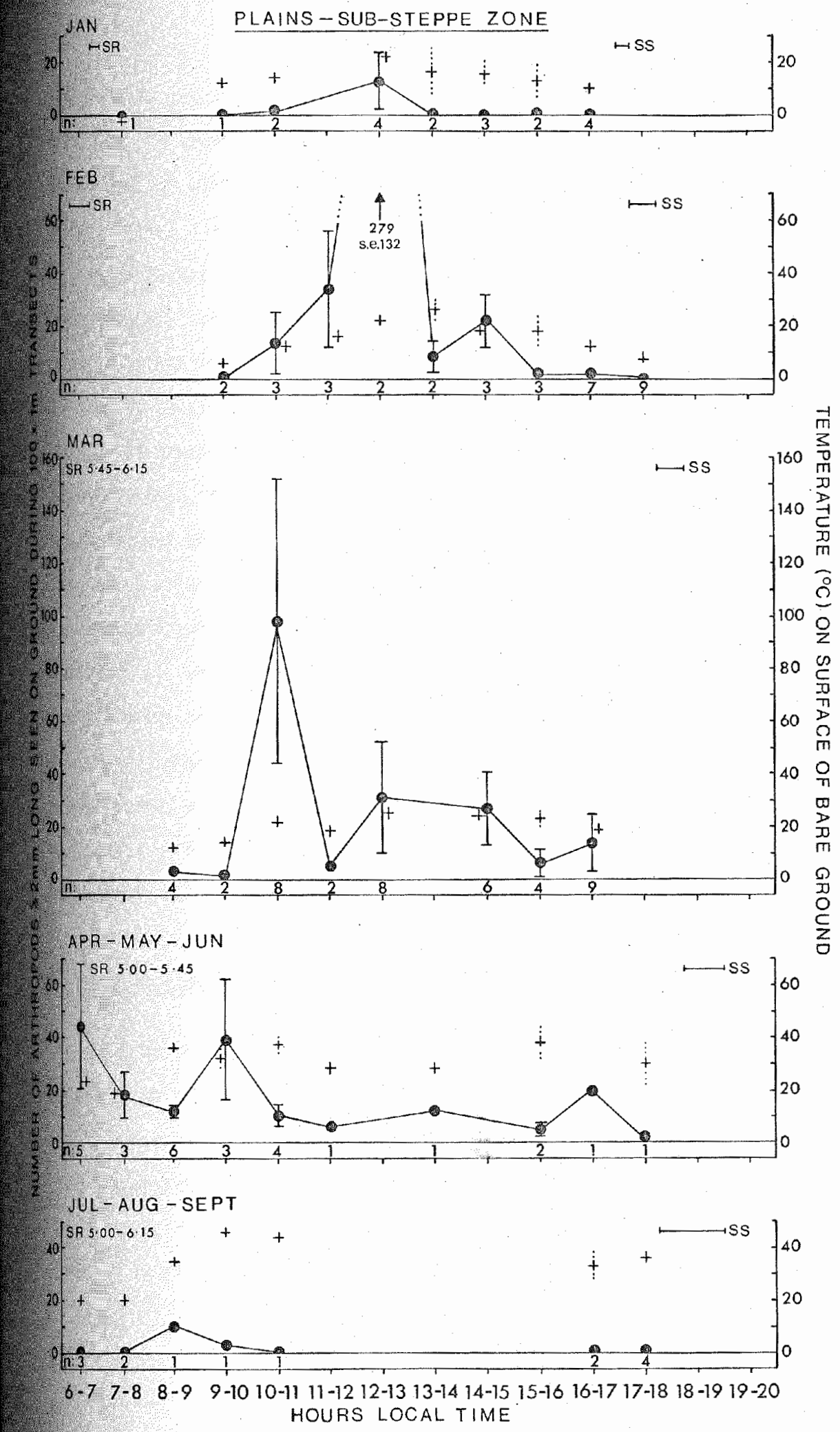

Figure 32. Numbers of arthropods ≥2mm long seen on the ground during 100 x 1m transects at various times of day during different months on plains with heavily grazed steppe vegetation in the sub-steppe zone of S. W. Iran.

KEY

The data are presented as means ± one standard error where this is greater than two.

• arthropods; + temperature °C; n number of transects; SR sunrise; SS sunset.

observations suggest that on the piedmonts and in the valley bottoms (fig. 31) and probably also on the plains (fig. 32) arthropod activity is unimodal in winter occurring mainly in the middle of the day while in the spring, summer and autumn the pattern of activity is bimodal with peaks in the morning and afternoon separated by a lull during the midday period. The validity of these indications is supported by three sorts of evidence: 1) The results from the piedmonts and valley bottoms are largely similar to those from the plains and are therefore corroborative. 2) Similar activity patterns have been reported from other arid areas (e.g. Bodenheimer 1935, Cloudesley-Thompson and Chadwick 1964, Holm and Edney 1973). 3) The results are consistent with what is known about arthropod behaviour in relation to temperature and humidity namely that roughly speaking arthropods tend to be inactive when environmental temperatures are below about 10°C or above about 40°C and to avoid conditions of low humidity (Allee et al. 1949, Cloudsley-Thompson 1961, Edney 1974). Therefore the unimodal winter activity patterns may be interpreted as avoidance of low morning and evening temperatures and the bimodal patterns seen at other times of year as avoidance of high temperatures and low humidities during the midday periods.*

2) SEASONAL VARIATIONS IN FOOD SUPPLY:

Four methods were employed to study seasonal variations in the supply of arthropods that was available to wheatears and the results are considered below:

A) Sweep-net sampling from vegetation:

The results of sweep-net sampling from low-growing vegetation are given in fig. 33. The samples were collected in the middle of the day between 13.00 and 15.00 hours and therefore took no account of possible diurnal activity patterns of arthropods or seasonal changes

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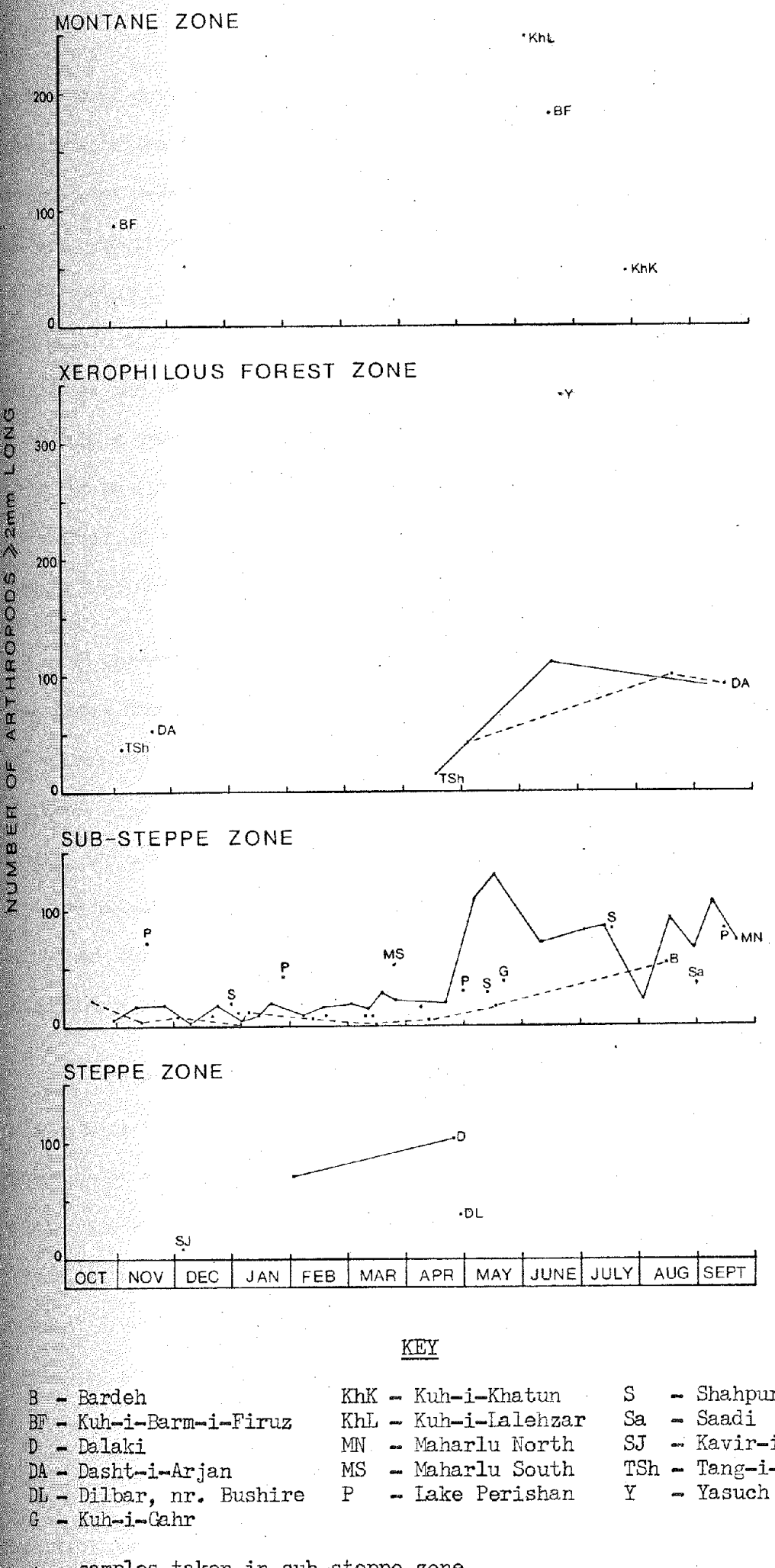
*Relative humidity at five cm above the ground in the shade was measured continuously using a thermohygrograph on 21 days in the period June-September and in every case the relative humidity fell below 10% during the midday period.

Temperatures on the surface of the ground that were recorded during the transects are given in figs. 30-32.



KEY

B - Bardeh	KhK - Kuh-i-Khatun	S - Shahpurjan
BF - Kuh-i-Barm-i-Firuz	KhL - Kuh-i-Lalehzar	Sa - Saadi
D - Dalaki	MN - Maharlu North	SJ - Kavir-i-Sirjan
DA - Dasht-i-Arjan	MS - Maharlu South	TSh - Tang-i-Shul
DL - Dilbar, nr. Bushire	P - Lake Perishan	Y - Yasuch
G - Kuh-i-Gahr		

· - samples taken in sub-steppe zone.

Figure 33. Numbers of arthropods ⩾2mm long in sweep-net samples taken from 100 shrublets growing on piedmonts or valley bottoms at various localities in S. W. Iran. (For method of sampling see text p.46. For localities see figure 7, p. 42.)

in such patterns. However I doubt whether the results will have been greatly affected by these factors since most of the arthropods in the samples were relatively sedentary leaf-dwelling forms such as caterpillars, Homoptera, Hemiptera and Araneida which probably do not have diurnal activity patterns that involve leaving the plants. They may move within the plants but this would not have greatly influenced the results as the sampling technique involved beating the whole of each plant into a sweep-net which was placed below it. The sweep-net samples therefore probably give a fair indication of seasonal fluctuations in the numbers of arthropods that were available to wheatears on low-growing vegetation.

Observations were reasonably comprehensive only in the sub-steppe zone where the results indicate a lean period during the winter and an upsurge in arthropod abundance during the spring with numbers remaining high until the autumn.* One of the reasons that arthropod numbers are maintained through the heat and drought of the summer and into the autumn is probably that several species of plant remain green throughout the period. These include Alhagi persarum, Glycyrrhiza glandulifera and several members of the family Chenopodiaceae.

Outside the sub-steppe zone too few observations were made to give more than rough indications of seasonal fluctuations in the abundance of arthropods on low-growing vegetation. Nevertheless the results are consistent with those from the sub-steppe zone and it seems likely, with the probable exception of the warm steppe zone, that seasonal fluctuations in the numbers of arthropods on low-growing vegetation are of a broadly similar pattern in all zones.

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*Statistical treatment of the sweep-net sample data from Maharlu North that were presented in fig. 33:

a) A Kruskall-Wallis one way analysis of variance showed that there was significant variation in the number of arthropods caught during the different seasons: winter (Nov-Feb), spring (Mar-Jun) and summer plus autumn (Jul-Oct) - $p < 0.01$.

b) Dunn's multiple comparison tests gave the following probabilities that arthropods were equally abundant during the different seasons:

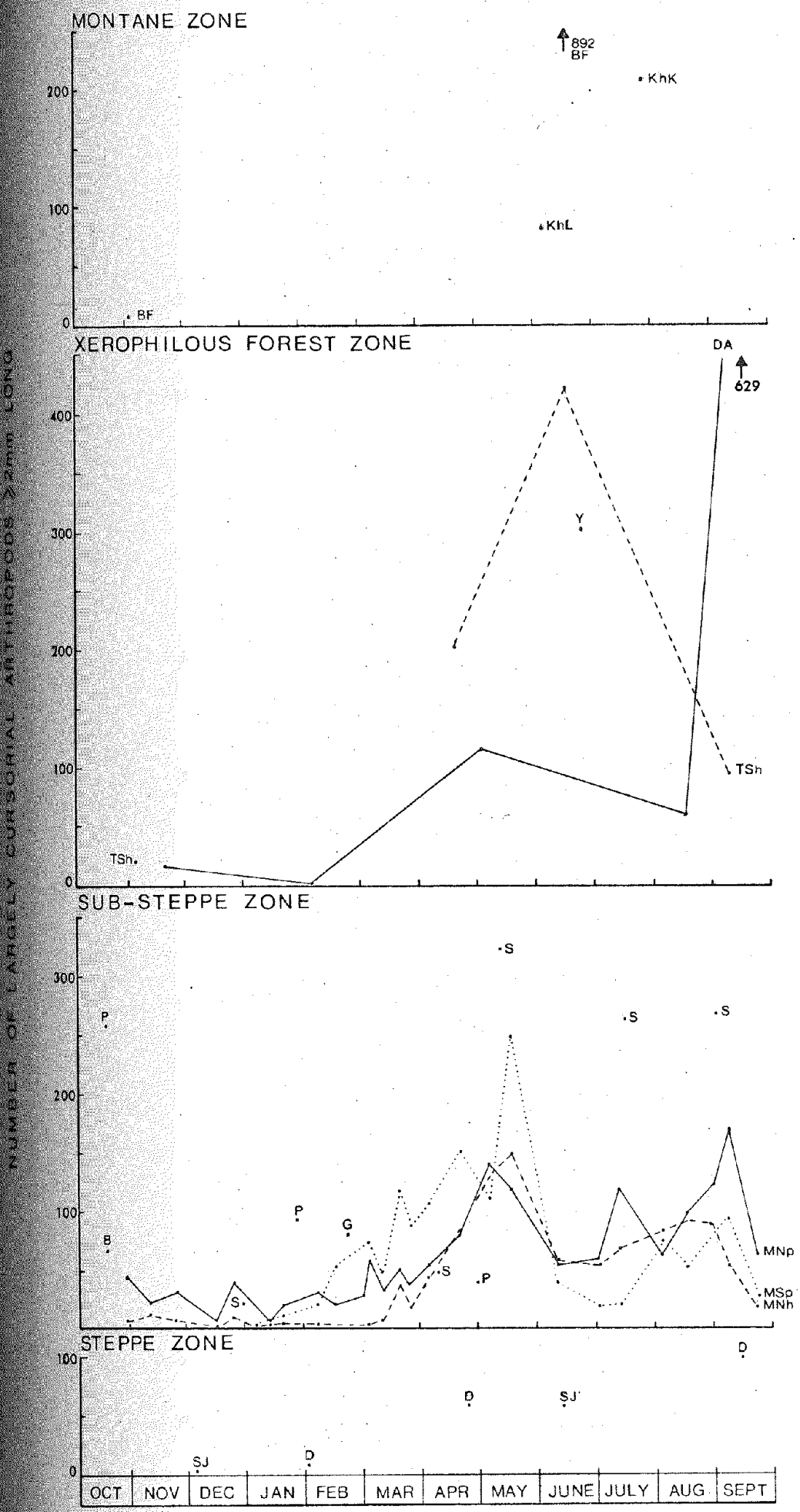
winter v. spring	$p < 0.05$
winter v. summer + autumn	$p < 0.01$
spring v. summer + autumn	$p > 0.90$

B) Pitfall sampling from bare ground:

The numbers of largely cursorial arthropods of two or more mm in length that were caught in pitfall traps at various localities and at various times of year in S. W. Iran are given in fig. 34. Many primarily flying insects, particularly Diptera (mostly Muscidae) and some Lepidoptera, which were probably attracted by the water in the traps were also caught but were eliminated from the samples since they are rarely taken by wheatears.

Pitfall trapping as a method for estimating variations in the supply of arthropod food available to wheatears has a number of advantages and disadvantages. These are discussed in appendix C where the following conclusions were reached: The method fails to adequately sample Araneida and Orthoptera but probably gives a good indication of variations in the abundance of ants, beetles and other running arthropods. Therefore since the latter form the bulk of the diets of most wheatear species the pitfall samples probably give a fair indication of the total amount of food that was available for wheatears in the various sampling localities on the different days. However the results give no information on the length of time that these arthropods were available to be caught by birds. This may be a serious drawback in mid-summer when diurnal activity of arthropods is probably strongly concentrated at dawn and dusk, but during the rest of the year comparison of figs. 34 and 35 suggests that there is a fairly close correlation between the total numbers of arthropods caught in the pitfalls and the number of daylight hours that arthropods were available at various densities.

Taking into account the drawbacks of the method I believe that the following conclusions may be drawn from the results of the pitfall sampling: In the sub-steppe zone, which is the only bioclimatic zone where sampling was reasonably comprehensive, there is a lean period during the winter (Nov-Feb) followed by a sharp increase in the number of arthropods at risk on bare ground during the period March to



KEY

B - Bardeh	KhK - Kuh-i-Khatun	P - Lake Perishan
BF - Kuh-i-Barm-i-Firuz	KhL - Kuh-i-Lalehzar	SJ - Kavir-i-Sirjan
D - Dalaki	MNh - Maharlu North-hillside	S - Shahpurjan
DA - Dasht-i-Arjan	MNp - Maharlu North-piedmont	TSh - Tang-i-Shul
G - Gumoon	MSp - Maharlu South-piedmont	Y - Yasuch

Figure 34. Numbers of largely cursorial arthropods ⩾2mm long caught between dawn and dusk in ten pitfall traps (pooled samples) in various localities in S.W. Iran. In each locality the traps were the same and set in exactly the same places each time. Unless otherwise stated the habitat was piedmont or valley bottom.

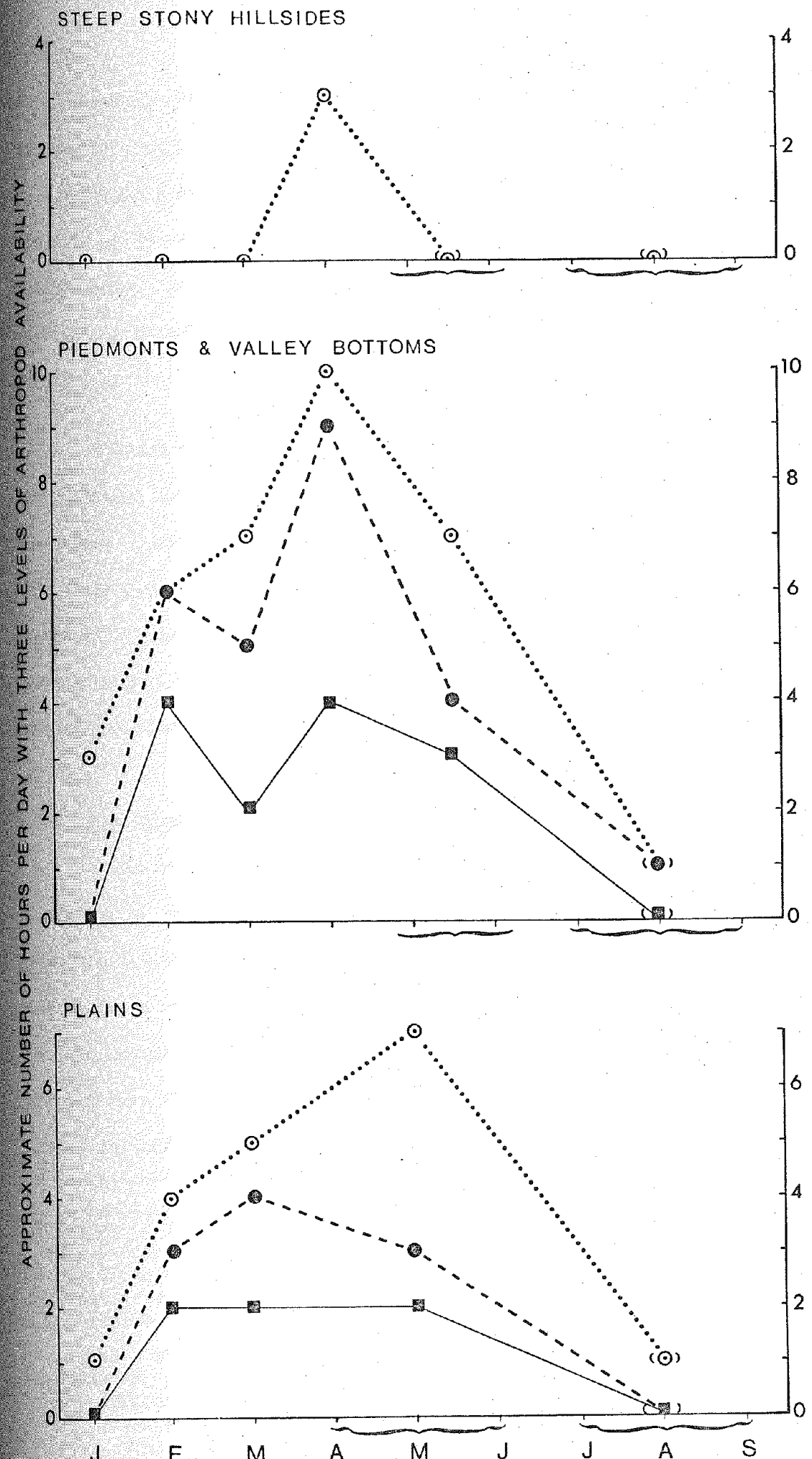


Figure 35. Seasonal variation in the number of hours per day that arthropods ≥2mm long were available on the surface of the ground at three densities in three habitats with heavily grazed steppe vegetation in the sub-steppe zone of S.W.Iran. The data are taken from figs. 30-32.

KEY

⊙·····⊙ Mean number of arthropods seen per 100 x 1m transect ≥10.
●---● Mean number of arthropods seen per 100 x 1m transect ≥20.
■——■ Mean number of arthropods seen per 100 x 1m transect ≥30.
( ) Data incomplete.

May coinciding with the spring flush of vegetation.* There is then apparently a fall in arthropod abundance during June and July followed by a resurgence during August and early September before numbers again diminish at the end of September.** Most of the arthropods that are active during the hot dry season are probably sustained by dried plant material, particularly seeds, and/or plants that are green during the period.

There are too few results from outside the sub-steppe zone to give detailed indications of seasonal fluctuations in arthropod abundance. However roughly speaking such results as there are agree with those from the sub-steppe zone and it seems likely, with the probable exception of the warm steppe zone, that seasonal fluctuations in the numbers of arthropods that are available to wheatears on bare ground have similar patterns in all zones.

C) Hundred-metre transects on bare ground:

The results of the pitfall sampling probably give a fair indication of variations in the total numbers of running arthropods that were available to wheatears in given localities on given days. However, for a bird, not only is the total abundance of prey important but also the length of time that it is available to be caught. Therefore the transect data that were presented in figs. 30-32 were further analysed to give an indication of seasonal variations in the number of hours per

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*Statistical treatment of the pitfall data from the sub-steppe zone which were presented in fig. 34 (data from all localities lumped).

a) A Kruskall-Wallis one way analysis of variance showed that there was significant variation in the number of arthropods caught during the different seasons; winter (Nov-Feb), spring (Mar-Jun) and summer plus autumn (Jul-Oct) - $p < 0.001$.

b) Dunn's multiple comparison tests (Hollander and Wolfe 1973) gave the following probabilities that arthropods were equally abundant during different seasons:

winter v. spring	$p < 0.001$
winter v. summer + autumn	$p < 0.001$
spring v. summer + autumn	$p > 0.90$

N.B. Similar results were obtained when the data from the Maharlu North piedmont, the Maharlu North hillside and the Maharlu South piedmont were analysed separately using the same methods.

**None of the fluctuations mentioned in this sentence could be shown to be statistically significant largely because of the nature of the data (see footnote p. 160). Nevertheless the fact that similar fluctuations were recorded in three different sites at Maharlu North and Maharlu South is strong evidence for the validity of these fluctuations.

day that arthropods were available on the surface of the ground at three different densities in three habitats in the sub-steppe zone. The results are given in fig. 35. These agree with the pitfall data in indicating poor feeding conditions for wheatears during the winter and a rapid improvement during the spring but differ from the pitfall results in suggesting poorer feeding conditions during the summer and autumn. However the latter indication is based on incomplete data and requires further study.

D) Inference from temperature:

Direct sampling of the arthropod food of wheatears was reasonably comprehensive only in the sub-steppe zone and even in this zone the observations on diurnal patterns of arthropod activity were incomplete (figs. 30-32). Therefore to augment these data an indirect method was employed. This is described fully in appendix D but the main steps in the reasoning behind it are outlined below:

1) Roughly speaking arthropod activity is restricted when environmental temperatures are below about 10°C or above about 40°C and most activity takes place when temperatures are between these values (Allee et al. 1949, Edney 1974, appendix D fig. 1).

2) In appendix D a method is given whereby the number of daylight hours that temperatures in the open on the surface of bare ground are likely to be between 10°C and 40°C on a given date can be roughly estimated for any locality of known altitude in S. W. Iran.

3) Since most arthropod activity takes place when environmental temperatures are within this range these estimates are used to give rough indications of seasonal and regional variations in the amount of time per day that good feeding conditions for wheatears may occur.

Estimates of seasonal fluctuations in the number of daylight hours that temperatures in the open on the surface of bare ground are likely to be between 10°C and 40°C at 100 m, 1,500 m, 2,000 m, and 2,800 m above sea level in S. W. Iran are given in fig. 36. While realising that these estimates are only rough, I believe that the broad

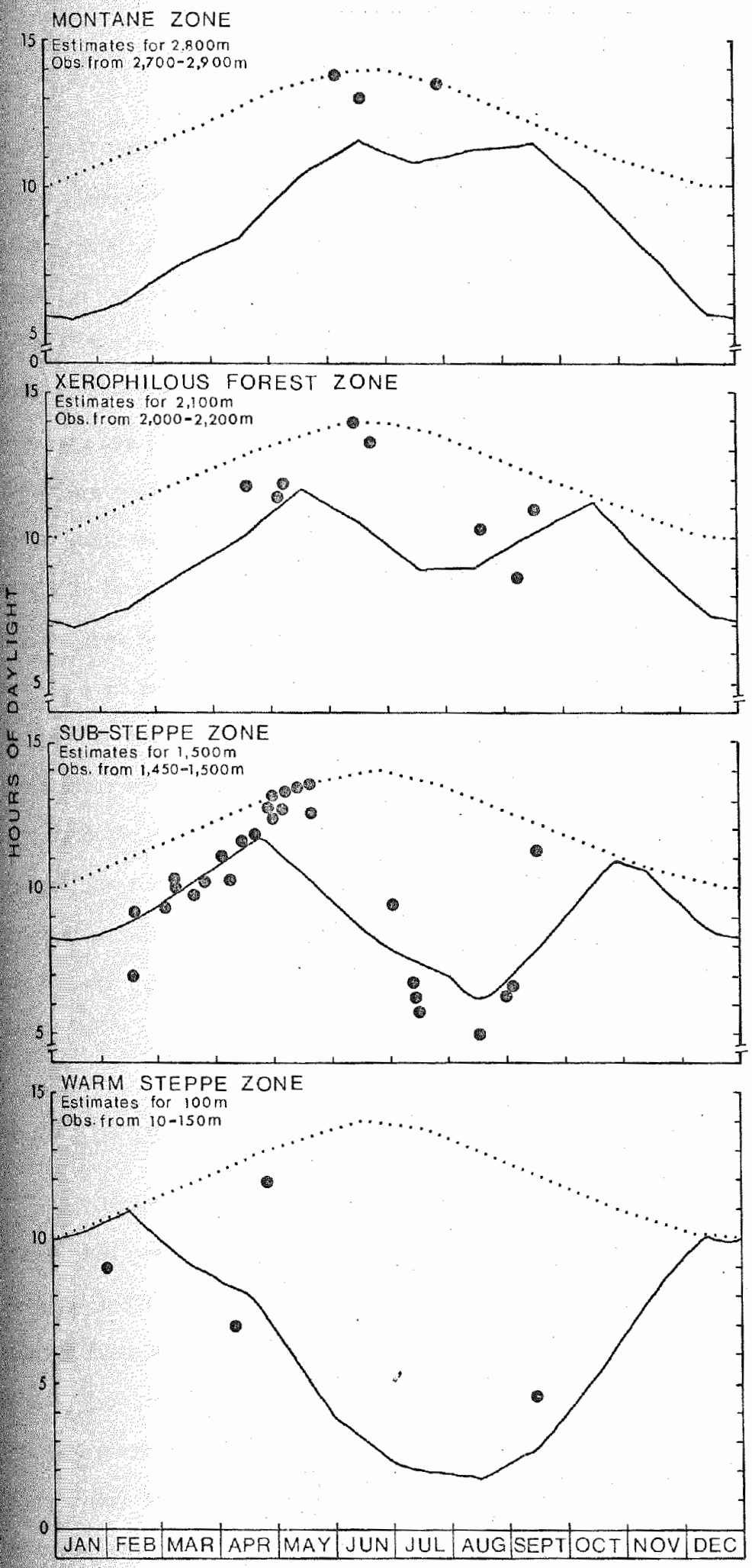

Figure 36. Seasonal changes in the number of daylight hours with ground surface temperatures in the open between 10°C and 40°C (i.e. temperatures between which arthropod availability is likely to be highest - see appendix D fig. 1) at various altitudes in S. W. Iran.

KEY

~~~ Estimated number of hours (from appendix D).

● Observed number of hours.

····· Day length.
~~~

patterns of seasonal and regional variation are valid and this belief is largely supported by the observed values that are included in the figure. However when these estimates are used to indicate feeding conditions for wheatears they must be treated with care. They do not indicate the lengths of time that arthropods will be active on bare ground in the open, but only the lengths of time that temperature conditions are likely to be favourable for such activity. Thus although temperature conditions are suitable for arthropod activity on the coastal plain of the Persian Gulf in winter this does not necessarily imply that large numbers of arthropods will be active since they may be restricted by some other factor such as drought. However the estimates probably give reliable indications of periods when few arthropods are likely to be active on bare ground in the open (i.e. when ground surface temperatures are below about 10°C or above about 40°C). Thus there are unlikely to be good feeding conditions for wheatears on bare ground in the open for more than about two hours per day on the coastal plain of the Persian Gulf during July and August or for more than about five-and-a-half hours per day during December and January at 2,800 m above sea level.

3) REGIONAL VARIATIONS IN FOOD SUPPLY:

Direct measurement of regional differences in the supply of arthropod prey that was available to wheatears was attempted using sweep-net sampling from low-growing vegetation (fig. 33) and pitfall sampling from bare ground (fig. 34). Although there are too few data to give more than tentative indications, the results nevertheless suggest that during the spring, summer and autumn more arthropods are available in the wetter bioclimatic zones than in the drier ones. Indeed during the spring (Mar-Jun) the pitfall catches in the xerophilous forest zone were significantly larger than those in the sub-steppe zone ($P = 0.007$ using a two-tailed Mann-Whitney U test).

FOOD SUPPLY

Further information about regional variations in the arthropod food supply of wheatears can be inferred from the regional differences in temperature regime that were discussed in the last section. Thus the data presented in fig. 36 indicate that the number of hours per day that temperatures in the open on bare ground are favourable for arthropod activity (i.e. approx. 10-40°C) decreases with increase in altitude during the winter while in summer the trend is reversed. As emphasised in the previous section these results must be treated with care if they are used to indicate feeding conditions for wheatears. Adverse environmental temperatures probably indicate reliably that feeding conditions for wheatears will be poor but the converse is not true since favourable environmental temperatures do not necessarily imply that feeding conditions for wheatears will be good.

4) INTER-HABITAT DIFFERENCES IN FOOD SUPPLY:

As background for the study of the feeding behaviour and habitat selection of wheatears an attempt was made to compare the availability of arthropod prey on bare ground in the three broad habitat types where wheatears mainly feed, namely plains, steep stony hillsides and piedmonts plus valley bottoms. For this purpose two methods were used: 100 m transects and pitfall trapping. The 100 m transects were carried out widely in the sub-steppe zone and the pooled results are presented in fig. 35. These suggest that on average more arthropods were available for wheatears on piedmonts and in valley bottoms than on plains and more on plains than on steep stony hillsides which is largely what one would expect from the distribution of vegetation which is generally more dense on piedmonts and in valley bottoms where run-off water and silt accumulate than on adjacent hillsides or plains. However these results represent only average conditions and there are undoubtedly many local variations associated with such factors as local differences in soil and aspect. This is borne out by the results of the pitfall sampling at Maharlu North and South (fig. 34) where more arthropods were caught on the piedmonts than on the hillside at most times of

year but during the summer fewer were caught on the south-facing gypsum piedmont, which got extremely hot and dry, than on the north-facing hillside which enjoyed more shade and where angles of insolation were more oblique.

5) SIZE DISTRIBUTION AND TAXONOMIC COMPOSITION OF ARTHROPOD FOOD SUPPLY:

The size distribution and taxonomic composition of largely cursorial arthropods of two or more mm in length that were caught in pitfall traps in S. W. Iran are given in fig. 37 and the taxonomic composition of those seen during the 100 m transects is given in fig. 38. Both series of data show the importance of worker ants and beetles and the transect data indicate that Orthoptera and Araneida are also sometimes common.

SUMMARY OF INFORMATION ON FOOD SUPPLY:

The studies of the food supply of wheatears in S. W. Iran indicate that it has the following important features:-

1) In cold weather arthropods are active mainly during the middle of the day while in hot periods they tend to be active in the early morning and late afternoon.

2) Peak food supply coincides with the spring flush of vegetation which begins when mean daily temperatures reach about 10°C and reaches its height when mean daily temperatures reach about 20°C.

3) Lean periods occur in winter in cold highland areas and in summer in the hot lowlands.

4) Other factors being equal food supplies are probably generally better in wetter than drier areas, better on piedmonts and in valley bottoms than on plains and better on plains than on stony hillsides.

5) The most abundant arthropod taxa available are Formicidae (workers), Coleoptera, Orthoptera and Araneida.

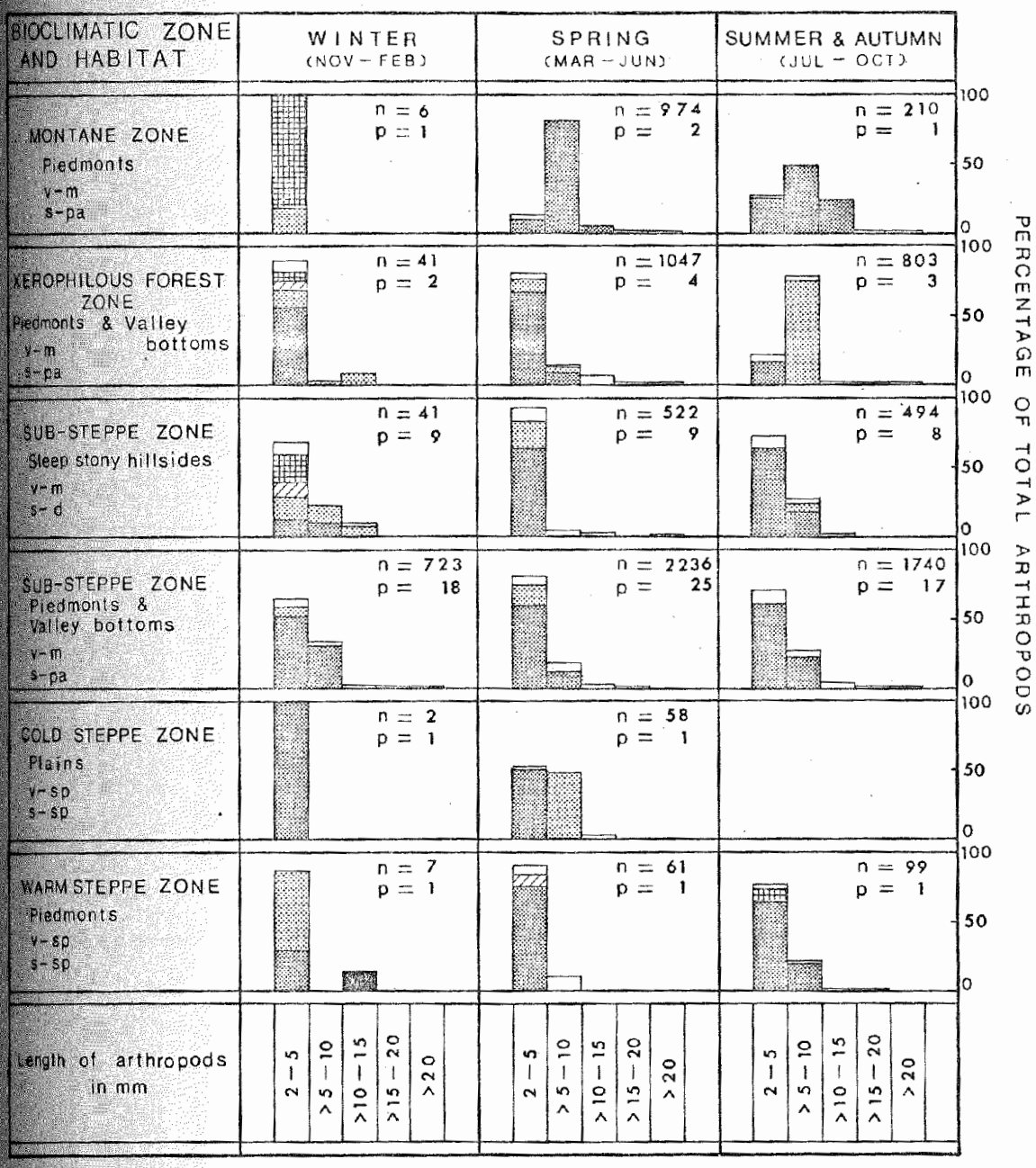

Figure 37. Size distribution and taxonomic composition of largely cursorial arthropods ⩾2 mm long caught in pitfall traps in S. W. Iran during 1970 - 1971.

KEY

Formicidae (workers) | Homoptera | Diplopoda

Coleoptera | Araneida | Other arthropods

n = total arthropods

p = number of pitfall samples (Each sample was the pooled dawn to dusk catch from ten pitfall traps. See p. 46 for procedure).

v = vegetation
s = stone-cover
d = dense
m = medium density
pa = patchy - sparse + dense
sp = sparse

} See pp 118-119 for definitions.

N.B. 1) Taxonomic groups of less than 5% occurrence have not been distinguished.

2) The number of pitfall samples is small from all bioclimatic zones except the sub-steppe zone.

3) See appendix E for measures of variation within these data.

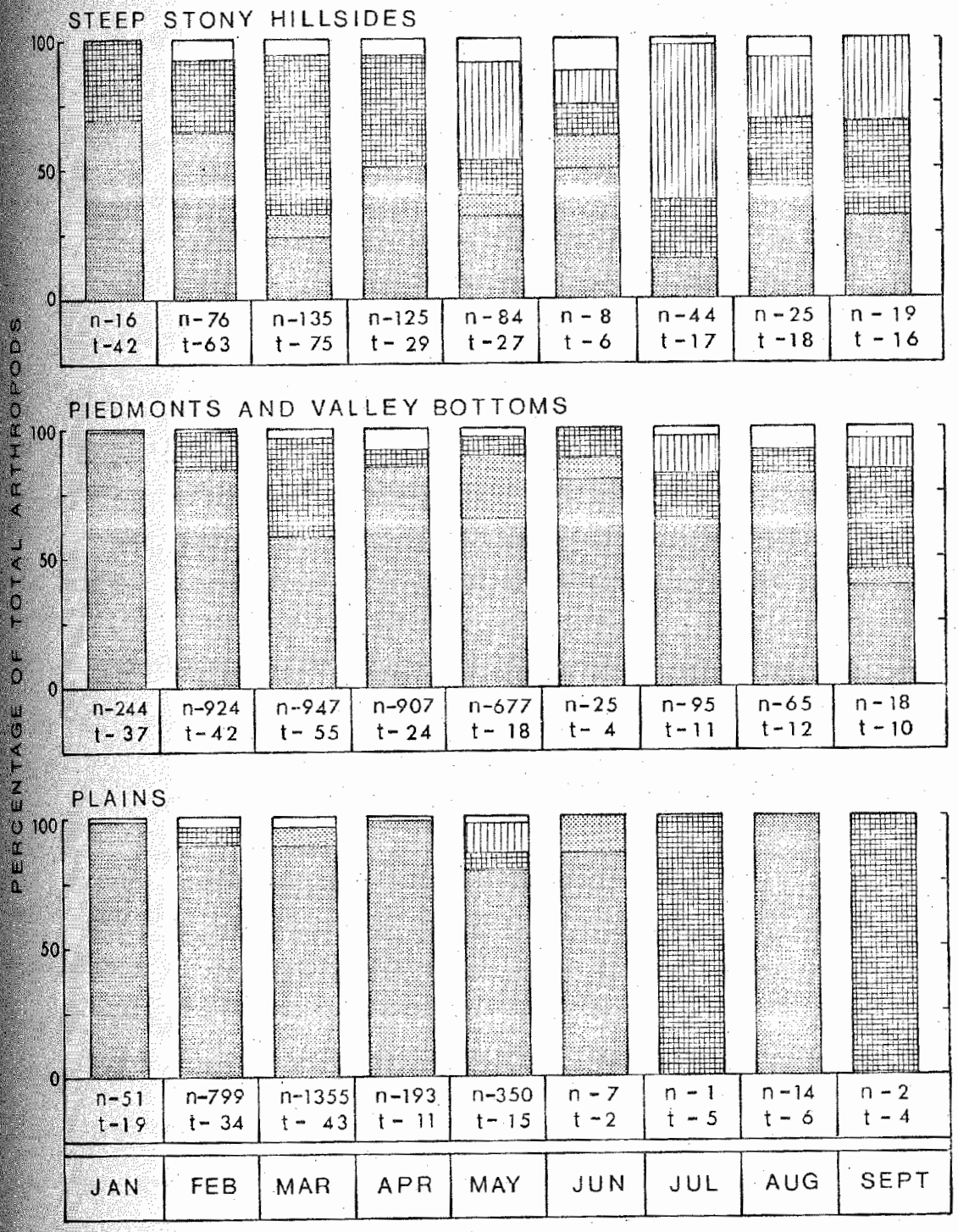

Figure 38. Taxonomic composition of arthropods ⩾2mm long seen on the ground during 100 x 1m transects in heavily grazed steppe in the sub-steppe zone of S. W. Iran.

KEY

- Formicidae (workers)
- Coleoptera
- Araneida
- Orthoptera
- Other arthropods

n Total arthropods

t number of transects

N. B. Taxonomic groups of less than 5 per cent occurrence have not been distinguished.

PART II. FORAGING:

Casual observations of many hundreds of wheatears in S. W. Iran suggested that they almost invariably feed solitarily and that most species use predominantly one or other of two main foraging patterns. These are described below:

Foraging pattern I (perch and pounce): Birds search for prey mainly from elevated watch-posts whence they launch aerial attacks chiefly against arthropods on bare ground. They move about mostly by making short flights. Species that use this technique fall into two groups:

Group I (often use flimsy perches): Species that perch a lot and with facility on vegetation which is often quite flimsy. This group includes O. deserti, O. hispanica, O. picata and O. pleschanka.

Group II (use mainly firm perches): Species which are too heavy and/or morphologically ill-adapted for perching on flimsy vegetation and which usually sit on firmer objects such as boulders, rock-outcrops or stones. This group includes O. alboniger, O. lugens, O. xanthoprymna and O. finschii when on its breeding grounds. On the few occasions that O. monacha was seen feeding it perched mainly on firm vantage points and employed the perch and pounce strategy but it also often pursued flying prey on the wing like a flycatcher and I gained the impression that it used this technique more than other wheatear species.

Foraging pattern II (dash and jab): Birds spend most of their time on the ground where they move about and hunt mainly by making rapid dashes and pursuits on foot. This group includes O. isabellina, O. oenanthe, O. finschii when on its wintering grounds and individuals of O. xanthoprymna that inhabit flat ground in winter.

To provide quantitative documentation of the foraging patterns employed by the various species of wheatear, continuous, usually five-minute, watches of birds were made during which all their overt actions were

recorded (see p. 45 for description of procedure). The majority of these actions was apparently concerned with foraging and fell into one or other of three categories: perching, locomotion or the pursuit and capture or attempted capture of prey. During the continuous watches four classes of data were recorded: 1) the types of perches used; 2) the methods of locomotion employed (movements in fig. 39); 3) the tactics used to pursue and capture or attempt to capture prey (feeding actions in fig. 39); and 4) where food was caught (feeding stations in fig. 39). Each class of data was divided into subclasses. These are given in fig. 39 and those that are not self-explanatory are defined below:

1) Perches:

a) Vegetation: Elevated often flimsy perches.

b) Boulders or rock-outcrops: Firm elevated perches. Boulders were defined as blocks of detached rock of more than 20 cm in diameter.

2) Movements:

a) Long flights: Flights of ten m or more.

b) Short flights: Flights of less than ten m.

c) Dashes along the ground: Movement was achieved by running or by a series of rapid hops.

3) Feeding actions:

a) Involving short flights: Attacks involving short flights were usually launched from elevated watch-posts but were sometimes initiated from the ground.

b) Stationary: Birds stayed in one place repeatedly pecking at the ground, at the base of a stone or at vegetation. Each series of pecks, between arrival and departure at a site was recorded as one feeding action unless more than one item was seen to be taken, in which case each item was recorded as a separate stationary feeding action.

FORAGING

Some feeding actions were seen to result in the capture of prey, but most took place at too great a distance from me for it to be possible to determine whether prey was taken or not. In such cases feeding actions were distinguished from movements by their terminating in a jab, apparently at prey.

RESULTS:

The results of the quantitative studies of the foraging patterns of wheatears are summarised in fig. 39. Each type of data (i.e. perches, movements etc.) is treated separately. The histograms show the percentage of the pooled observations from all individuals watched that fell into the various categories. The number of observations made on each individual varied. Hence lumping these data introduces bias towards the behaviour of individuals for which most observations were made. Therefore to give an indication of the amount of variation between individuals the means and standard deviations are given of the percentage utilization of the various types of perch, movement, feeding action and feeding station by individual wheatears for which twenty or more observations were made.

As a basis for making generalisations about the foraging behaviour of the various species of wheatear the results of these quantitative studies must be treated with caution for two reasons:

1) Seasonal variations in foraging behaviour: Except in the cases of O. alboniger and O. finschii observations were made during only part of the year (fig. 39) and hence took no account of possible seasonal variations. However, apart from O. finschii and O. xanthoprymna, the species of wheatear that occur in S. W. Iran are unlikely to show much seasonal variation in their patterns of foraging activity since this behaviour is probably strongly influenced by the nature of the habitat and except for O. finschii and O. xanthoprymna the wheatear species that occur in S. W. Iran live mainly in similar habitats throughout the year (see chapter V - especially cf. figs. 26, 27, 28 and 29, pp. 121-124 and tables 19 and 20, pp. 153-154).

KEY

Histograms – % of pooled observations (n) from all individuals watched.

i – Number of individuals for which ≥ 20 observations made (= larger samples).

l – Total observations in larger samples.

┼ – The crossbar gives the mean and the vertical line the standard deviation about the mean of the percentage utilization of the various types of perch, movement, feeding action and feeding station by individual wheatears for which ≥ 20 observations were made.

▒ – i = ≥ 3 + results support casual observations.

▒ – i = < 3 + results support casual observations.

□ – Results do not agree with casual observations. See discussion p. 182.

↑↓ – Results expected on basis of casual observations.

Habitat code (= same categories as were used in figs. 26–29 pp. 121–124).

Slope: a = flat; b = flat and/or gentle; c = combination of b + d; d = steep or steep + cliff.

Boulders + rock-outcrops: a = none; b = scattered boulders; c = pile(s) of boulders and/or rock-outcrops; d = b + c.

Stones: a = none or sparse; b = patchy a + c; c = dense.

Vegetation: a = sparse or very short; b = patchy a + c; c = medium density; d = patchy c + dense; bs = bushes; t = trees.

N. B. See pp. 116–119 for definitions of these terms.

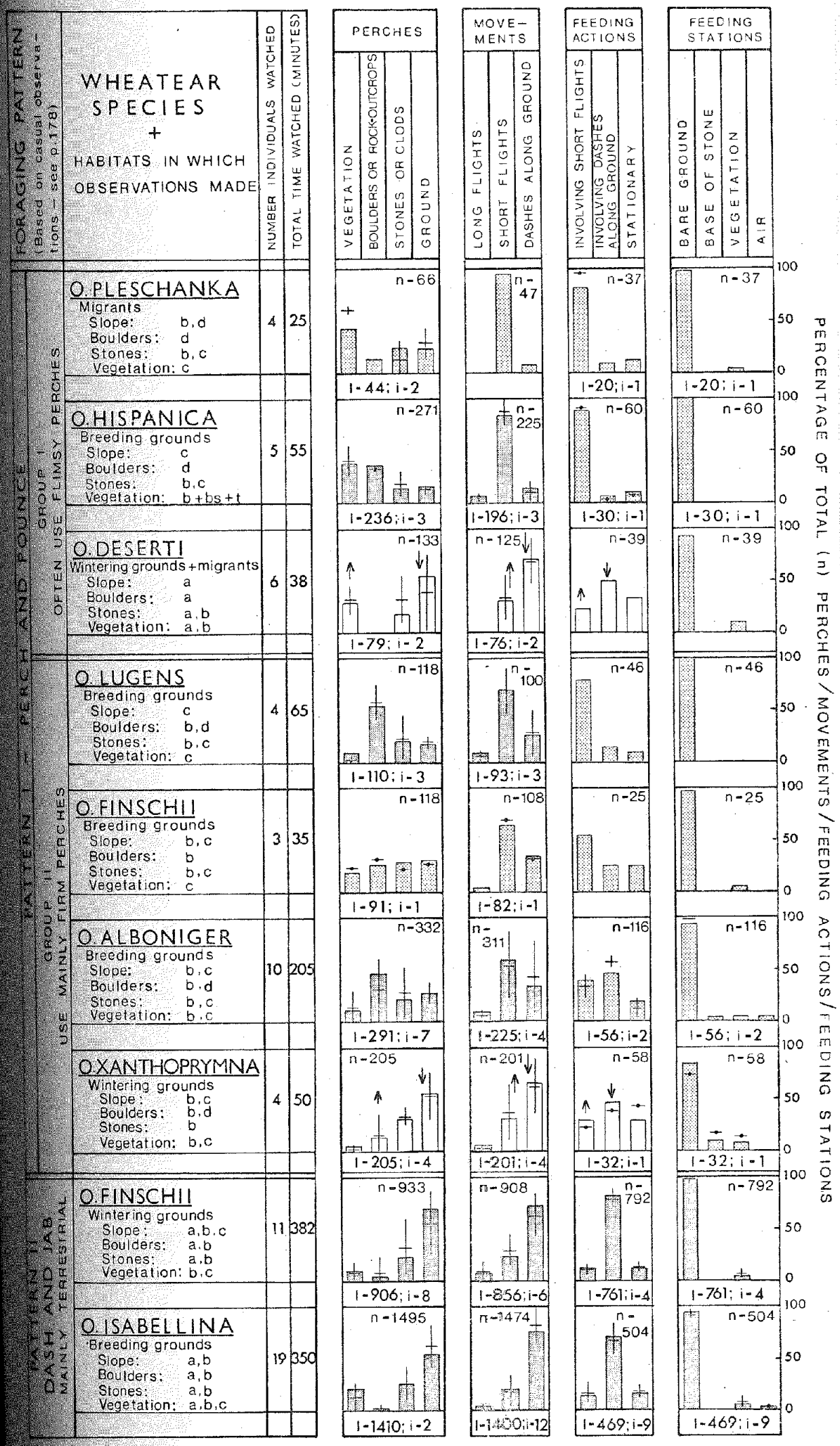

Figure 39. Foraging patterns of wheatears in S. W. Iran. The four classes of data are treated separately. The species are arranged with those that use elevated perches and fly a lot at the top and those that are mainly terrestrial at the bottom. For key see opposite and for explanation of terms and method of analysis see pp. 178–180 and for statistical treatment see pp. 182–183 and table 21.

2) Small sample sizes: The second reason why the results of the quantitative studies of foraging behaviour must be treated with caution is that for most species the number of individuals studied and the number of observations made on each was small. Nevertheless, except in the cases of O. deserti and O. xanthoprymna, I believe that the results provide reliable summaries of the patterns of foraging behaviour employed by the various species. I believe this for two reasons: first because the results agree with the impressions gained from casual observations (p. 178) and second because for each species the observations were made in a representative range of habitat situations (cf. figs. 26-29, pp. 121-124 with fig. 39) which probably evoked typical behavioural responses since much of avian behaviour takes the form of stereotyped adaptive responses to stimuli in the external environment (Hinde 1961).

In the case of O. deserti my impression from casual observations was that the species perched more on vegetation and used aerial locomotion more than is suggested by the quantitative data (fig. 39) and I believe that more comprehensive quantitative studies would confirm these impressions. This view is supported by numerous reports in the literature of the partiality of O. deserti for perching on vegetation (e.g. Whitaker 1905, Ticehurst 1922, Ticehurst et al. 1922 and Meinertzhagen 1930). In the case of O. xanthoprymna I believe that more extensive quantitative studies, particularly during the breeding season, would support the impression gained from casual observations that the species is mainly one of rocky hillsides where it perches a great deal on boulders and rock-outcrops whence it frequently darts to the ground after prey. However, as the quantitative studies show, under some circumstances both O. deserti and O. xanthoprymna can become largely terrestrial.

Statistical treatment of results presented in figure 39:

To test whether the various wheatear species used the different types of perch, movement and feeding action to different extents two-by-two contingency tables were constructed for the numerous

comparisons and analysed using chi-squared tests. Thus to test whether O. pleschanka perched on vegetation to a different extent from O. hispanica the following contingency table was constructed:

	Perched on vegetation	Used other types of perch
O. pleschanka	27	39
O. hispanica	99	172

The chi-squared analysis incorporating Yate's correction was then used to test the null hypothesis that O. pleschanka perched on vegetation to the same extent as O. hispanica. Similar procedure was used for other comparisons. The results are presented in table 21. Since numerous comparisons were carried out the significance levels have been adjusted to take account of the number of possible comparisons using the following formula given by Langley (1970):

$$\text{Significance level between members of pairs selected from three or more samples.} \simeq \frac{\text{Significance level using a two sample test}}{\text{Number of possible comparisons.}}$$

Even though this procedure is very conservative most of the differences that are apparent in fig. 39 are statistically significant at the five per cent level.

ADAPTIVE SIGNIFICANCE OF FORAGING PATTERNS:

This topic is discussed in chapter VIII (pp. 264-267), together with other adaptations of the various species of wheatear.

FORAGING RATES AND RHYTHMS:

All day watches were made on nests of O. finschii, O. isabellina and O. monacha during which the rates at which the parents brought food to the young were recorded. The results together with data on the foraging rates of O. finschii and O. isabellina,

		O. PLESCHANKA (Migrants)	O. HISPANICA (Breeding grounds)	O. LUGENS (Breeding grounds)	O. FINSCHII (Breeding grounds)	O. ALBONIGER (Breeding grounds)	O. FINSCHII (Wintering grounds)
O. HISPANICA (Breeding grounds)	V	0.27					
	F	2.60					
	G	1.70					
	M	1.76					
	FA	0.05					
O. LUGENS (Breeding grounds)	V	23.87*	28.68*				
	F	23.15*	20.49*				
	G	0.58	0.09				
	M	7.12	5.56				
	FA	6.11	1.28				
O. FINSCHII (Breeding grounds)	V	11.55*	13.94*	2.38			
	F	4.26	0.65	9.68			
	G	0.71	10.14*	4.65			
	M	12.28*	15.53*	1.03			
	FA	2.83	6.74	1.50			
O. ALBONIGER (Breeding grounds)	V	38.86*	60.16*	0.00	3.47		
	F	16.51*	14.59*	3.17	3.81		
	G	0.15	9.78	3.40	0.45		
	M	16.00*	29.11*	2.65	0.09		
	FA	18.60*	33.76*	17.47*	2.40		
O. FINSCHII (Wintering grounds)	V	71.27*	139.00*	0.15	9.71	1.17	
	F	3.78	54.42*	116.73*	41.21*	165.13*	
	G	51.81*	230.51*	110.83*	62.58*	170.03*	
	M	99.35*	262.18*	88.73*	71.01*	133.60*	
	FA	141.50*	227.73*	151.48*	44.74*	67.82*	
O. ISABELLINA (Breeding grounds)	V	15.76*	35.67*	7.20	0.42	17.42*	63.57*
	F	2.36	48.71*	110.92*	35.92*	166.56*	1.33
	G	22.27*	131.70*	55.98*	23.28*	79.85*	47.45*
	M	127.21*	357.19*	120.67*	99.64*	198.27*	3.82
	FA	91.58*	147.76*	96.83*	27.48*	35.47	4.87

Table 21. Statistical treatment of the data presented in figure 39.

KEY

The numbers are values of chi-squared calculated using Yates' correction.
* = Statistically significant at the 5% level taking into account the 21 possible comparisons using Langley's formula (see p. 183).
V = Vegetation v. other perches.
F = Firm elevated perches (boulders, rock-outcrops, stones or clods) v. other perches.
G = Ground v. other perches.
M = Dashes along the ground v. short flights.
FA = Feeding actions involving short flights v. feeding actions involving dashes along the ground.

obtained by making five-minute continuous watches (see p. 45 for description of procedure), are presented in figs. 40-42. These studies were carried out because, as far as I am aware, no detailed information has been published on the feeding rates or diurnal patterns of foraging of wheatears and because I was interested in the amount of effort put into foraging and how far diurnal rhythms of foraging were related to prey availability and ambient temperature.

Although the data are few and any conclusions must be regarded as tentative I think the following points are worth making:

1) In winter at Maharlu North although O. finschii foraged throughout the day there was no evidence of a peak of foraging activity during the middle of the day when arthropods were probably most abundant (cf. figs. 31 and 40). On the contrary foraging rates tended to be higher towards evening. The reason for this is not known but it is possible that the birds were preparing for their overnight fast by stocking up with food immediately before going to roost as has been reported for the Bullfinch (Pyrrhula pyrrhula) by Newton (1969).

2) The very marked increases in the feeding rates of the two male O. finschii at Maharlu North on the evenings prior to their departures on migration (fig. 40) were probably associated with taking on fuel for their journeys.

3) In March O. isabellina foraged throughout the day but by May feeding was concentrated in the morning and evening with a lull during the middle of the day (fig. 41). This fits in well with the pattern of arthropod availability (fig. 31). The midday lull in activity may also be influenced directly by environmental temperatures which rise to between 30°C and 40°C on the ground surface during the heat of the day in May and if foraging continued these active ground-dwelling birds which do not drink and which maintain their body temperatures at 38.5-43°C* would probably face problems of water balance associated with thermoregulation.

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* Oral temperatures of 32 birds measured with a mercury thermometer.

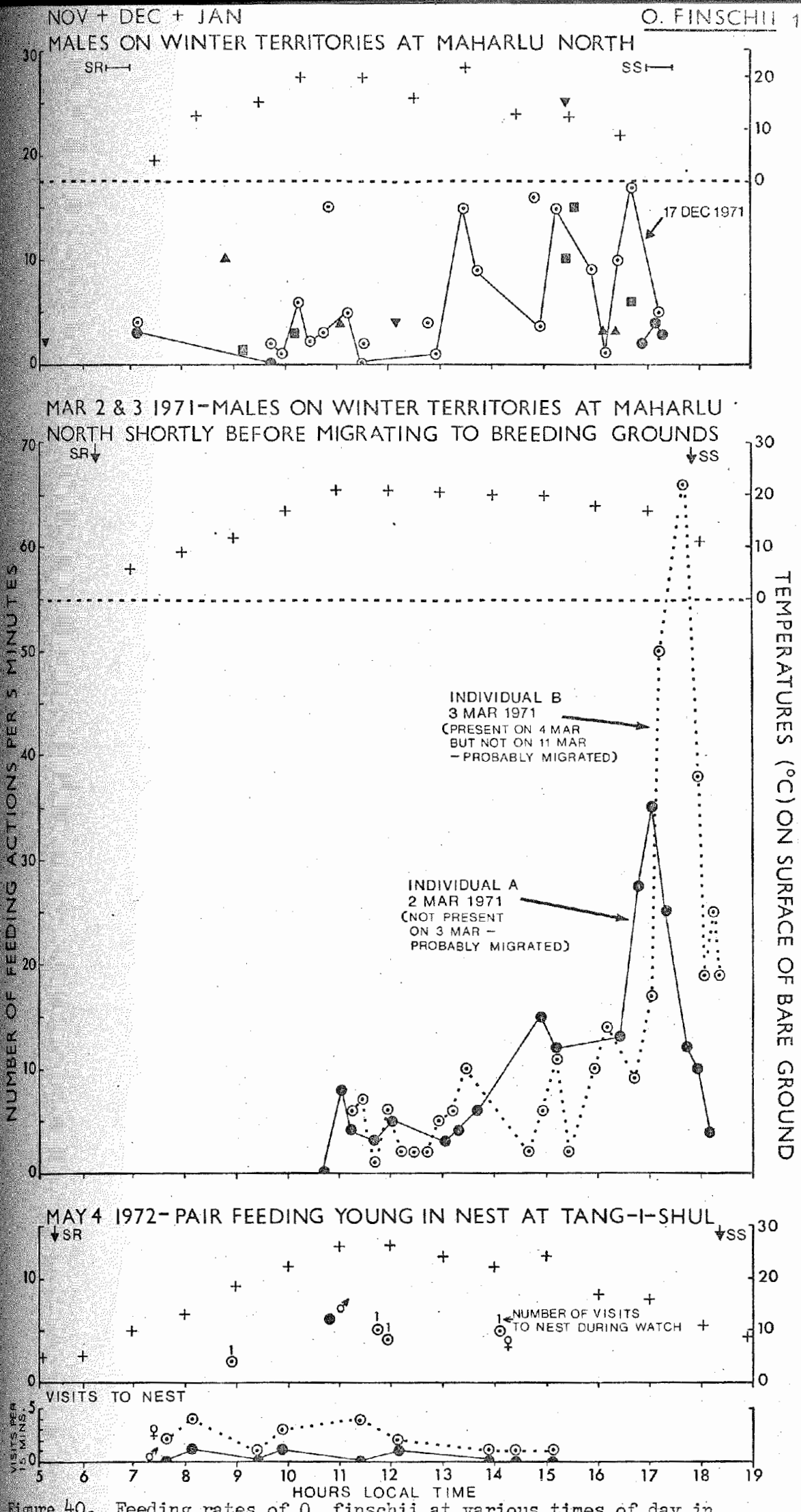

Figure 40. Feeding rates of O. finschii at various times of day in different months on piedmonts and plains in several localities in S.W.Iran.

KEY

+ = Temperature. The values given in the top section of the figure are the means of readings taken in association with 100 m transects during January (see fig. 31).

SR = Sunrise; SS = Sunset.

Other symbols represent feeding rates of various individual wheatears with those joined by lines having been recorded on the same day.

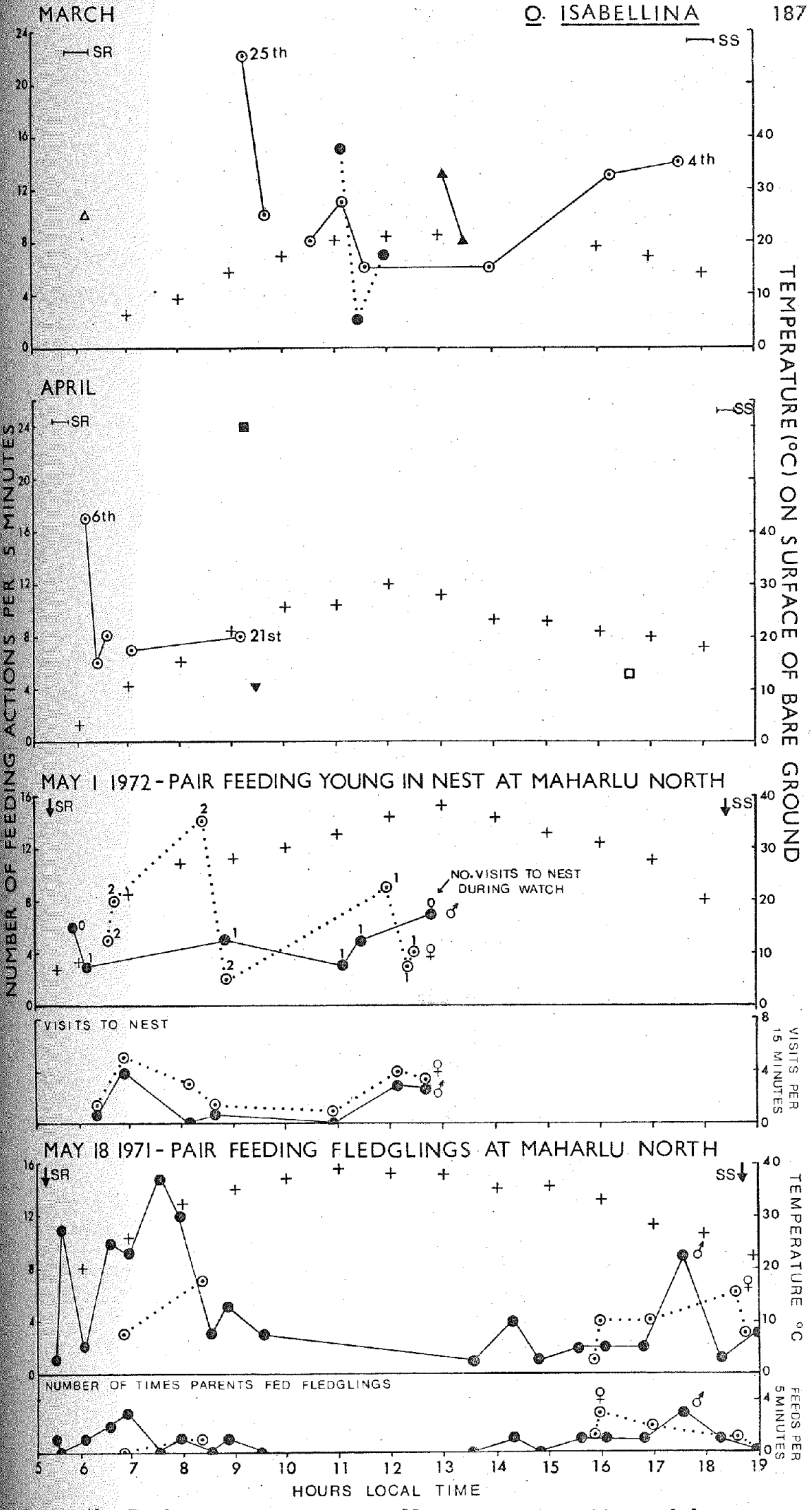

Figure 41. Feeding rates of O. isabellina at various times of day in different months on piedmonts at the Maharlu North study area (1,450 m in sub-steppe zone).

KEY

+ = Temperature. The values for March and April are the means of the readings taken on days when feeding rates were recorded.

SR = Sunrise ; SS = Sunset.

Other symbols represent feeding rates of various individual wheatears with those joined by lines having been recorded on the same day.

8-9 APRIL 1972 — A PAIR OF O. MONACHA FEEDING YOUNG IN NEST AT PASSA BANDAR, PERSIAN BALUCHISTAN

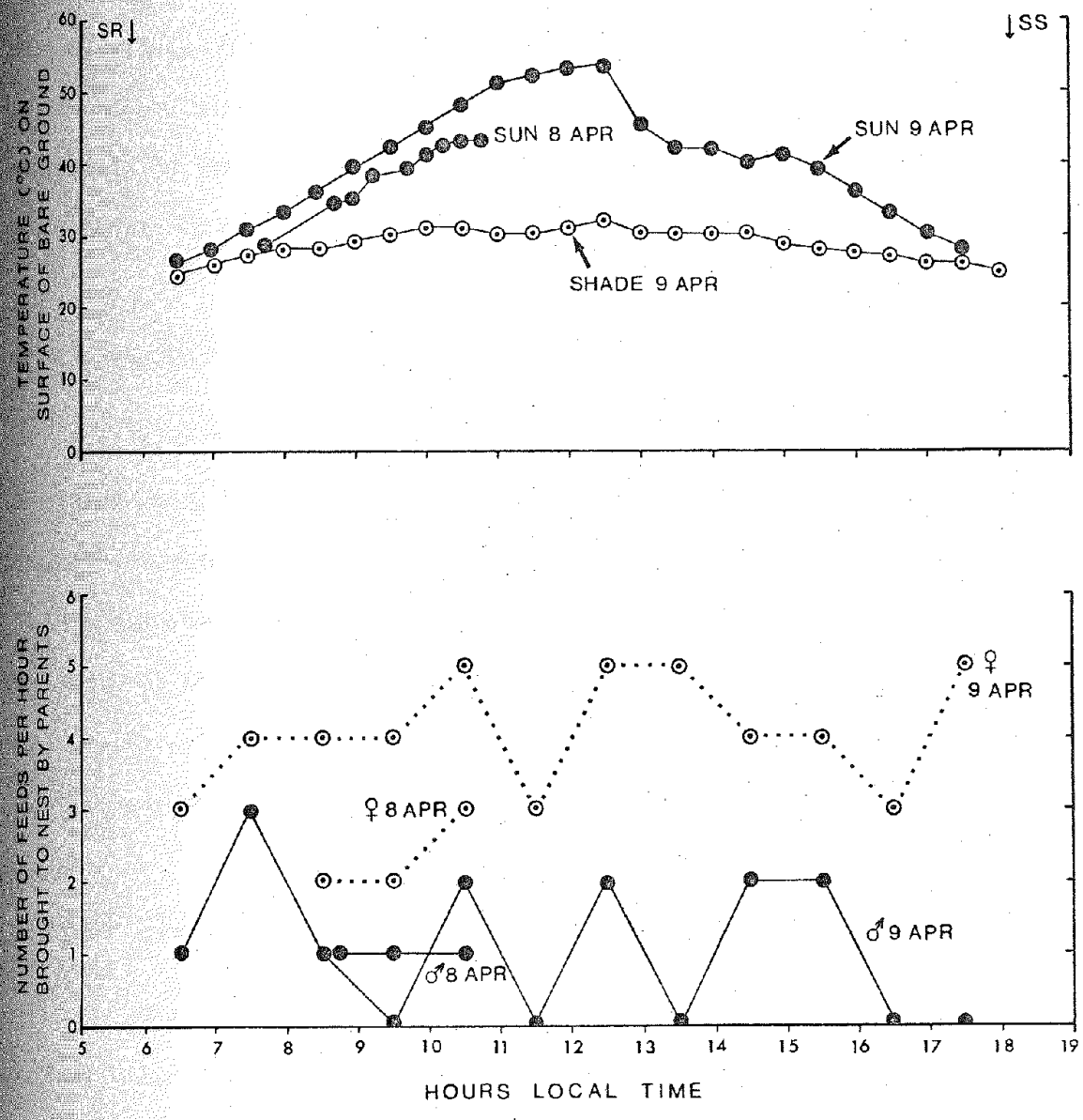

Figure 42. Rates at which food was brought by parent O. monacha to young in a nest on 8 and 9 April 1972 at Passa Bandar on the coast of Persian Baluchistan near the Pakistani border. The observations at the nest were shared with R. F. Porter.

KEY

SR = sunrise SS = sunset

4) In marked contrast to the behaviour of the ground-dwelling O. isabellina was that of the pair of O. monacha (fig. 42) which continued to bring food to their young even when ground surface temperatures were over 50°C. I can think of two reasons why these O. monacha were apparently unaffected by the high midday temperatures. First, they perched mainly on elevated objects where temperatures would have been lower than on the ground surface and second, they frequently took flying arthropods in the air and these, unlike ground-dwelling forms, continue to be active through the heat of the day.

PART III. DIET:

No detailed information has been published on the diet of wheatears in S. W. Iran and the present account is based on data collected during this study. These are of two types and consist of 1) 91 field observations in which wheatears of nine species were seen to take food items which were identified and 2) analyses of the gut-contents from 226 wheatears of 11 species. The field observations are self-explanatory but the gut-analyses require further description.

METHOD OF COLLECTION AND ANALYSIS OF GUT-CONTENTS:

The gut-contents were taken from specimens collected for the Pahlavi University Museum in Shiraz. Since these were obtained by a number of people and under differing circumstances, collecting procedure varied. However within a few hours of collection, all birds were either dissected and the gut-contents preserved in 70% ethyl alcohol or were deep-frozen pending dissection. In hot weather specimens were kept cool in insulated ice-boxes while awaiting dissection in the field or during transport to the deep freezer.

In the alimentary canal of wheatears the majority of identifiable food items were found in the gizzard. They consisted mostly of broken chitinous fragments of arthropods with sometimes a few seeds or bits of berry. In the analysis an attempt was made to identify and place in size classes as many items as possible.

DIET

Identifications were made only to order or family. More detailed determinations were not made for the following reasons: 1) this would have been extremely difficult owing to the fragmented nature of the material and the lack of identification keys for Iranian arthropods; 2) the large number of different types of food items taken by wheatears would have produced cumbersome tables and made comparisons more difficult and 3) it is doubtful whether finer taxonomic categorisation would have been helpful. There was no evidence that wheatears of different species were specialising on particular prey species. Indeed the large number of prey species in the gut-contents of all the wheatear species strongly suggested that they, as predicted for most species of bird by MacArthur (1961), probably take almost any prey item they encounter within a certain size range. All references to arthropod taxa follow the nomenclature of Borror and DeLong (1971).

Food items were placed in size classes using the following measurements: the longest dimension for seeds, berries and gastropods and the length from the anterior point of the head capsule to the tip of the abdomen for arthropods. In the samples few items were intact, but with experience and a reference collection of whole animals it was possible in many cases to estimate the size of items from fragments such as head capsules, wing cases or legs.

RESULTS:

The taxonomic composition of food items in the gut-contents of wheatears and of items observed to be taken by the various species are given in tables 22-32. The field observations are given simply as the numbers of records of each class of food being taken. The results of the gut-analyses are expressed in two ways designed to give an indication of the relative importance of the various kinds of food: First the percentage of guts containing each type is given and second the percentage contribution of each type of item to the total number of items in each sample. The results are presented fully as a source of reference for the present study and for their intrinsic interest since published information on the food of wheatears is mainly anecdotal.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS
REPTILIA																					
Lacertidae									2			1									3
ARTHROPODA																					
COLEOPTERA	67	6		100	11		100	17		83	8		100	8		100	13		100	4		89	10	
HYMENOPTERA																					
Formicidae (workers)	100	77	2	100	69	1	86	62		67	33					100	75		50	66	2	81	59	5
Apoidea	17	+								8	+											6	+	
Others	33	2								8	+											8	+	
DIPTERA							14	+		42	2								50	1		19	1	
HEMIPTERA	33	1					29	1		8	+					100	6					17	1	
ISOPTERA	17	4								17	4											8	2	
NEUROPTERA							14	+		25	1											11	+	
ORTHOPTERA	17	+					14	+	2	50	10											22	2	2
Insect larvae	17	+		14	+		14	+		50	26					100	6					25	6	
Insect pupae	17	+																				3	+	
Unidentified insects	83	7		43	1		86	8		58	5		100	8					100	29		67	7	
ISOPODA	17	+		14	1		14	+		25	7		100	82								19	4	
CHILOPODA										8	1											3	+	
ARANEIDA	17	+											100	3								6	+	
ACARINA							14	+														3	+	
SCORPIONIDA							14	+														3	+	
PLANT MATERIAL																								
Seeds	17	1		71	18		43	9		17	4											31	8	
Miscellaneous							29			8									50			11		
SAMPLE SIZES																								
No. guts	6			7			7			12			1			1			2			36		
No. items in all guts		302			349			249			305			39			16			77			1337	
No. field observations			2			1			4			1									2			10

Table 22. Composition of the diet of O. alboniger in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined. For key see opposite.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS
ARTHROPODA																		
COLEOPTERA				80	12		60	5		75	29					57	11	
HYMENOPTERA																		
Formicidae (workers)	100	35		80	81		90	10		75	38		100	29		87	37	
Bees and wasps				20	1		60	6								30	2	
Others	100	65		20	1		40	3		25	3		67	33		39	10	
DIPTERA							20	1		50	1		33	1		22	1	
HEMIPTERA				20	1		20	1		75	10		33	4		30	4	
ISOPTERA										25	16		67	28		13	9	
NEUROPTERA							20	1								9	1	
ORTHOPTERA				20	1		50	5								26	2	
HOMOPTERA							10	1		25	1					9	+	
LEPIDOPTERA							10	1								4	+	
Insect larvae				20	1		30	55								17	19	
Unidentified insects				20	1		30	5		25	1		67	5		30	3	
ISOPODA							30	4		25	1					17	2	
ARANEIDA							20	2		25	1					13	1	
PLANT MATERIAL																		
Seeds				20	1					25	1					9	+	
SAMPLE SIZES																		
No. guts	1			5			10			4			3			23		
No. items in all guts		23			153			221			149			115			662	
No. field observations																		

Table 23. Composition of the diet of O. deserti in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined. For key see opposite.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.
ARTHROPODA																																	
COLEOPTERA	56	3		50	1				2													100	1										
HYMENOPTERA																																	
Formicidae (workers)	100	86	3	50	79											75	74		100	93				1	100	95		86	84	2	90	88	6
Others	11	+																							25	+		29	2		16	1	
HEMIPTERA	33	1														25	5		100	5					25	+		29	6		29	3	
ISOPTERA	33	8		50	13																										13	3	
NEUROPTERA				50	1																										3	+	
ORTHOPTERA																25	21								13	+					7	+	
HOMOPTERA	11	+																													3	+	
Insect larvae	11	+		50	2							1			7												1	14	1		10	+	9
Unidentified insects	33	1																	100	1					25	+		71	2		29	1	
ISOPODA	11	+		50	1				10																13	+		14	+		13	+	10
ARANEIDA	22	+																													7	+	
PLANT MATERIAL																																	
Seeds	22	1		50	3																				13	+		29	1		19	1	
Miscellaneous																			100						38			14			16		
SAMPLE SIZES																																	
No. guts	9			2												4			1						8			7			31		
No. items in all guts		662			96												19			87					625			671			2160	
No. field observations			3						12			1			7								1			1			2			27

Table 24. Composition of the diet of O. finschii in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined. For key see opposite.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	Oct. % OCCURRENCE	Oct. % ITEMS	Oct. FLD OBS. No.	Nov. % OCCURRENCE	Nov. % ITEMS	Nov. FLD OBS. No.	Dec. % OCCURRENCE	Dec. % ITEMS	Dec. FLD OBS. No.	Jan. % OCCURRENCE	Jan. % ITEMS	Jan. FLD OBS. No.	Feb. % OCCURRENCE	Feb. % ITEMS	Feb. FLD OBS. No.
ARTHROPODA															
COLEOPTERA	91	14					25	3					57	8	
HYMENOPTERA															
Formicidae (workers)	73	42					88	61		50	68		76	53	
Bees and wasps	18	7											10	3	
Others	36	5								50	8		24	4	
DIPTERA	9	1											5	+	
HEMIPTERA	73	13					25	7					48	8	
ORTHOPTERA	27	3					38	10					29	4	
LEPIDOPTERA	18	3											10	1	
Insect larvae	36	7				1							19	3	1
Unidentified insects	27	4					25	4		50	2		29	3	
ARANEIDA	9	1					13	1					10	1	
PLANT MATERIAL															
Seeds							13	1					5	+	
Berries (Daphne sp.)							63	5*					24	1	
Berries (unidentified)							13	8	12	100	23		14	8	12
SAMPLE SIZES															
No. guts	11						8			2			21		
No. items in all guts		135						77			65			277	
No. field observations						1			12						13

Table 25. Composition of the diet of O. hispanica in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined. For key see opposite.

*Ground up berries of Daphne sp. filled most of one gut, about half of another and about a fifth of another.

Table 26. Composition of the diet of *O. isabellina* in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.
REPTILIA																																	
Lacertidae															1																		1
ARTHROPODA																																	
COLEOPTERA	50	1		100	8		100	29	1	100	4				4	75	14		100	29		100	6		100	20				1	83	3		78	9	6
HYMENOPTERA																																	
Formicidae (workers)	100	99		100	88		60	66		100	9		75	75		100	38		100	50		100	92		50	77		100	60		100	59		84	61	
Apoidea										25	1	1																					3	+	1
Others										50	1					25	1					100	2							50	1		19	1	
DIPTERA										25	1																			17	6		5	1	
HEMIPTERA				100	1		20	1		25	4					50	1		100	21					50	1		100	20	17	+		30	1	
ISOPTERA							10	+		50	7		50	22														100	20	33	29		22	8	
ORTHOPTERA															1	25	4													50	1		11	+	1
EMBIOPTERA										50	72																						5	14	
LEPIDOPTERA										25	+				2																		3	+	2
ODONATA																											1								1
Insect larvae							40	2		25	+	5	25	3																			16	+	5
Insect pupae																25	34																3	2	
Unidentified insects				50	3		10	1		50	1					25	6								50	2							16	2	
DIPLOPODA	50	+																															3	+	
ISOPODA							20	1		25	+																			17	+		11	+	
ARANEIDA										25	+																			33	2		30	1	
SCORPIONIDA															2																				2
PLANT MATERIAL																																			
Seeds																														17	+		3	+	
Berries																								2											2
Miscellaneous							10			25															50					50			16		
SAMPLE SIZES																																			
No. guts	2			2			10			4			4			4			1			1			2			1			6			37		
No. items in all guts		225			277			300			446			36			141			14			219			158			5			526			2347	
No. field observations									1			6			10									2			1			1					21

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS
ARTHROPODA																					
COLEOPTERA	100	5								100	14		50	2				1	100	5		82	5	1
HYMENOPTERA																								
Formicidae (workers)	100	80		100	78					50	19		100	98					100	92		82	85	
Others	50	5		100	3					50	28											36	3	
DIPTERA				100	3					25	3											11	1	
HEMIPTERA				100	6					25	6								100	2		36	2	
ISOPTERA																			50	1		9	+	
ORTHOPTERA									2	25	3											9	+	2
HOMOPTERA										25	8											9	1	
Insect larvae	50	3								25	17											18	2	
Unidentified insects	50	5		100	9					25	3								50	1		36	2	
ARANEIDA	50	3																				9	+	
PLANT MATERIAL																								
Miscellaneous	50									25			50									27		
SAMPLE SIZES																								
No. guts	2			1						4			2						2			11		
No. items in all guts		40			32						36			126						188			422	
No. field observations									2									1						3

Table 27. Composition of the diet of O. lugens in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined. For key see opposite.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS
ARTHROPODA												
COLEOPTERA							100	20		50	5	
HYMENOPTERA												
Formicidae (workers)	100	21								50	16	
Others	100	57								50	42	
NEUROPTERA							100	20		50	5	
ORTHOPTERA	100	7					100	40		50	16	
ODONATA			1									1
LEPIDOPTERA						1						1
Unidentified insects	100	14								50	11	
SAMPLE SIZES												
No. guts	1						1			2		
No. items in all guts		14						5			19	
No. field observations			1			1						2

Table 28. Composition of the diet of O. monacha in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined.

For key see opposite.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.	% OCCURRENCE	% ITEMS	No. FLD OBS.
ARTHROPODA																		
COLEOPTERA	100	31		100	5		100	11		100	13		67	18		88	16	
HYMENOPTERA																		
Formicidae (workers)	100	65		50	8		100	6		100	88		100	72		88	55	
Apoidea													67	3		25	2	
Others													67	3		25	2	
HEMIPTERA	100	2		50	85		100	11					33	1		38	1	
Insect larvae	100	2											33	1		25	1	
Unidentified insects				50	1								67	2		38	1	
ARANEIDA													33	1		13	+	
MOLLUSCA																		
GASTROPODA							100	22								13	1	
PLANT MATERIAL																		
Seeds				50	1								33	1		25	1	
SAMPLE SIZES																		
No. guts	1			2			1			1			3			8		
No. items in all guts		48			85			9			8			187			34	
No. field observations																		

Table 29. Composition of the diet of O. oenanthe in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined. For key see opposite.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS
ARTHROPODA																								
COLEOPTERA	50	5		100	8		100	29					100	17		100	18					86	9	
HYMENOPTERA																								
Formicidae (workers)	100	93		100	92		100	40					100	83		100	65					100	86	
Bees and wasps							50	3														14	+	
Others							50	3								100	6					29	1	
HEMIPTERA							50	9														14	1	
NEUROPTERA							100	9														29	1	
HOMOPTERA							50	3														14	+	
LEPIDOPTERA																100	6					14	+	
Insect larvae												1												1
Unidentified insects							100	6														29	1	
DIPLOPODA	50	2																				14	1	
ARANEIDA																100	6					14	+	
PLANT MATERIAL																								
Berries																				1				1
SAMPLE SIZES																								
No. guts	2			1			2						1			1						7		
No. items in all guts		190			113			35						6			17						361	
No. field observations												1								1				2

Table 30. Composition of the diet of O. picata in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined. For key see opposite.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS	% OCCURRENCE	% ITEMS	No. FLD OBS
ARTHROPODA																		
COLEOPTERA	67	22		50	4		100	13		91	41		75	.16				
HYMENOPTERA																		
Formicidae (workers)	83	50		100	59		67	67		73	16		82	48				
Apoidea										18	1		7	+				
Others				25	2					18	3		14	2				
HEMIPTERA	50	5		13	+		67	7		55	11		43	4				
ISOPTERA										9	8		4	2				
ORTHOPTERA	17	1					67	7					11	1				
HOMOPTERA				38	2					9	1		14	1				
ODONATA	17	1											4	+				
Insect larvae	33	3		25	1					36	2		29	2				
Unidentified insects	50	16		63	25		33	4		73	11		61	19				
ISOPODA	33	2											7	+				
ARANEIDA				13	+					18	4		11	1				
ACARINA										18	1		7	+				
PLANT MATERIAL																		
Seeds				25	1		33	2		18	1		18	1				
Berries				75	5								21	3				
Drupe of Pistacia			9*												9			
SAMPLE SIZES																		
No. guts	6			8			3			11			28					
No. items in all guts		100			471			45			213			829				
No. field observations			9												9			

Table 31. Composition of the diet of O. pleschanka in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined. For key see opposite.

*The drupes were small (average diameter 5mm) and had fleshy endocarps.

KEY

% OCCURRENCE = the percentage of guts in which each type of food item was identified.

% ITEMS = the number of items of each type of food in the combined contents from all guts obtained during the period concerned expressed as a percentage of the total number of food items in the sample.

No. FLD OBS = number of field observations of the various types of food being eaten.

\+ = less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.
Months for which there are no data have been omitted.

FOOD ITEMS	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.	% OCCURRENCE	% ITEMS	No. FIELD OBS.
ARTHROPODA																											
COLEOPTERA	100	25		100	29		100	34		75	16	1							75	8		75	3		77	15	1
HYMENOPTERA																											
Formicidae (workers)	100	47	1	100	14	1	100	14		50	52		100	100		100	83		100	82		100	91		91	66	2
Bees and wasps							67	14		25	8														14	1	
Others	50	1					33	16											25	1					18	1	
DIPTERA							33	2																	5	+	
HEMIPTERA	25	1					33	9		25	4					100	8		50	2		25	+		32	1	
ISOPTERA	25	1																				25	+		9	1	
ORTHOPTERA												1				100	8								5	+	1
LEPIDOPTERA										25	4								25	1					9	+	
Insect larvae	25	3		100	29														50	2					18	2	
Unidentified insects	25	1		100	14		67	7		75	12								75	6		25	4		46	3	
ISOPODA				100	14																				5	+	
ARANEIDA	25	+					33	2		25	4								25	1		25	+		23	1	
ACARINA							33	2																	5	+	
PLANT MATERIAL																											
Seeds	25	21																				25	1		9	9	
Berries (Daphne sp.)													100												5		
Miscellaneous	25									25												25			14		
SAMPLE SIZES																											
No. guts	4			1			3			4			1			1			4			4			22		
No. items in all guts		368			7			44			25			5			12			183			257			901	
No. field observations			1			1						2															4

Table 32. Composition of the diet of O. xanthoprymna in S. W. Iran based on gut analyses and field observations. The data were collected between 1964 and 1973 and those from all years have been combined. For key see opposite.

DIET

The size distribution and taxonomic composition of measurable items found in the gut-contents of the ten commonest wheatear species in S. W. Iran are given in fig. 43. For each wheatear species and period of the year all available data have been pooled and the histograms show the numbers of measurable food items in various size classes and taxonomic groups expressed as percentages of the total number of measurable items in the pooled samples. This method of presentation, which has been used by many workers (e. g.: Ashmole and Ashmole 1967, Root 1967, Ashmole 1968, Schoener and Gorman 1968), summarises all the data available for each species. However lumping data from a number of individuals, in this way, means that the results are influenced by any given individual in proportion to the number of data contributed by it. Hence with the rather small number of guts from each wheatear species the importance of an unusual food could be exaggerated if a large number of items of that unusual food was contributed by a single bird. However inspection of the data showed that the contents of most guts were rather similar and hence lumping the data was deemed justifiable. A measure of the variation between the contents of the different guts is given in appendix F where I list for each sample the mean and standard deviation of the percentage occurrence of items in each size class and taxonomic group in all gut-contents from which twenty or more items were measured.

INTERPRETATION OF THE FOOD DATA:

Gut-contents as an indicator of the diet of birds must be treated with care since more resistant food items are liable to be over-represented. Small and soft-bodied items are more easily crushed and are digested and pass through the gut more quickly than large chitinous ones (Koersveld 1951, Dillery 1965 and Newton 1967) and hence the latter are more likely to be found and identified in gut-contents. Moreover Koersveld (1951) showed for two species of Corvidae (*Corvus monedula* and *Corvus corone cornix*) and Dillery (1965) for the Savannah Sparrow

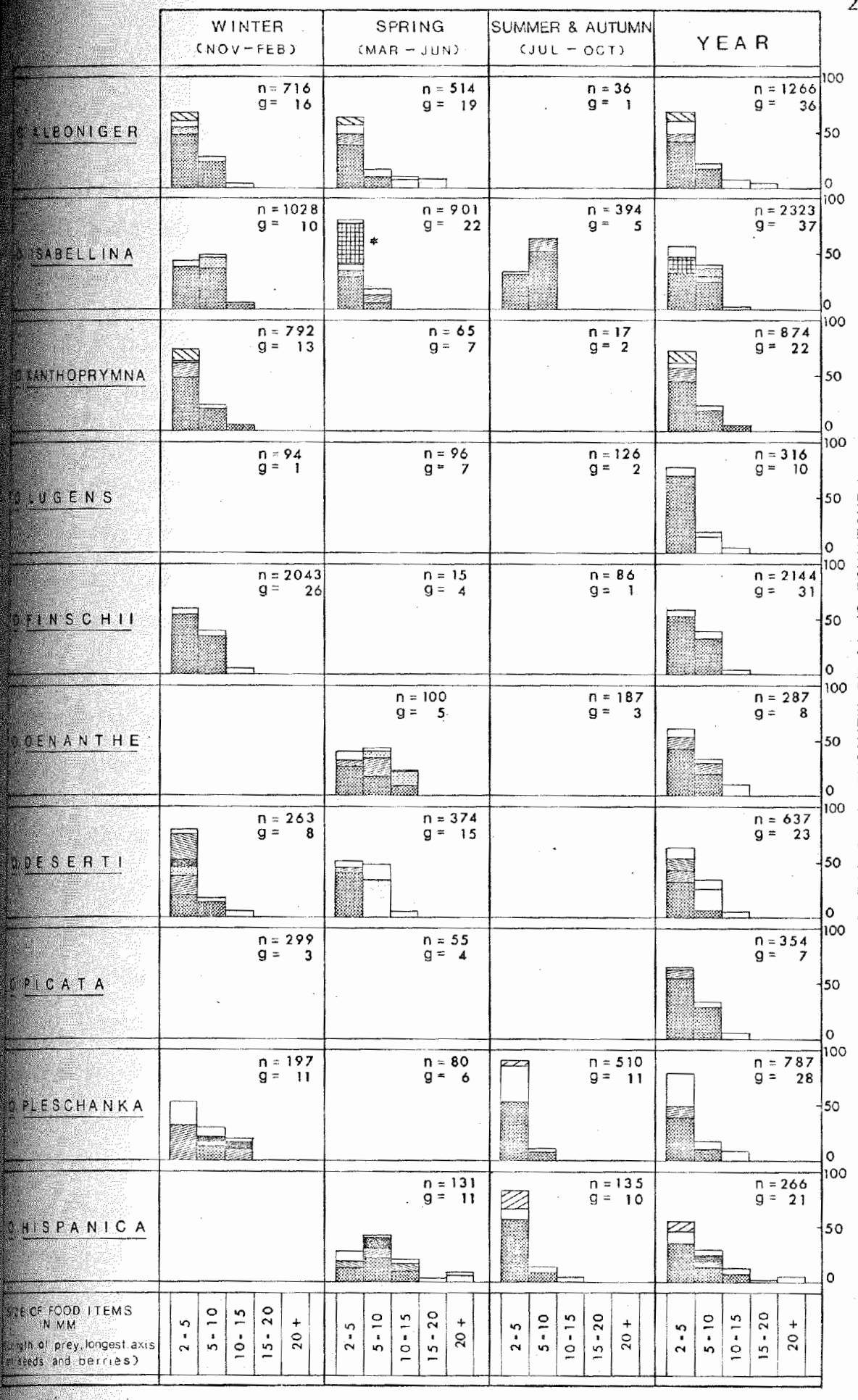

Figure 43. Size distribution and taxonomic composition of measurable items in the gut contents of wheatears obtained in S. W. Persia. The species are arranged in descending order of mean bill length of males.

KEY

- Formicidae (workers)
- Winged Hymenoptera
- Coleoptera
- Isoptera
- Hemiptera
- Embioptera
- Insect larvae
- Other insects
- Seeds
- Berries
- n = total items measured
- g = number of guts

*Embioptera were found in only two guts.

N. B. Samples of less than 100 items and from less than five guts have been omitted. Taxonomic groups of less than 5% occurrence have not been distinguished.

(Passerculus sandwichensis) that digestion continued after death and that unless this was checked by introducing 10% formalin into the alimentary canal immediately upon the death of the birds the results of subsequent gut-analyses were biased in favour of more resistant items.

The gut-contents of wheatears collected during this study consisted mainly of broken chitinous fragments of arthropods and a few seeds and bits of berry, all of which were relatively resistant to digestion. Since, apart from cooling, no measures were taken to arrest post-mortem digestion and since smaller and softer food items are digested more quickly than larger more schlerotized ones it is possible that small and/or soft-bodied food items are important in the diets of wheatears but are under-represented in the gut-contents. This possibility will be considered in the light of what is known about the availability of such prey in the environment:

1) Minute arthropods (0-2 mm) mainly Collembola, Acarina and Thoptera, were common in the pitfall samples (see p. 160) but were not found in the gut-contents. This may have been due either to wheatears not bothering with such tiny prey or to these delicate animals having been digested before the gut-contents were examined. Wheatears feed predominantly by spotting prey from a distance and then darting to catch it. Such small prey items would probably only attract attention and be energetically worth fetching if they were very close or had a clumped distribution for which there is no evidence. Hence I doubt whether these small animals were quantitatively an important part of the diet of wheatears and therefore if their absence from the gut-contents was due to rapid digestion I think this is unlikely to have introduced serious error into the results.

2) Diptera were abundant in the pitfall samples but were only rarely found in the gut-contents of wheatears (tables 22-32, fig. 43). I believe that this paucity of Diptera and other flying insects in the gut-contents of wheatears is a genuine omission from their diets which

reflects their feeding strategies (fig. 39). This view is supported by the discovery that the wings of even such delicate insects as aphids were resistant to digestion and remained intact in the faeces of House Martins (Delichon urbica) (Bryant 1971) and Pied Wagtails (Motacilla alba yarrellii) (N. B. Davies pers. comm.). These findings suggest that had winged insects been an important part of the diet of wheatears more remains of them would have been found in the gut-contents.

3) Araneida and Homoptera of from 2-5 mm in length were better represented in samples from the environment (figs. 37 and 38) than in the gut-contents of wheatears. This was probably partly due to rapid digestion of these soft-bodied forms. However Araneida and Homoptera were rarely in abundant supply and I doubt whether either group formed a large proportion of the diet of any species of wheatear.

No other small or soft-bodied arthropods that might have been suitable prey for wheatears were recorded on bare ground which is where the birds mainly foraged. It therefore seems likely that the birds eat mostly items that have parts that are relatively resistant to digestion and as a result the gut-contents probably give a fair indication of what the wheatears had actually been eating.

DIET AND PREY AVAILABILITY:

Prey availability was studied by pitfall trapping (pp. 160, 167, 175 and fig. 37) and 100 m transects (p. 160 and fig. 38). The results suggest that in all the areas investigated the prey available on bare ground where wheatears mainly forage was broadly similar and consisted chiefly of Formicidae (workers) with smaller numbers of Coleoptera, Orthoptera, Homoptera and Araneida mostly of 2-10 mm in length. Comparison of these data with the results of the gut-analyses (tables 22-32 and fig. 43) shows that roughly speaking the prey taken by wheatears are similar in taxonomic composition and size distribution to the arthropods available in the environment. This is consistent with the hypothesis that wheatears eat any prey item that they encounter as long as it is large enough to be worth fetching and not too large

to handle. However this indication must be regarded as tentative since the wheatear specimens and the data on food supply were collected in different localities.

COMPARISON OF THE DIETS OF WHEATEAR SPECIES IN S. W. IRAN:

Figure 43 shows visually that all ten of the commoner wheatear species that occur in S. W. Iran take food items of similar sizes and in similar taxonomic groups, Formicidae (workers) and Coleoptera of 2-10 mm in length being predominant in the diets of all of them.

To assess numerically the degree of similarity between the diets of the various wheatear species I have followed Holmes and Pitelka (1968) and used percentage overlap. This was calculated by comparing the percentage composition of the diets of each pair of wheatear species in turn and adding the values in all food classes that were shared. The method is illustrated by the following simple example:

	Percentage occurrence in diet	
	Food class 1	Food class 2
Wheatear species A	80	20
Wheatear species B	10	90
% overlap	10	20

In this case the overlap in the diets of species A and species B is 30 per cent. If the diets had been identical the overlap would have been 100 per cent.* The percentage overlap in the size distribution and taxonomic composition of the food of the various wheatear species were calculated separately. The results are presented in table 33.

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*The same method was used by Schoener (1970) to measure spatial overlap in lizards and he gave the following formula for the calculations:

$$\text{Percentage overlap} = 100\left(1 - \tfrac{1}{2}\sum_i \left[P_{x,\,i} - P_{y,\,i}\right]\right)$$

where $P_{x,\,i}$ and $P_{y,\,i}$ are the frequencies for species x and y respectively for the ith category.

Percentage overlap, rather than a more complicated index such as one of those discussed by Horn (1966), was chosen as the measure of similarity because it is easier to understand and was considered adequate for the present purposes.

They show that the overlap in the size range of food items taken by the members of the various species pairs was over 80% in the majority of cases and over 50% in all except one case. The overlap in taxonomic composition was not so great but was over 50% in most cases and over 25% in the remainder. Since wheatears probably do not select particular prey species but take most items they encounter within a certain size range (see pp. 190, 206) the degree of overlap in the sizes of food items is probably more pertinent than the overlap in taxonomic composition. Hence the results of the gut-analyses suggest that there is considerable similarity in the diets of the various species of wheatear and this is in spite of the fact that the specimens were collected from all over S. W. Persia and from a diversity of habitats.

However there are also differences between the diets of some species of wheatear. For example there is some evidence that species with larger bills can take larger prey than species with smaller bills. Thus of the wheatears that occur in S. W. Iran the only species that have been recorded taking small lizards (5-7 cm in length) are O. alboniger (table 22) and O. isabellina (table 26, Hollom 1959) both of which have relatively long bills (table 1, p. 3). In contrast Smith (1971) observed that an O. deserti, which has a comparatively short and delicate bill (table 1, p. 3), ate small locust hoppers but failed in its attempt to eat fourth and fifth instars. The ability to take a wide range of prey sizes could be of crucial importance to survival under conditions of food shortage and may be one of the factors allowing O. alboniger and O. monacha to inhabit the arid warm steppe zone bordering the Persian Gulf where food is comparatively scarce (pp. 173-174).

	a	87.4 (62.2)								
X	w	94.7 (89.7)	72.3 (66.4)							
	s	-	-	X						
	a	-	-							
	y	95.8 (82.2)	83.2 (61.6)							
L	w	-	-	-						
	s	-	-	-	L					
	a	-	-	-						
	y	90.9 (64.5)	78.6 (55.8)	93.7 (68.3)						
F	w	89.8 (81.1)	86.6 (81.5)	84.8 (76.2)	-					
	s	-	-	-	-	F				
	a	-	-	-	-					
	y	84.5 (68.5)	97.9 (69.7)	85.3 (73.8)	80.5 (73.3)					
O	w	-	-	-	-	-				
	s	63.9 (48.6)	58.5 (49.8)	-	-	-	O			
	a	-	-	-	-	-				
	y	87.6 (75.0)	92.5 (67.1)	87.3 (77.8)	81.4 (63.7)	94.4 (71.6)				
D	w	89.1 (48.8)	66.6 (46.2)	94.2 (53.7)	-	79.3 (46.2)	-			
	s	70.0 (53.8)	69.8 (41.1)	-	-	-	83.5 (35.4)	D		
	a	-	-	-	-	-	-			
	y	88.6 (57.0)	93.9 (47.7)	89.4 (53.7)	84.1 (47.7)	96.0 (47.1)	96.3 (57.4)			
P	w	-	-	-	-	-	-	-		
	s	-	-	-	-	-	-	-	P	
	a	-	44.4 (43.6)	-	-	-	-	-		
	y	90.3 (71.1)	92.2 (67.4)	91.1 (76.5)	86.4 (75.9)	94.0 (88.5)	95.1 (74.8)	98.6 (49.0)		
PL	w	84.4 (34.3)	78.4 (27.8)	80.2 (37.2)	-	84.8 (28.5)	-	74.4 (44.8)	-	
	s	-	-	-	-	-	-	-	-	PL
	a	-	-	-	-	-	-	-	-	
	y	90.4 (62.9)	75.9 (54.7)	92.7 (66.3)	96.5 (57.1)	78.0 (57.1)	81.2 (68.8)	82.1 (55.2)	83.8 (61.2)	
H	w	-	-	-	-	-	-	-	-	-
	s	56.9 (37.1)	47.3 (35.5)	-	-	-	87.6 (53.3)	73.7 (29.4)	-	-
	a	-	49.4 (43.1)	-	-	-	-	-	-	91.7 (69.1)
	y	87.5 (59.1)	86.2 (59.2)	84.1 (60.0)	78.4 (56.9)	87.0 (59.5)	90.8 (63.9)	87.5 (52.6)	86.7 (58.6)	78.0 (59.6)

of mean tail lengths of males. For method of calculation of percentage overlap see text p. 202.

KEY

w = winter
s = spring
a = summer and autumn
y = year

- = No data or less than 100 items from less than five guts.
▒ = ⩾ 80% overlap.

A = O. alboniger
D = O. deserti
F = O. finschii
H = O. hispanica
I = O. isabellina
L = O. lugens
O = O. oenanthe
P = O. picata
PL = O. pleschanka
X = O. xanthoprymna

CHAPTER VII

ECOLOGICAL ISOLATION

INTRODUCTION:

The background and theoretical basis of the problem of ecological isolation in wheatears was discussed fully in chapter I, pp. 4-10, and only the crux of the problem will be reiterated here. Eight species of wheatear breed commonly in S. W. Iran (+ three species breed or probably breed in small numbers) and three species are abundant in the area in winter (+ four species winter or probably winter in small numbers) (fig. 2, p. 11). All these species are rather similar in size (table 1, p. 3), morphology (plate 1, p. 2) and broadly speaking in ecology, particularly feeding ecology (pp. 178-208). In S. W. Iran some of these species have different distributions or live in different habitats. However many of them overlap to some extent in both range and habitat and different species were often found side by side in the same habitat and appeared to have very similar ecology. This situation presented two problems which are considered in this chapter:

1) In view of the principle of competitive exclusion, that two species cannot coexist on the same limiting resources (see p. 8), how do so many such similar and potentially competing species of wheatear coexist in S. W. Iran? In other words how are the various species of wheatear that occur in S. W. Iran ecologically segregated?

2) How much ecological overlap is there between different species of wheatear in S. W. Iran and how can this overlap be reconciled with the principle of competitive exclusion?

Ecological segregation (= ecological isolation) in birds is accomplished in several ways (see reviews by Lack 1971, Diamond 1972 and Cody 1974). These can be classified under two headings and will be briefly described below:

1) Spatial segregation: Species with similar ecological

requirements generally avoid competition by living in different places. This spatial segregation is achieved by the species having different altitudinal ranges, different geographical distributions or living in different habitats or parts of habitats. In places where such species meet they have sometimes been found to hold interspecific territories.

2) Within-habitat segregation: Species that live together in the same habitat usually differ in their requirements for resources. The resource for which competition most commonly occurs is probably food (Lack 1966) and species that coexist in the same habitat often differ in size and usually take different foods or feed in different places, at least at certain times of year.

The similarity of the ecological requirements of the various species of wheatear that occur in S. W. Iran and the simple one-layered nature of the habitats of most of them make it unlikely that any of these species could coexist in the same place for any length of time without competing. It is therefore probable that most of these species are segregated spatially and in the present analysis the various means by which this might be achieved are considered first.

Investigation of the means of ecological segregation between the various species of wheatear that occur in S. W. Iran is complicated by the number of species and the fact that most of them spend only part of the year in the area. Two groups of species of wheatear coexist in S. W. Iran for considerable periods during each year. These are: 1) species on their breeding grounds (residents and summer visitors) and 2) species on their wintering grounds (residents and winter visitors) (fig. 21, p. 97). These groups are considered in separate sections.

METHOD OF ANALYSIS:

In each section a similar procedure is followed. Analysis is carried out on a species to species basis. For each pair of species the altitudinal range, geographical distribution and habitat selection

of the members are compared and in cases where the species overlap in all these respects the relationships between them are examined in detail. The method of comparison and the categories used to denote the amount of overlap (or lack of it) between species are given below for each of these aspects of their ecology.

1) Altitudinal range and geographical distribution:

The altitudinal ranges and geographical distributions of the members of each pair of wheatear species were compared by superimposing the appropriate overlays (overlays 5-17) and consulting the maps showing their probable altitudinal ranges and geographical distributions (figs. 22-24, pp. 99-101). Each pair of species was allotted to one of the following categories describing altitudinal range and one of the following categories describing geographical distribution.

Altitudinal range:

a) Altitudinal ranges totally separate ("ALT" in tables).

b) Altitudinal ranges largely separate ("alt" in tables): Pairs of species where each member had at least 65 per cent of its total altitudinal range separate from that of the other, in areas where they overlapped geographically.

c) Considerable overlap in altitudinal range (altitudinal range space blank in tables): Pairs of species not classified in categories a) or b).

Geographical distribution:

a) Geographical distributions totally separate ("GEOG" in tables): Pairs of species where the members had totally separate geographical distributions and where the differences were not due simply to differences in altitudinal range.

b) Geographical distributions largely separate ("geog" in tables): Pairs of species where the members had largely separate geographical distributions and where the differences were not due simply to differences in altitudinal range. Judgements were made visually.

c) Considerable overlap in geographical distribution (geographical distribution space blank in tables): Pairs of species not classified in categories a) or b).

It must be emphasised that in this chapter the terms altitudinal range and geographical distribution are used literally and where differences are reported this does not imply ecological segregation by range in the sense of Lack (1971) (i. e. that one species replaces another as a result of competitive exclusion). Discussion of the factors which influence the distribution patterns is deferred to chapter VIII.

B) Habitat:

Comparisons of the habitats of the various species of wheatear were based on the data presented in figs. 26-29, pp. 121-124. The method used to assess the similarity between the habitats of different species was percentage overlap (and the corollary percentage difference) in the occurrence of various habitat characteristics in the territories of the species being compared. This method is analogous to that employed to measure the overlap in the diets of the various species of wheatear and the calculations were made in precisely the same way (see pp. 206-207). This procedure was used by Schoener (1970) to compare the habitats of lizards and it, rather than one of the more complex indices of overlap that are now available (see Horn 1966), has been followed in this study because it is easier to understand and was considered adequate for the present purposes.

The data on the habitats of the various species of wheatear were compared on a species to species basis and each pair of species allotted to one of the following categories:

a) Habitats largely distinct ("hab" in tables): Pairs of species of wheatear in which 75 per cent or more of the territories of one species differed from those of the other in at least one of the following respects: topography, the occurrence of rock-outcrops and boulders, stone-cover and/or vegetation.

b) Considerable overlap in habitat (habitat space blank in tables): Pairs of species not classified in category a).

The procedures described in this section for investigating the means of ecological segregation between different species of wheatear in S. W. Iran are now put into practice.

1) ECOLOGICAL SEGREGATION BETWEEN SPECIES OF WHEATEAR ON THEIR BREEDING GROUNDS IN S. W. IRAN:

Nine species of wheatear breed regularly in S. W. Iran (eight commonly and one, O. picata, in small numbers - fig. 2, p. 11) and are included in the main analysis (table 34). In addition O. monacha probably breeds in small numbers and is considered separately on pp.215-16.* The seasonal occurrence and status of the various species are summarised in table 17, p. 96 and fig. 21, p. 97.

Altitudinal range, geographical distribution and habitat:

Comparisons of the altitudinal ranges, geographical distributions and habitats of the various species of wheatear while on their breeding grounds in S. W. Iran were based on the following data: 1) overlays 5-8 which show the altitudes and localities of proven and probable breeding records of wheatears in S. W. Iran; 2) overlays 9-17 which show the altitudes and localities of wheatears that were on their breeding grounds or probably on their breeding grounds outside the breeding season; 3) figs. 22 and 23, pp. 99-100, which show the probable altitudinal ranges and geographical distributions of the breeding grounds of the various species; and 4) figs. 26 and 27, pp. 121-122, where the characteristics of the habitats of the various species while on their breeding grounds are given. The results of the comparisons are summarised in table 34 and form the basis for the following discussions of the ecological relationships between the various species of wheatear while on their breeding grounds in S. W. Iran.

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*O. pleschanka may breed occasionally in S. W. Iran but it has been omitted from the analysis for want of data.

SPECIES	MEANS OF SEPARATION				
	ALT	alt	GEOG	geog	hab/(hab)
ALLOPATRIC (10 pairs of species)					
O. alboniger/O. oenanthe	+				(+) (t)
O. alboniger/O. xanthoprymna	+				
O. deserti/O. oenanthe	+				(+) (trsv)
O. deserti/O. xanthoprymna	+				(+) (trs)
O. isabellina/O. oenanthe	+				(+) (r)
O. isabellina/O. xanthoprymna	+				(+) (tr)
O. lugens/O. picata	+				(+) (t)
O. oenanthe/O. xanthoprymna			+		(+) (trsv)
O. oenanthe/O. finschii			+		(+) (trsv)
O. oenanthe/O. hispanica					
ALLOPATRIC (5 pairs of species)					
O. alboniger/O. xanthoprymna		(+)			
O. alboniger/O. finschii		(+)			(+) (t)
O. alboniger/O. hispanica		(+)			(+) (t)
O. finschii/O. oenanthe		(+)			
O. finschii/O. xanthoprymna		(+)			
O. hispanica/O. oenanthe		(+)			(+) (t v)
O. hispanica/O. xanthoprymna		(+)			
O. lugens/O. oenanthe		(+)			(+) (t)
O. deserti/O. isabellina				(+)	
O. finschii/O. hispanica				(+)	(+) (v)
O. finschii/O. picata				(+)	
O. hispanica/O. lugens				(+)	(+) (v)
O. hispanica/O. picata				(+)	
CONSIDERABLE SYMPATRY (11 pairs of species)					
O. alboniger/O. deserti					(+) (tr v)
O. alboniger/O. isabellina					(+) (tr)
O. alboniger/O. lugens					(+) (t)
O. deserti/O. lugens					(+) (trs)
O. deserti/O. picata					(+) (trs)
O. finschii/O. isabellina					(+) (r)
O. hispanica/O. isabellina					(+) (tr v)
O. isabellina/O. lugens					(+) (tr)
O. isabellina/O. picata					(+) (tr)
O. oenanthe/O. xanthoprymna					(+) (t)
O. oenanthe/O. picata					
O. finschii/O. lugens					
O. lugens/O. picata					
SYMPATRIC (36 pairs of species)	8	8	2	5	24

Where both members of these pairs of species were found in the same locality they were invariably holding separate territories.

Table 24. Summary of comparisons between the altitudinal ranges, geographical distributions and habitats of wheatears on their breeding grounds in S. W. Iran.

	O. alboniger	O. deserti	O. finschii	O. hispanica	O. isabellina	O. lugens	O. oenanthe	O. picata
O. deserti	hab (trv)							
O. finschii	alt hab (t)	GEOG (hab) (trsv)						
O. hispanica	alt hab (t)	GEOG (hab) (trsv)	geog hab (v)					
O. isabellina	hab (tr)	geog	hab (r)	hab (trv)				
O. lugens	hab (t)	hab (trs)		geog hab (v)	hab (tr)			
O. oenanthe	ALT (hab) (t)	ALT (hab) (trsv)	alt	alt hab (tv)	ALT (hab) (r)	alt hab (t)		
O. picata		hab (trs)	geog	geog	hab (tr)		ALT (hab) (t)	
O. xanthoprymna	ALT	ALT (hab) (trs)	alt	alt	ALT (hab) (tr)	alt	hab (t)	ALT

KEY

ALT	=	Altitudinal ranges totally separate.
alt	=	Altitudinal ranges largely separate.
GEOG	=	Geographical distributions totally separate.
geog	=	Geographical distributions largely separate.
hab	=	Sympatric pairs of species with largely distinct habitats.
(hab)	=	Allopatric pairs of species with largely distinct habitats.
(t)	=	Habitats differ in topography.
(r)	=	Habitats differ in the occurrence of rock-outcrops and boulders.
(s)	=	Habitats differ in stone-cover.
(v)	=	Habitats differ in vegetation.
+	=	Total separation.
(+)	=	Partial separation.
	=	Blank space indicating overlap.

N.B. For definitions of categories denoting means of separation see pp. 210-212.

ECOLOGICAL ISOLATION - BREEDING GROUNDS

Main means of ecological segregation on the breeding grounds:

Nine species of wheatear are considered in the main analysis which gives 36 different combinations of pairs of species where the members could compete while on their breeding grounds in S. W. Iran. The data given in table 34 show that of these 36 pairs of species the members of ten pairs of species are allopatric; the members of six pairs of species are largely allopatric and have largely distinct habitats; the members of seven pairs of species are largely allopatric and the members of ten pairs of species show considerable sympatry but have largely distinct habitats. Therefore of the 36 pairs of species the members of 33 pairs of species are totally or largely separated spatially.

This leaves three pairs of species of wheatear (*O. picata*/*O. alboniger*, *O. picata*/*O. lugens* and *O. finschii*/*O. lugens*) where the members show considerable sympatry and occupy similar habitats in S. W. Iran. However comparisons of the world-wide breeding distributions of the members of these pairs of species show that in all three cases the areas of overlap in S. W. Iran are parts of relatively small zones of overlap and that the members of these pairs of species are largely segregated geographically (cf. fig. 18, p. 86 with fig. 10, p. 56 and fig. 15, p. 78 and the latter also with fig. 12, p. 65). The relationships between the members of these pairs of species in the areas where they overlapped in S. W. Iran are considered in the next section.

In addition to the nine species of wheatear that have been proved to breed in S. W. Iran, and which have already been discussed in this section, *O. monacha* probably breeds in small numbers and the means of ecological segregation between this species and the other nine will now be briefly considered. In the breeding season *O. monacha* is probably confined mainly to the badlands bordering the Persian Gulf but it may occur also in the sub-desert zone in the east of S. W. Iran. Its altitudinal range is probably from sea level to perhaps 1,000 m above sea level.* In S. W. Iran *O. monacha* is therefore sympatric only with

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* *O. monacha* was found breeding at about 1,000 m above sea level near Semman in northern Iran by D. A. Scott in July 1972.

O. alboniger from which it is probably largely segregated by habitat since it seems to be able to exist in badland areas with relatively little shade (see pp. 188-189 for clues to the reasons for this) whereas O. alboniger, especially in the hot lowland areas where it is sympatric with O. monacha, probably requires steep hillsides and cliffs which provide shaded feeding areas (see p. 126).

Relationships between species of wheatear that overlapped to some extent in range and habitat on their breeding grounds in S. W. Iran:

In the previous section it was shown that all the species of wheatear that breed in S. W. Iran are totally or largely segregated from one another while on their breeding grounds by spatial means. However table 34 shows that the members of 26 pairs of species overlapped to some extent in both range and habitat.* These pairs of species are singled out in table 35 and the aim of this section is to investigate the relationships between the members of these pairs of species in areas where they occurred together. This task was greatly facilitated by the fact that on their breeding grounds wheatears invariably live in well-defined territories where they both nest and feed. Studies of marked birds showed that they rarely left their own ground, even to drink, and could not usually be chased off it. When pursued they invariably circled back onto home-ground if a territorial boundary was reached. Such territorial tenacity, which is common to all the species of wheatear that occur in S. W. Iran, was well illustrated by Meinertzhagen (1954) who described the following case: "I found a pair of O. alboniger at Naft Khaneh in eastern Iraq. Their territory was a small vegetationless hill slope, made ugly by oil seepage; I endeavoured to drive them from their territory, which was mainly bitumen seepage, but they refused to go even a short distance from their inhospitable home in spite of many shots fired in their direction to alarm them ". Therefore by mapping territories, using the methods described on pp. 44-45, I was able to compare the areas of exploitation of all the wheatears in any locality.

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*The members of the 13 pairs of species of wheatear that were largely allopatric were sympatric at the edges of their ranges and the habitats of all species overlapped to some degree.

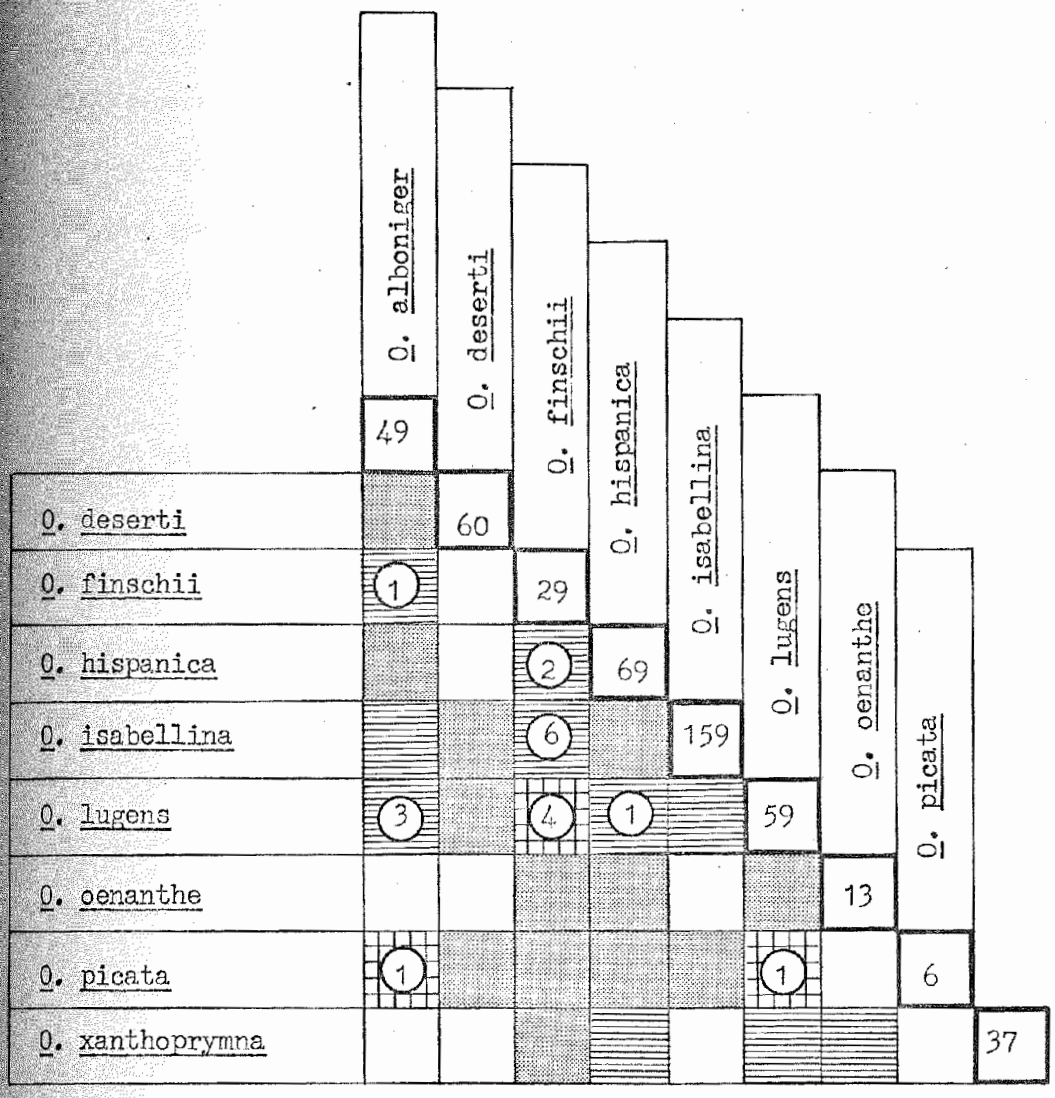

Table 35. Relationships between the members of pairs of species of wheatear that overlapped to some extent in range and habitat on their breeding grounds in S. W. Iran (based on table 34).

KEY

= Considerable overlap in range and habitat.

= Marginal overlap* + members recorded in same locality.

= Marginal overlap* + members not recorded in same locality.

71 = Number of breeding or probable breeding territories studied.

(3) = Number of records of interspecific territoriality (includes all cases where the territories of different species of wheatear were found to share a common boundary).

*The members of these pairs of species were either largely allopatric and overlapped only at the edges of their ranges or they showed considerable sympatry but lived in largely distinct habitats and overlapped only where these merged.

ECOLOGICAL ISOLATION - BREEDING GROUNDS

1) Pairs of species of wheatear where the members showed considerable overlap on their breeding grounds: In the previous section it was shown that the members of three pairs of species of wheatear (O. picata/O. alboniger, O. picata/O. lugens and O. finschii/O. lugens) showed considerable sympatry and occupied similar habitats while on their breeding grounds in S. W. Iran. The relationships between the members of these pairs of species will be discussed first:

O. picata/O. alboniger and O. picata/O. lugens: The members of these pairs of species do not present serious ecological overlap since O. picata, although widespread, is rare in S. W. Iran. Indeed the members of these pairs of species were found breeding in sight of one another at only one locality, the Shahpurjan study area, where in the spring of 1971 all three species bred side by side. In this situation the three species occupied apparently very similar habitat but their territories, although close together, were largely non-overlapping (fig. 44).

O. finschii/O. lugens: These species are partially segregated by their habitat preferences since O. finschii is found breeding on gently sloping hillsides and piedmonts more often than O. lugens while the latter often breeds high up on steep hillsides where O. finschii was not found breeding (fig. 26, p. 121 and table 36). However where gently sloping hillsides or piedmonts merge with steep hillsides both species are commonly found breeding in apparently identical habitats (cf. the territories of O. lugens, L1 and L2, in fig. 44 with the territories of O. finschii, F1-7, in fig. 45). In most of the localities where O. finschii and O. lugens were found breeding in S. W. Iran only one of the species was present and so there was no question of interspecific competition for territories in the intermediate foothill habitat. However, of the breeding territories of these species that I studied, nine territories of each species were in sight of breeding territories of the other. In these situations, although the territories of the two species were sometimes contiguous, they were never found to overlap more than marginally. Furthermore the intermediate foothill habitat was usually occupied by O. finschii while O. lugens was

SPATIAL RELATIONSHIP BETWEEN *O. FINSCHII* AND *O. LUGENS*	WHEATEAR SPECIES	NUMBER OF TERRITORIES STUDIED	PERCENTAGE OF TERRITORIES IN EACH HABITAT CATEGORY			PERCENTAGE OVERLAP IN HABITAT
			a) Gently sloping hillside or piedmont	b) Combination of a) and c)	c) Steep hillside	
ALLOPATRY + SYMPATRY: All territories of each species regardless of whether there were territories of the other species in sight or not - as in fig. 26, p. 121.	*O. FINSCHII*	29	52	48		63
	O. LUGENS	59	2	34	63	
ALLOPATRY: Territories of each species where there were no territories of the other species in sight.	*O. FINSCHII*	20	70	30		34
	O. LUGENS	50	4	38	58	
SYMPATRY: Territories of each species where there were territories of the other species in sight.	*O. FINSCHII*	9	11	89		11
	O. LUGENS	9		11	89	

Table 36. Habitat distribution of breeding territories of *O. finschii* and *O. lugens* in S. W. Iran both when the species were allopatric and when they were sympatric. For the method of calculating the percentage overlap in habitat see p. 212 and pp. 206-207.

mainly confined to steep hillsides (table 36, figs. 45 and 46). Although the difference between the habitat distribution of O. lugens in the presence of O. finschii and its habitat distribution in the absence of O. finschii is not statistically significant (chi-squared with two degrees = 2.842. P = 0.2 - 0.3) I think it is likely that in places where both species occurred O. lugens was excluded from the foothill habitat by competition from O. finschii but was able to breed unhindered high up on steep hillsides since these are apparently not favoured by O. finschii (table 36). This view is supported by the relative positions of the territories of the two species in localities where they both occurred, typical examples of which are shown in figs. 44 and 45. This view is also supported by the fact that three interspecific territorial border clashes involving O. finschii and O. lugens were observed, in all of which the former species was dominant.* In conclusion the ecological relationships between O. finschii and O. lugens may be summarised as follows: The two species are mainly segregated by having different world-wide breeding distributions but where they occurred side by side in S. W. Iran they usually occupied different habitats.

2) Pairs of species of wheatear where the members showed marginal overlap on their breeding grounds: The members of 23 pairs of species of wheatear overlapped marginally on their breeding grounds in S. W. Iran. These included 13 pairs of species where the members were largely allopatric and overlapped only at the edges of their ranges, and ten pairs of species where the members showed considerable sympatry but lived in largely distinct habitats and overlapped only where their habitats merged (table 34). These pairs of species are singled out and the relationships between their members are summarised in table 35. This shows that the members of only ten of these pairs of species were recorded in the same locality and the relationships between the members of these pairs are considered below:

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*In each case the clashes involved different individual birds. See chapter VIII, pp. 252-254 for full discussion of interspecific territorial border clashes.

ECOLOGICAL ISOLATION - BREEDING GROUNDS

O. alboniger/O. finschii, O. alboniger/O. isabellina, O. finschii/O. hispanica, O. finschii/O. isabellina, O. hispanica/O. xanthoprymna, O. isabellina/O. lugens and O. oenanthe/O. xanthoprymna: In localities where both the members of these pairs of species were found the members of the different species usually held widely separated territories in different habitats. However in a few cases (see table 35 for numbers) where their habitats merged, members of three of these pairs of species (O. alboniger/O. finschii, O. finschii/O. hispanica and O. finschii/O. isabellina) shared common territorial boundaries along which interspecific clashes were sometimes observed. Examples of the relative positions of the breeding territories of some of these pairs of species in localities where they both occurred are given in figs. 45 and 46.

O. alboniger/O. lugens: In localities where both these species were found breeding their territories were usually widely separated and in rather different habitats, those of O. alboniger almost always including some flat or gently sloping ground together with a section of steep hillside and/or cliff while the territories of O. lugens were usually confined to steep hillsides. However in a few cases O. lugens was found in territories that included cliffs and adjacent areas of more gently sloping ground, in other words in habitat typical of O. alboniger. Indeed the habitat in these territories of O. lugens was apparently very similar to the habitat in nearby territories of O. alboniger (e.g. cf. the territory of O. alboniger, A, with the territories of O. lugens, L1 and L2, in fig. 44 and the territories of O. alboniger, Aa, Ab, and Ac, with those of O. lugens, L1 and L2 in fig. 46). In most cases where O. alboniger and O. lugens occurred in the same area and occupied similar habitat their territories were widely separated but in two cases territories of the different species were found to lie side by side and to share a common boundary. Along these common boundaries interspecific skirmishes were observed in which O. alboniger was always dominant. This suggests that in the event of competition between these species for ground O. alboniger would exclude O. lugens and I think it is likely that O. lugens can occupy habitat suitable for O. alboniger

only when this is not disputed by the latter.* Some examples of the relative positions of breeding territories of O. alboniger and O. lugens in areas where they both occurred are given in figs. 44 and 46.

O. hispanica/O. lugens: O. hispanica and O. lugens were found breeding in the same locality only once. This was in the Tang-i-Shul study area where, in the spring of 1971, the two species occupied contiguous but largely non-overlapping territories (fig. 45). The habitat in these territories was apparently very similar steep rocky hillside and valley bottom. It therefore seems likely that if these species were both common in an area they would compete for ground to some extent.

O. lugens/O. xanthoprymna: These species were found breeding within sight of one another in only one locality. This was at about 2,700 m above sea level on Kuh-i-Lalehzar in eastern S. W. Iran during June 1971. On this mountain O. lugens and O. xanthoprymna were largely segregated from one another by differences in altitudinal range, the former occurring below about 2,700 m above sea level and the latter above this altitude. In the area where they occurred together both species held territories in similar habitat, namely on steep hillsides or in steep sided valleys. These territories were mostly widely separated but on one occasion an O. xanthoprymna was observed to twice attack an O. lugens which both times retreated. It seems probable, therefore, that these species would compete for ground if they were both common in the same area.

Ecological segregation on the breeding grounds in S. W. Iran - summary and conclusions:

1) Main means of segregation: Of the 36 pairs of species of wheatear where the members might compete while on their breeding grounds in S. W. Iran the members of 34 pairs of species were totally or largely

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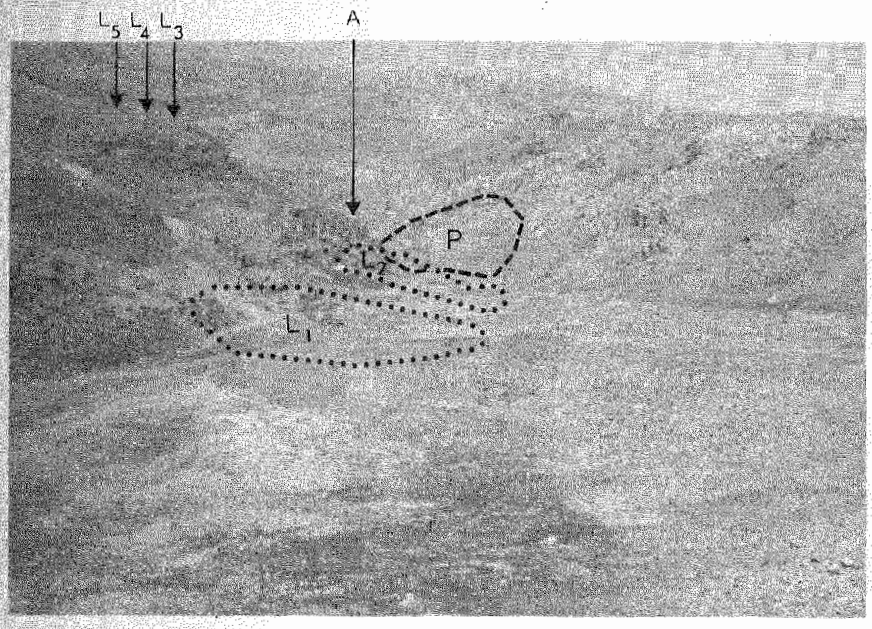
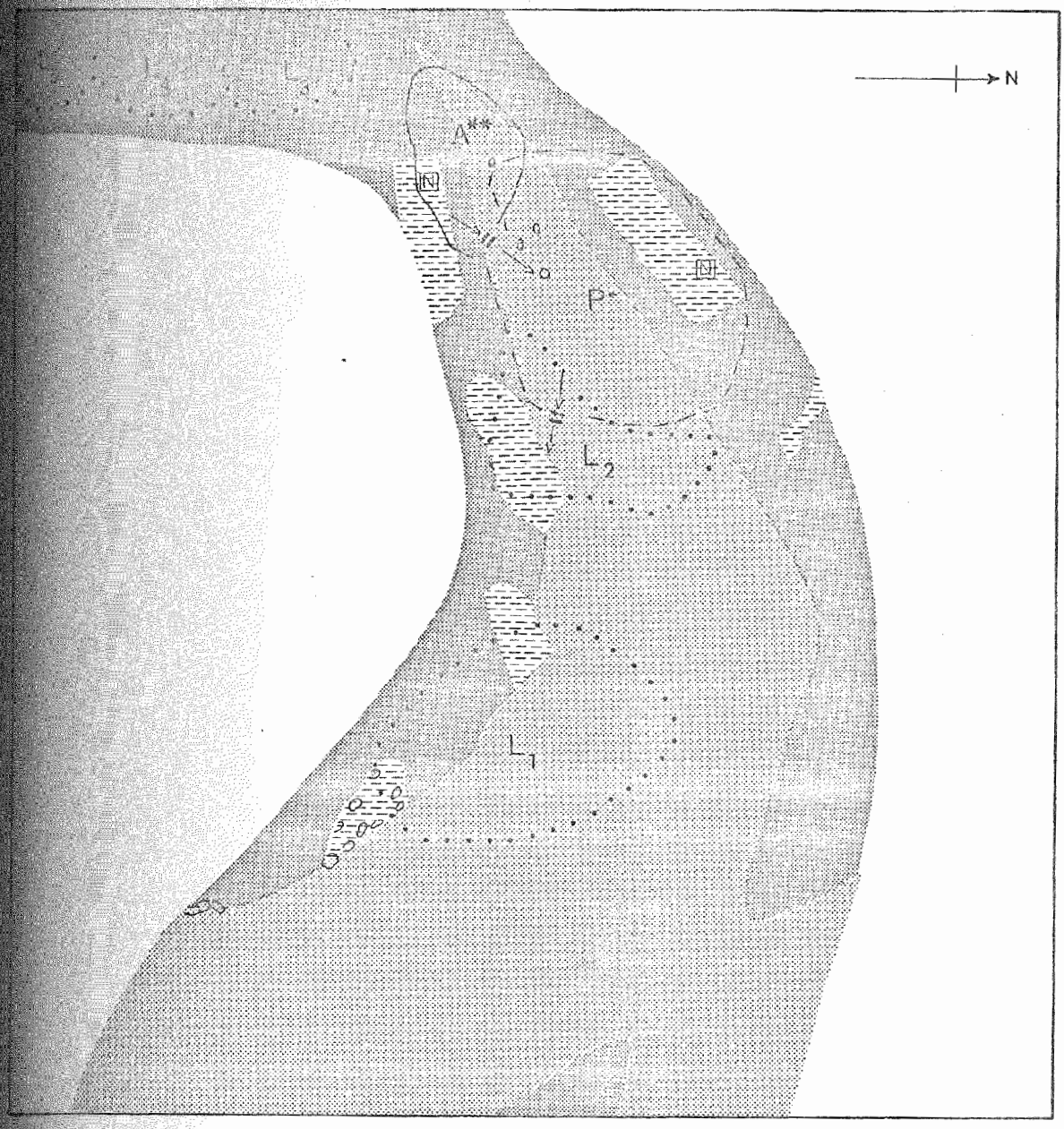
*See pp.252-254 for fuller discussion of interspecific competition.





Approximate scale: 0 100 metres

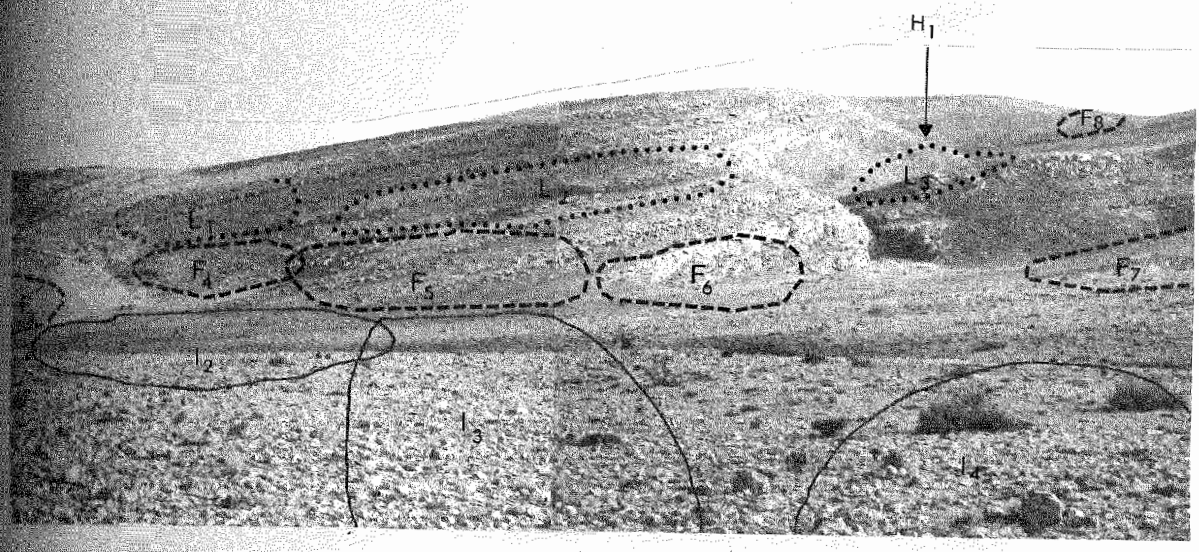
= Cliffs
= Steep hillsides
= Piedmont and valley bottom
= Not covered in detail
= Boulders
N = Nest

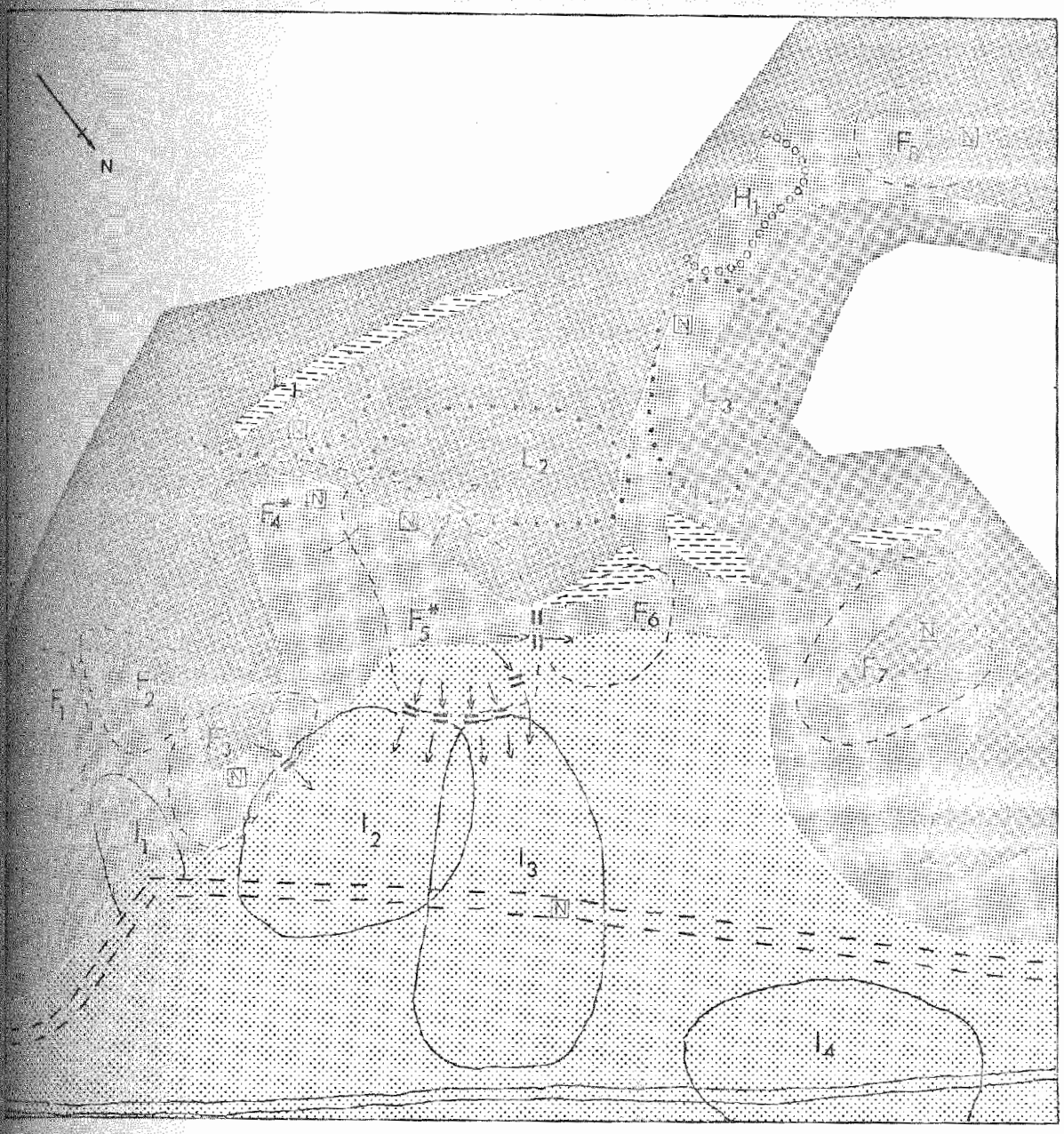
* = One member of pair colour-ringed
** = Both members of pair colour-ringed
→‖→ = Clash between wheatears with arrows indicating direction of movement of combatants

Approximate territorial boundaries:

O. alboniger (A) ····· O. lugens (L) ---- O. picata (P)

Figure 44. The Shahpurjan study area showing the breeding territories of wheatears in the spring of 1971.





Approximate scale: 0 ____ 100 metres

= Cliffs
= Steep hillsides
= Piedmont and valley bottom
= Flat open ground
= Not covered in detail
= Shallow dry runnel
= Road

N = Nest
* = One member of pair colour-ringed
→||→ = Clash between wheatears with arrows indicating direction of movement of combatants.

Approximate territorial boundaries:

- - - - - O. finschii (F)
~~~~~ O. isabellina (I)
°°°°°°°° O. hispanica (H)
. . . . . O. lugens (L)

Figure 45. The Tang-i-Shul study area showing the breeding territories of wheatears in the spring of 1971.
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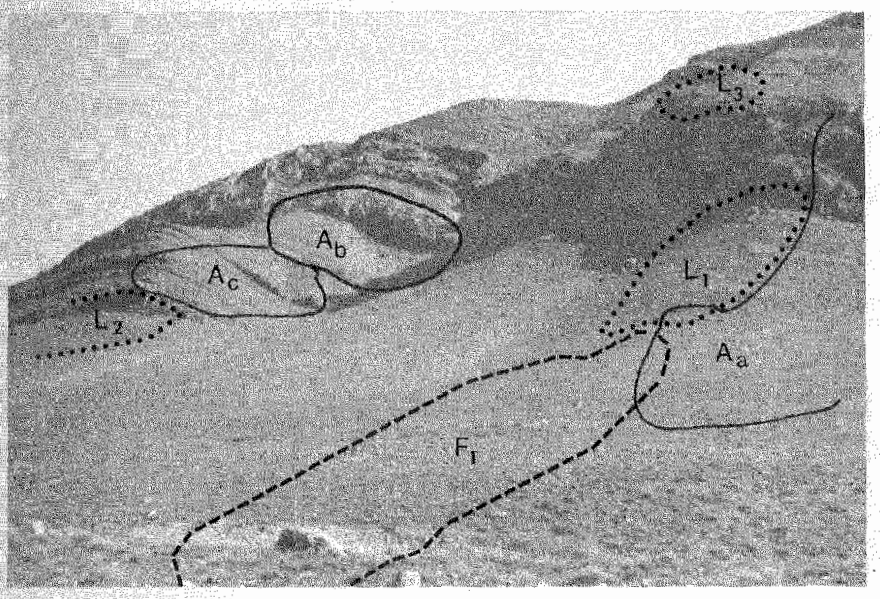

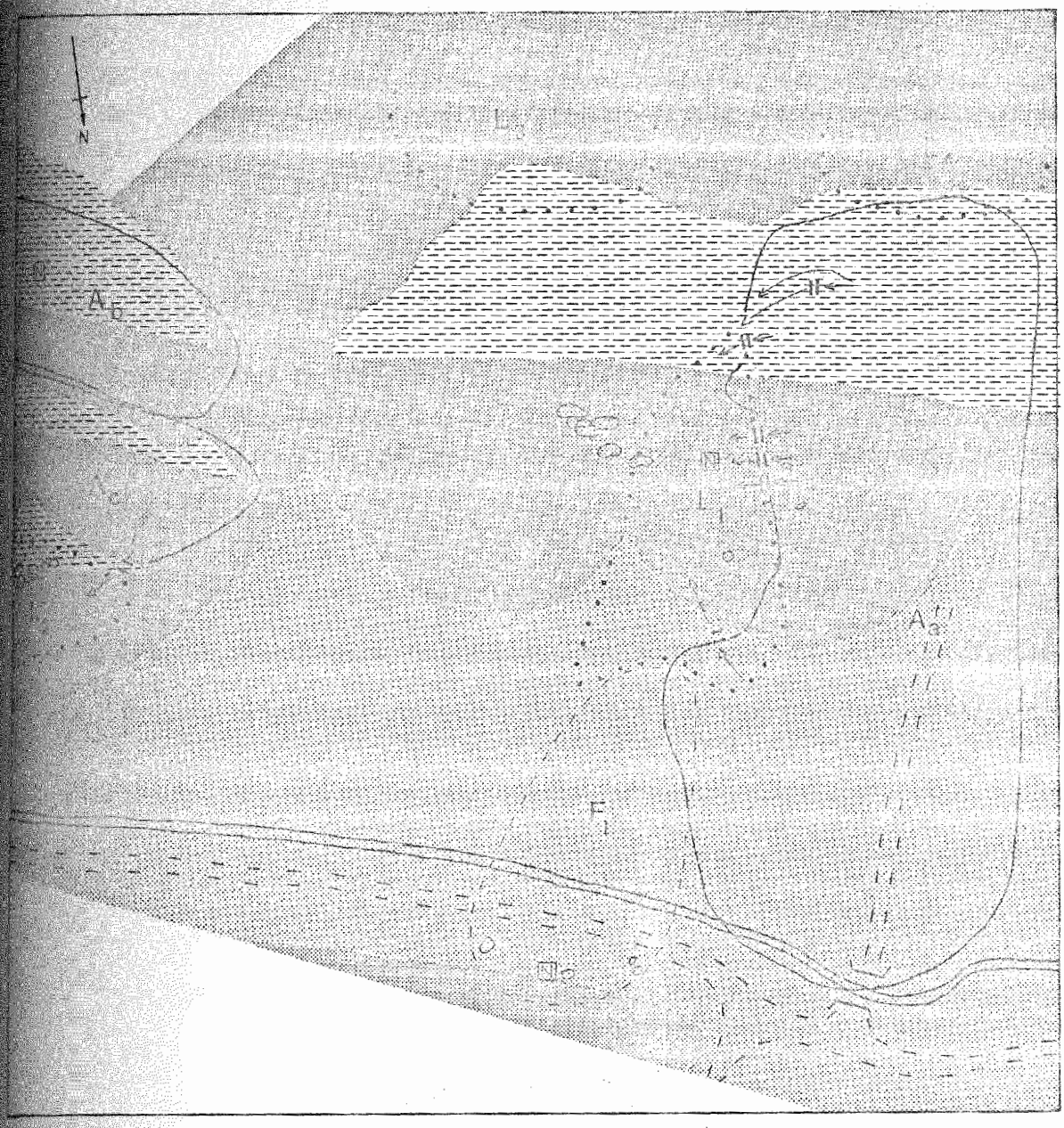

Approximate scale: 0 ——— 100 metres

= Cliffs
= Steep hillsides
= Piedmont and valley bottom
= Not covered in detail
= Boulders
= Shallow dry runnel
= Road
[N] = Nest
→||→ = Clash between wheatears with arrows indicating direction of movement of combatants.

Approximate territorial boundaries:

~~~ O. alboniger (A) - - - - - O. finschii (F) · · · · · O. lugens (L)

Figure 46. The Saadi study area showing the breeding territories of wheatears in the spring of 1971. (N.B. Individuals are identified by the same notations on this map and in table 5, p.57 & table 11, p.80.)
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segregated by differences in altitudinal range, geographical distribution and/or habitat.* The members of the remaining two pairs of species overlapped considerably in both range and ecology but they did not contravene Gause's hypothesis as they were rarely found in the same locality. The differences in the ranges and habitats of the various species are summarised in table 34 and in figs. 22 and 23, pp. 99-100.

2) Relationships between species that overlapped in range and habitat to some extent: The members of 26 pairs of species of wheatear overlapped to some extent in range and habitat on their breeding grounds in S. W. Iran (table 34) but of these the members of only 13 pairs of species were found together in the same locality. Of these 13 pairs of species the members of eight held territories in different habitats and shared common territorial boundaries only in a few cases where their habitats merged. The members of the remaining five pairs of species were sometimes found holding territories near one another in apparently very similar habitats. However these territories were never found to overlap more than marginally and they were always in areas where there was apparently suitable, untenanted ground nearby which suggested that there was unlikely to have been severe interspecific competition for territories. It may therefore be stated in conclusion that little ecological overlap was found between species of wheatear on their breeding grounds in S. W. Iran and that in the few cases where ecological overlap was found, that is where different species occupied similar habitat in the same locality, the birds were spatially separated in largely non-overlapping territories and were at low densities which suggested that there was little competition for ground.

2) ECOLOGICAL SEGREGATION BETWEEN SPECIES OF WHEATEAR ON THEIR WINTERING GROUNDS IN S. W. IRAN:

Five species of wheatear are considered in this section. These include O. alboniger, O. finschii and O. xanthoprymna which are common

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*This includes the 33 pairs of species shown to be segregated in these ways in table 34 and O. finschii/O. lugens (see pp. 218-220).

and widespread in S. W. Iran during the winter and O. deserti and O. isabellina which probably winter in small numbers, mainly on the coastal plain of the Persian Gulf.* Of these, most O. alboniger and possibly a few O. deserti and O. finschii are residents while the rest are winter visitors (fig. 21, p. 97). The aim of this section is to consider the ecological relationships between these species with a view to determining whether they are ecologically segregated from one another in winter as well as during the breeding season.

Altitudinal range, geographical distribution and habitat:

Comparisons of the altitudinal ranges, geographical distributions and habitats of the various species of wheatear that winter in S. W. Iran were based on the following data: 1) overlays 9-12 and 17 which show the altitudes and localities of records of wheatears wintering or probably wintering in S. W. Iran; 2) fig. 24, p. 101 which shows their probable altitudinal ranges and geographical distributions in S. W. Iran; 3) fig. 10, p. 56; fig. 11, p. 59; fig. 12, p. 65; fig. 14, p. 72 and fig. 20, p. 92 which show the world-wide wintering distributions of the various species; and 4) fig. 28, p. 123 which gives the characteristics of the habitats in the winter territories of the various species in S. W. Iran. The results of the comparisons are summarised in table 37 and form the basis of the following discussions of the ecological relationships between species of wheatear on their wintering grounds in S. W. Iran.

Main means of ecological segregation on the wintering grounds:

Five species of wheatear are considered in this section which gives ten combinations of pairs of species where the members might compete. The members of all these pairs of species show considerable sympatry in S. W. Iran in winter but the members of five of them live in largely distinct habitats (table 37). This leaves five pairs of species where the members overlap considerably in both range and habitat in S. W. Iran in winter and the relationships between the members of these pairs of species are considered in the next section. However before proceeding

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* In addition O. monacha and O. picata probably winter in S. W. Iran in small numbers but these species have been omitted from the analysis as they were recorded only occasionally.

	O. alboniger	*O. deserti*	*O. finschii*	*O. isabellina*
O. deserti	(geog) hab (trs)			
O. finschii	hab (t)	(geog)		
O. isabellina	(geog) hab (tr)		(geog)	
O. xanthoprymna		hab (trs)		hab (trs)

Table 37. Summary of comparisons 1) between the world-wide wintering distributions of the five species of wheatear that winter in S. W. Iran and 2) their habitats in S. W. Iran in winter.

N. B. All five species show considerable sympatry in winter within S. W. Iran.

KEY

(geog) = World-wide wintering distributions largely separate.

hab = Habitats in S. W. Iran largely distinct (see p. 212).

(t) = Habitats differ in topography.

(r) = Habitats differ in the occurrence of rock-outcrops and boulders.

(s) = Habitats differ in stone-cover.

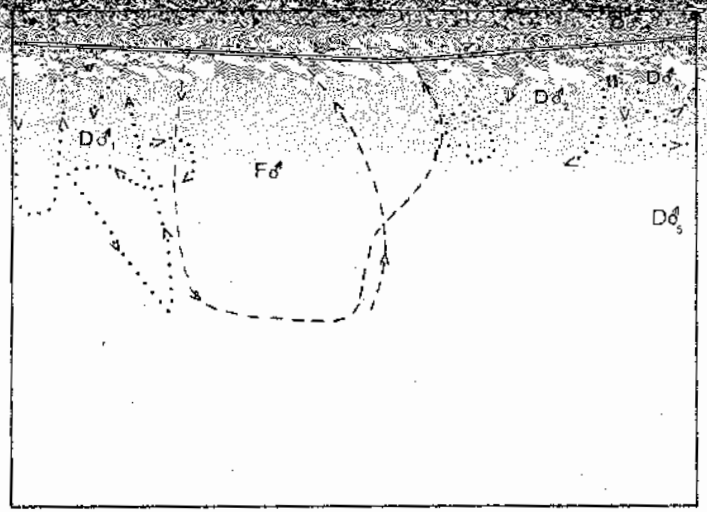
= Blank space indicating considerable overlap.

to the next section it is worth pointing out that comparisons of the world-wide wintering distributions of the members of these five pairs of species showed that the members of two of them (O. finschii/O. deserti and O. finschii/O. isabellina) are largely segregated geographically and that the areas of overlap in S. W. Iran are parts of relatively small zones of overlap (cf. fig. 12, p. 65 with fig. 11, p. 59 and fig. 14, p. 72).

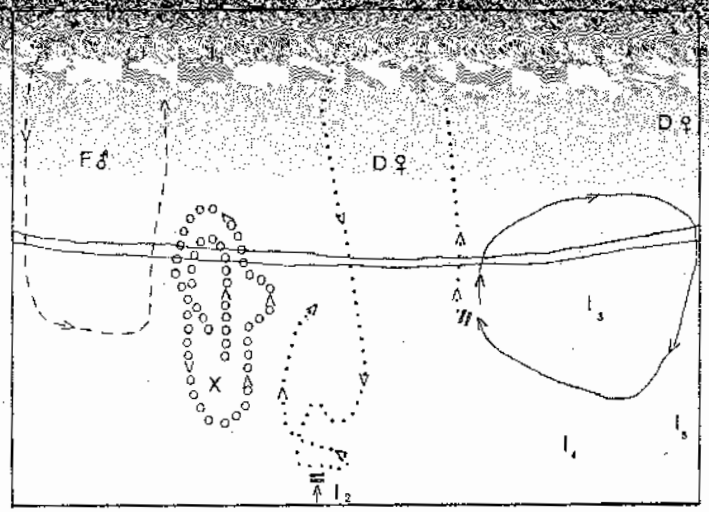
Relationships between species of wheatear that overlapped to some extent in range and habitat on their wintering grounds in S. W. Iran:

1) Pairs of species of wheatear where the members showed considerable overlap on their wintering grounds: The members of five pairs of species of wheatear showed considerable overlap in distribution and habitat in S. W. Iran during the winter (table 37) and the relationships between the members of these pairs will be considered below:

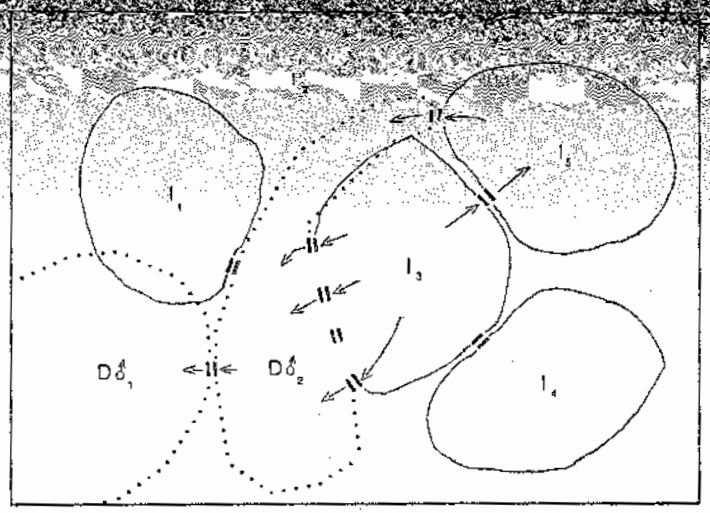
O. deserti/O. finschii, O. deserti/O. isabellina and O. finschii/O. isabellina: In S. W. Iran O. deserti, O. finschii and O. isabellina were all found wintering or probably wintering on plains from sea level to about 800 m above sea level (fig. 24, p. 101). However little ecological overlap was found between the members of these pairs of species of wheatear since their numbers were small and the different species were rarely found in the same locality. Indeed the members of the pairs of species O. deserti/O. finschii and O. deserti/O. isabellina were found together in only five localities while O. finschii and O. isabellina were found together only twice. In these localities where two or more species of wheatear occurred, all the wheatears present were found to be holding individual territories which were largely non-overlapping although members of different species sometimes had common territorial boundaries (see fig. 47 for examples). The habitat in all these localities was uniform, dry, largely bare, alluvial plain with scattered shrublets and the different species of wheatear appeared to have very similar ecology. However there was always some ground which was not tenanted by wheatears and I think it is probable that the different species were able to coexist side by side in the same habitat,



20 January 1973. Near Bandar Mashur, Khuzistan (about 80km WNW of Butari).



21 January 1973. Near Butari.



1 February 1971. Near Dalaki (for location see fig.7, p.42). In this map only outer limits of movements of each bird are shown.

Approximate scale: 0 ——— 100 metres

Habitat: In all three localities the habitat was similar, flat alluvial plain with scattered shrublets (mostly Chenopodiaceae) in patches.

KEY

= Oil pipe-line

= Track

→‖→ = Clash between wheatears with arrows indicating direction of movement of combatants.

Movements of wheatears:

..... O. deserti (D)

- - - - - - - O. finschii (F)

~~~~~ O. isabellina (I)

°°°°°°°°°° O. xanthoprymna xanthoprymna (X)

Figure 47. Distribution of wheatears at three localities on the coastal plain of the Persian Gulf in winter.
~~~~~

in these cases, because the densities of birds were low with the result that there was little competition for territories. Indeed if interspecific competition had been severe I believe that the various species would probably have been found in different areas. In interspecific clashes O. finschii was invariably dominant to both O. deserti and O. isabellina (see pp. 252-254). Therefore in the event of competition O. finschii would probably occupy all the ground for which it competed. However O. deserti and O. isabellina are probably better adapted for life on plains than O. finschii and they could probably survive in drier less productive areas unhindered by competition from O. finschii.* In clashes between O. deserti and O. isabellina the latter was invariably dominant (see pp.252-254) and therefore in the event of competition between these species O. isabellina would probably oust O. deserti from from all disputed ground. However O. deserti can probably live in even drier and less productive areas than O. isabellina* and it would probably be able to remain unhindered in such areas.

O. alboniger/O. xanthoprymna: These species were found to be sympatric over large areas of S. W. Iran in winter (fig. 24, p. 101) and both species were commonly found near one another on steep hillsides and especially along the bases of rocky hillsides (fig. 28, p. 123). As with other species of wheatear O. alboniger and O. xanthoprymna hold solitary territories during the winter and in localities where both species occurred their territories rarely overlapped more than marginally. Indeed their territories were mostly widely separated although in eight cases members of the different species shared territorial boundaries. Some examples of the relative positions of territories of O. alboniger and O. xanthoprymna in localities where they were both found wintering are given in figs. 48-50. Therefore although O. alboniger and O. xanthoprymna do not overlap spatially in winter in S. W. Iran they apparently have very similar ecology. However in localities where the two species occurred side by side there was always some ground which looked suitable

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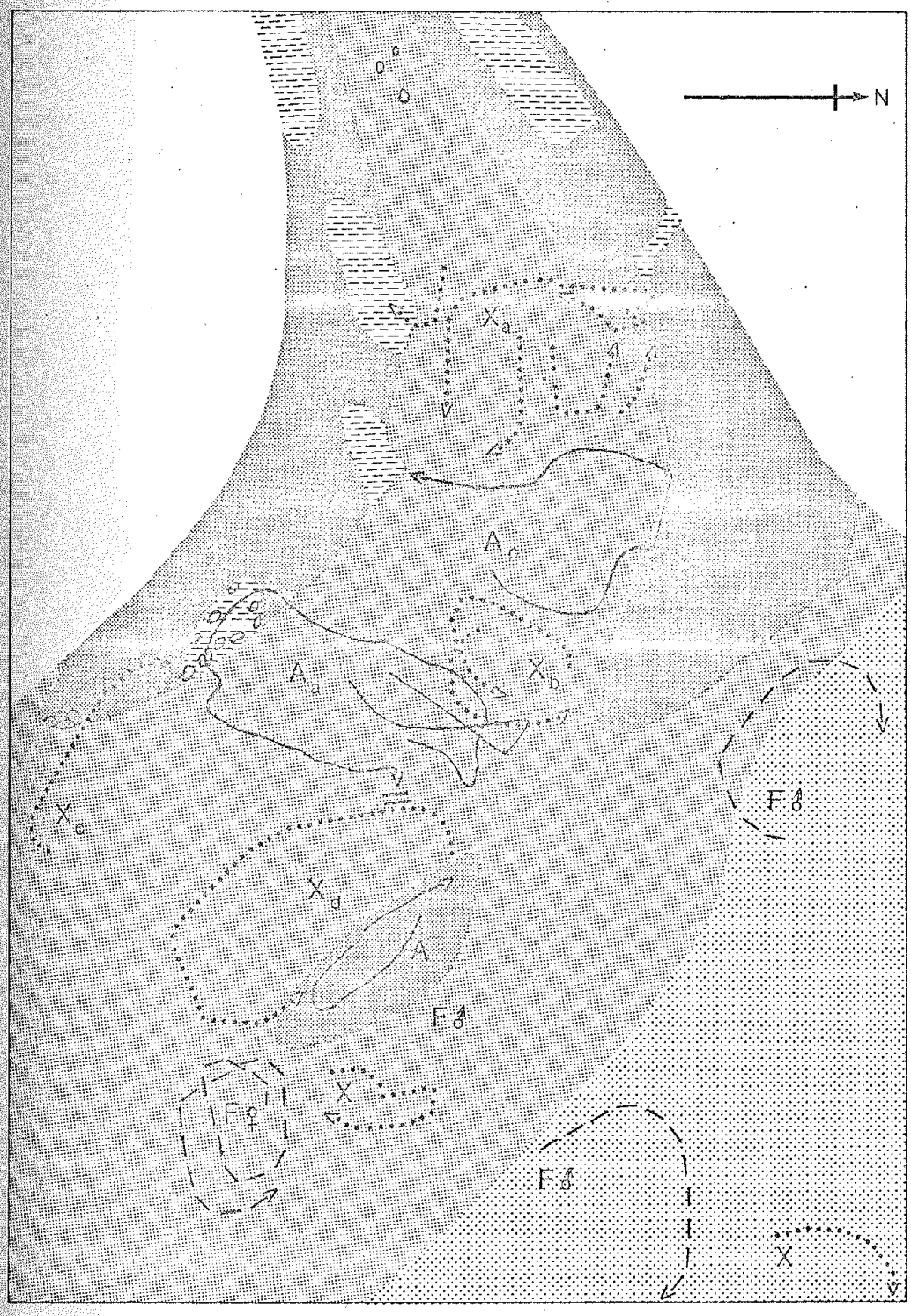
*See chapter VIII for discussions of the adaptations of the various species of wheatear.



Approximate scale: 0 100 metres

= Cliffs
= Steep hillsides
= Piedmont and valley bottom
= Flat stony plain
= Boulders

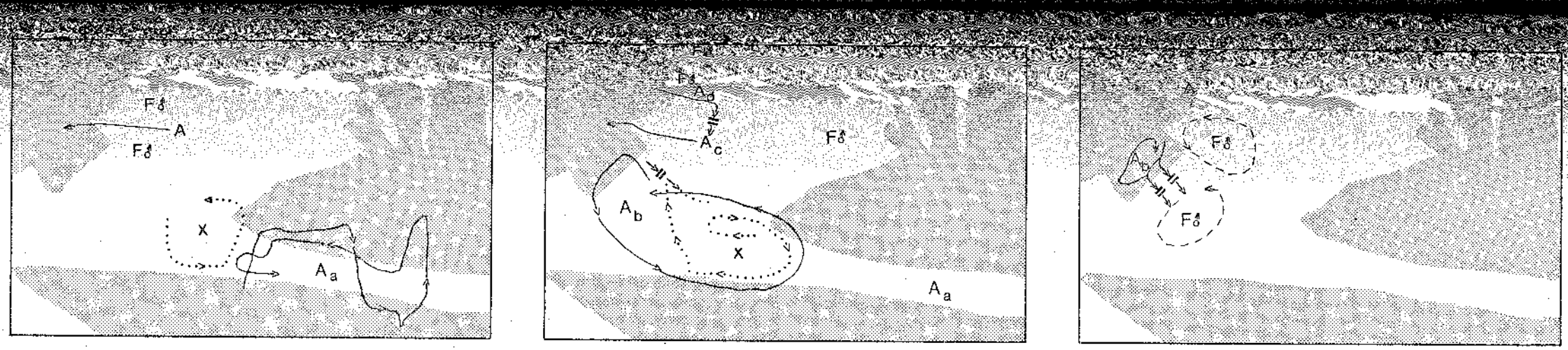
= Not covered
= Clash between wheatears with arrows indicating direction of movement of combatants

Movements of wheatears:

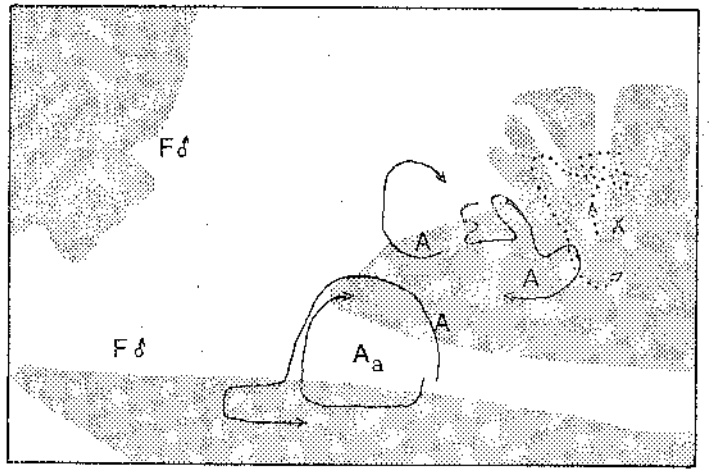
———— O. alboniger (A)
– – – – – O. finschii (F)
..... O. xanthoprymna (X)

Figure 48. Distribution of wheatears at the Shahpurjan study area on 30 December 1970 (see fig. 44, p. 223 for photograph of the area).

(N. B. Individuals are identified by the same notations on this map and in table 5, p. 57 & table 15, p. 93.)



18 FEBRUARY 1971



Approximate scale: 0 100 metres

KEY

= Rocky hillsides and cliffs

= Flat plain, piedmont and valley bottom

→II→ = Clash between wheatears with arrows indicating direction of movement of combatants

Movements of wheatears:

~~~ O. alboniger (A)

- - - - - O. finschii (F)

..... O. xanthoprymna (X)

Figure 49. Distribution of wheatears at Maharlu Valley, near Shiraz, on four days in January-February 1971. (N. B. Individuals are identified by the same notations on these maps and in table 5, p. 57 & table 15, p. 93.)
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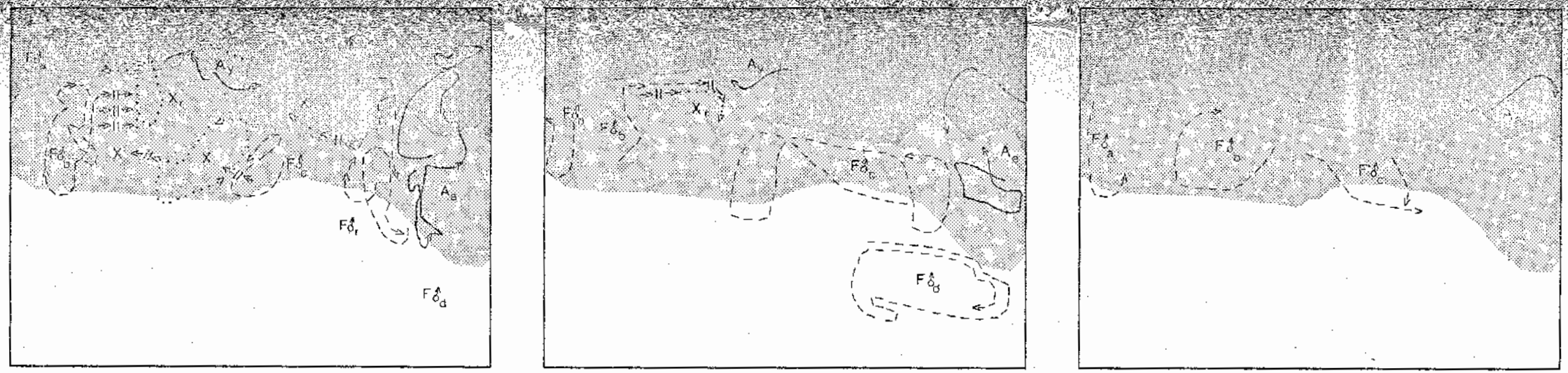

KEY

= Rocky hillsides
= Piedmont
= Flat plain

→||→ = Clash between wheatears with arrows indicating direction of movement of combatants

y = yellow coloured ring

r = red and yellow coloured rings

N.B. On 7 January $F\delta_r$ was caught and released 20km away at Bardeh. He was not seen again at Maharlu South.

Movements of wheatears:

~~~~ O. alboniger (A)

------- O. finschii (F)

..... O. xanthoprymna (X)

Figure 50. Distribution of wheatears in the Maharlu South study area, near Shiraz, on three days in January 1971.

(N. B. Individuals are identified by the same notations on these maps and in table 5, p. 57 & table 15, p. 93.)
~~~~

for these species but which was untenanted. This suggests that competition for territories was not severe and I believe that this is the reason why these species were able to coexist in this way. Indeed in skirmishes O. alboniger was invariably dominant to O. xanthoprymna (see pp. 252-254) and in the event of competition for territories O. alboniger would probably oust O. xanthoprymna from all disputed ground. In fact this is probably what happened in the Maharlu Valley in January 1971 (see fig. 49). Therefore if competition between these species were severe it seems likely that O. alboniger would prevail on all contested ground and that O. xanthoprymna would be forced into habitats and/or parts of its range which were not disputed by O. alboniger.

O. finschii/O. xanthoprymna: The world-wide wintering range of O. xanthoprymna is largely within the world-wide wintering range of O. finschii (cf. figs. 12, p. 65 and fig. 20, p. 92) and the two species are sympatric in winter over large areas of S. W. Iran (fig. 24, p. 101). In S. W. Iran in winter the two species differ to some extent in their selection of habitats, O. finschii being found more on open plains and O. xanthoprymna more along the bases of rocky hillsides and also high up on steep rocky hillsides where O. finschii was not found (fig. 28, p. 123). Nevertheless O. finschii and O. xanthoprymna were often found in the same locality holding territories in similar habitat.* These territories were usually widely separated but in ten cases individuals of the different species were found holding contiguous territories (see figs. 48-51 for examples). In two cases (illustrated in figs. 50 and 51) territories of O. finschii and O. xanthoprymna were found to overlap, but in both

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*The figures for the percentage overlap in the occurrence of various habitat characteristics in the territories of O. finschii and O. xanthoprymna in S. W. Iran in winter were as follows: topography 47%, the occurrence of rock outcrops and boulders 63%, stone-cover 60% and vegetation 92% (see pp. 211-212 for method of calculation). These figures are based on all the territories of each species that were studied regardless of whether the other species was present (i.e. the data presented in fig. 28, p. 123). However similar results were obtained when sympatric territories and allopatric territories were compared separately. There was therefore no indication that the habitat distribution of either species was influenced by the presence of the other.

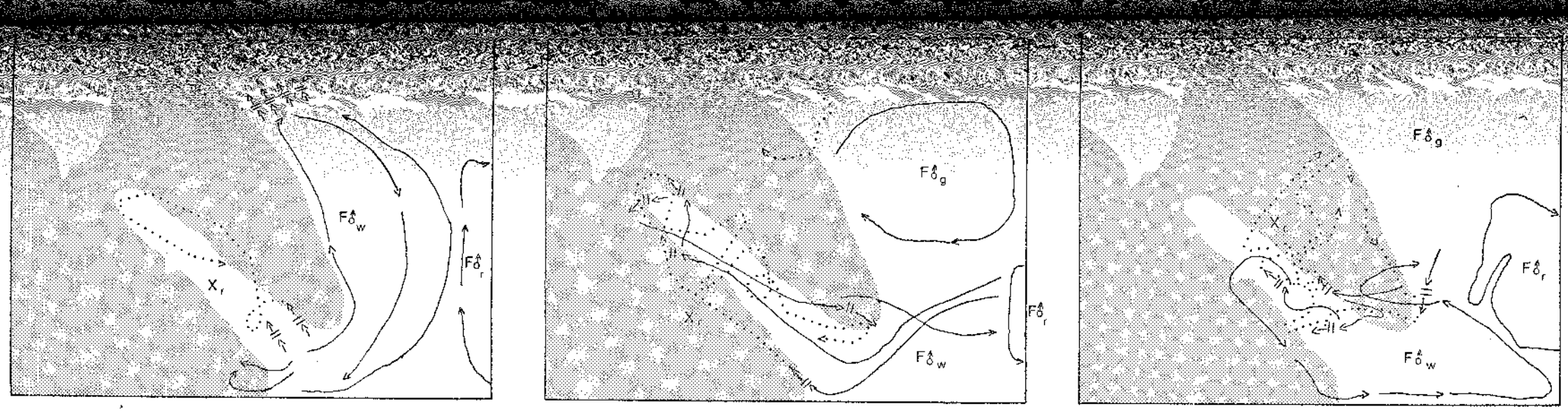

Figure 51. Distribution of wheatears in part of the Maharlu North study area, near Shiraz, on four days during the 1970-71 winter.

(N. B. Individuals are identified by the same notations on these maps and in table 8, p. 66 & table 15, p. 93.)

instances the period of overlap was relatively short and, after much interspecific skirmishing, ended with the disappearance of the O. xanthoprymna. Thus in S. W. Iran in winter O. finschii and O. xanthoprymna were rarely found to overlap spatially but they appeared to overlap considerably in ecology. However, as in the other cases of ecological overlap in winter that were discussed above, O. finschii and O. xanthoprymna were never found side by side in areas where all the apparently suitable ground was occupied by wheatears. Therefore, as in the other cases, I believe that O. finschii and O. xanthoprymna were able to coexist in similar habitats because the densities of birds were low with the result that there was probably little competition for territories. Indeed in interspecific clashes O. finschii was invariably dominant to O. xanthoprymna (see pp.252-254) and if the two species competed for territories O. finschii would probably prevail. In fact this is probably what happened in the cases of territorial overlap shown in figs. 50 and 51. Therefore in the event of severe competition between these species O. xanthoprymna would probably be forced into habitats and/or areas which were not contested by O. finschii. However these species may rarely compete in winter since for two reasons it seems likely that wintering ground may be superabundant: 1) The wintering ranges of both species are larger than their breeding ranges (fig. 12, p. 65 and fig. 20, p. 92) and this is especially true in the case of O. xanthoprymna which winters from sea level to about 2,000 m above sea level whereas it is restricted to ground above about 2,500 m above sea level in the breeding season. 2) Both species occur in a wider range of habitats during the winter than during the breeding season (cf. figs. 26, p. 121 with fig. 28, p. 123 and see pp. 132 and 151).

2) Pairs of species of wheatear where the members showed marginal overlap in winter: The members of five pairs of species of wheatear showed considerable sympatry in S. W. Iran in winter but were largely segregated from one another by living in distinct habitats (table 37). However the members of all these pairs of species of wheatear overlapped in habitat to some extent and the relationships between the members of these pairs of species in localities where they both occurred are

examined below:

O. alboniger/O. deserti and O. alboniger/O. isabellina: The members of these pairs of species were never found together in the same locality.

O. alboniger/O. finschii: These species were often found in the same locality but in most cases their territories were widely separated with those of O. alboniger usually including areas of steep rocky hillside while those of O. finschii were mainly confined to flat or gently sloping ground. However in 11 cases on piedmonts or on flat ground adjacent to steep hillsides O. alboniger and O. finschii were found holding contiguous territories. Some examples of the relative positions of territories of O. alboniger and O. finschii in localities where they both occurred are given in figs. 48-50. O. alboniger and O. finschii were therefore never found to show serious spatial overlap in S. W. Iran although they showed marginal overlap in ecology. However in all clashes between these species, that I observed, O. alboniger was dominant (see pp.252-254) and so in the event of competition for ground O. alboniger would probably prevail.

O. deserti/O. xanthoprymna and O. isabellina/O. xanthoprymna: The members of these pairs of species were found together at only one locality. This was near Butari on the coastal plain of the Persian Gulf where, in January 1973, all three species were found holding largely non-overlapping territories on an apparently uniform plain (fig. 47). However there was plenty of ground in the vicinity which was apparently suitable for wheatears but which was not occupied and I therefore doubt whether these territories were held in the face of severe interspecific competition.

Ecological segregation on the wintering grounds in S. W. Iran - summary and conclusions:

1) Main means of ecological segregation: Of the ten pairs of species of wheatear where the members might compete while on their wintering grounds in S. W. Iran the members of five pairs of species were

largely segregated by living in different habitats (table 37). The members of the remaining five pairs of species overlapped considerably in both range and ecology. However none of these pairs of species represented exceptions to Gause's hypothesis as their members were either rarely found in the same locality or occurred in such low densities that interspecific competition was unlikely. The ecological relationships between the various species of wheatear that occur in S. W. Iran in winter are summarised in table 37 and fig. 24, p. 101.

2) Relationships between species that overlapped in range and habitat to some extent: The members of all of the ten pairs of species of wheatear that were considered in this section overlapped in range and habitat to some extent (table 37). Of these the members of two pairs of species (O. alboniger/O. deserti and O. alboniger/O. isabellina) were never found in the same locality; the members of six pairs of species were occasionally found near one another in the same habitat while the members of the remaining two pairs of species (O. alboniger/O. xanthoprymna and O. finschii/O. xanthoprymna) were often found side by side in the same habitat. In cases where different species were found side by side in the same habitat they appeared to have very similar ecology. However their territories were rarely found to overlap more than marginally and there was invariably ground nearby which looked suitable for wheatears but which was unoccupied. I therefore believe that the wheatears of different species that wintered side by side in the same habitat were able to do so because their densities were low with the result that there was little interspecific competition. However in skirmishes between the members of the different pairs of species of wheatear the same species was invariably dominant (see pp. 252-254) which suggests that in the event of severe interspecific competition the dominant species would oust the subordinate one from all disputed ground. However the subordinate species all differed to some extent from the dominant ones in both range and habitat and it seems likely that in the event of severe interspecific competition they would be able to survive in habitats and/or areas which were not contested by the dominant species.

Therefore although, as in some other areas (see p. 7), some species of wheatear appeared to be imperfectly segregated in S. W. Iran in winter I believe that mechanisms for their segregation exist and that if there were severe interspecific competition the various species would become clearly segregated by differences in habitat and/or range.

GENERAL CONCLUSIONS:

The ecological relationships between different species of wheatear while on their breeding and wintering grounds in S. W. Iran are summarised in table 38, and the following general comments may be made about these relationships:

1) Although the patterns of coexistence between different species of wheatear in S. W. Iran are rather complex, careful comparisons of their ranges and habitats revealed that most of them avoid competition by living in different places. This spatial segregation is achieved by the species having different altitudinal ranges, different geographical distributions or living in different habitats. In places where different species were found side by side in the same habitat they were invariably holding largely non-overlapping territories. Since the various species of wheatear have similar ecological requirements and would probably compete if they remained on the same ground for any length of time their spatial segregation in S. W. Iran is consistent with, and provides indirect evidence for Gause's hypothesis (p. 8).

2) Nevertheless different species of wheatear were frequently found holding territories near one another in the same habitat and appeared to have very similar ecology. Initially I gave inflated importance to these cases which led me to believe that the species concerned were imperfectly segregated. However when viewed in the context of the total ranges and habitat distributions of the species in question, cases of ecological overlap were seen to be relatively few and to occur mainly where the ranges or habitats of species overlapped marginally. Furthermore ecological overlap was observed only in places where there was some

RELATIONSHIPS BETWEEN MEMBERS OF PAIRS OF SPECIES OF WHEATEAR	BREEDING GROUNDS		WINTERING GROUNDS	
	No.of pairs of species	Proportion	No.of pairs	Proportion
A Totally or largely segregated by:				
1) Altitudinal range.	16	44%		
2) Geographical distribution.	7	19%		
3) Habitat.	11	31%	5	50%
B Overlapped considerably in both range and ecology but:				
1) Rarely found in the same locality.	2	6%	3	30%
2) Where the different species occurred side by side there was always apparently suitable, untenanted ground nearby which suggested that inter-specific competition was unlikely to have been severe.			2	20%
TOTALS:	36		10	

Table 38. Summary of the ecological relationships between different species of wheatear while on their breeding and wintering grounds in S.W. Iran.

apparently suitable ground that was unoccupied by wheatears which suggested that interspecific competition was unlikely to have been severe. Therefore, since competitive exclusion is a theoretical necessity only when two species compete for a limited resource, these cases of ecological overlap did not contravene Gause's hypothesis. Indeed if interspecific competition had been severe I have no doubt that the various species would have been more perfectly segregated by range and/or habitat.

CHAPTER VIII

FACTORS THAT INFLUENCE THE RANGES AND HABITAT DISTRIBUTIONS OF WHEATEARS IN S. W. IRAN

INTRODUCTION:

In chapters IV, V and VII the ranges and habitat distributions of wheatears in S. W. Iran were described and compared and the results were summarised in figures 22-24, pp. 99-101. In this chapter an attempt is made to explain these distribution patterns.

The range and habitat distribution of a species depend upon the interactions of two sorts of factors: 1) the characteristics of the species which define the environmental conditions in which it can survive; and 2) the opportunities and restraints presented by the complex array of physical and biological variables that make up the environment. As a result a species will be found only in areas: a) which are within the range of its powers of dispersal; b) where the environmental conditions do not exceed its range of tolerance; c) where its minimum requirements are satisfied; and d) where it is not eliminated by disease, predation or competition. Furthermore the principle of competitive exclusion (p. 8) carries with it the implication that in a mature community, where the member species are in dynamic equilibrium with one another and with the other components of the environment, each species will be better adapted to exploit its own range and habitat than any competitor.

In the light of the foregoing ideas the distribution patterns of wheatears in S. W. Iran present two related problems which are considered in this chapter:

1) The ranges and habitat distributions of the various species of wheatear in S. W. Iran are more or less restricted and the environmental factors that limit these distributions are often obscure since their boundaries rarely coincide with any obvious deficiency or restraint in the environment.

2) The ranges and/or habitat distributions of most species of wheatear in S. W. Iran differ from one another and since these distribution patterns are probably mature and in equilibrium with the environment* this suggests that the various species have different adaptations which enable them to survive in their respective ranges and habitats. However these adaptations are often obscure since the various species are all rather similar in size, morphology and broadly speaking in their ecological requirements.

Therefore in this chapter I aim a) to discover the environmental factors that limit the ranges and habitat distributions of the various species of wheatear that occur in S. W. Iran; and b) to determine the adaptive differences between the various species that account for the interspecific differences in range and habitat.

It would be a prodigious task to try and consider all the environmental factors that might influence the ranges and habitat distributions of wheatears in S. W. Iran or to consider all the possible adaptive differences between the various species. Therefore in this study I consider only environmental factors and adaptations that are likely to be critical in explaining the distribution patterns. These include the following: 1) Environmental factors: climate, particularly temperature, rainfall and humidity; the availability of food and habitat requirements; predation and interspecific competition. I have no evidence that disease limits the distribution of wheatears. 2) Adaptations: adaptations for survival under different climatic conditions; and adaptations for life in different habitats such as differences in coloration, feeding strategies and morphology.

The chapter is divided into two parts: In part I some of the environmental limiting factors and adaptations are considered in general terms and then in part II the factors that influence the range and habitat

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* I know of no evidence to suggest that there have been any recent ecological changes in S. W. Iran which might have upset the equilibrium between the various species of wheatear and their environments, nor is there any evidence that any species of wheatear have recently extended their ranges into the area or become extinct there.

distribution of each species of wheatear in S. W. Iran are considered for each species in turn.

PART I. ENVIRONMENTAL LIMITING FACTORS AND ADAPTATIONS OF WHEATEARS - GENERAL TREATMENT:

1) CLIMATE AND ADAPTATIONS TO CLIMATE:

If climate influences the distributions of wheatears in S. W. Iran it is most likely to affect the broad patterns of altitudinal range and geographical distribution and the aims of this section are: 1) to assess in general terms the possible role of climate in limiting the distributions of wheatears in S. W. Iran; and 2) to consider whether any of the inter-specific differences in distribution might be explained in terms of inter-specific differences in tolerance to climatic factors.

The climatic factors that are most likely to influence the distributions of wheatears are temperature, rainfall and humidity and their affects are likely to be both direct and indirect.

Direct influence of climate:

The climatic factors that are most likely to have direct influence on the distribution of wheatears in S. W. Iran, and those that are considered here, are temperature and humidity. These factors are thought likely to be important for the following reasons:

1) Wheatears are homoiothermic and maintain their body temperatures at between 38.5° - 43°C.*

2) The ability of a species to maintain its body temperature depends on its powers of thermoregulation in relation to ambient temperatures and humidities. Humidity is important as it influences the rate at which cooling can be effected by evaporation from respiratory surfaces.

3) The ambient temperatures in S. W. Iran vary widely both above and below the body temperatures of wheatears (pp. 22-25 and fig. 36, p. 172). Ambient humidities also vary widely, particularly during the

*Oral temperatures of 56 wheatears of seven species measured with a mercury thermometer in S. W. Iran.

summer, when this factor is likely to be of critical importance in the thermoregulation of wheatears. Mean monthly actual vapour pressures during July at various stations in S. W. Iran are given in figure 52.

4) Birds vary in their adaptations for thermoregulation and in some cases even species which are superficially similar have been shown to differ in their powers of temperature regulation. For example Wallgren (1954) studied the metabolism of two similar species of Eurasian bunting (genus Emberiza) in relation to temperature and showed that the Yellowhammer (E. citrinella) has better insulation, greater tolerance to cold, poorer tolerance to heat and is exposed to lower environmental temperatures than the Ortolan Bunting (E. hortulana). In another study Salt (1952) compared the powers of thermoregulation of three similar species of finch in the genus Carpodacus where they occur in the Sierra Nevada of California, and he showed: 1) that C. cassinii which breeds at high altitudes had little ability to withstand high temperatures; 2) that C. purpureus which breeds in middle altitudes was able to thermoregulate efficiently in both moist and dry air; while 3) C. mexicanus which breeds in arid lowlands was able to regulate its temperature in dry air but soon died when exposed to high temperatures if the air was moist.

As far as I am aware no work has been done on the thermoregulation of wheatears but in view of the studies described above and the wide range of climatic conditions found in S. W. Iran it seems likely that interspecific differences in thermoregulatory ability may in some cases contribute to interspecific differences in distribution. The adaptive differences that seem most likely to be important are differences in insulation, coloration, behaviour and in ability to dissipate heat by evaporation from the respiratory surfaces. Laboratory studies will be necessary to compare the powers of thermoregulation of the various species of wheatear that occur in S. W. Iran, but in lieu of such studies and to provide a basis for discussing the sorts of adaptations that the different species might have, estimates were made of: 1) the range of temperature in which each species was recorded; and 2) the range of humidity occurring within the breeding distribution of each species during July which is the hottest month and

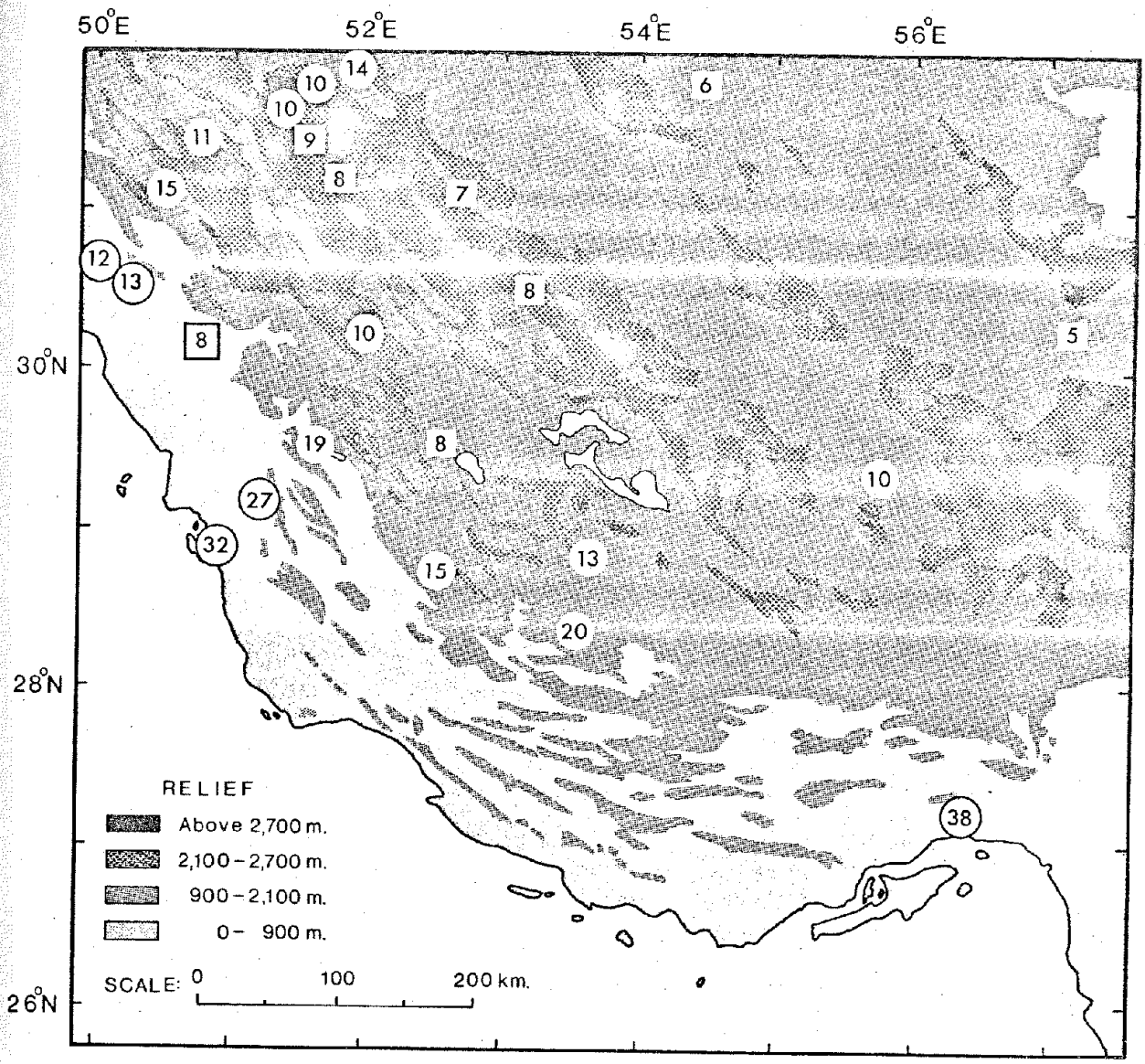


Fig. 52. Mean monthly actual vapour pressures (mbars) for July at various stations in S. W. Iran, based on five years' data.

KEY

[8] = Mean monthly actual vapour pressure <10 mbars (= "dry").

(25) = Mean monthly actual vapour pressure ≥ 10 mbars (= "moist").

(Calculated from observations of temperature and humidity made at 0300 and 1500 G. M. T. and published by the Iranian Meteorological Department, Tehran in Meteorological Year Books 1965–1969.)

therefore the month when humidity is most likely to be important in the thermoregulation of wheatears. The results are given in figure 53 and a few general comments about them are made below, but most comments are deferred to the discussions of individual species in part II.

1) The lower limits of the ranges of temperature experienced by most species of wheatear in S. W. Iran fall between 2.5° - 7.5°C (estimated mean daily) and hence, with the possible exceptions of O. hispanica, O. picata and O. monacha, there is no suggestion in these data of interspecific differences in tolerance to cold. This is not surprising since, provided they have plenty of food, adult birds have considerable resistance to low ambient temperatures (e. g. Kendeigh 1934). Indeed the lower limits of the ranges of temperature in which wheatears can survive are more likely to be determined by the restricting influence of low temperatures on the availability of arthropod food (pp. 170-173 and appendix D).* Nevertheless it must be pointed out that there may be interspecific differences in metabolic efficiency at different temperatures which could influence their distributions.

2) The upper limits of the ranges of temperature to which most species of wheatear are exposed in S. W. Iran lie between about 22° - 28°C and the factors that are most likely to determine these limits are the abilities of the various species to thermoregulate and/or the influence of temperature on the availability of arthropod food (pp. 170-173 and appendix D). O. alboniger and O. monacha live in hotter regions than the other species and the factors that enable them to do this are discussed in the sections dealing with the individual species in part II of this chapter.

3) The humidity in July within the breeding ranges of the different species of wheatear in S. W. Iran varies considerably. Thus O. oenanthe, O. xanthoprymna, O. deserti and O. finschii are confined to

*Regardless of date and altitude wheatears in S. W. Iran begin laying when estimated mean daily temperatures are between about 7° - 14°C and this is probably another example of the influence of temperature on the life of wheatears working through the availability of food.

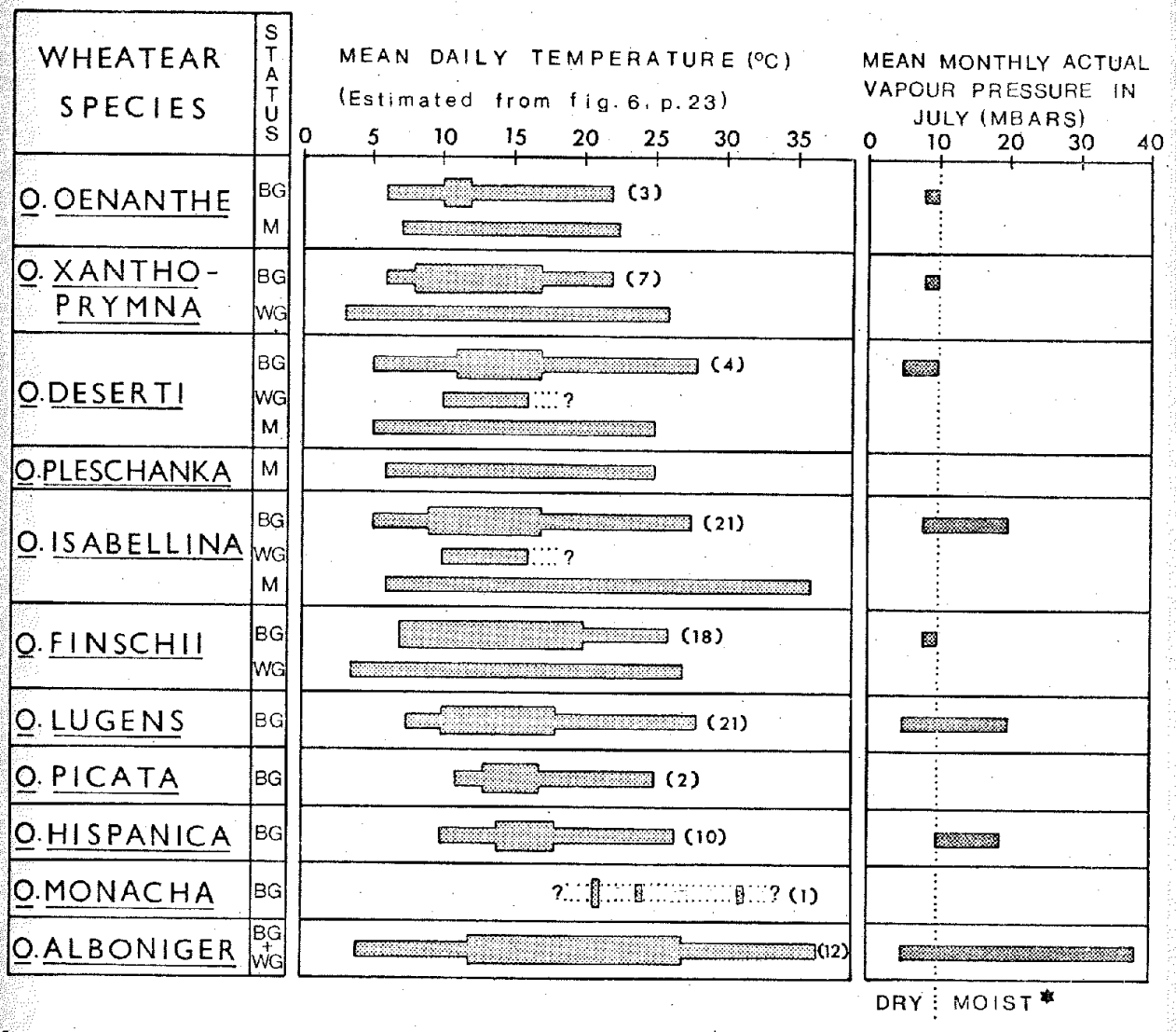


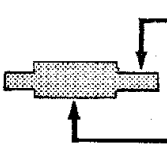
Figure 53. Estimates of temperatures and humidities in areas where wheatears occurred in S. W. Iran.

KEY

Status:

BG = On breeding grounds.
WG = On wintering grounds.
M = Migrants.

Temperature:



Range of mean daily temperatures in localities where wheatears were recorded.**

Rough estimates of ranges of temperature within which laying probably took place.***

(n) = Number of breeding records used in estimating laying periods.
? = Limits of range uncertain.

Humidity:



Rough estimates of ranges of mean monthly actual vapour pressures for July within the breeding distributions of the various species of wheatear.****

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*A vapour pressure of 0.3 inches of mercury (≡ 10.2 mbars) was designated by Salt (1952) as the division between "moist" and "dry" air.

**This was estimated by superimposing overlays 9-17 and breeding records plotted on similar figures, over fig. 6, p. 23 from which the mean daily temperature in the locality of any record could be estimated.

***Laying dates were roughly estimated from various sorts of evidence of breeding using the schedule given in table 4, p. 51. The mean daily temperatures during the laying period were then estimated from fig. 6, p. 23.

****Based on figs. 22-23, pp. 99-100 and fig. 52.

areas with dry air; O. hispanica occurs only in areas with moist air and O. isabellina, O. lugens and O. alboniger occur in areas with both dry and moist air. Wheatears were frequently seen panting during hot weather and therefore evaporative cooling is probably an important means of heat dissipation in these birds. Evaporative cooling in birds is strongly influenced by ambient humidity and as shown by Salt (op. cit.) even some similar species differ in their capacities to thermoregulate, some being more efficient in dry air and others in moist air. Moreover the ambient vapour pressures within the ranges of the finches that Salt studied varied between about 0.1-0.5 inches of mercury (3.4-16.9 mbars) which is considerably narrower than the range of 5-38 mbars that occurs in S. W. Iran (fig. 52). It therefore seems possible that interspecific differences in ability to thermoregulate in relation to humidity could be a factor influencing the distributions of wheatears in S. W. Iran.

Indirect influence of climate:

In addition to their direct role, climatic factors, particularly temperature and rainfall, probably have a strong indirect influence on the distribution of wheatears through their effect on vegetation and food supplies. These factors have already been discussed in general terms in chapters II and VI and their influence on the distributions of individual species is considered in part II of this chapter.

2) COMPETITION:

In this study the term competition is used in the sense of Ricklefs (1973) who defined it as follows: "Competition occurs when the use of a resource—food, water, space, light and so on—by one individual reduces the availability of that resource to another individual, whether of the same species (intraspecific competition) or of a different species (interspecific competition)".

It is now generally accepted that the potential distribution and ecological expression of one species can be restricted by competition from another or a combination of other, usually similar, species. Indeed

interspecific competition is regarded as a major factor in the organisation of ecosystems (e. g. Darwin 1859; Lack 1944a, 1971; Hutchinson 1957, 1965; Elton 1958; Miller 1967; MacArthur 1972; Ricklefs 1973). It seems likely, for three main reasons, that interspecific competition may play a role in determining the ranges and habitat distributions of wheatears in S. W. Iran. These reasons are as follows: 1) All wheatears have similar ecological requirements and hence are potential competitors. 2) The pattern of coexistence between the various species is complex and in many areas several species occur side by side. 3) Evidence for competition between different species of wheatear has been reported from a number of areas outside S. W. Iran (e. g. by: Eggebrecht 1943; Hartley 1949, 1950; Simmons 1951; Ali and Ripley 1973) and within S. W. Iran frequent interspecific territorial skirmishes observed during this study suggested interspecific competition. However, in nature, it is extremely difficult to assess the role of interspecific competition in shaping the distribution and ecology of an animal species since the process is rarely observed while actually occurring. What is usually seen is the situation after the poorer competitor has been eliminated, when it is difficult to know whether the observed distribution patterns are the result of competition or due to other factors. Moreover, as pointed out by MacArthur (1972), to be important competition does not need to occur very often and even if two species compete only once every 20 years this may be sufficient to influence their ecology during the intervening period. Nevertheless, even if competition is not actually observed, various sorts of data provide indirect evidence of competition (see Miller 1967 for review of these) and those that are relevant to detecting interspecific competition in wheatears are reviewed in general terms below as background for investigating specific cases in part II of this chapter:

1) Evidence from distribution patterns:

a) Contiguous allopatry: When two species show contiguous allopatry and the boundaries do not coincide with any obvious environmental discontinuity this is strong circumstantial evidence for interspecific competition.

b) Ecological release: When a species expands its altitudinal range, habitat distribution or foraging repertoire in the absence of a closely related species or several similar species this is indirect evidence of interspecific competition where the species are sympatric.

2) Evidence from interspecific territorial interactions:

Except on migration wheatears invariably hold territories which rarely overlap more than marginally with the territories of any other wheatears regardless of species. This is brought about by various sorts of territorial behaviour including singing, "chacking", peaceful border confrontations and skirmishes often involving chases. Since wheatears live in open habitats the results of skirmishes can often be observed, and during this study 223 skirmishes were witnessed in which a wheatear of one species, the dominant, attacked a wheatear of another species, the subordinate, which retreated. These involved 139 different pairs of individuals and 26 combinations of species. The results are summarised in table 39 together with the results of similar observations by other workers, the details of which are listed in a footnote below.*

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*Aggressive interactions between different species of wheatear reported by other workers:

1) O. alboniger/O. xanthoprymna: Meinertzhagen (1954) reported a case of O. alboniger chasing an O. xanthoprymna in S. W. Iran in late winter.

2) O. finschii/O. isabellina: M. C. Harrison (pers. comm.) saw a male O. finschii attack and chase away an O. isabellina near Ereğli in southern central Turkey on 15 September 1971.

3) O. finschii/O. hispanica: In the same locality as the previous observation M. C. Harrison saw a male O. finschii attack a male O. hispanica which retreated.

4) O. hispanica/O. oenanthe: Dr. P. R. Grant (in litt.) saw an O. hispanica chase an O. oenanthe in northern Greece in June 1972.

5) O. lugens/O. deserti and O. lugens/O. hispanica: Hartley (1950) reported that he observed several attacks by a breeding O. lugens on migrants of O. deserti and O. hispanica.

6) O. lugens/O. oenanthe: Simmons (1951) described the following case which took place at Adabiya on the Bay of Suez in October 1949: An O. oenanthe took up a territory on the borders of the territories of two O. lugens which repeatedly attacked the O. oenanthe until it disappeared five days after its arrival.

7) O. lugens/O. monacha: Hartley (1949) reported the following observations which he made in an arid wadi near Cairo in Egypt where both O. lugens and O. monacha were winter visitors: "The scrubby area was first occupied by Hooded Chats [O. monacha], each taking a section of the ground and defending its marches. Later Mourning Chats [O. lugens] arrived and fought with the Hooded Chats. The Hooded Chats disappeared, either completely or from most of the ground previously owned, and the area was divided anew between the Mourning Chats". During this take-over two clashes involving different individuals were observed in which an O. lugens attacked and chased an O. monacha.

(footnote continued on p. 254)

	O. ALBONIGER	O. FINSCHII	O. PICATA	O. XANTHOPRYMNA	O. LUGENS	O. ISABELLINA	O. OENANTHE	O. PLESCHANKA	O. HISPANICA	O. DESERTI
O. FINSCHII	4 (6)									
O. PICATA	1									
O. XANTHOPRYMNA	12(14)* +1 / 1	12(16)**	2 +n / 1							
O. LUGENS	4 (9)	3	2 / 1	1(2) / +1						
O. ISABELLINA	4 (5)	22(71)** +1	1	1	1					
O. OENANTHE					+m	2				
O. PLESCHANKA			2		2(4)	8(10)	+			
O. HISPANICA		4(6)		1	1 +s	3	+1			
O. DESERTI		7(9)			2 +s	13(15)**		1		
O. MONACHA					+2					

Table 39. Results of aggressive territorial interactions between different species of wheatear. Each pair of species is represented by a rectangle, which is divided in half if a clash between the members has been observed. Cases where the species at the top of the table was dominant are scored in the top, shaded half of the rectangle. If the other species prevailed it is recorded in the bottom half of the rectangle.

KEY

n = Number of interactions involving different individuals - present study.
(n) = Total number of interactions if this is greater than n - present study.
+ = Interactions observed by other workers. (These are listed in a footnote, pp. 252 and 254.)
m = "Many" or "repeatedly".
s = "Several".
* = The difference between the number of individuals of each species that were dominant in interactions and those that were subordinate is statistically significant using a chi-squared one-sample test with one degree of freedom. *$p < 0.01$; **$p < 0.001$.

FACTORS INFLUENCING RANGE AND HABITAT DISTRIBUTION

The observations of aggressive encounters between different species of wheatear (table 39) show that the same member of each pair of species was almost always dominant, suggesting a hierarchical relationship between the different species. However only in four cases were there enough observations to establish statistically that one species was dominant to another. The information on interspecific interactions presented in table 39 also suggests a dominance hierarchy within the genus. Thus at the top O. alboniger was dominant to all species with which it was seen to clash. In second place O. finschii was superior to all except O. alboniger while at the bottom O. deserti and O. monacha fled from all attackers. In the table the species are arranged in order of dominance as implied by the available data.

Although the data on interspecific territorial interactions are few, they suggest that in the event of competition between different species of wheatear the dominant species in skirmishes would prevail by excluding the subordinate species from its territories.

3) HABITAT REQUIREMENTS AND ADAPTATIONS TO HABITAT:

The habitat requirements of a bird depend on its biological properties, for example on its adaptations for foraging, thermoregulation and escaping from predators, and it will occur only in habitats where its minimum requirements are satisfied. The habitat requirements of wheatears in S. W. Iran were discussed in chapter V and summarised in tables 19 and 20, pp. 153-154. However the adaptations of wheatears have not yet been discussed and in this section adaptations which are thought likely to influence their habitat distributions are considered. These are coloration, foraging strategies, weight and morphology.

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8) O. oenanthe/O. pleschanka: Eggebrecht (1943) reported a case in the southern Ukraine where O. oenanthe successfully competed for ground with two O. pleschanka.

9) O. picata/O. xanthoprymna: Ali and Ripley (1973) wrote as follows concerning interactions between O. picata and O. xanthoprymna in Pakistan and N. W. India: "In winter [O. xanthoprymna] almost everywhere in direct food competition with the more domineering O. picata by which it is mercilessly chivvied and chased".

10) O. xanthoprymna/O. lugens: Major M. D. Gallagher (in litt.) saw an O. xanthoprymna attack an O. lugens in Bahrain in winter.

FACTORS INFLUENCING RANGE AND HABITAT DISTRIBUTION

A. COLORATION:

The coloration, during the breeding season, of the 11 species of wheatear that occur in S. W. Iran is shown in plate 1, p. 2 and fig. 2, p. 11. The black and white or red and white tails apart, wheatears are broadly speaking either bright black and white, bright grey and black and white or a dull dun-colour, and on the basis of their coloration the various species can be divided into the following four groups (see table 40):

1) Both sexes black and white. (Two species)

2) Male: black and white. (Three species)
   Female: dun.

3) Male: black and white or grey and black and white during the breeding season; dun in winter.
   Female: dun. (Three species)

4) Both sexes largely dun. (Three species)

The aim of this section is to investigate the adaptive significance of the coloration of the various species of wheatear that occur in S. W. Iran with a view to evaluating the role of coloration in determining their habitat distributions.

1) Dun-coloured wheatears:

The plumage of these birds is often very similar in colour to the ground on which they live and when they are still they are extremely difficult to see and even in flight they are by no means conspicuous. This is strong circumstantial evidence for the now generally accepted hypothesis that the main function of cryptic dun-coloration in prey species that live in deserts is protection from predators (e. g. Cott 1940, Cloudsley-Thompson and Chadwick 1964, Willoughby 1969, Serventy 1971, Nelson 1973). However there is rather little direct evidence in support of this hypothesis and several authors (e. g. Buxton 1923, Bodenheimer 1954, Meinertzhagen 1954) have opposed it. Therefore the evidence for and against the procryptic function of the dun-coloration of wheatears will be examined below:

The chief arguments against the hypothesis are:

1) that many species with dun-coloration have no important predators and

(For Oenanthe see plate 1, p. 2 and fig. 2, p. 11.)		Steep rocky hillsides and gorges. Background: general shadow + variegated light and dark especially in bright sunlight.	Open steep rocky hillsides. Background variegated light and dark especially in bright sun.	Combination of b + d.	Flat and/or gently sloping ground – usually dun coloured.	
ADULTS	FLEDGLINGS				+ cover: e.g. bushes, trees, runnels, rock-outcrops.	Largely featureless.
1) Both sexes black & white.						
O. alboniger	Black & white.	B, W				
O. lugens	Dun.		B, W?	(B), W?		
2) ♂ black and white. ♀ dark brown or dun.						
O. picata (♀ dark brown)	Dark smoky brown.	B		B, W	W	
O. monacha (♀ dun)	Undescribed.			B, W		
O. finschii (♀ dun)	Dun.			B, W		W
3) ♂ black & white or grey & black & white in breeding season, dun in winter. ♀ dun.						
O. hispanica	Dun.		B	B	W	
O. pleschanka	Dun.		B, W	B, W	B, W	
O. oenanthe	Dun.			B, W	B, W	W
4) Both sexes largely dun.						
O. xanthoprymna	Dun.		B, (W)	B, W		W
O. deserti	Dun.				B, W	B, W
O. isabellina	Dun.				B, W	B, W

Table 4C. The coloration of wheatears that occur in S. W. Iran in relation to their typical breeding and wintering habitats. The species are arranged with those that have the most black and white plumage at the top and those that are mainly dun-coloured at the bottom.

KEY

B = Breeding habitat. ( ) = A few.
W = Wintering habitat. ? = Unconfirmed.

hence have no need of camouflage; 2) that prey species with cryptic coloration do not take advantage of it since they render themselves visible by moving about and do not take notice of predators; and 3) that it is difficult to apply to nocturnal and fossorial animals. The latter argument has been successfully countered by Cott (1940, pp. 153-154) and will not be considered further. The first two arguments are opposed here and below I list evidence to show that dun-coloured wheatears are subject to predation and that their coloration is procryptic:

i) Remains of two O. isabellina which had evidently been taken by predators were found at Dasht-i-Arjan, one in November 1970 and the other in September 1971.

ii) Passburg (1966) reported seeing a Hobby (Falco subbuteo) chasing an O. isabellina near Bandar Pahlavi on the south coast of the Caspian on 29 September 1958.

iii) Jackson (1938) reported that in northern Uganda many O. isabellina are snapped up by hawks and kestrels during the migration season.

iv) O. oenanthe is taken in Europe by a number of predators that also occur in wheatear habitat in S. W. Iran. These include: Sparrow Hawk (Accipiter nisus) (I. Newton in litt. 1973); Peregrine (Falco pregrinus) (Witherby et al. 1939) and Hobby (Witherby et al. 1939).

v) On 19 August 1971 an O. isabellina was seen mobbing a Little Owl (Athene noctua) at Dasht-i-Arjan.

vi) R. E. Smith and M. Wright (in litt.) observed a case, in October 1971 on the Calf of Man in the Irish Sea, where a female O.oenanthe and a female O. hispanica crouched motionless when a Sparrow Hawk went over low.

vii) In Nigeria Macgregor (1950) noted that often when a Pallid Harrier (Cirus macrourus) came near a nest of the Red-breasted Chat (O. bottae heuglini), which is a dun-coloured wheatear resembling O. isabellina, it gave an alarm call which caused the young to retreat into their nest-burrow. However occasionally a harrier appeared suddenly, and both the adults and young crouched motionless until the predator had passed.

viii) Wheatears are probably most vulnerable to predators during the fledgling period. Therefore the predominance of dun-coloration in the

fledgling plumage of wheatears (table 40) is indirect evidence of its procryptic survival value.

For the above reasons I believe that dun-coloration in wheatears has concealment value which affords them protection against predators and is an important factor in enabling them to survive in open habitats with little cover. Furthermore Heppner (1970) has shown that pale-coloured birds absorb less radiant energy than dark-coloured ones and it seems likely that the pale dun-coloration of wheatears may also have survival value by reducing their heat load during hot weather.

2) Black and white wheatears:

These birds can be extremely conspicuous and Cott (1947) put forward the hypothesis that the main function of their coloration was to warn predators of their repugnant taste. He supported this hypothesis with two sorts of evidence. First he regarded the behaviour of black and white wheatears as appropriate for aposematic animals and noted: a) that: "Everyone who has observed these chats in the field knows that they are in fact extremely conspicuous objects, even when at rest: moreover, they seldom long keep still, being active and restless in their habits." and b) that: "I am also informed by Col. Meinertzhagen that, unlike the desert larks, the black and white chats never crouch or flatten at the sight of a hawk". The second sort of evidence that he used to support his hypothesis was the results of experiments on the food preferences of a hornet, Vespa orientalis, which showed that the flesh of O. leucopyga (The White-rumped Black Wheatear), O. lugens and O. monacha was less well liked than the flesh of 32 other species of bird, although O. pleschanka came near the edible end of his edibility scale. Finally Cott concluded: "If it be allowed, as seems almost certain in the light of recent evidence, that the flesh of these black and white chats is highly unpalatable, then their coloration is readily explained on the theory of warning colours.... In short, they are aposematic animals".

I made the following observation which may support Cott's hypothesis: On 21 January 1971 at the Maharlu North study area a male

O. finschii with an orange colour ring (table 8, p. 66) was killed by a Kestrel (Falco tinnunculus). I followed the predator with its prey and watched it go to ground beside a bush at some considerable distance from me. Long before I cameup with the Kestrel it flew off and on investigating the place where it had been I was astonished to find the headless, but otherwise unmutilated, corpse of the wheatear. There was no indication that the Kestrel had been frightened away from its prey by my approach and it is possible that it left the wheatear because it found it distasteful.

However the following evidence is against the hypothesis that the black and white plumage of wheatears is primarily aposematic in function:

i) Some black and white wheatears react to predators by hiding. On 15 March 1971 a Sparrow Hawk came over the Shahpurjan study area causing an O. lugens to dart behind a rock, uttering a high-pitched alarm call.

ii) Some black and white wheatears are eaten by predators. Cott (1947) quoted as follows from a letter to him from Major P. H. T. Hartley: "On one occasion, in the Wadi el Gibbu [near Cairo, Egypt] , I found the scattered feathers and other rejectamenta where a Mourning Chat [O. lugens] had been eaten by a hawk".

iii) The male of O. oenanthe in its grey and black and white breeding plumage can be every bit as conspicuous as a purely black and white wheatear. However it was considered good eating in England where large numbers used to be caught for the table (Dresser 1871-1881). It seems unlikely that a species that is acceptable to the pernickety tastes of Englishmen would be unpalatable to other predators. Hence it is unlikely that the breeding plumage of the male O. oenanthe is aposematic.

iv) If the black and white plumage of wheatears is effective warning coloration the following facts are puzzling: a) Table 40 shows that, with the exception of O. finschii in winter, black and white wheatears are rarely found in featureless dun-coloured plains where they would be most conspicuous and hence aposematic plumage most effective. b) In males of O. oenanthe, O. hispanica and O. pleschanka only the breeding

plumage is bright black and white or grey and black and white. After the breeding season they moult into cryptic dun-coloured plumage. c) In six species of wheatear the male, at least in breeding plumage, is black and white or grey and black and white but the females are cryptically dun-coloured (table 40). It is difficult to believe that the sexes taste different and therefore to explain why aposematic plumage should have been developed in one sex only. The argument that the female needs cryptic coloration for camouflage during incubation cannot be invoked in this case since wheatears nest hidden in holes.

Although some species of wheatear may be distasteful to predators and this may afford them some protection I am unconvinced, for the above reasons, that the black and white plumage of most species is primarily aposematic in function. Therefore I investigate below the adaptive significance of the black and white plumage of wheatears that occur in S. W. Iran.

a) O. alboniger: Table 40 shows that, of the species of wheatear that occur in S. W. Iran, only O. alboniger has its adults of both sexes and its fledglings black and white. I think the most reasonable explanations for the black and white plumage in this species are as follows: First O. alboniger can be extremely difficult to see when it is sitting motionless in the deep shadow of a rock or even when it is feeding on a shade-darkened hillside or in a sunless gorge. O. alboniger is commonly found in such situations, and in these places their black and white plumage probably renders them more difficult to see than dun-coloured birds. It therefore seems reasonable to suggest a procryptic role for the black and white plumage of O. alboniger. Since these birds are probably most vulnerable to predation during the fledgling period, this hypothesis is supported by the fact that the fledglings have black and white plumage. In bright sunlight against dun-coloured backgrounds O. alboniger is very conspicuous and this may account for the fact that they are rarely found far from rocky hillsides where the variegated background of light and shade renders them relatively cryptic and there are always places at hand in which to hide. Heppner (1970) has shown that black plumage absorbs more radiation than paler plumage and he suggested that it could be an adaptation for

reducing energy expenditure when ambient temperatures are below the thermoneutral point. Therefore the black plumage of O. alboniger may also be important to the birds in reducing the metabolic costs of staying warm.

b) O. lugens: In this species the adults of both sexes remain black and white throughout the year but the fledglings are dun-coloured. Since these birds are probably most vulnerable to predation during the fledgling period the dun-coloration of the fledglings suggests that this coloration affords the best protection from predators. This is consistent with my impression that on open rocky hillsides motionless black and white wheatears are difficult to see but dun-coloured ones are even more cryptic. This raises the question of why the adults are black and white instead of remaining dun-coloured. I offer the following possible explanation: In their typical habitat of open rocky hillsides experienced adult O. lugens are probably fairly safe from predation by virtue of the abundance of places to hide and the cryptic qualities of black and white disruptive plumage against a variegated light and dark background. It is therefore possible that the reduction in energy expenditure conferred by black coloration when ambient temperatures are below the thermoneutral point may outweigh the disadvantages of loss of some measure of crypsis. The increased liability to heat stress which is also conferred by black coloration is not a problem in the habitat of O. lugens since there is ample shade in which the birds find relief from high temperatures.

c) Species of wheatear where the breeding plumage of the males is black and white or grey and black and white and the plumage of the females and fledglings dun-coloured (= groups 2 and 3 in table 40*): Table 40 shows that the species of wheatear in this category live mainly in open habitats which include some flat and/or gently sloping ground together with some cover such as a section of rocky hillside, a rock-outcrop, a runnel or a few scattered bushes. In these habitats dun-coloration is less conspicuous and probably has greater procryptic survival value than black and white or grey and black and white. This view is

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*N.B. I include O. monacha in this section but this is not strictly valid as the plumage of the fledglings has not been described.

supported by the fact that the fledglings of these species* are dun-coloured. I therefore believe that the dun-coloration of the females of all these species and of the males of O. hispanica, O. oenanthe and O. pleschanka in non-breeding plumage is primarily an adaptation for concealment from predators.

This leaves the question of how to account for the black and white plumage of the males. Nelson (1973) has suggested that the sexual dimorphism in O. finschii may have evolved to reduce competition between the sexes and he wrote: "It now appears that, at least in Oenanthe finschii, there is a distinct tendency for the males to inhabit shadow-patched (boulder-strewn) ground and the females open, sandy areas contiguous to those of the males". I looked for this tendency in breeding O. finschii and O. hispanica in S. W. Iran but found no difference between the habitat utilization of the sexes. However further study might reveal differences. Nelson suggested that the advantage of the black and white coloration of the males was its cryptic properties against shadow-patched backgrounds and implied that it was superior to the dun-coloration of the females in such situations. However this is inconsistent with the facts that the nests of wheatears that show sexual dimorphism are invariably in the rockiest parts of the territories and yet the females and fledglings are dun-coloured. I therefore suggest that the males are black and white mainly for some other reason and that they are largely confined to rocky areas because these afford them some protection from predators in the form of escape holes and variegated backgrounds against which they are much less conspicuous than against plain dun-coloured backgrounds.

Willoughby (1969) proposed a social function for the black and white plumage of the Southern Anteater Chat (Myrmecocichla formicivora) and the Mountain Chat (Oenanthe monticola) in the Namib Desert of S. W. Africa and I think that the black and white and the grey and black and white plumage of the male wheatears considered in this section may also have a social function. In display flights black and white wheatears can be extremely conspicuous and I think the most likely social functions of

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* N.B. I include O. monacha in this section but this is not strictly valid as the plumage of the fledglings has not been described.

this coloration are in territorial defence and particularly in attracting mates of the right species. Several species of wheatear frequently breed in the same vicinity and since they are all rather similar there is a risk of hybridization. It therefore seems reasonable to suggest that natural selection has favoured the development of species specific plumage patterns in the males to facilitate correct mate selection. The reason why black and white or grey and black and white have been selected in the species of wheatear considered in this section is probably that birds with these colour combinations can be conspicuous if they move about but can also be cryptic if they keep still. The black elements in this plumage may also confer an advantage by reducing energy expenditure when ambient temperatures are below the thermoneutral point.

Indirect support for the hypothesis that the black and white and the grey and black and white plumage of wheatears serves a social function is provided by O. xanthoprymna which is the only hill-species which does not have such coloration in the male. I suggest that the reason for this is that the red rump and tail in O. xanthoprymna fulfils the social function of the black and white and the grey and black and white plumage of the other species.

Coloration of wheatears - summary and conclusions:

1) Dun-coloration in wheatears probably has survival value in two main ways: a) concealment from predators in open habitats; b) reduction of heat load when ambient temperatures are above the thermoneutral point. Both these factors are probably important in enabling dun-coloured wheatears to survive in open habitats, particularly in areas with little cover.

2) Black and white, and grey and black and white plumage in wheatears probably has survival value in three main ways: a) concealment from predators in habitats with dark, and with variegated dark and light backgrounds; b) reduction of the metabolic costs of staying warm when ambient temperatures are below the thermoneutral point; and c) facilitating territorial defence and mate selection. The price of these

advantages is probably restriction of these wheatears to habitats with cover, usually in the form of stones, rock-outcrops and boulders which, in addition to providing hiding places, furnish backgrounds against which they can be cryptic.

B. FORAGING STRATEGIES:

Food is crucial for survival. Therefore the abilities of wheatears to forage in different habitats are likely to influence their habitat distributions. The foraging patterns of wheatears in S. W. Iran were described in chapter VI, pp. 178-189 (see particularly fig. 39, p.181) and the aim of this section is to investigate the adaptive significance of the foraging strategies of the various species in order to assess the role of these strategies in determining habitat distributions. The analysis follows the classification of foraging patterns given on p. 178 and used in fig. 39, p. 181.

1) Species of wheatear that use predominantly the perch and pounce foraging strategy (see p. 178):

In this strategy birds locate their prey mainly from elevated watch-posts whence they launch aerial attacks usually against arthropods on bare ground. They move about chiefly by making short-flights.

This strategy has two main advantages: 1) Sitting on elevated watch-posts enables birds to search large areas of ground for prey with little expenditure of energy; and 2) pursuing prey on the wing enables birds to cross ground which would be difficult or impassable on foot. Species that use this technique fall into two groups:

Group I (often use flimsy perches). The species in this group perch a lot and with facility on vegetation which is often quite flimsy.

a) O. hispanica and O. pleschanka: These species occur in areas with relatively high rainfall and where in most springs much of the ground surface becomes obscured by a sward of lush herbaceous vegetation (e. g. see plate 6, p. 36 and plate 20, p. 156). These wheatears do not

feed among thick vegetation and rely for hunting ground on bare patches which are often small and isolated. The perch and pounce foraging strategy appears to be adaptive in this situation since it enables the birds to survey one or more bare patches from a distance and then to attack prey without having to negotiate thick vegetation on foot. In areas where these birds occur the only vantage points that command views of bare patches are often flimsy. It therefore seems reasonable to suggest that the ability of O. hispanica and O. pleschanka to perch on flimsy vegetation is probably an important contributory factor to their survival in areas that are subject to dense flushes of ground vegetation.

b) O. deserti and O. picata: These species are often found in open bare habitats in areas with scanty rainfall and where in consequence arthropod prey is probably usually scarce (pp. 173-174). In these areas the perch and pounce foraging strategy probably has survival value since it enables birds to survey large areas of ground in search of prey with minimum expenditure of energy. In these habitats many and often the only elevated perches are provided by flimsy vegetation and hence the ability of O. deserti and O. picata to use these vantage points is probably a factor contributing to their survival in open bare habitats in the drier parts of S. W. Iran.

Group II (use mainly firm perches): The species in this group are too heavy and/or morphologically ill-adapted for perching on flimsy vegetation and instead usually sit on firmer objects such as boulders, rock-outcrops or stones. The group includes O. alboniger, O. lugens, O. monacha*, O. xanthoprymna and O. finschii while on its breeding grounds. These species live mainly on rocky, stony terrain where the perch and pounce foraging strategy probably has two main advantages: 1) It enables birds to locate prey among stones; and 2) to pursue it without having to cross rough and/or steep ground on foot.

2) Species of wheatear that use predominantly the dash and jab foraging strategy (see p. 178):

Species of wheatear that use this strategy search for and pursue

*In addition to using the perch and pounce foraging strategy O. monacha flycatches a good deal and the adaptive significance of this is considered on p. 294.

most of their quarry on foot. These include O. isabellina, O. oenanthe, O. finschii when on its wintering grounds and individuals of O. deserti and O. xanthoprymna while on flat featureless ground. The strategy is used by wheatears foraging in areas where there are few elevated perches, such as on bare plains or on ground with short grass. It is an efficient foraging strategy probably only in areas where: 1) the ground is relatively smooth so that birds can locate prey from quite large distances and pursuit on foot is unimpeded; and 2) where the density of prey is relatively high.

The question arises, however, of why the birds pursue their prey on foot rather than on the wing. The answer is probably related to the relative energetic costs of making short flights and short runs. For animals of the same body size the energy cost of flying to a distant point is less than the energy cost of running to the same place (Schmidt-Nielsen 1972). However take-off consumes more energy than level flight (Savile 1957) and absorbing the shock of landing is also probably energetically expensive. Therefore, although I can find no figures for the energetic costs to small birds of making short flights and short runs, it seems likely that over short distances the energetic cost of running may be less than that of flying. If this is the case it seems likely that on smooth bare ground with relatively high densities of prey the dash and jab foraging technique is more efficient, in terms of energy gained from prey per unit of energy expended to capture it, than the perch and pounce technique. It therefore seems reasonable to suggest that the dash and jab foraging strategy is an adaptation for feeding on smooth ground with relatively high densities of prey and few elevated perches. A concomitant adaptation is probably the ability to run rather than hop. Hopping involves the energy cost of raising the weight of the bird through a vertical component and absorbing the shock of landing, while in running the weight of the bird is always supported by the ground. It therefore seems likely that the energetic cost of running is less than that of hopping and it is probably significant that the only species of wheatear that were observed to run were O. isabellina and O. oenanthe, the species that make the most use of the dash and jab foraging strategy. All other species of wheatear hop regardless of whether they are on smooth or rough ground. This may

be associated with the fact that they usually live in terrain where there are obstacles that would trip a running bird.

C. WEIGHT AND MORPHOLOGY:

A number of workers have demonstrated adaptive relationships between the morphology of the members of groups of closely related species of birds and their patterns of habitat utilization (e. g. Dilger 1956, Newton 1967, Raikow 1973, Gaston 1974); and the aim of this section is to determine whether the wheatears of S. W. Iran show morphological adaptations for life in their respective habitats which might help to explain their habitat distributions.

Morphological adaptations of a species for life in a particular habitat can be considered meaningfully only in the context of the ways in which it behaves in that habitat. In chapter VI, pp. 178-183 (see particularly fig. 39, p. 181) it was shown that the majority of overt actions of wheatears, while in their habitats in S. W. Iran, were apparently concerned with foraging and that the various species could be divided into three groups on the basis of their foraging patterns. The membership and the characteristics of the foraging patterns of the members of these groups, referred to here as foraging groups, are briefly reiterated below:

Foraging group I*: Species that use mainly the perch and pounce foraging strategy, move around their habitats mostly by making short flights and perch a lot and with facility on vegetation which is often quite flimsy. This group includes: O. deserti, O. hispanica, O. picata and O. pleschanka.

Foraging group II*: Species that use chiefly the perch and pounce foraging strategy, move around their habitats mainly by making short flights but usually sit on firm perches. This group includes: O. alboniger, O. lugens, O. monacha, O. xanthoprymna and O. finschii while on its breeding grounds.

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*See p. 178 et seq. for full descriptions of foraging patterns.

Foraging group III*: Species that use predominantly the dash and jab foraging strategy, move around their habitats to a large extent on foot and invariably perch on firm objects, often the ground. This group includes: O. isabellina, O. oenanthe and O. deserti, O. finschii and O. xanthoprymna when on flat featureless ground in winter.

In the previous section the adaptive significance of the foraging patterns of the various species of wheatear for life in their respective habitats was suggested. It is therefore likely that any morphological adaptations that might help to explain their habitat distributions will be associated with their foraging patterns. This is especially to be expected as food is crucial for survival and hence any morphological modifications that facilitated foraging are likely to have been favoured by natural selection.

The chief interspecific differences in foraging pattern involve the types of perches used (flimsy v. firm) and the methods of locomotion employed (short flights v. short dashes along the ground) (see table 41 for summary). It is therefore likely that any adaptive differences in

Type of perch used		Type of locomotion usually used	
Often use flimsy perches	Usually use firm perches	Short flights	Short dashes on foot along ground
O. deserti	O. alboniger	O. alboniger (R)	O. isabellina (LM ?some SM)
O. hispanica	O. finschii	O. deserti (LM ?some SM)	O. oenanthe (LM)
O. picata	O. isabellina	O. finschii (SM)	(O. deserti) (LM ?some SM)
O. pleschanka	O. lugens	O. hispanica (LM)	(O. finschii) (SM)
	O. monacha	O. lugens (SM)	(O. xanthoprymna (SM)
	O. oenanthe	O. monacha (R)	
	O. xanthoprymna	O. picata (SM)	
		O. pleschanka (LM)	
		O. xanthoprymna (SM)	

Table 41. Types of perches and methods of locomotion used by wheatears while in their habitats in S. W. Iran, based on casual observations and the quantitative data presented in fig. 39, p. 181. The migratory status of the various species is also given. ( ) = when on flat featureless ground in winter, LM = Long migration, SM = Short migration, R = Resident.

*See p. 178 et seq. for full descriptions of foraging patterns.

morphology will be related to these activities. The features of the birds that are most likely to show adaptive modifications for these activities and those which are examined here are weights, tarsi, wings and tails.

1) Weights:

Birds can perch only on objects that are strong enough to bear their weights. Hence the lighter the bird the flimsier the perches that it can use. Weights of wheatears obtained in S. W. Iran are summarised in fig. 54. This shows that the lightest species are O. hispanica, O. pleschanka, O. deserti and O. picata which are the species that often use flimsy perches (table 41). Indeed these species are significantly lighter than species that usually use firm perches.** The ability of O. hispanica, O. pleschanka, O. deserti and O. picata to use flimsy perches is probably in part due to their low weights which may therefore be regarded as adaptations to this habit and hence to habitats where the use of flimsy perches is an advantage (see pp. 264-265). These findings are similar to those of Newton (1967) who, in a study of some British finches (Fringillidae), showed that, apart from the Crossbill (Loxia curvirostra), the heaviest finches were less adept at feeding from vegetation than the lightest ones.

Weight gives an indication of body size. Small birds require less food than large ones. O. deserti and O. picata live in the dry eastern regions of S. W. Iran where food is probably often relatively scarce (pp. 173-174). Hence in these species natural selection may have favoured small size not only because it enables them to utilize flimsy perches but also because it reduces the amount of food they require.

2) Tarsi:

Tarsal lengths of wheatears from S. W. Iran are presented in fig. 55. Two series of measurements are given: 1) actual lengths of tarsi; and 2) lengths of tarsi corrected for body size by dividing by the cube roots of the weights, a method proposed by Amadon (1943) and used successfully by a number of workers (e. g. Dilger 1956, Grant 1966, Gaston 1974). To minimise errors due to seasonal fluctuations in weight only

**The weights of all males, males on their breeding grounds during the breeding season and all females (= the categories used in fig. 54) were compered separately using two-tailed Mann-Whitney U tests. In each case $p<0.00006$.

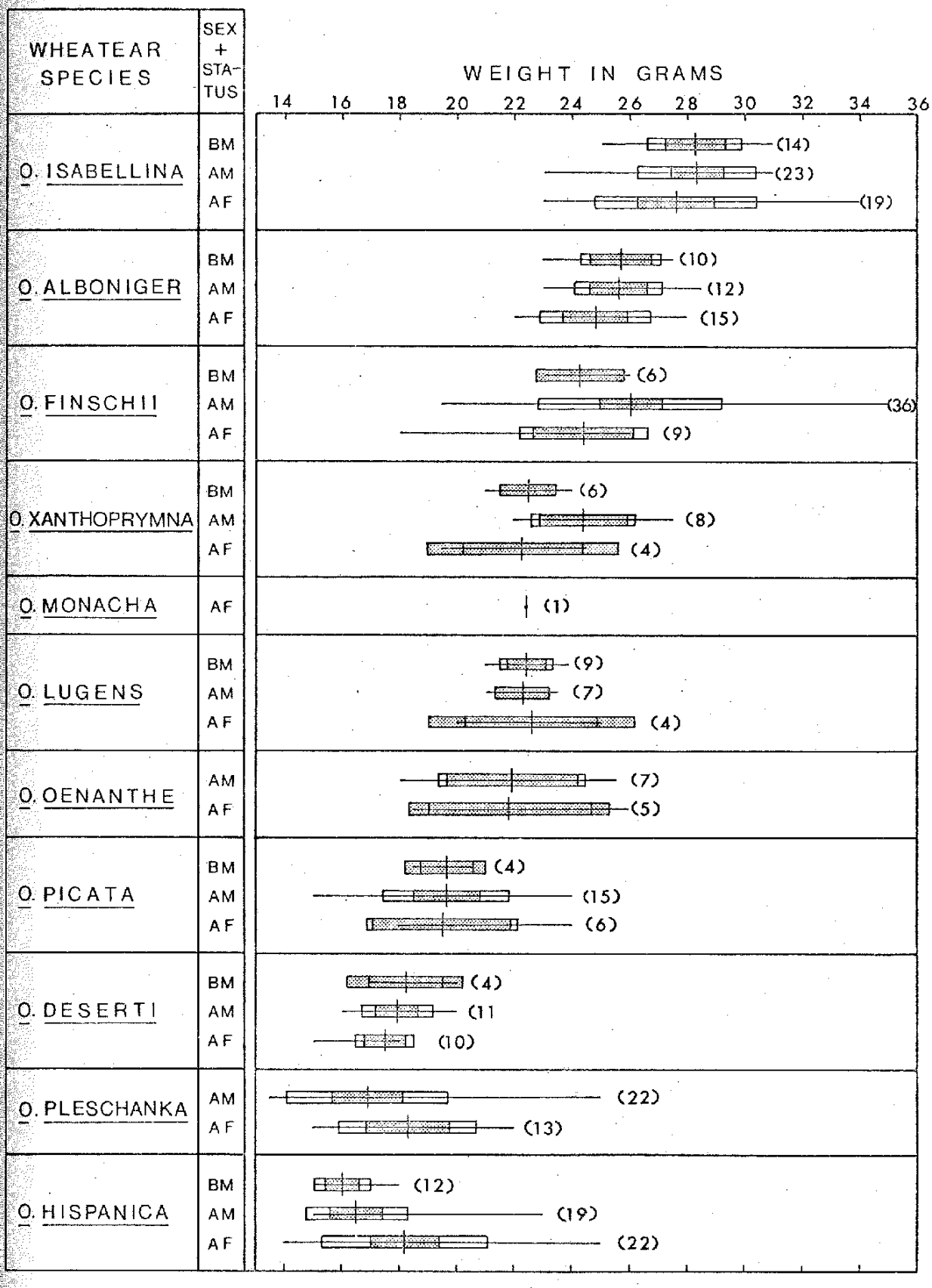
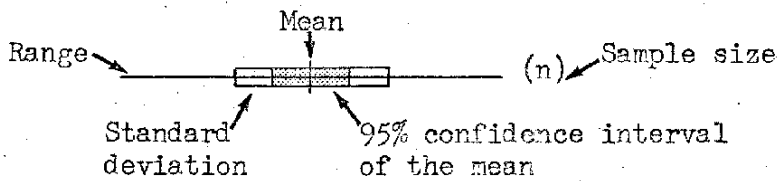
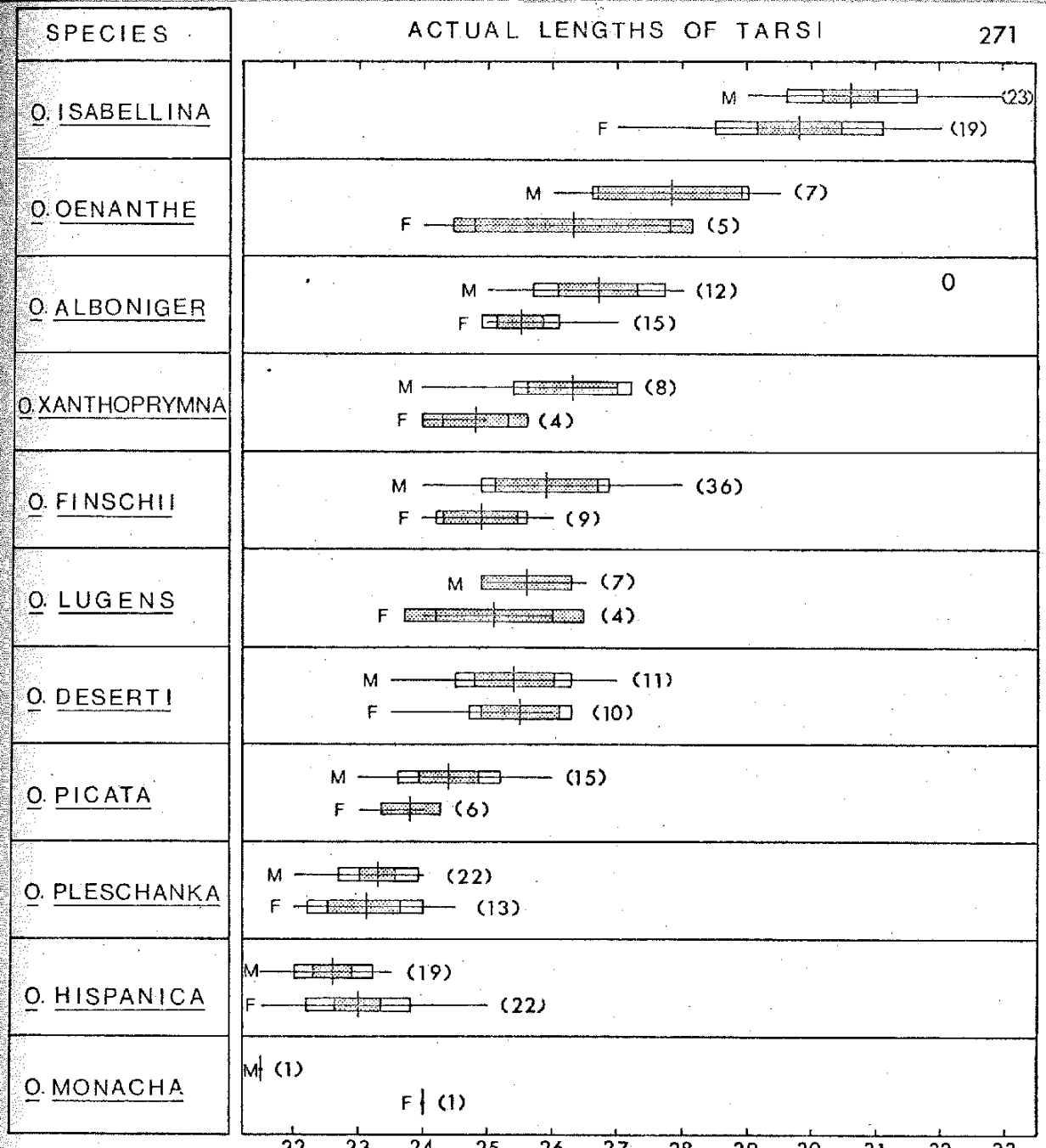


Figure 54. Weights of wheatears obtained in S. W. Iran.

KEY

BM = Males on the breeding grounds during the breeding season.
AM = All males.
AF = All females.





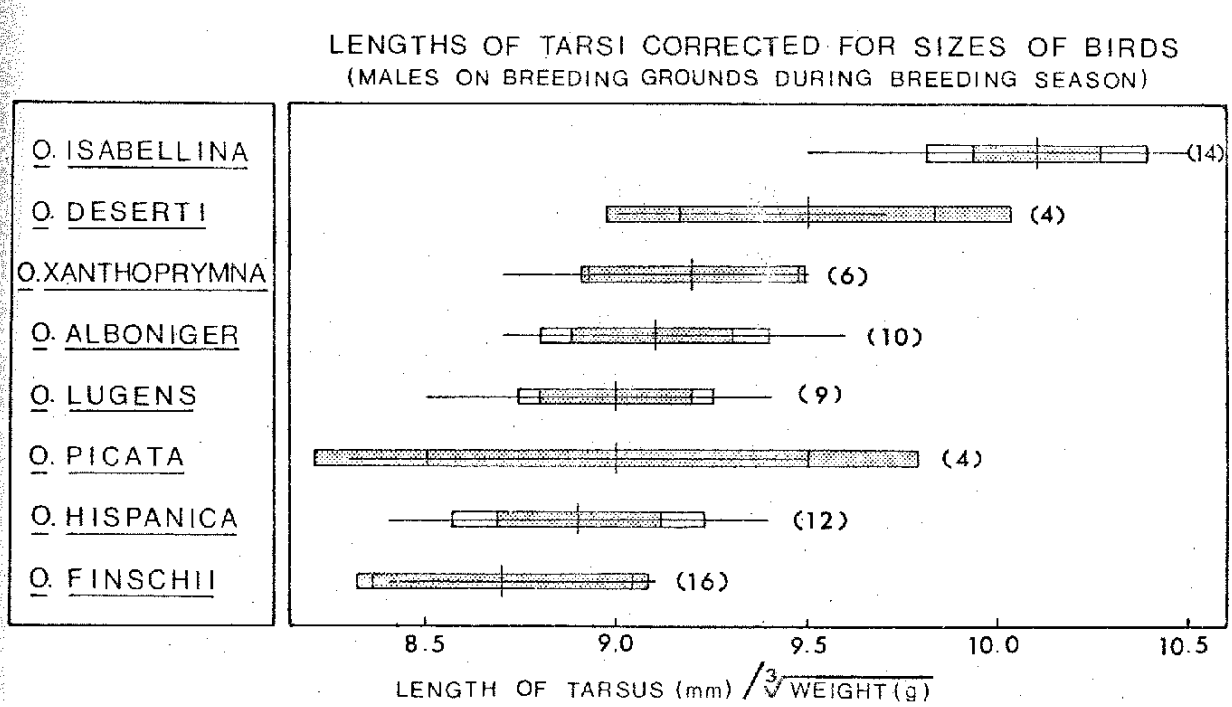
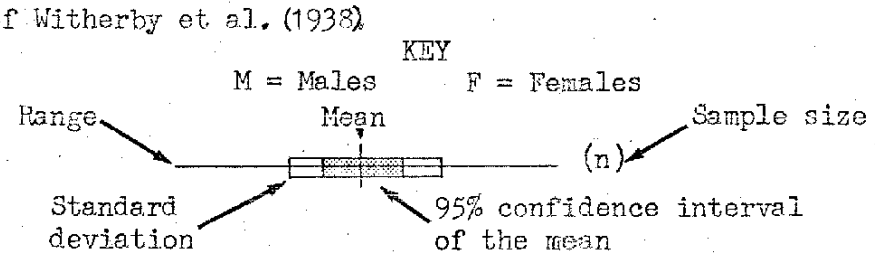


Figure 55. Measurements of tarsi of wheatears from S. W. Iran made using the method of Witherby et al. (1938).



data from males on their breeding grounds during the breeding season were used in the calculation of tarsus length/cube root of weight ratios. These ratios allow comparisons of tarsal length that are independent of body size.*

Generally speaking ground-dwelling birds have longer tarsi than birds of similar size that perch a lot in vegetation (e. g. Engels 1940; Dilger 1956; Grant 1965, 1966; Newton 1967; Gaston 1974). Long legs are an obvious advantage to cursorial birds since they allow them to cover ground more quickly and increase their fields of view. Therefore since O. isabellina and O. oenanthe and to a lesser extent O. deserti, O. finschii and O. xanthoprymna are the most cursorial of the wheatears that occur in S. W. Iran (see table 41) it is reasonable to expect that natural selection will have favoured longer tarsi in these species. The data presented in fig. 55 show that this is to a large extent true. Of the species of wheatear that occur in S. W. Iran O. isabellina and O. oenanthe have the longest tarsi both in absolute terms and per unit body weight.[1,2] O. deserti and O. xanthoprymna also have relatively long tarsi per unit body weight. However the tarsi of O. finschii are relatively short which is puzzling in view of its saltatorial habits while in winter quarters (see fig. 39, p. 181). The only explanation for this that I can suggest is that the disadvantage of short tarsi for life in winter quarters is outweighed by their advantage for life on the breeding grounds where the species often perches on vegetation.

Grant (1966) suggested that short tarsi are an advantage to birds that use non-rigid perches since they facilitate the maintenance of balance. Of the species of wheatear that occur in S. W. Iran O. deserti O. hispanica, O. picata and O. pleschanka often use flimsy perches (see

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*N.B. Similar procedure was used to eliminate allometric effects in comparisons of the lengths of wings and tails.

[1]No weights were available of male O. oenanthe while on their breeding grounds during the breeding season in S. W. Iran but the mean tarsal length/cube root of the mean weight of seven migrant males gave the high value of 9.94 (cf. fig. 55).

[2]A two-tailed Mann-Whitney U test showed that the tarsus/cube root of weight ratio of male O. isabellina while on their breeding grounds during the breeding season was significantly larger than the combined ratios for the other species included in fig. 55 — $p < .00006$.

table 41) and hence it seems likely that short tarsi would be an advantage to these species. The data presented in figure 55 show that O. hispanica and O. picata do in fact have relatively short tarsi. O. pleschanka also probably has relatively short tarsi. No weights were available for breeding males but the mean tarsal length/cube root of the mean weight of 22 migrant males obtained in S. W. Iran gave the relatively low value of 9.07 (cf. fig. 55). O. deserti appears to have relatively long tarsi which are probably associated with the cursorial habit it often adopts.

It therefore seems that the tarsi of the various species of wheatear that occur in S. W. Iran are well adapted to life in their respective habitats.

3) Wings:

A number of studies have related the aerodynamic properties of the wings of birds to their flight performance (e. g. Savile 1957, Brown 1963, Barlee 1964, Raikow 1973, Gaston 1974); and the aim of this section is to determine whether there are any adaptive differences between the wings of wheatears that employ short flights as their main means of locomotion while foraging and moving around their habitats, and the wings of wheatears that move around their habitats mainly on foot and use their wings more in fast direct flight, as for example when on migration (see table 41).

The aerodynamic properties of wings that are adapted to fast direct flapping flight are rather different from the aerodynamic properties of wings that are adapted to making numerous short flights and to manoeuvring in restricted places (e. g. see Savile 1957). The features of these two types of wings, referred to respectively as high-speed and elliptical wings after Savile (loc. cit.), are briefly reviewed below:

a) High-speed wings: High-speed wings have the following main characteristics: 1) They tend to have rather small wing areas relative to body weight (= high wing loadings), a feature that reduces drag and which can be afforded since at high speeds small wing areas give high

lift.* 2) They tend to be rather long, narrow and pointed, a shape which is reflected in relatively high aspect ratios (wing span/mean wing breadth) and which is an advantage since it reduces the drag caused by wing-tip vortices (Barlee 1964).

b) Elliptical wings: Elliptical wings, exemplified by the wing of O. lugens (fig. 56), have the following main characteristics: 1) They tend to be relatively short which is an advantage in restricted places. 2) They tend to have rather large wing areas relative to body weight (= low wing loadings), a feature which is achieved by broadening the whole wing to give the elliptical shape and which facilitates manoeuvre and repeated take-offs by providing high lift at slow speeds.* This shape is reflected in relatively low aspect ratios. 3) They tend to have well-developed mid-wing and wing-tip slots, the former provided by the alula and the latter by emargination of the distal primaries. These slots help to provide high lift at slow speeds since lift is proportional to the angle of attack up to the point at which stalling occurs and slots delay stalling to higher angles of attack (Brown 1963).* Wing-tip slots also serve to reduce drag produced by wing-tip vortices.

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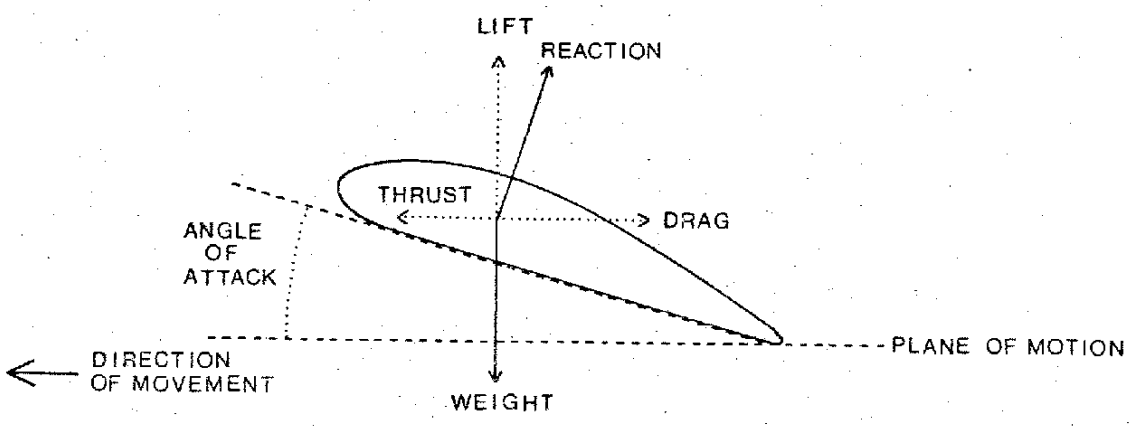
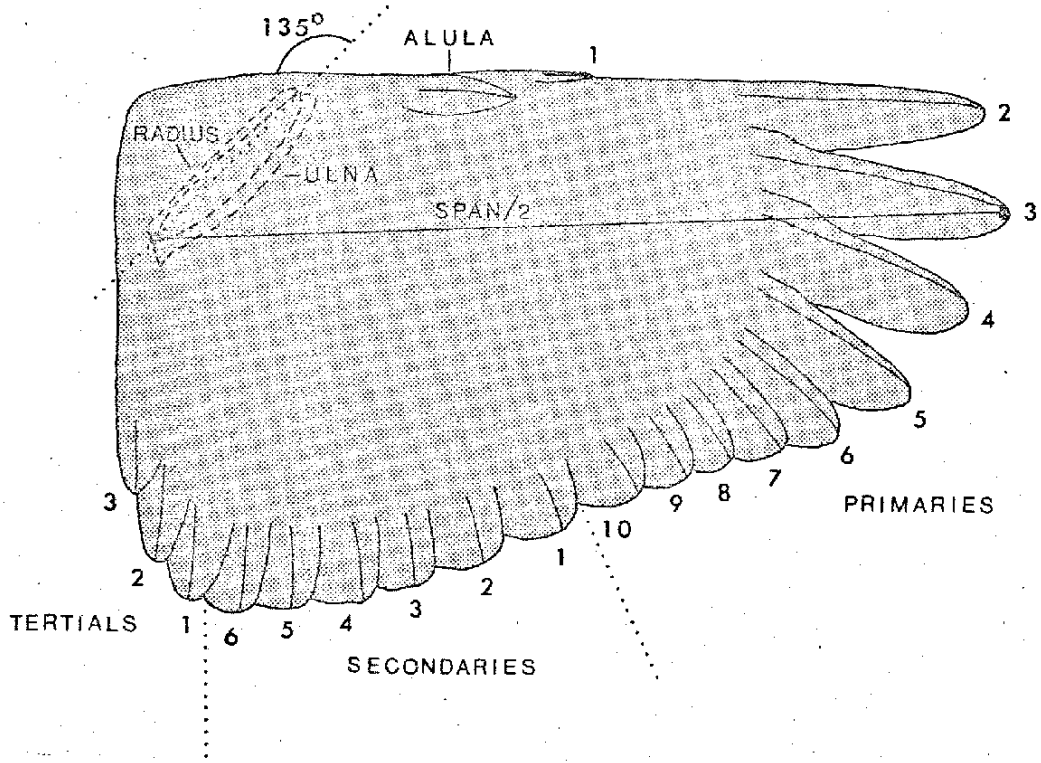
*The wings of birds are aerofoils and when they move forward through the air a force, known as the reaction, is produced almost at right angles to the plane of motion. This force can be resolved into two components, the lift and the drag, at right angles to one another. In order for a bird to become or remain airborne the lift produced by its wings must be equal to its weight and the propulsive force forward, the thrust in flapping flight, must be sufficient to overcome the drag. The angle that the wing makes with the plane of motion is called the angle of attack. These forces and the various other terms mentioned are illustrated below:



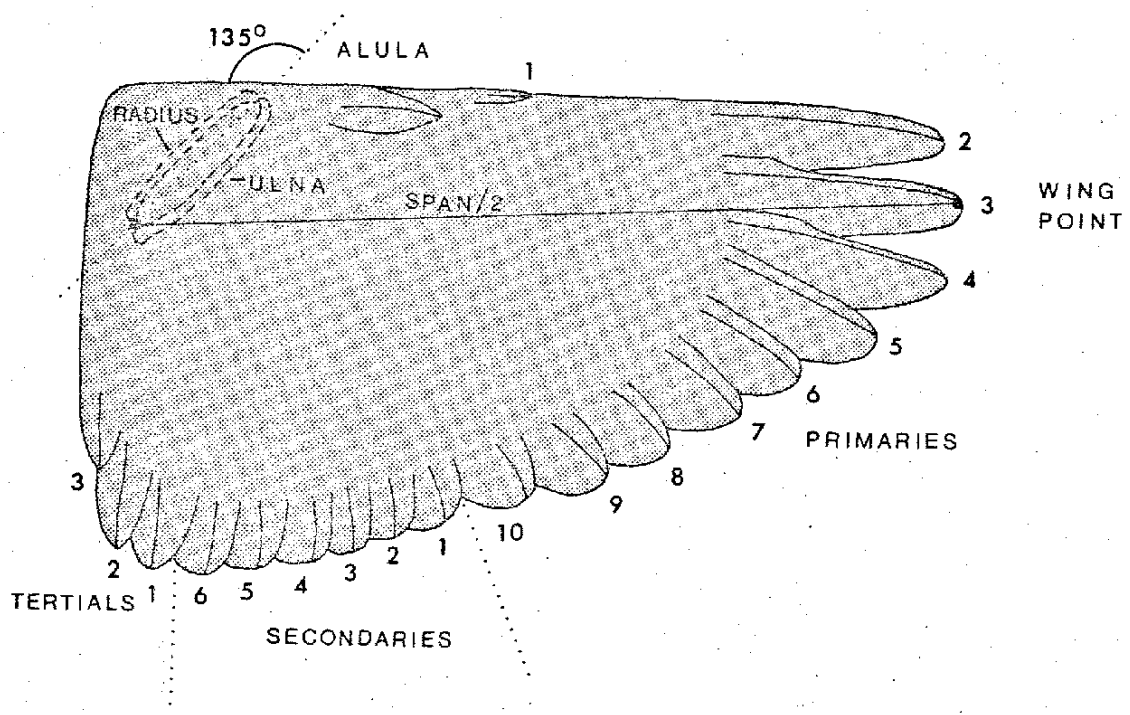
A cross section of an aerofoil showing the forces that are active during motion and various terms used in describing bird flight (modified after Brown 1963, Barlee 1964).

The reaction (i.e. both lift and drag) is proportional to the square of the velocity, to the wing area and to the angle of attack until it reaches about 12-15 degrees when lift begins to decrease due to stalling (Brown 1963, Barlee 1964).



WING OF O. LUGENS MALE

Wing length = 95 mm
Wing span = 224 mm Length of emargination as % of wing length = 85.0%
Aspect ratio = 3.69 Length of 10th primary as % of wing length = 76.3%
Wing area (cm^2)/Mean weight of males on breeding grounds during breeding season = 5.8cm^2



WING OF O. OENANTHE FEMALE

Wing length = 95 mm Length of emargination as % of wing length = 48.9%
Wing span = 218 mm Length of 10th primary as % of wing length = 70.8%
Aspect ratio = 4.32
Wing area (cm^2)/Mean weight of migrant females = 5.1cm^2

Figure 56. Wings of wheatears showing: 1) the method of pinning them out for measurement of areas and spans; and 2) examples of wings with differing aerodynamic properties: a) the wing of O. lugens which has characteristics that provide high lift economically at low speeds - e.g. it is relatively rounded, has large wing tip slots, low wing loading (wt./wing area) and low aspect ratio; b) the wing of O. oenanthe which has less well developed devices for lift at low speeds but has properties which are an advantage in fast direct flight - e.g. it is relatively pointed, has only two primaries with emargination and has relatively high wing loading and aspect ratio. See text for details.

Thus wings adapted for manoeuvrability and numerous short flights tend to be shorter and more rounded, and to have lower wing loadings and greater slotting than wings adapted to fast direct flight. Data on the lengths, shapes, wing loadings and slotting of the wings of wheatears from S. W. Iran are presented in figure 57. These data are first described and then used as a basis for comparing the wings of the various species.

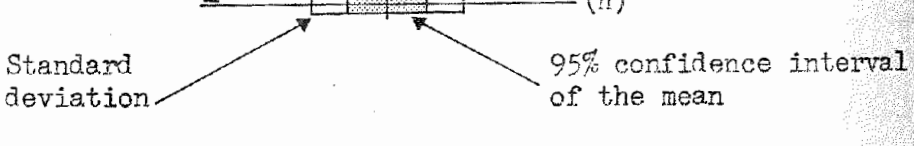
i) Wing length: As for tarsi (pp. 269, 272), wing lengths were corrected for the body size of the birds by dividing by the cube roots of their weights and to minimise errors due to seasonal fluctuations in weight the data, except when otherwise stated, refer only to males on their breeding grounds during the breeding season.

ii) Wing area: Wing areas have been measured by a number of workers (e. g. Poole 1938, Hartman 1961, Raikow 1973) by stretching the wings to their fullest extent, tracing the outlines on paper and measuring the areas enclosed. I tried this method for measuring the areas of the wings of wheatears but found that when repeated measurements of the same wing were taken the results differed considerably due to variations in the profile of the wing caused by differences in the fall of the feathers each time the wing was stretched. Therefore the following method was developed: The wings were removed from the birds at the joint where the humerus meets the radius and ulna. Each wing was then pinned out on graph paper so that: 1) the axis of the radius and ulna was at $45^{\circ}/135^{\circ}$ to the leading edge of the wing; 2) the wing-tip slots were fully open; 3) the tertials were at right angles to the leading edge; and 4) so that the intervening primaries and secondaries were arranged evenly (see fig. 56). The outlines of the wings were then traced and the areas measured with a planimeter. When the same wing was measured several times, using this method, the results varied relatively little.

iii) Wing span: With the wings pinned out, as described above, for the measurement of wing areas, wing spans were taken as the sum of the distances between the proximal ends of the radii and ulnae and the wing points (see fig. 56).

KEY

● = Individual measurements



Foot-notes:

*Wing length was measured from the carpal joint to the tip of the longest primary using the method of Witherby et al. (1938).

[a]Migrant males: Mean wing length (mm)/$\sqrt[3]{\text{Mean weight (g)}}$

[b]A female

[c]Wing area (cm^2)/ Mean weight of males on breeding grounds during breeding season.

[d]Wing area (cm^2)/ Mean weight of migrant males.

[e]The primaries were numbered from the distal end of the wing inwards and so the tenth primary is the innermost one.

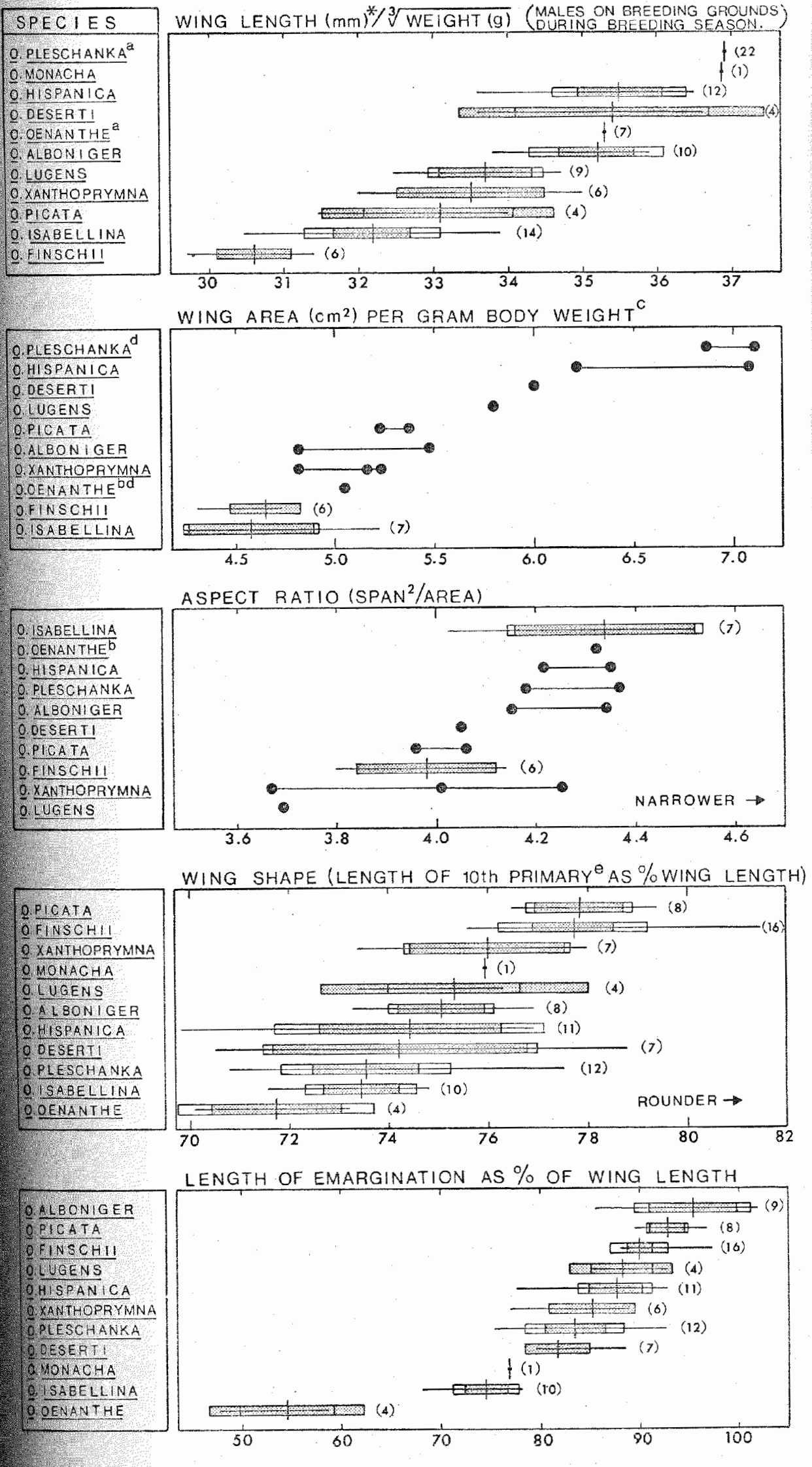


Figure 57. Some characteristics of the wings of wheatears from S. W. Iran. Unless otherwise stated the data refer to males. For actual wing lengths see table 1, p. 3. For key see opposite.

iv) Aspect ratio: A measure of wing shape is given by the aspect ratio which is the ratio of the wing span to the mean wing breadth. The latter is difficult to measure and so it was replaced by the mean aerodynamic chord which is: total wing area/span. The aspect ratio then becomes: $span^2$/area (see Savile 1957). Clearly the narrower is the wing the higher is the aspect ratio.

v) Wing shape: A measure of the roundness of the wings was given by expressing the length of the innermost primary as a percentage of the length of the longest primary (= wing length), and clearly the percentage is highest in the roundest wings.

vi) Length of emargination: As a basis for interspecific comparisons of the lengths of wing-tip slots, the total length of emargination of the outer webs of the distal primaries of each wing was expressed as a percentage of the wing length.

The data presented in figure 57 are now examined to test the working hypothesis that species of wheatear that employ short flights as their main means of locomotion while foraging and moving around their habitats have wings that are adapted to this mode of locomotion; that is, that they have wings that are shorter, rounder, have lower wing loadings and more emargination than the wings of species that are largely cursorial when in their habitats and use their wings mostly in fast direct flight. The species in the two categories, together with their migratory status, are listed in table 41, p. 268.

i) Wing length: Figure 57 shows that there is no indication that the cursorial species, O. isabellina and O. oenanthe, have longer wings than the species that make numerous short flights. Indeed O. isabellina has relatively short wings. However, apart from O. isabellina and O. monacha, the species that make long migrations (O. deserti, O. hispanica, O. oenanthe and O. pleschanka) have relatively longer wings than the species that are sedentary or make only short migrations (O. alboniger, O. finschii, O. lugens, O. picata, O. xanthoprymna). It therefore seems likely that

the advantage of long wings for long distance migration outweighs the advantage of short wings for negotiating restricted openings in vegetation or among rocks. This finding is consistent with the tendency among birds for long distance migrants to have longer wings than similar more sedentary birds (e. g. Kipp 1958, Hamilton 1961, Gaston 1974). O. isabellina and O. monacha are exceptions to this trend. O. monacha is relatively sedentary and yet the single available measurement suggests that it has rather long wings. This may be associated with the fact that, unlike other species of wheatear, O. monacha often makes high aerial chases after insects. O. isabellina has relatively short wings and this is puzzling in view of the fact that the species is extremely cursorial and makes long distance migrations. However the wintering grounds of the O. isabellina that breed in S. W. Iran are not known and it is possible that this population makes relatively short migrations and has relatively short wings.

ii) Wing area: Although the sample sizes are small the data suggest that the species that make numerous short flights (see table 41, p. 268) have larger wing areas per gram of body weight (i. e. have lower wing loadings) than the more cursorial species. This trend would appear to be adaptive since wings with low loadings provide high lift at slow speeds and hence are an advantage to species that take off repeatedly.

iii) Wing shape: Two measures of wing shape are given, aspect ratio and the length of the innermost primary expressed as a percentage of the wing length. Although sample sizes are small, the results support the hypothesis that the species that make a lot of short flights have broader, rounder wings than the more cursorial species. Thus the latter, O. isabellina and O. oenanthe, have the most pointed wings and those with the highest aspect ratios. The data also show that the species that make long migrations (O. deserti, O. hispanica, O. isabellina, O. oenanthe, O. pleschanka) have higher aspect ratios and more pointed wings than the species that make only short migrations or are relatively sedentary (O. alboniger, O. finschii, O. lugens, O. monacha, O. picata, O. xanthoprymna).*

* A two-tailed Mann-Whitney U test showed that the species of wheatear that make long migrations have significantly more pointed wings than species that make only short migrations or are relatively sedentary - $p < .00006$.

iv) Length of emargination: Although the data are rather few, they show that the species that make a lot of short flights tend to have more emargination than the more cursorial species.* Indeed all of the species that make a lot of short flights have well developed emargination on the outer webs of the third, fourth and fifth primaries (numbering from the distal end of the wing inwards). In contrast the two cursorial species, O. isabellina and O. oenanthe, have less well developed emargination. Thus O. isabellina shows emargination on the third and fourth primaries but only very slightly on the fifth while O. oenanthe has emargination on only the third and fourth primaries.

It therefore seems that the wings of the various species of wheatear that occur in S. W. Iran show differences that may be regarded as adaptations to their particular modes of habitat utilization and migratory status. Thus species that make a lot of short flights tend to have more rounded wings with lower wing loadings and more emargination than the more cursorial ones. Furthermore the species that make long migrations tend to have longer, more pointed wings with higher aspect ratios than the species that have shorter migrations or are relatively sedentary. Examples of wings of wheatears with differing aerodynamic properties are given in figure 56.

4) Tails:

Some measurements of the lengths of the tails of wheatears from S. W. Iran are given in figure 58. These were corrected for the sizes of the birds by dividing by the cube roots of their weights and to minimise errors due to seasonal fluctuations in weight, the data, except where otherwise stated, refer only to males on their breeding grounds during the breeding season. These measurements reveal a number of interesting features which will be discussed below:

i) Species of wheatear that make numerous short flights (see table 41, p. 268) have relatively longer tails than the two cursorial

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* A two-tailed Mann-Whitney U test showed that the difference is significant - $p < .00006$.

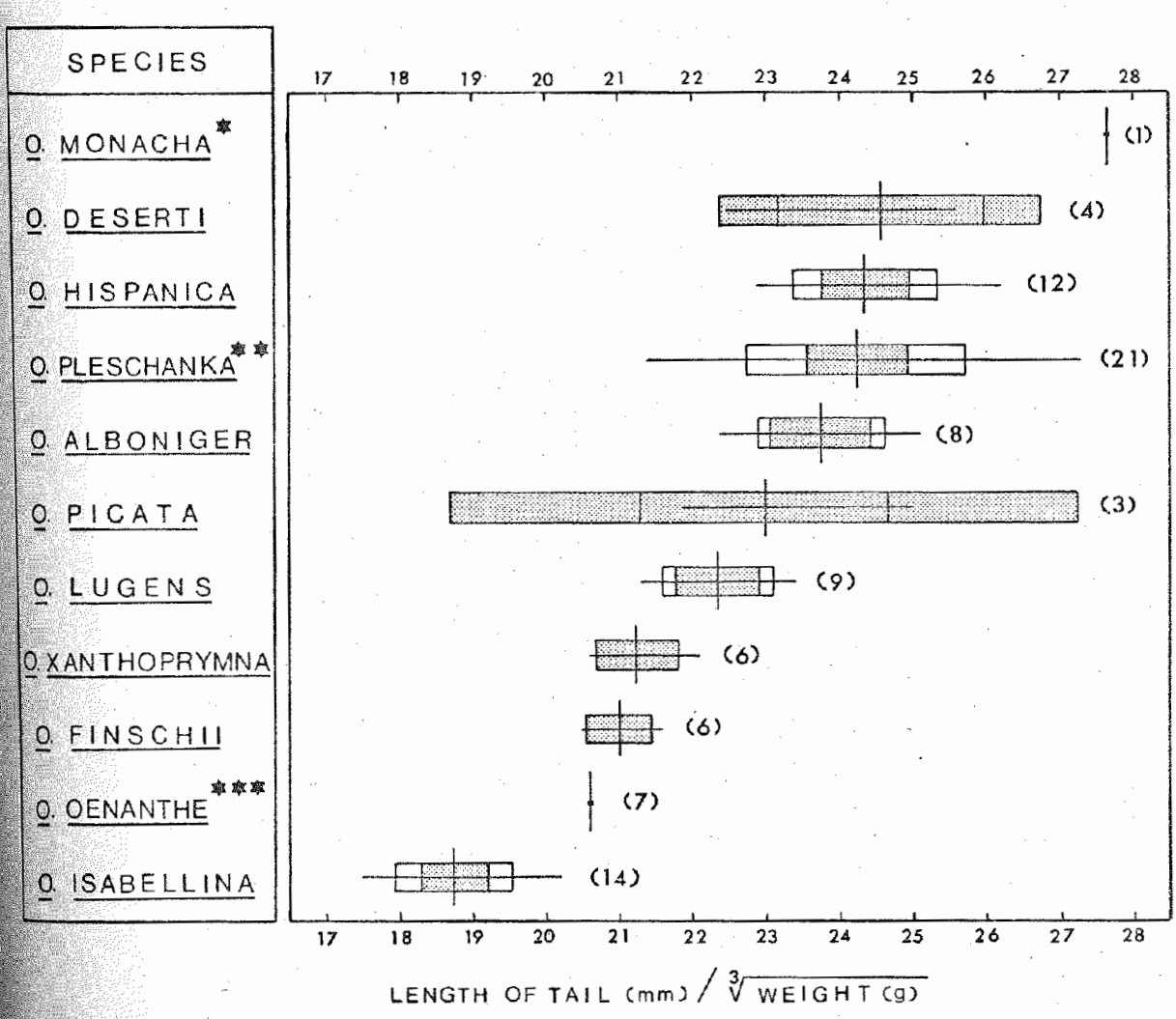


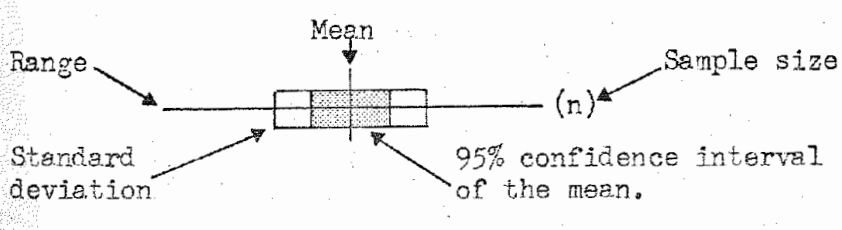
Figure 58. Measurements of tails of wheatears from S. W. Iran corrected for the sizes of the birds. The tail measurements were made using the method of Witherby et al.(1938) and except where otherwise stated are of males on their breeding grounds during the breeding season. The weights used to indicate size were taken from the same birds. For actual tail lengths see table 1, p. 3.

KEY

*Female taken in winter.

**Migrant males.

***Migrant males Mean tail length (mm)/$\sqrt[3]{\text{Mean weight (g)}}$



species, O. oenanthe and O. isabellina.* I suggest the following reasons for this difference: The tail acts as a brake when landing and as a rudder during flight and hence relatively long tails are an advantage to species that make repeated landings and for which manoeuvrability is important. It is noteworthy that the species that has the longest tail relative to body size is O. monacha which is the only species that was often seen making high twisting flights after insects in the air. Such aerobatics require good manoeuvrability and it seems reasonable to suggest that the long tail of O. monacha is an adaptation to aerial feeding. The relatively short tail of the cursorial O. isabellina, I suggest, is an adaptation that allows it to adopt its characteristic upright, searching posture (see plate 1, p. 2) without dragging its tail on the ground.

ii) The data presented in figure 58 show that, disregarding O. monacha, the species of wheatear that habitually use flimsy perches (O. deserti, O. hispanica, O. pleschanka, O. picata) have relatively longer tails than the species that use mainly firm, elevated perches (O. alboniger, O. finschii, O. lugens, O. xanthoprymna).* While perching the tails of birds are used in balancing and it is possible that the longer tails of the species that often use non-rigid perches help them to maintain balance when sitting on unstable objects.

PART II. SYSTEMATIC TREATMENT OF SPECIES:

So far in this chapter various factors that are likely to influence the ranges and habitat distributions of wheatears in S. W. Iran have been considered in general terms. In this section the distribution of each species is examined, in the light of the foregoing discussions, to try and determine the main factors that influence its range and habitat distribution.

1) O. ALBONIGER (Hume's Wheatear):

O. alboniger is a resident in S. W. Iran where it occurs widely but is restricted to areas below about 1,900 m above sea level (pp. 55-58,

* A two-tailed Mann-Whitney U test showed that the difference is significant - $p < .00006$.

fig. 22, p. 99) and is seldom found far from steep, usually rocky, boulder-strewn hillsides and gorges (pp. 120-123, 125-127). Factors that may help to explain this distribution pattern are considered below:

1) O. alboniger is a large wheatear (fig. 54, p. 270) and in clashes with other species of wheatear it was invariably the winner (table 39, p. 253). Its distribution is therefore unlikely to be influenced by interspecific competition.

2) The restriction of O. alboniger to areas below 1,900 m above sea level is puzzling as there is habitat above this altitude that appears to be suitable for the species, namely that which is occupied by O. xanthoprymna during the breeding season (p. 91; fig. 22, p. 99; figs. 26-27, pp. 121-122; p. 149). A possible explanation is that O. alboniger is kept out by competition from O. xanthoprymna. However I think this is unlikely as in winter when the two species often occur side by side O. alboniger is socially dominant to O. xanthoprymna (table 39, p. 253). Another possible explanation is that it is too cold for O. alboniger above about 1,900 m above sea level. However low temperature is unlikely to be a limiting factor during the breeding season since O. alboniger winters up to about 1,900 m above sea level when it survives lower temperatures than prevail above this altitude during the breeding season (cf. the ranges of temperature in the breeding distributions of O. alboniger and O. xanthoprymna which are given in fig. 53, p. 249). The only other possible explanation that I can suggest for the restriction in the altitudinal range of O. alboniger is that its sedentary habits have prevented it from colonising areas at higher altitudes since these cannot be occupied throughout the year due to the paucity of arthropod food during the winter (see pp. 171-173).

3) Apart from O. monacha, O. alboniger is the only species of wheatear that occupies areas below about 1,400 m above sea level during the summer. Indeed it is common right down to sea level. I suggest that a reason why O. alboniger can survive in these hot regions is that it lives in habitats that provide a) abundant shade where the birds can shelter from the heat; and b) shaded feeding areas where the birds can feed without

problems of overheating and where arthropod food supplies are not restricted by high ground surface temperatures (see pp. 170-173 and appendix D).

4) Habitat features which may be important in habitat selection were discussed in chapter V, pp. 125-126.

5) O. alboniger is well adapted to occupation of boulder-strewn rocky ground with abundant shade by virtue of its black and white plumage which can be extremely cryptic in such places (pp. 260-261) and its employment of the perch and pounce foraging strategy (pp. 178-181, p. 265) for which its well-slotted, high-lift, elliptical wings and relatively long tail are an advantage (pp. 277-282).

2) O. DESERTI (Desert Wheatear):

In S. W. Iran O. deserti breeds in flat, usually bush-clad plains in the cold steppe zone and probably winters in similar habitat below 800 m above sea level in the warm steppe zone (pp. 58-63; figs. 22-23, pp. 99-100; figs. 26-28, pp. 121-123; pp. 127-129). Factors that may help to explain these distribution patterns are considered below:

A) Breeding distribution:

1) O. deserti is a small slender wheatear (fig. 54, p. 270) and in skirmishes with other species of wheatear it was invariably subordinate (table 39, p. 253). It therefore seems likely that competition from other species of wheatear may be an important factor in restricting O. deserti to its relatively inhospitable range and habitat. The following evidence supports this hypothesis: a) In the Pamirs where O. deserti is one of the commonest breeding birds its habitat includes areas covered with large boulders, rocky defiles and high mountain passes (Dementiev and Gladkov 1968). The species therefore can survive on rocky hillsides and I postulate that it is restricted to plains in S. W. Iran by competition from O. alboniger, O. lugens and O. picata which occupy the hillsides within its range. b) In S. W. Iran O. deserti occurs in similar habitat to that occupied by O. isabellina and the two species show contiguous allopatry (see fig. 23, p. 100). O. deserti is socially subordinate to O. isabellina (table 39, p. 253). It therefore seems likely that the breeding distribution of

O. deserti in S. W. Iran may be limited along its common boundary with O. isabellina by competition from the latter species.

The above evidence suggests that O. deserti is restricted to an uncontested refuge which implies that it has a combination of adaptations for life on the desolate plains of the cold steppe zone that its competitors lack. I suggest that these adaptations include the following: i) the ability to thermoregulate efficiently in dry air (see fig. 53, p. 249); ii) small size which reduces its food requirements (pp. 269-270); iii) the ability to use flimsy perches and the perch and pounce foraging strategy (pp. 178-181, p. 265), to which it is well adapted by virtue of its light weight (pp. 269-270); high-lift, elliptical wings and relatively long tail (pp. 277-282); and iv) dun-coloration which renders it cryptic in the largely dun-coloured plains when it is still and reduces its heat load when temperatures are above the thermoneutral point (pp. 255-258).

2) Other factors which may be important in habitat selection were discussed in chapter V, pp. 127-128.

3) In view of the restriction of O. deserti to open habitats where there is little shade I suggest that a factor contributing to the lower altitudinal limit of its breeding range is high summer temperatures, working largely through their restricting influence on the availability of arthropod prey (pp. 170-173 and appendix D).

B) Winter distribution:

I postulate that O. deserti is confined to lowland areas of S. W. Iran in winter for two main reasons: 1) paucity of food on its breeding grounds; and 2) competition from O. finschii in other parts of S. W. Iran (see pp. 60-62; table 39, p. 253).

3) O. FINSCHII (Finsch's Wheatear):

A) Breeding distribution:

The breeding range of O. finschii in S. W. Iran is restricted to the wetter parts of the sub-steppe zone (p. 64; fig. 23, p. 100) where it is usually found on gently sloping hillsides, piedmonts or along the bases

of steep rocky hillsides (figs. 26-27, pp. 121-122; pp. 130-131). The factors that govern this distribution pattern are largely obscure but some factors that may help to explain it are considered below:

1) It is unlikely that the breeding distribution of O. finschii is influenced by competition from other species of wheatear since it is a heavy (fig. 54, p. 270), aggressive species which was socially dominant to all other species of wheatear, except O. alboniger, with which it was seen to clash (table 39, p. 253); and it is unlikely that O. alboniger competes seriously with O. finschii since it has rather different habitat requirements (pp. 120-123, 125-127) and the two species were rarely found in the same vicinity (see table 34, p. 214; table 35, p. 217; p. 221).

2) The lower altitudinal limit is probably controlled by high summer temperatures working largely through their restricting influence on the availability of arthropod prey (pp. 170-173 and appendix D).

3) Above about 2,500 m above sea level O. finschii is replaced in similar habitat by O. oenanthe (fig. 23, p. 100) and it is possible that this is due to interspecific competition. However I think this is unlikely since although no interactions were observed between these species, their relative positions in the dominance hierarchy, which appears to exist among the members of the genus Oenanthe, suggests that in the event of competition O. finschii would prevail over O. oenanthe (see pp. 253-254). An obvious alternative hypothesis is that it is too cold for O. finschii above about 2,500 m above sea level. However this is also unlikely since the range of temperature experienced by O. oenanthe while on its breeding grounds is similar to that experienced by O. finschii while on its breeding grounds (fig. 53, p. 249). Clearly the factors governing the upper altitudinal limit of O. finschii require further study.

4) In the west of its range O. finschii may be limited by an inability to feed in areas where much of the ground is often obscured in spring by a flush of dense herbaceous vegetation (see pp. 264-265 where problems of feeding in such areas are discussed).

5) In the east of its range the most likely limiting factor is low humidity (see fig. 52, p. 247; fig. 53, p. 249).

6) Habitat features which may be important in habitat selection were discussed in chapter V, pp. 130-131.

B) Winter distribution:

In S. W. Iran O. finschii is widespread in winter from sea level to about 1,900 m above sea level (pp. 67-68; fig. 24, p. 101) where it occurs mainly on plains, gently sloping hillsides or at the bases of steep rocky hillsides (fig. 28, p. 123; pp. 131-132). The upper altitudinal limit is probably determined by cold winter temperatures working largely through their influence on the availability of arthropod prey (pp. 170-173 and appendix D).

4) O. HISPANICA (Black-eared Wheatear):

O. hispanica is a summer visitor to S. W. Iran where it usually breeds on hillsides and in valley bottoms, particularly in lightly wooded areas, between about 1,600 m and 2,700 m above sea level in the xerophilous forest zone (pp. 69-71; fig. 22, p. 99; figs. 26-27, pp. 121-122; pp. 132-133). Factors that may help to explain this rather restricted distribution are reviewed below:

1) O. hispanica is a small, slender species which is socially subordinate to most other species of wheatear (table 39, p. 253). It therefore seems likely that interspecific competition may be an important limiting factor for this species and I postulate that it is restricted in range by competition from the following species: a) O. xanthoprymna at the upper limit of its range; b) O. alboniger, O. picata, O. isabellina and particularly O. finschii and O. lugens in the east; and O. alboniger at the lower limit of its range. Indirect support for this hypothesis is given by the fact that in Morocco, where these competitors are either absent or extremely rare, O. hispanica extends into drier country as far as the 200 mm (mean annual precipitation) isohyet (Brosset 1961) whereas in S. W. Iran it is confined largely to areas where the mean annual precipitation is greater than 400 mm (cf. overlay 1 and fig. 22, p. 99).

It seems reasonable to suggest therefore that O. hispanica has been able to colonise S. W. Iran because it has adaptations which enable it to survive in an uncontested refuge, namely the xerophilous forest zone where, except at the edges of the zone, O. hispanica is the only species of wheatear that breeds. I postulate that these adaptations include the following: i) the ability to thermoregulate efficiently in moist air (fig. 53, p. 249); ii) the ability to use flimsy perches and the perch and pounce foraging strategy which I suggest is critical for survival in the xerophilous forest zone since in the spring dense flushes of herbaceous vegetation often obscure much of the ground and the above abilities enable them to feed under such conditions (see pp. 264-265 for discussion of this topic); iii) low weights (fig. 54, p. 270); short tarsi (fig. 55, p. 271); high-lift, elliptical wings (fig. 57, p. 277) and long tails which facilitate the above foraging strategy.

2) Other factors that may influence the habitat distribution of O. hispanica were discussed in chapter V, pp. 133-134.

5) O. ISABELLINA (Isabelline Wheatear):

O. isabellina is a summer visitor to the sub-steppe zone of S. W. Iran where it breeds abundantly on plains. It probably winters in small numbers on plains below about 800 m above sea level in the warm steppe zone (pp. 71-77; figs. 23-24, pp. 100-101; pp. 136-138; figs. 26-28, pp. 121-123). Factors that may help to explain these distributions are considered below:

A) Breeding distribution:

1) O. isabellina may be prevented from inhabiting rocky hillsides and to some extent piedmonts in S. W. Iran by competition from the species that occupy these habitats (O. alboniger, O. finschii, O. picata and O. lugens) to which it is socially subordinate (table 39, p. 253). Some indirect evidence in support of this hypothesis is given by the report that in the Caucasus, where its only congeneric competitor is probably O. finschii, the preferred breeding habitat of O. isabellina is stonefields and scree (Dementiev and Gladkov 1968 citing work by Satunin 1907 and Bobrinskii 1915).

2) The socially dominant competitors of O. isabellina (O. alboniger, O. finschii, O. picata and O. lugens) are largely restricted to rocky hillsides and the bases of hillsides, probably mainly because of their need for shade, cover and nest-sites that are provided by rocky ground; their predominant use of the perch and pounce foraging strategy with its associated morphological adaptations; and because their black and white plumage would be conspicuous and render them vulnerable to predators in open habitats with little cover (see sections dealing with these species in this chapter). However O. isabellina is not restricted in these ways and I postulate that it can survive in open, bare plains because it has the following adaptations: i) Dun-coloration which renders it cryptic on the largely dun-coloured plains when it is still and reduces its heat load when temperatures are above the thermoneutral point (pp. 255-258); ii) the ability to make efficient use of the dash and jab foraging strategy which is an advantage on featureless bare ground where there are few elevated perches (pp. 265-267); and iii) its upright posture and relatively long tarsi which facilitate the above foraging strategy.

3) O. isabellina is socially dominant to all other species of wheatear that occur on plains in S. W. Iran (i. e. O. deserti and O. oenanthe) and hence its distribution on plains is unlikely to be restricted by competition from other species of wheatear (table 39, p. 253).

4) The eastern boundary of the range of O. isabellina virtually coincides with the eastern limit of the sub-steppe zone and the species hardly enters the cold steppe zone where it is replaced by O. deserti. I suggest that the following factors may contribute to this boundary: a) O. isabellina may be unable to thermoregulate efficiently in very dry air (see fig. 53, p. 249). b) Due to the greater aridity arthropod prey is probably usually scarcer in the cold steppe than in the sub-steppe zone (pp. 173-174) and for the following reasons it seems likely that paucity of prey may help to prevent O. isabellina from colonising the cold steppe zone: i) O. isabellina employs predominantly and is morphologically well adapted to the dash and jab foraging strategy which is probably effective only in areas with relatively high densities of prey (p. 266); ii) by virtue of its

heavy weight, long tarsi, short tail, and relatively high-speed wings O. isabellina is probably unable to make efficient use of the perch and pounce foraging strategy or use flimsy perches which, in connection with O. deserti (p. 265), I suggested were adaptations to foraging in areas with low prey densities.

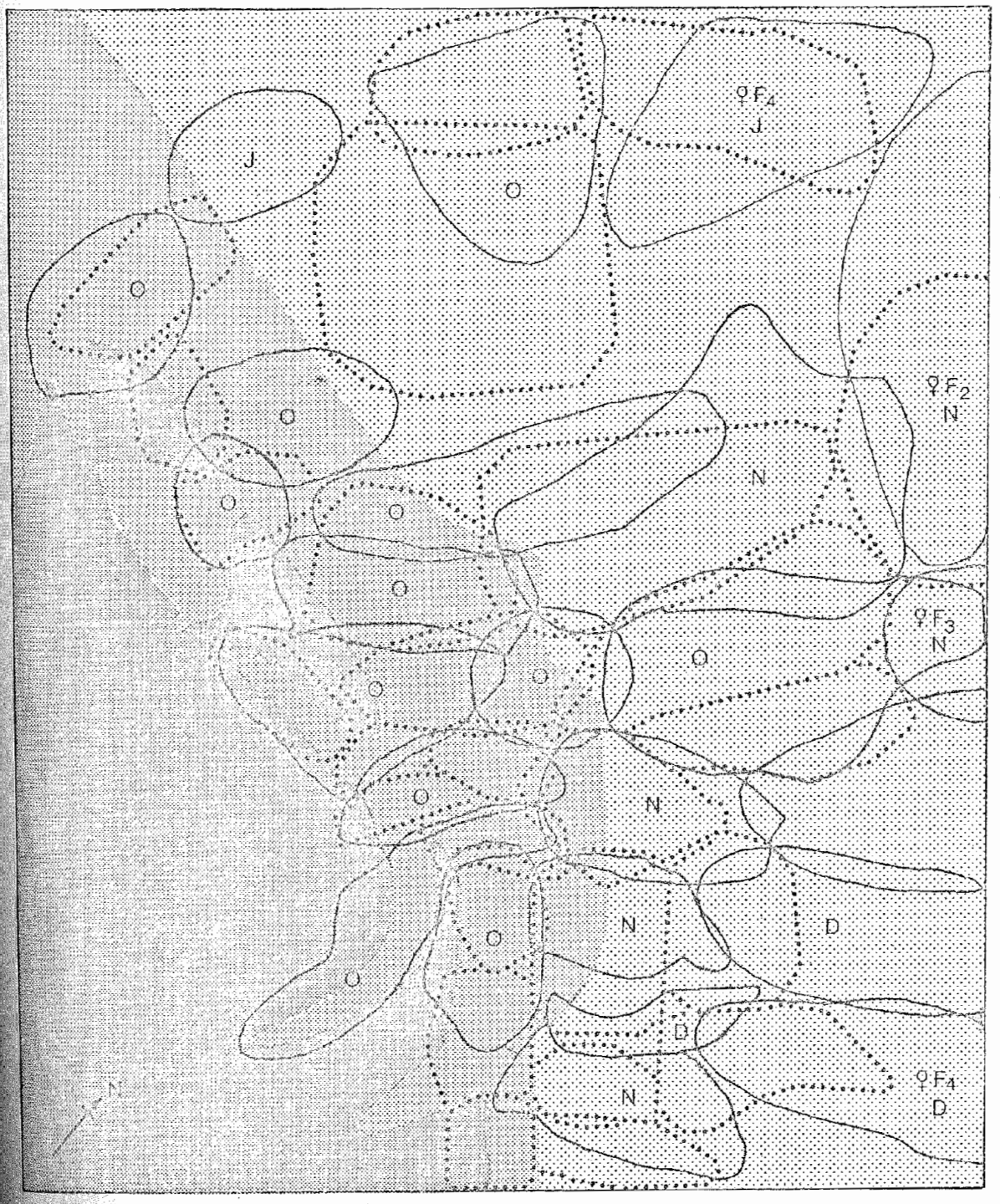
5) In view of its restriction to open habitats with little shade it seems likely that the lower altitudinal limit of the breeding range of O. isabellina may be controlled by high temperatures, probably working largely through their restricting influence on the availability of arthropod prey (pp. 170-173 and appendix D).

6) Habitat features which may be important in habitat selection were discussed in chapter V, pp. 136-138.

B) Winter distribution:

In winter O. isabellina is replaced on its breeding grounds in S. W. Iran by O. finschii which is a common winter visitor to the area. Indeed in many localities O. finschii occupied precisely the same ground in winter as was occupied in the breeding season by O. isabellina. An example of this replacement was documented at the Maharlu North study area near Shiraz and is illustrated in figure 59. Although most of the breeding population of O. isabellina has departed before the arrival of the O. finschii at the beginning of September (see p. 73) I postulate that, in evolutionary terms, a factor in the departure of O. isabellina is competition from O. finschii which is the socially dominant member of this pair of species (table 53, p. 249). An obvious alternative hypothesis is that it is too cold for O. isabellina on its breeding grounds in winter. However the data, presented in fig. 53, p. 249, on the ranges of ambient temperature in areas where the various species of wheatear occurred do not suggest that O. isabellina has poorer cold tolerance than O. finschii which winters up to 1,900 m above sea level.

It will be noted that O. isabellina coexists with O. finschii in winter in the warm steppe zone below about 800 m above sea level (fig. 24, p. 101). However during this study neither of these species was common in this area with the result that competition for ground was unlikely to have been severe (see pp. 229-231).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6) O. LUGENS (Mourning Wheatear):

O. lugens is a summer visitor to S. W. Iran where it breeds on open, usually steep, rocky hillsides and piedmonts in the sub-steppe zone and probably also in the cold steppe zone (pp. 77-81; fig. 22, p. 99; figs. 26-27, pp. 121-122; p. 136). Factors which may help to explain this distribution are considered below:

1) O. lugens is replaced above about 2,700 m above sea level by O. xanthoprymna which occurs in similar habitats to those occupied by O. lugens. Interactions between these species while on their breeding grounds were observed on only one occasion. This was on Kuh-i-Lalehzar at about 2,700 m above sea level where an O. xanthoprymna was twice seen to attack an O. lugens which both times retreated (see p. 222). In view of the hierarchical relationship between most species of wheatear (pp. 252-254) it seems likely that on their breeding grounds O. xanthoprymna is socially dominant to O. lugens in which case the upper altitudinal limit of the range of O. lugens may be influenced by competition from O. xanthoprymna.

2) O. lugens is usually found on open hillsides which provide little general shade. It therefore seems likely that the lower altitudinal limit of this species may be controlled by high summer temperatures working chiefly through their restricting influence on the availability of arthropod prey (pp. 170-173 and appendix D). This is in contrast to O. alboniger which occurs down to sea level and which, in hot areas, invariably occurs in habitats that provide shaded feeding grounds throughout most of the day (see pp. 126, 283-284). A factor which may prevent O. lugens from occupying such habitats is competition from O. alboniger which is socially dominant to O. lugens (table 39, p. 253).

3) O. lugens is very similar, both in physiognomy and ecology, to O. finschii and yet in S. W. Iran it extends into drier country than the latter (figs. 22-23, pp. 99-100). I postulate that this difference in range may be associated with interspecific differences in ability to thermoregulate in dry air (see fig. 53, p. 249).

4) I suggest that in the west of its range O. lugens is prevented from colonising the wetter parts of the xerophilous forest zone by an inability, probably associated with its relatively heavy weight, to use flimsy perches which I believe is of critical importance for foraging in areas where much of the ground is often obscured by a flush of herbaceous vegetation (see pp. 264-265 where problems of feeding in such areas are discussed).

5) Habitat features which may be important in habitat selection were discussed in chapter V, pp. 139-140.

6) O. lugens is well adapted for life on boulder-strewn rocky hillsides by virtue of: i) its black and white plumage which can be extremely cryptic against variegated light and dark backgrounds and probably affords the additional advantage of reducing the metabolic costs of staying warm when ambient temperatures are below the thermoneutral point (see p. 261); and ii) its use of the perch and pounce foraging strategy for which its well-slotted, high-lift elliptical wings and fairly long tail are an advantage (pp. 273-282).

7) In localities where O. lugens and O. finschii were found together O. lugens was mainly confined to territories high up on steep hillsides while O. finschii occupied territories along the bases of hills. However where O. lugens was found in the absence of O. finschii it occupied both these habitats. I suggest that this is an example of ecological release and that where the two species were sympatric O. lugens was excluded from the foothill habitat by competition from O. finschii which is socially dominant to it (table 39, p. 253). The relationships between these two species were discussed more fully on pp. 218-220.

7) O. MONACHA (Hooded Wheatear):

In S. W. Iran O. monacha is probably resident in small numbers in desolate, arid wadis and badlands in the hot lowlands bordering the Persian Gulf. In addition it may occur in the sub-desert zone (pp. 81-83, 141, 215-216). Factors which may help to explain this rather restricted distribution are considered below:

FACTORS INFLUENCING RANGE AND HABITAT DISTRIBUTION

1) Few interactions have been documented between O. monacha and other species of wheatear (table 39, p. 253). However in view of the dominance hierarchy that appears to exist among the members of the genus Oenanthe and the fact that O. monacha is probably socially subordinate to O. lugens it is probably subordinate also to O. alboniger, O. finschii, O. picata and O. xanthoprymna. Its social status in relation to the other species is unknown (see pp. 252-254). It therefore seems reasonable to postulate that a factor contributing to the restriction of O. monacha to its dreary domain may be competition from other species of wheatear.

2) In areas where O. monacha occurs it is the only species of wheatear and adaptations which may contribute to its ability to survive in such inhospitable places will now be briefly considered: a) Unlike other species of wheatear O. monacha frequently takes flying arthropods in the air and I submit that this ability has the following advantages for life in its often hot, relatively shade-free habitat: i) Flying arthropods, unlike ground-dwelling forms, continue to be active and available throughout the heat of the day. ii) By feeding in the air the birds avoid high temperatures near the ground. When at rest they take advantage of local shade if temperatures are high. These ideas are supported by and were largely derived from the observations reported on pp. 188-189. b) O. monacha is well adapted for aerial pursuits which require high manoeuvrability by virtue of its relatively long rounded wings (fig. 57, p. 277) and exceptionally long tail (fig. 58, p. 281; p. 282).

8) O. OENANTHE (Wheatear):

O. oenanthe is a summer visitor to S. W. Iran where it was found breeding at the bases of rocky hillsides largely in the montane zone above about 2,700 m above sea level (p. 83; fig. 23, p. 100; fig. 26, p. 121; p. 142). Factors which may help to explain this rather restricted distribution are discussed below:

1) O. oenanthe is probably socially subordinate to all other species of wheatear that occur in S. W. Iran except possibly O. pleschanka, O. deserti and O. monacha (pp. 252-254). It therefore seems reasonable

to postulate that competition from other species of wheatear may be a factor contributing to the restriction in range of O. oenanthe. The most likely competitors are O. finschii, O. hispanica, O. lugens and O. isabellina which occupy similar habitats to O. oenanthe but at lower altitudes. Indirect support for this hypothesis was given by the observations of Wettstein (1938) and Watson (1964) a) that on Aegean islands where both O. hispanica and O. oenanthe occurred the former was found largely at lower altitudes than the latter which was confined to the tops of the mountains; but b) that where O. oenanthe occurred alone on an island it was found at all altitudes.

2) The above hypothesis implies that O. oenanthe has adaptations, that its competitors lack, which enable it to survive in the montane zone. An obvious suggestion is that O. oenanthe has greater cold tolerance than species that occur at lower altitudes. However the data given in fig. 53, p. 249 do not support this suggestion. I know of no alternative hypotheses that have been put forward and so clearly this matter requires further study.

3) Habitat features that may be important in habitat selection were discussed in chapter V, pp. 142-143.

9) O. PICATA (Eastern Pied Wheatear):

In S. W. Iran O. picata breeds widely, but in only very small numbers, between about 450 m and 2,400 m above sea level in the xerophilous forest, sub-steppe and steppe zones where it was found on steep rocky hillsides and on adjacent gently sloping ground. In winter it was recorded in a few localities up to about 1,500 m above sea level (overlay 6; pp. 83, 86-87, 144; fig. 26, p. 121; p. 144). Factors that account for the rarity of O. picata in S. W. Iran are largely obscure but I suggest that the following may play a part: i) competition from O. alboniger, O. finschii and O. lugens which occur in similar habitats to O. picata; and ii) inability to thermoregulate efficiently in moist air.

10) O. PLESCHANKA (Pied Wheatear):

In S. W. Iran O. pleschanka occurs mainly as a passage migrant, but it may breed or attempt to breed occasionally (pp. 87-89). Although the factors that account for its failure to breed regularly in S. W. Iran are undoubtedly complex I suggest that competition from other species of wheatear may be contributory since O. pleschanka is socially subordinate to most other species of wheatear that occur in the area (table 39, p. 253).

11) O. XANTHOPRYMNA (Red-tailed Wheatear):

A) Breeding distribution:

In S. W. Iran O. xanthoprymna is a summer visitor to mountainous areas above about 2,500 m above sea level where it breeds mainly in rocky valleys; on steep, stony, boulder-strewn hillsides; and along the bases of rocky hillsides (p. 91; fig. 22, p. 99; figs. 26-27, pp. 121-122). Factors that may help to explain this rather restricted distribution are considered below:

1) O. xanthoprymna overlaps in habitat with O. alboniger, O. finschii, O. hispanica, O. lugens and O. picata which replace it at lower altitudes (see table 34, p. 214). O. xanthoprymna is socially subordinate to O. alboniger, O. finschii and probably O. picata (table 39, p. 253) and so competition from these species may contribute to the restriction in altitudinal range of O. xanthoprymna. However O. xanthoprymna is probably socially dominant to O. lugens and O. hispanica and hence it is unlikely that O. xanthoprymna is kept out of the habitats of these species by competition from them.

2) I suggest that the failure of O. xanthoprymna to colonise the xerophilous forest zone, the domain of O. hispanica, may be influenced by the following factors: i) an inability to thermoregulate efficiently in moist air (fig. 53, p. 249); and ii) an inability, associated with its relatively heavy weight (fig. 54, p. 270), long tarsi (fig. 55, p. 271) and short tail (fig. 58, p. 281), to perch on flimsy vegetation which I contend is crucial for foraging in the xerophilous forest zone where much of the ground is often obscured by a dense flush of herbaceous vegetation in spring (see pp. 264-265 for discussion of problems associated with

foraging in such areas).

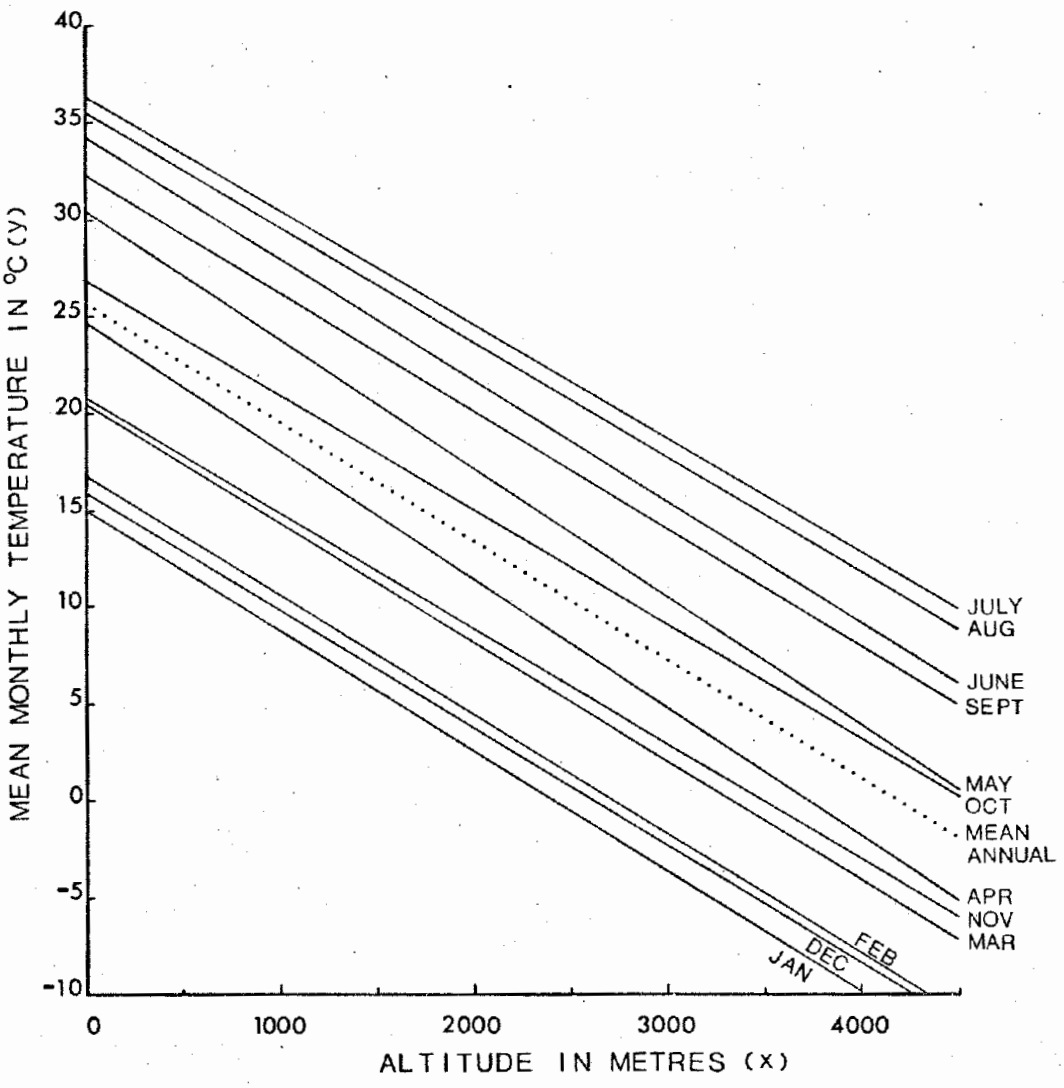
3) O. xanthoprymna is morphologically very similar to O. lugens (pp. 267-282), both species being well adapted to employment of the perch and pounce foraging strategy on rocky hillsides where solid, elevated perches are abundant (see p. 265). In view of this, and the fact that O. xanthoprymna is probably socially dominant to O. lugens the only explanation that I can suggest for O. xanthoprymna not usurping the province of O. lugens is interspecific differences in thermoregulatory ability (see fig. 53, p. 249).

4) Habitat features which may be important in habitat selection were discussed in chapter V, pp. 149-150.

B) Winter distribution:

O. xanthoprymna is a common winter visitor to S. W. Iran where it occurs widely on plains, rocky hillsides, and particularly along the bases of rocky hillsides in the lower deforested parts of the xerophilous forest zone, and in the sub-steppe and warm steppe zones (pp. 94-95; fig. 24, p. 101; fig. 28, p. 123; pp. 150-151). The upper altitudinal limit of this range is about 2,100 m above sea level and is probably controlled largely by low temperatures working through their restricting influence on the availability of arthropod prey (pp. 170-173 and appendix D).

APPENDIX A



Fitted linear regression lines of mean monthly temperature (y) on altitude (x) in S. W. Iran.

NOTES:

1) The regressions are based on data from 24 stations located between 4-2,600m. Twenty-two had data covering five or more years and the remaining two had data for four years. The data were taken from the Meteorological Year Books (1956-1968) published by the Iranian Meteorological Department.

2) For each regression the following additional data are given: The regression equation in the form

$y = a + bx \pm S_{y.x}$, F and r^2 where:-

a = the y-intercept.

b = the regression coefficient.

$S_{y.x}$ = the standard error of estimate.

F = the sample variance ratio.

r^2 = the coefficient of determination.

JAN:	$y = 15.019 - 0.006x \pm 1.410$	$F = 314.082$	$r^2 = 0.935$
FEB:	$y = 17.005 - 0.006x \pm 1.483$	$F = 290.282$	$r^2 = 0.930$
MAR:	$y = 20.471 - 0.006x \pm 1.463$	$F = 280.387$	$r^2 = 0.927$
APR:	$y = 24.793 - 0.007x \pm 1.426$	$F = 354.087$	$r^2 = 0.942$
MAY:	$y = 30.613 - 0.007x \pm 1.646$	$F = 261.612$	$r^2 = 0.922$
JUN:	$y = 34.414 - 0.006x \pm 1.936$	$F = 170.588$	$r^2 = 0.886$
JUL:	$y = 36.253 - 0.006x \pm 1.953$	$F = 139.290$	$r^2 = 0.864$
AUG:	$y = 35.616 - 0.006x \pm 2.021$	$F = 137.452$	$r^2 = 0.862$
SEPT:	$y = 32.320 - 0.006x \pm 1.708$	$F = 201.267$	$r^2 = 0.901$
OCT:	$y = 27.077 - 0.006x \pm 1.304$	$F = 334.777$	$r^2 = 0.938$
NOV:	$y = 20.980 - 0.006x \pm 1.387$	$F = 298.996$	$r^2 = 0.931$
DEC:	$y = 16.057 - 0.006x \pm 1.369$	$F = 316.919$	$r^2 = 0.935$
YEAR:	$y = 25.905 - 0.006x \pm 1.190$	$F = 432.981$	$r^2 = 0.952$

In all cases the arithmetic mean of x ($\bar{x}$) = 1350.330, the sum of the squares of x (x^2) = 15,728,400, and the number of degrees of freedom = 22. $F_{0.001[1,22]} = 14.4$ and it is, therefore, clear that in every case a large and significant portion of the variance of y has been explained by regression on x. A measure of this portion is given by r^2.

3) The above analyses give the following relationships between temperature and altitude:-

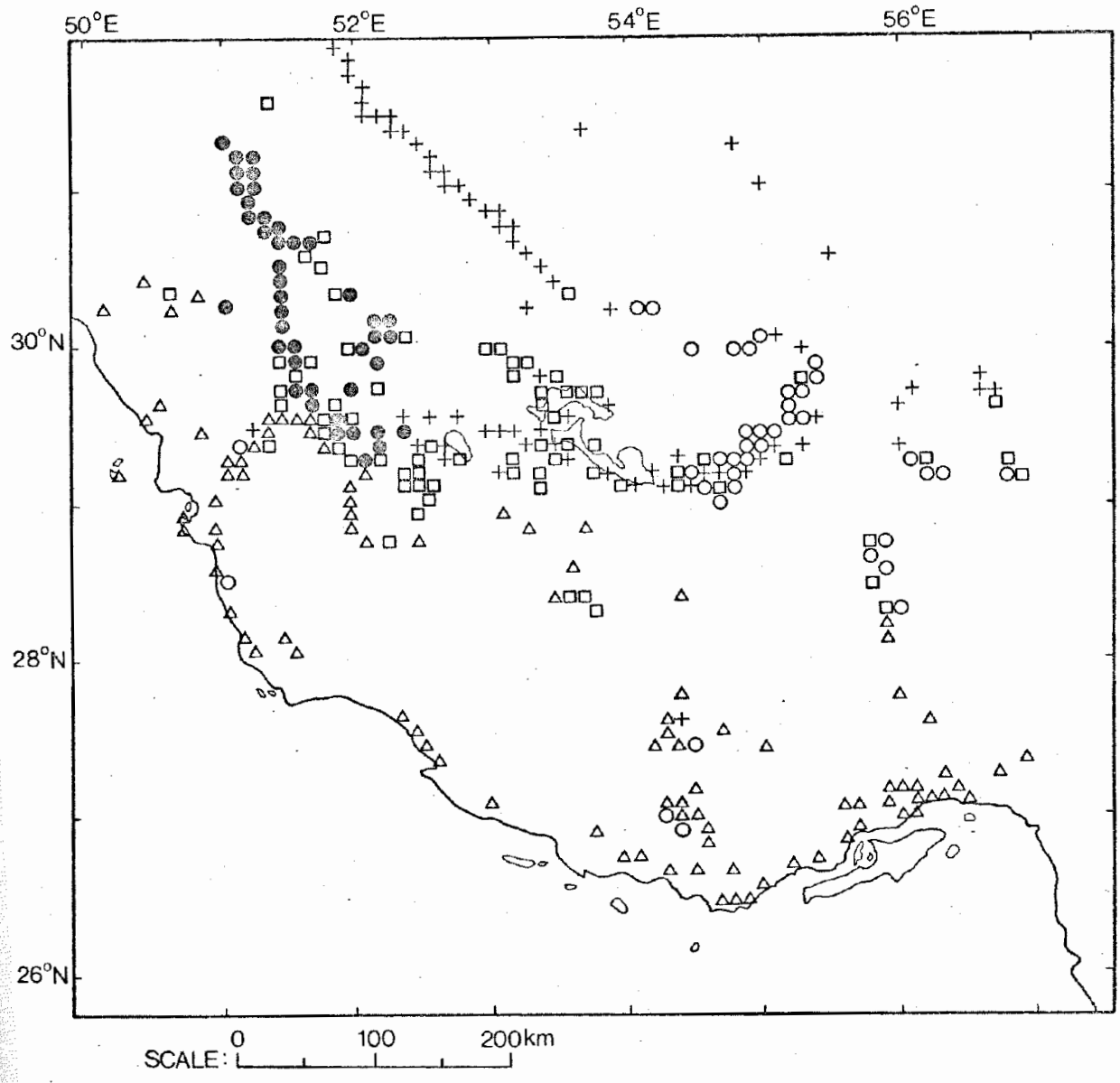
Mean annual temperature: 1°C lost for every 164m rise in altitude.

Mean monthly temperature: 1°C lost for every 150-170m rise in altitude.

These figures are close to those quoted for normal lapse rate:-

1°C lost for every 150m rise in altitude (Trewartha 1954).

1°C lost for every 162m rise in altitude (Horrocks 1957).



KEY

- ● – Xerophilous forest dominated by Quercus brantii.
- □ – Wooded steppe with scattered trees of Pistacia atlantica, and/or bushes of Amygdalus scoparia and/or Amygdalus eburnea.
- \+ – Steppe dominated by Artemisia spp., mostly Artemisia herba-alba.
- ○ – Bushland dominated by Zygophyllum atriplicoides.
- △ – Warm steppe zone species: cultivated date palms (Phoenix dactylifera) and/or scattered trees of Acacia spp. and/or Ziziphus spp. and/or bushes of Calotropis procera.

Locations of records in S. W. Persia of vegetation types used, together with climatic data, to define the boundaries of the various bioclimatic zones.

APPENDIX C. DISCUSSION OF THE ADVANTAGES AND DISADVANTAGES OF PITFALL SAMPLING:

Pitfall trapping as a method for sampling the arthropod food that is available to wheatears has a number of advantages including the following: 1) It requires few man-hours during daylight. 2) The catch can be retained for study. 3) The method gives good results when sampling running fauna from bare ground (Williams 1958, Greenslade 1964) and is therefore appropriate for sampling the food supply of wheatears since they prey mainly on ants and beetles which they catch chiefly on bare ground. 4) The pitfall traps were left open from dawn to dusk and so took account of diurnal variations in arthropod activity and of differences in day length. The results therefore give an indication of the total amount of prey available during daylight hours which is pertinent since wheatears do not feed at night.

Unfortunately pitfall trapping also has a number of problems (see Williams 1958, Greenslade 1964, Southwood 1966) and the results must be treated with caution. The most serious of these problems will be considered below:-

1) Although the pitfall samples probably give a good indication of the total abundance of running prey available during daylight hours, they give no information on the length of time this prey is available to be caught by birds.

2) Other factors being equal the size of pitfall catches depends primarily on the number of arthropods at risk and their level of locomotor activity (Williams 1958, Greenslade 1964). The latter is strongly influenced by weather, particularly rainfall, humidity and temperature. Since rain is rare in S. W. Iran this factor as a cause of variation in arthropod activity was eliminated by taking samples only on dry, usually sunny, days. Temperature influences arthropod activity and hence pitfall catches in two ways: Not only does the number of arthropods active on the surface of the ground increase as temperatures rise between about 10°C and 40°C (appendix D fig. 1), but activity levels probably also rise causing increased pitfall catches

without the number of arthropods at risk increasing. This effect was not studied in the field but since most species of arthropod become active only within relatively narrow ranges of temperature (Wigglesworth 1972) this bias may not be serious. Indeed as arthropods become more active they probably become more conspicuous and hence more likely to be taken by wheatears, in which case their increased likelihood of being caught in the pitfalls may be regarded as a strength rather than as a drawback of the method.

3) The water used in the pitfalls to drown captures could have acted as an attractant and if the lure varied between species or seasonally this would have biased the results. However in this study most of the animals caught were worker ants or beetles which were apparently not attracted by water since neither form took advantage of water thrown out from our camps.

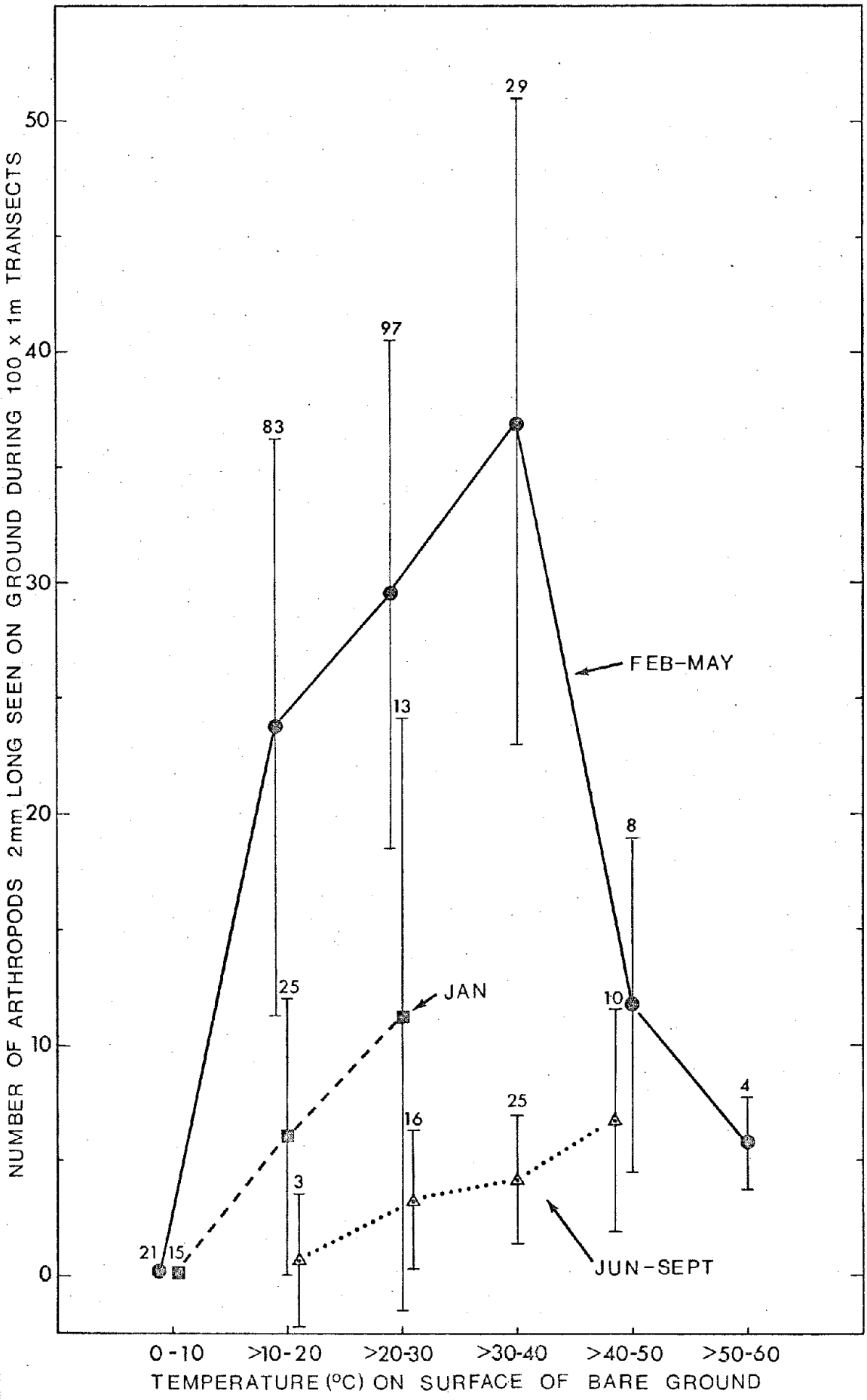
4) Some species of arthropod are more susceptible to capture in pitfalls than others. Thus it is a poor way of sampling grasshoppers due to their mode of locomotion, but is generally good for catching running forms although some of these evade capture by recovering balance when on the lip of the trap or simply by seeing and avoiding the traps. In the results of the present study comparison of the taxonomic composition of arthropods caught in the pitfalls (fig. 37, p. 176 and appendix E) with that of those seen during the transects (fig. 38, p. 177) shows that more Orthoptera and Araneida were seen during the transects, particularly those on the hillsides, than were caught in the pitfalls. These deficiencies in the pitfall catches probably represent genuine sampling errors and must be taken into account when using the pitfall results as an index of food available to wheatears.

APPENDIX D. INFERENCE OF FLUCTUATIONS IN THE AVAILABILITY OF ARTHROPOD PREY FOR WHEATEARS FROM MEAN DAILY SCREEN TEMPERATURES:

The activity of arthropods is strongly influenced by temperature. Roughly speaking they are most active when environmental temperatures are between about 10°C and about 40°C and become inactive when temperatures are outside this range (Allee et al. 1949, Edney 1973). Evidence that these generalisations apply to the activity of arthropods in the open on bare ground in S. W. Iran is provided by the data presented in appendix D fig. 1. Information about environmental temperatures can therefore be used to make predictions about arthropod activity. Thus few arthropods are likely to be active on bare ground when surface temperatures are below about 10°C or above about 40°C and the greatest densities can be expected when temperatures are between these values. Variations in the number of hours per day that temperatures on bare ground are between about 10°C and about 40°C can therefore be used to give indications of variations in the supply of arthropod prey for wheatears.

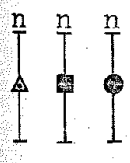
Temperatures in the open on the surface of bare ground were measured at hourly intervals during daylight on 42 days on piedmonts or plains at various localities in S. W. Iran. Analysis of the relationship between these observations and mean daily screen temperatures showed significant correlations between the latter and the number of daylight hours that ground surface temperatures rose above 40°C and above 10°C if this was not curtailed by day length.* The correlation coefficients and the forms of the relationships as shown by regression analyses are given in appendix D fig. 2. The mean daily temperature at any locality of known altitude in S. W. Iran can be estimated for any date from fig. 6, p. 23 and from this using the regression lines given in appendix D fig. 2, rough predictions can be made of the number of daylight hours

*Cases where temperatures remained above 10°C throughout the day were omitted from the analysis as in these instances the periods of daylight for which temperatures were above 10°C were determined by day length rather than being directly related to the ambient temperature.



Appendix D fig. 1. Number of arthropods ⩾2mm long seen on the ground during 100 x 1m transects at various temperatures in heavily grazed steppe on plains, piedmonts and in valley bottoms in the sub-steppe zone of S. W. Iran.

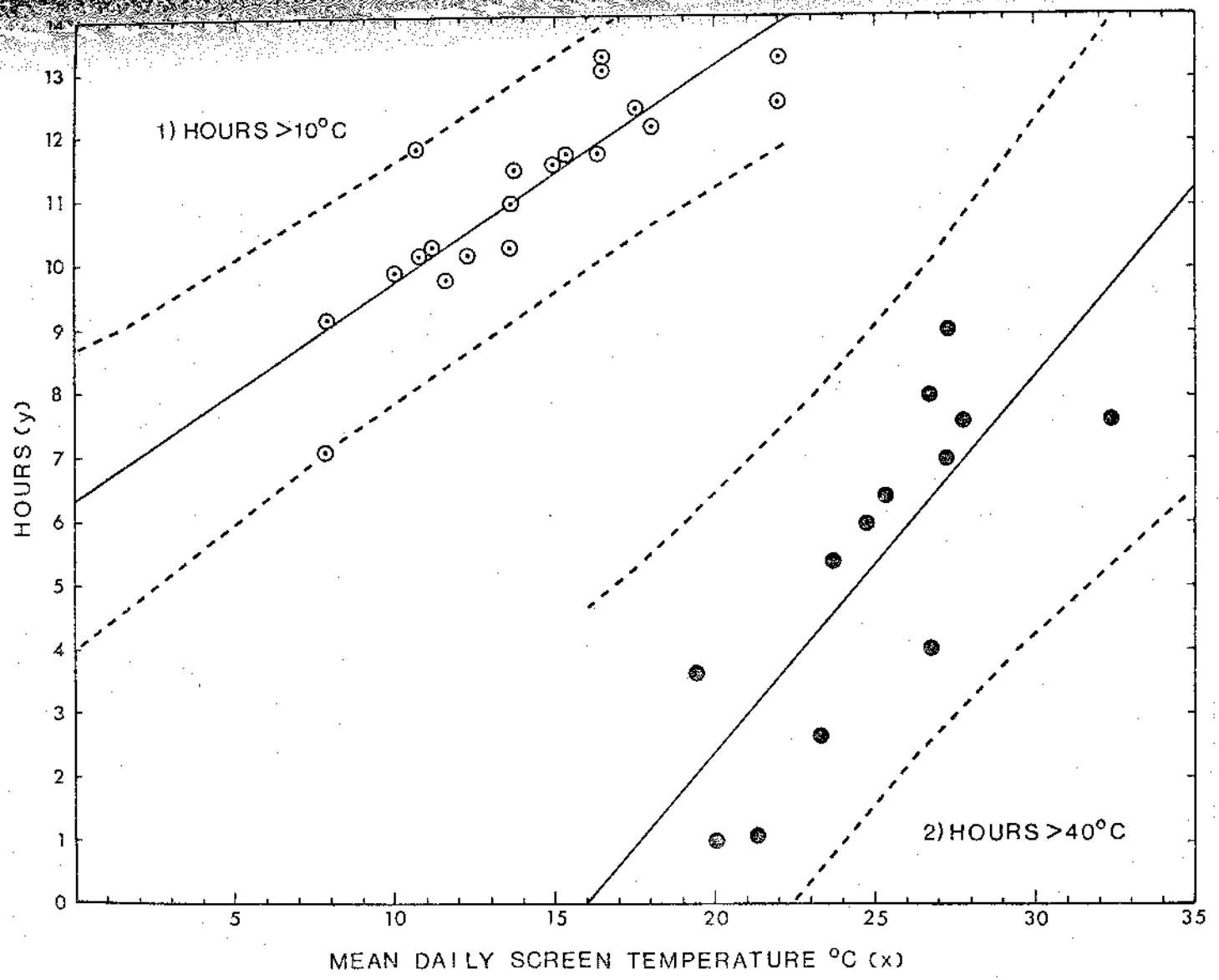
KEY



——— Number of transects.

——— Mean number of arthropods per transect.

——— 95% confidence intervals of the mean where this is >0.05.



Appendix D fig. 2. The number of daylight hours when temperatures in the open on the surface of bare ground at various localities in S. W. Iran were: 1) >10°C (⊙) and 2) >40°C (●) expressed in relation to mean daily screen temperatures as indicated by fig. 6 p. 23. Cases where temperatures on the ground were >10°C throughout the day have been excluded - see text for reasons. The lines have been fitted using regression analyses of hours (y) on mean daily temperatures (x) and the dashed lines give 95% confidence limits for the prediction of values of y from values of x. The regression equations and correlation coefficients are:-

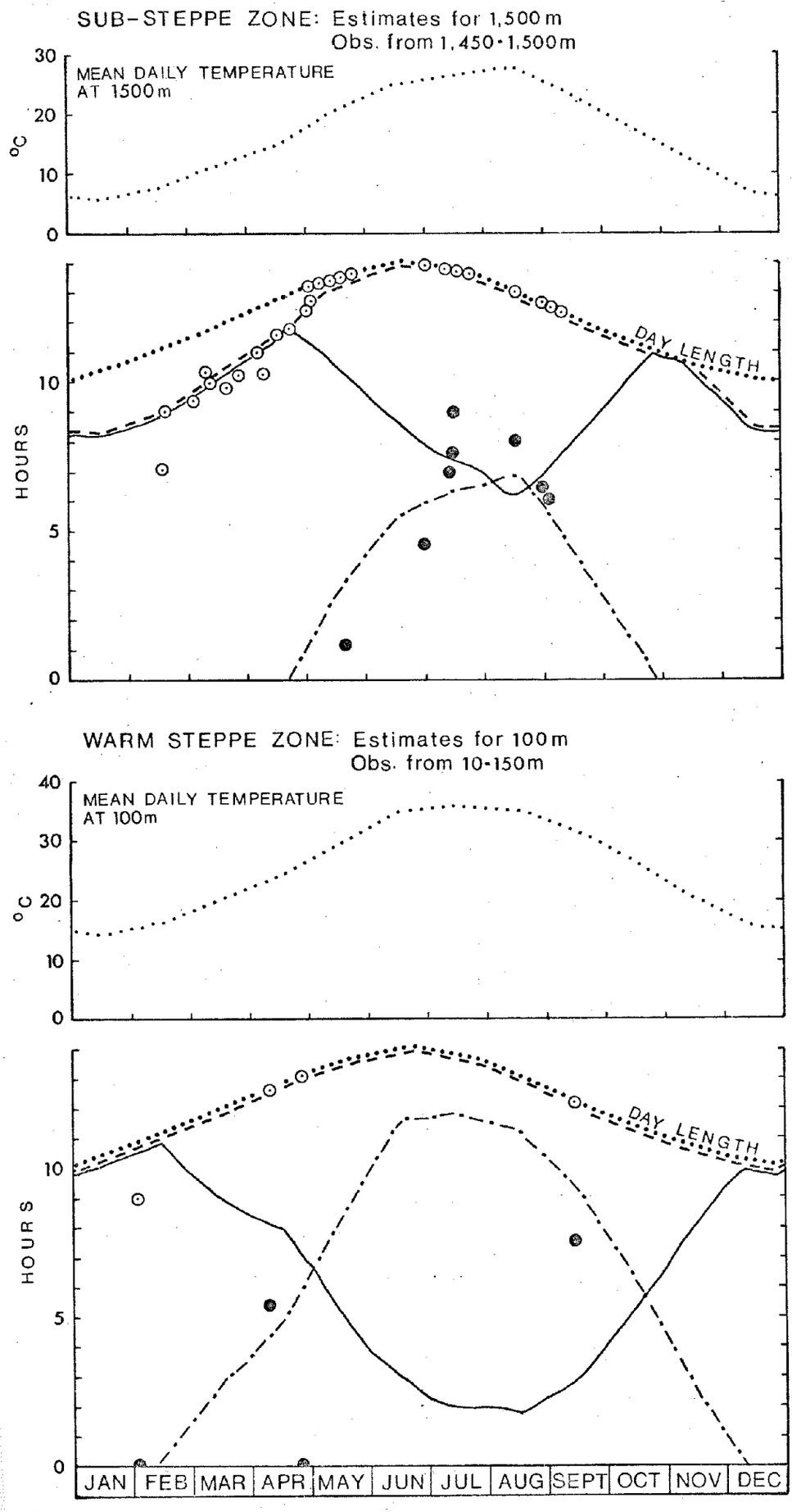
1) For hours >10°C $y = 0.342\,x + 6.337$
$r = 0.858$ with 18 d.f. ($p > 0.001$).

2) For hours >40°C $y = 0.588\,x - 9.372$
$r = 0.799$ with 11 d.f. ($p > 0.01$).

that temperatures on the surface of bare ground are likely to be a) above 10°C and b) above 40°C. These predictions must be appropriately corrected if they exceed the day length. Since twilight never exceeds 35 minutes per day within the latitudinal range of S. W. Iran day length was taken as sunrise to sunset and for given dates was obtained from Berry et al. 1954.

The method is demonstrated in appendix D, fig. 3 where it is used to estimate seasonal changes in temperature on the surface of bare ground at 100 m and 1,500 m above sea level in S. W. Iran. For each altitude seasonal variation in the mean daily temperature obtained from fig. 6, p. 23 is given. From these figures seasonal variation in the numbers of daylight hours that temperatures on the surface of the ground were likely to be greater than 10°C and greater than 40°C were estimated using the regression lines in appendix D, fig. 2. Where these predictions exceeded day length they were corrected to equal day length. Then, taking each day in turn, by subtracting the number of hours that temperatures rose above 40°C from the number of hours that they were above 10°C seasonal changes in the daily number of hours that temperatures were between these values were obtained. Similar procedures were carried out to give estimates of seasonal changes in the number of hours per day that temperatures on the surface of bare ground were between 10°C and 40°C at 2,100 m and 2,800 m above sea level. The results together with those for 100 m and 1,500 m above sea level are given in fig. 36, p. 172.

The validity of the method as a means of inferring variations in the availability of arthropod prey for wheatears is discussed on pp. 173-174.



Appendix D fig. 3. Estimation of seasonal changes in the number of daylight hours with ground surface temperatures in the open between 10°C and 40°C (i.e. temperatures between which arthropod availability is likely to be highest - see appendix D fig. 1) at 1,500m and 100m above sea level in S. W. Iran.

KEY

..... Mean daily temperature.

- - - - Number of daylight hours with ground temperatures >10°C (- - -)
-·-·- and >40°C (-·-) estimated from mean daily temperatures using appendix D fig. 1.

~~~ Number of daylight hours with ground temperatures between 10°C and 40°C deduced from the above information.

⊙ Number of daylight hours with ground temperatures >10°C (⊙)
● and >40°C (●) observed at localities close to 1,500m (upper fig.) and 100m (lower fig.).
~~~

APPENDIX E

BIOCLIMATIC ZONE, HABITAT AND PERIOD OF YEAR	SAMPLE SIZES		BEST REPRESENTED TAXONOMIC GROUPS (Defined as those which contributed ≥ 5% of at least one sample in any size class)													
	No. pitfall samples	Total items	LENGTH OF ARTHROPODS (mm)					FORMICIDAE WORKERS			COLEOPTERA			HEMIP-TERA	HOMOP-TERA	ARAN-EIDA	DIPLO-PODA
			2-5	>5-10	>10-15	>15-20	>20	2-5	>5-10	>10	2-5	>5-10	>10	2-5	2-5	2-5	10-15
MONTANE ZONE																	
Piedmonts (v-m; s-p)																	
Nov-Feb																	
% of total	1	6	100								17					83	
Mar-Jun																	
% of total	2	974	12	82	5	1	+	10	80	5	1	+	1		2	+	
Mean %	2	974	23	46	30	1	1	19	44	30	1	+	1				
S.d. of mean %			±18	±62	±42	++	±1	±16	±62	±42	±1	++	++				
Jul-Oct																	
% of total	1	210	26	49	24	+	+	24	48	24			+		2	+	
XEROPHILOUS FOREST ZONE																	
Piedmonts & valley bottoms (v-m; s-p)																	
Nov-Feb																	
% of total	2	41	90	2	7			56			12	2	7	2	7	7	
Mar-Jun																	
% of total	4	1047	80	13	6	1	+	67	9	4	9	5	2	+	2	1	+
Mean %	4	1047	78	15	6	1	+	63	9	3	10	6	3	+	2	2	+
S.d. of mean %			±7	±7	±1	±1	±1	±13	±9	±7	±6	±5	±3		±2	±1	
Jul-Oct																	
% of total	3	803	21	78	1	+	+	16	2	1	2	75	+	1	1	+	
Mean %	3	803	58	41	3	+	1	42	5	2	8	35	+	2	2	1	
S.d. of mean %			±47	±48	±3	++	±2	±36	±8	±3	++	±52	±1	±3	±2	±1	

(continued overleaf)

APPENDIX E

BIOCLIMATIC ZONE, HABITAT AND PERIOD OF YEAR	SAMPLE SIZES		LENGTH OF ARTHROPODS (mm)					BEST REPRESENTED TAXONOMIC GROUPS (Defined as those which contributed ⩾ 5% of at least one sample in any size class)								
								FORMICIDAE WORKERS			COLEOPTERA			HEMIP-TERA	HOMOP-TERA	ARAN-EIDA	DIPLO-PODA
	No. pitfall samples	Total items	2-5	>5-10	>10-15	>15-20	>20	2-5	>5-10	>10	2-5	>5-10	>10	2-5	2-5	2-5	10-15
SUB-STEPPE ZONE																	
Steep stony hillsides (v-m; s-d)																	
Nov-Feb																	
% of total	9	41	68	22	10			12	10	2	17	12	7		10	20	
Mar-Jun																	
% of total	9	522	93	4	2		+	64	2	1	19	1	1	4	2	3	
Mean %	6	496	94	3	2		1	65	2	1	18	1	1	7	2	2	
S.d. of mean %			±2	±2	±2		±1	±16	±2	±2	±16	±1	±1	±7	±2	±2	
Jul-Oct																	
% of total	8	494	72	26	2			64	17	1	1	6	1	1	1	2	
Mean %	7	484	70	28	2			62	17	1	1	6	1	1	1	2	
S.d. of mean %			±13	±12	±2			±14	±7	±2	±1	±5	±2	±1	±2	±2	
SUB-STEPPE ZONE																	
Piedmonts & valley bottoms (v-m; s-p)																	
Nov-Feb																	
% of total	18	723	65	34	1	+	+	52	30	+	7	2	+	+	+	3	+
Mean %	10	651	76	23	1	+	+	51	18	+	14	2	1	+	1	6	+
S.d. of mean %			±19	±19	±2	++	++	±26	±21	±1	±19	±4	±2	±1	±2	±7	++
Mar-Jun																	
% of total	25	2236	81	17	2	+		60	12	2	15	3	1	+	2	2	+
Mean %	25	2236	83	15	2	+		60	9	2	14	3	1	+	2	2	+
S.d. of mean %			±19	±18	±2	±1		±26	±16	±7	±14	±6	±1	±1	±3	±2	±1
Jul-Oct																	
% of total	17	1740	71	26	3	+	+	61	22	1	1	1	1	+	2	4	
Mean %	17	1740	62	33	5	+	+	52	28	2	1	1	2	+	2	4	
S.d. of mean %			±20	±18	±8	±1	++	±19	±17	±5	±1	±1	±4	±1	±3	±4	

(continued overleaf)

APPENDIX E

BIOCLIMATIC ZONE, HABITAT AND PERIOD OF YEAR	SAMPLE SIZES		LENGTH OF ARTHROPODS (mm)					BEST REPRESENTED TAXONOMIC GROUPS (Defined as those which contributed ⩾ 5% of at least one sample in any size class)								
	No. pitfall samples	Total items	2-5	>5-10	>10-15	>15-20	>20	FORMICIDAE WORKERS 2-5	>5-10	>10	COLEOPTERA 2-5	>5-10	>10	HEMIPTERA 2-5	HOMOPTERA 2-5	ARANEIDA 2-5	DIPLOPODA 10-15
COLD STEPPE ZONE																	
Plain (v-sp; s-sp)																	
Nov-Feb																	
% of total	1	2	100					100									
Mar-Jun																	
% of total	1	58	52	47	2			50				47	2				
WARM STEPPE ZONE																	
Piedmont (v-sp; s-sp)																	
Nov-Feb																	
% of total	1	7	86		14			29			57						14
Mar-Jun																	
% of total	1	61	90	10				75	3		3	3			8	2	
Jul-Oct																	
% of total	1	99	76	22	1	1		64	20					2		8	

Appendix E. Size distribution and taxonomic composition of largely cursorial arthropods ⩾2 mm long caught in pitfall traps in S. W. Iran during 1970-1971.

KEY

Pitfall sample = Pooled dawn to dusk catch from ten pitfall traps (see p. 46 for procedure).

% of total = Percentage of arthropods from pooled pitfall samples falling into various categories.

Mean % = Means of the percentage occurrence of arthropods in various categories in individual pitfall samples containing ⩾20 items.

S.d. = Standard deviations of the mean percentages.
\+ = Less than 0.5%
v = vegetation
s = stone-cover
d = dense
m = medium density
p = patchy, sparse + dense
sp = sparse

See pp 118-119 for definitions.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.

APPENDIX F

| WHEATEAR SPECIES AND PERIOD OF YEAR | SAMPLE SIZES | | LENGTH OF FOOD ITEMS (mm) | | | | | BEST REPRESENTED TAXONOMIC GROUPS (Defined as those which contributed ⩾ 5% of at least one sample in any size class) | | | | |

WHEATEAR SPECIES AND PERIOD OF YEAR	SAMPLE SIZES No. guts	SAMPLE SIZES Total items	LENGTH OF FOOD ITEMS (mm) 2-5	>5-10	>10-15	>15-20	>20	BEST REPRESENTED TAXONOMIC GROUPS (Defined as those which contributed >5% of at least one sample in any size class) FORMICIDAE WORKERS 2-5	>5-10	>10	WINGED HYMENOPTERA 2-5	>5-10	>10	COLEOPTERA 2-5	>5-10	>10	ISOPTERA 2-5	>5-10	>10	HEMIPTERA 2-5	>5-10	>10	EMBIOPTERA 2-5	INSECT LARVAE 5-10	>10	ISOPODA 2-5	SEEDS 2-5	BERRIES 2-5
O. DESERTI, cont.																												
Year																												
% of total	23	637	61	34	5	1		31	5	2	10	+	+	9	2		4	2		3	+			20		2	+	
Mean %	10	489	72	25	3	+		32	10	3	10	+		11	1		5	4		5				9			+	
S.d.of mean %			±34	±33	±4	±+		±38	±14	±4	±27	±+		±26	±2		±16	±14		±14				±27			±+	
O. FISCHII																												
Nov-Feb																												
% of total	26	2043	58	38	4	1		51	32	4	1	+		2	2	+	+	3		2		+		+	+	+	+	
Mean %	22	1994	61	35	4	+		53	31	4	1			2	1			3		4		+		+	+		+	
S.d.of mean %			±24	±23	±4	±+		±24	±21	±4	±5			±4	±2			±12		±16		±+		±+	±+		±+	
Mar-Jun																												
% of total	4	15	13	67	13		7	13	67	13																		
Jul-Oct																												
% of total	1	86	58	38	4			57	34	4											5							
Year																												
% of total	31	2144	58	38	4	1	+	51	33	4	1	+		2	2	+	+	3		2	+	+		+	+	+	1	
Mean %	23	2080	61	35	4	+		53	31	4	+			2	1			3		4	+	+		+	+		+	
S.d.of mean %			±23	±22	±4			±24	±20	±4	±+			±4	±2			±12		±16	±+	±+		±+	±+		±+	
O. HISPANICA																												
Mar-Jun																												
% of total	11	131	27	42	20	3	8	13	21	10	5	2	6	3	8	1				4	9			7				
Mean %	2	51	42	43	12		4	28	29	2	10	2	10	2	7						6			4				
S.d.of mean %			±1	±1	±5		±6	±4	±6	±3	±4	±3	±8	±3	±9						±8			±6				
Jul-Oct																												
% of total	10	135	82	14	4			56	8	3	4				1						4							16
Mean %	2	89	100					85			4																	11
S.d.of mean %			±0					±21			±6																	±16

(continued overleaf)

APPENDIX F

WHEATEAR SPECIES AND PERIOD OF YEAR	SAMPLE SIZES		LENGTH OF FOOD ITEMS (mm)					BEST REPRESENTED TAXONOMIC GROUPS (Defined as those which contributed ⩾5% of at least one sample in any size class)																										
								FORMICIDAE WORKERS			WINGED HYMENOPTERA			COLEOPTERA			ISOPTERA			HEMIPTERA			EMBIO-PTERA	INSECT LARVAE		ISO-PODA	SEEDS	BERRIES					
	No. guts	Total items	2-5	>5-10	>10-15	>15-20	>20	2-5	>5-10	>10	2-5	>5-10	>10	2-5	>5-10	>10	2-5	>5-10	>10	2-5	>5-10	>10	2-5	5-10	>10	2-5	2-5	2-5				
O.HISPANICA cont.																																
Year																																
% of total	21	266	55	28	12	2	4	35	14	6	4	1	3	2	5	+				2	6				3			8				
Mean %	4	140	71	22	6		2	56	14	1	7	1	5	1	3						3				2			6				
S.d.of mean %			±34	±25	±7		±4	±35	±17	±2	±5	±2	±7	±2	±7						±6				±4			±11				
O. ISABELLINA																																
Nov-Feb																																
% of total	10	1028	45	50	6	1		38	32	1	+			2	2	+	15			1	+		+			+		+				
Mean %	9	1011	47	46	7	1		40	33	7	+			2	3	1	9			+	+		+			+		+				
S.d.of mean %			±15	±15	±10	±1		±19	±14	±10	±+			±2	±4	±1	±26			±+	±+		±+			±+		±+				
Mar-Jun																																
% of total	22	901	79	18	2	+		29	6	1	+	1	+	6	7	1	3			2	1		36	+	1							
Mean %	8	756	50	47	3	1		32	9	2		1	+	7	13	1	+						23	1								
S.d.of mean %			±14	±13	±6	±1		±36	±12	±4		±4	±+	±10	±31	±1	±+						±40	±3								
Jul-Oct																																
% of total	5	394	34	64	1	1		31	53	1	1			1	11	1				1	1											
Mean %	3	371	33	67				30	32		1			+	35					1												
S.d.of mean %			±55	±55				±53	±52		±1			±+	±56					±1												
Year																																
% of total	37	2323	56	40	4	+		33	26	3	+	+	+	3	5	1	8			1	+		14	+	+	+		+				
Mean %	20	2138	46	49	4	+		35	23	4	+	1	+	4	12	1	4			2	1		8	1				+				
S.d.of mean %			±34	±34	±8	±+		±31	±24	±8	±1	±2	±+	±7	±29	±1	±17			±8	±4		±25	±2				±+				

(continued overleaf)

APPENDIX F

WHEATEAR SPECIES AND PERIOD OF YEAR	SAMPLE SIZES No. guts	SAMPLE SIZES Total items	LENGTH OF FOOD ITEMS (mm) 2-5	>5-10	>10-15	>15-20	>20	BEST REPRESENTED TAXONOMIC GROUPS (Defined as those which contributed ≥5% of at least one sample in any size class) FORMICIDAE WORKERS 2-5	>5-10	>10	WINGED HYMENOPTERA 2-5	>5-10	>10	COLEOPTERA 2-5	>5-10	>10	ISOPTERA 2-5	>5-10	>10	HEMIPTERA 2-5	>5-10	>10	EMBIOPTERA 2-5	INSECT LARVAE 5-10	>10	ISOPODA 2-5	SEEDS 2-5	BERRIES 2-5
Q. LUGENS																												
Nov-Feb																												
% of total	1	94	100					81						6			1			11								
Mar-Jun																												
% of total	7	96	58	28	9	4		47	16	4	1		3	1	3	2				4				7				
Mean %	2	53	71	25	2	2		66	21	2	2					2				4				2				
S.d.of mean %			±17	±23	±3	±3		±25	±24	±3	±2					±3				±5				±3				
Jul-Oct																												
% of total	2	126	74	24	2			73	22	2				1	2													
Mean %	2	126	71	26	3			70	25	3				1	2													
S.d.of mean %			±21	±15	±4			±19	±16	±4				±1	±2													
Year																												
% of total	10	316	76	19	4	1		69	14	2	+		1	3	2	1	+			2				2				
Mean %	5	273	77	20	2	1		70	18	2	1			1	1	1	+			4				1				
S.d.of mean %			±19	±18	±3	±2		±17	±8	±3	±1			±3	±1	±2	±+			±5				±2				
Q. OENANTHE																												
Mar-Jun																												
% of total	5	100	38	41	21			25	18	7				5	16		3	6	13	1	1				1		1	
Mean %	2	80	38	33	30			27	7	9				3	16		5	10	21	1					1			
S.d.of mean %			±18	±11	±28			±30	±1	±1				±4	±22		±6	±13	±29	±1					±1			
Jul-Oct																												
% of total	3	187	70	28	2			51	20		3	2	2	12	6						1			1			1	
Mean %	3	187	56	43	1			40	39		5	2	1	8	3						1			1			1	
S.d.of mean %			±32	±32	±1			±29	±35		±5	±2	±2	±9	±5						±2			±2			±1	
Year																												
% of total	8	287	59	33	8			42	20	2	2	1	1	10	9		1	2	5	+	1			+	+		1	
Mean %	5	267	43	40	12			35	26	3	3	1		6	8		2	4	8	+	1			1	+		+	
S.d.of mean %			±26	±24	±22			±26	±30	±5	±4	±1		±7	±13		±4	±8	±18		±1			±1	±+		±+	

(continued overleaf)

APPENDIX F

WHEATEAR SPECIES AND PERIOD OF YEAR	SAMPLE SIZES		LENGTH OF FOOD ITEMS (mm)					BEST REPRESENTED TAXONOMIC GROUPS (Defined as those which contributed ≥5% of at least one sample in any size class)																				
								FORMICIDAE WORKERS			WINGED HYMENOPTERA			COLEOPTERA			ISOPTERA			HEMIPTERA			EMBIOPTERA	INSECT LARVAE			ISOPODA	SEEDS	BERRIES
	No. guts	Total items	2-5	>5-10	>10-15	>15-20	>20	2-5	>5-10	>10	2-5	>5-10	>10	2-5	>5-10	>10	2-5	>5-10	>10	2-5	>5-10	>10	2-5	5-10	>10	2-5	2-5	2-5
O. PICATA																												
Nov-Feb																												
% of total	3	299	68	29	3			62	29	3				6														
Mean %	3	299	64	32	4			59	29	4				6														
S.d.of mean %			±28	±24	±5			±24	±28	±5				±5														
Mar-Jun																												
% of total	4	55	40	49	9	2		18	29	7	4		2	9	11						6							
Year																												
% of total	7	354	64	32	4	+		55	29	4	1		+	7	2						1							
Mean %	3	299	64	32	4			59	29	4				6														
S.d.of mean %			±28	±24	±5			±24	±28	±5				±5														
O. PLESCHANKA																												
Nov-Feb																												
% of total	11	197	52	28	18	2	1	4	11	3	2	2	1	29	5	9	4			2	2	2		1	1		1	
Mean %	5	117	62	18	20			5	16	5	1	1	2	33		6				2		6			1		2	
S.d.of mean %			±25	±16	±28			±6	±14	±7	±2	±2	±2	±16		±14				±2		±14			±2		±2	
Mar-Jun																												
% of total	6	80	58	30	11		1	35	18	10				16	8					1	3			3	1			
Mean %	2	41	49	27	23		3	22	17	20				23	5					3	5				3			
S.d.of mean %			±8	±23	±18		±4	±16	±23	±14				±25	±7					±4	±7				±4			
Jul-Oct																												
% of total	11	510	89	9	1	+	1	52	7	1	2	+		2	1					1	+						1	5
Mean %	7	476	82	16	3			47	15	3	3	+		5	+					1	+						1	6
S.d.of mean %			±26	±25	±5			±27	±25	±5	±7	++		±11	++					±3	++						±2	±8
Year																												
% of total	28	787	77	16	6	1	1	39	9	2	2	5	+	10	3	2	1			1	2	1		+	+		1	3
Mean %	14	634	70	18	33		0	28	15	6	2	+	1	18	1	2				2	1	2			1		1	4
S.d.of mean %			±26	±20	±89		±1	±28	±20	±9	±5	±1	±1	±19	±3	±9				±3	±3	±9			±2		±2	±8

(continued overleaf)

APPENDIX F

WHEATEAR SPECIES AND PERIOD OF YEAR	SAMPLE SIZES		LENGTH OF FOOD ITEMS (mm)					BEST REPRESENTED TAXONOMIC GROUPS (Defined as those which contributed ⩾5% of at least one sample in any size class)																				
								FORMICIDAE WORKERS			WINGED HYMENOPTERA			COLEOPTERA			ISOPTERA			HEMIPTERA			EMBIOPTERA	INSECT LARVAE		ISOPODA	SEEDS	BERRIES
	No. guts	Total items	2-5	>5-10	>10-15	>15-20	>20	2-5	>5-10	>10	2-5	>5-10	>10	2-5	>5-10	>10	2-5	>5-10	>10	2-5	>5-10	>10	2-5	5-10	>10	2-5	2-5	2-5
O. XANTHOPRYMNA																												
Nov-Feb																												
% of total	13	792	72	23	5	+	+	47	19	4	+	+	+	13	1	+	+			+				1	+	+	10	
Mean %	9	749	67	25	7	+		47	22	6				9	1	+	+			1				1		9		
S.d.of mean %			±23	±19	±8	±1		±26	±19	±8				±17	±3	±+	±+			±2				±3		±26		
Mar-Jun																												
% of total	7	65	48	35	11	3	3	22	6	2		15	8	14	9	2				3	3							
Jul-Oct																												
% of total	2	17	88	6			6	82	6											6								
Year																												
% of total	22	874	71	23	5	1	1	46	18	4	+	1	1	13	2	+	1			1	+			1	+	+	9	
Mean %	9	749	67	25	7	+		47	22	6				9	1	+	+			1				1		9		
S.d.of mean %			±23	±19	±8	±1		±26	±19	±8				±17	±3	±+	±+			±2				±3		±26		

Appendix F. Size distribution and taxonomic composition of measurable items in the gut contents of wheatears obtained in S. W. Iran.

KEY

% of total = Percentage of items from pooled samples falling into various categories.

Mean % = Means of the percentage occurrence of items in various categories in the gut contents of individual wheatears which included ⩾ 20 measurable items.

S. d. = Standard deviations of above means.

\+ = Less than 0.5%.

N. B. All percentages have been corrected to the nearest whole number, 0.5 being corrected up.

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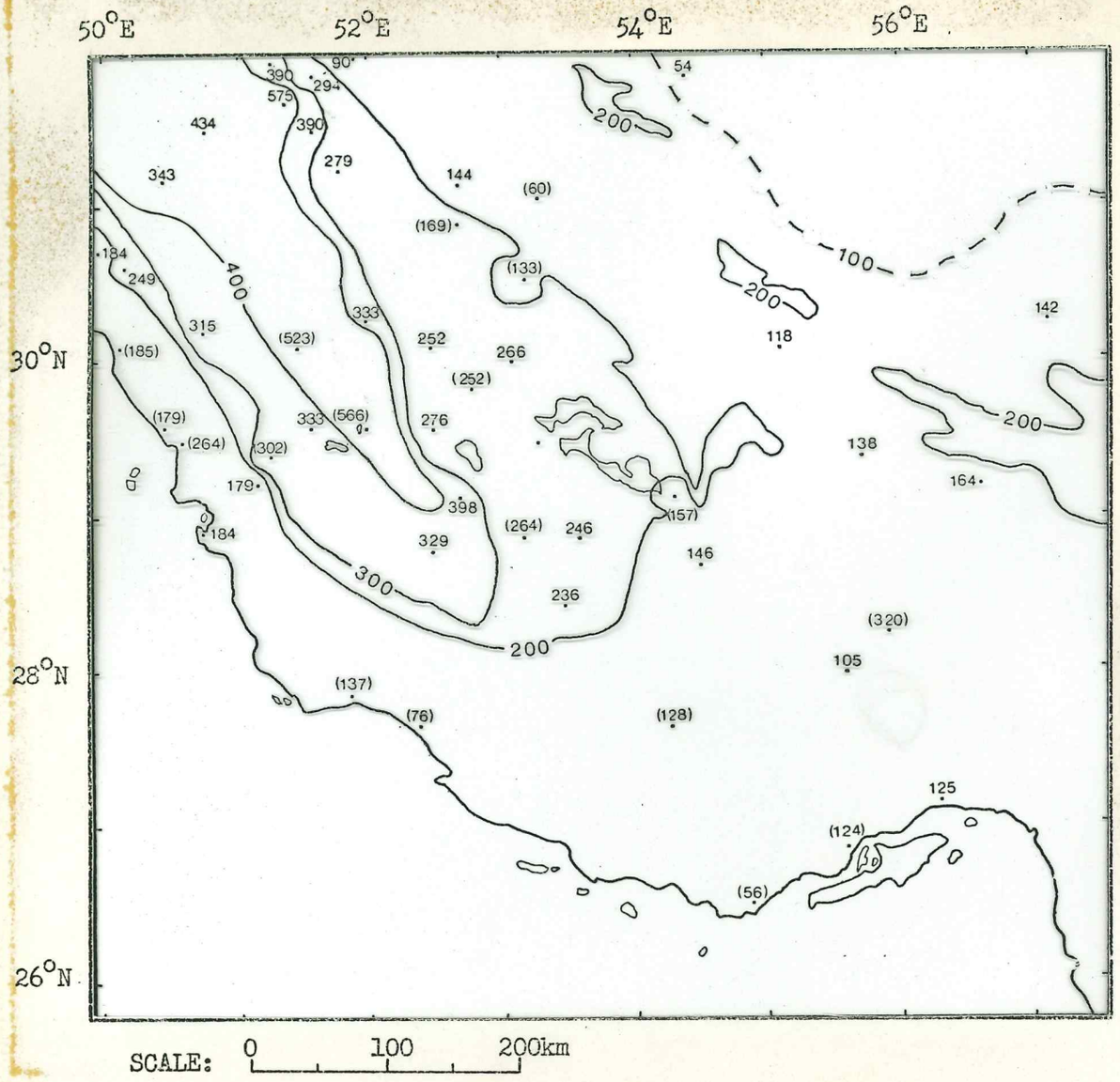
MEAN ANNUAL PRECIPITATION

Overlay 1



KEY

127 Mean annual precipitation based on five or more years of data.

(128) Mean annual precipitation based on two-four years of data.

Isohyets drawn with reference to the plotted values and the local relief.

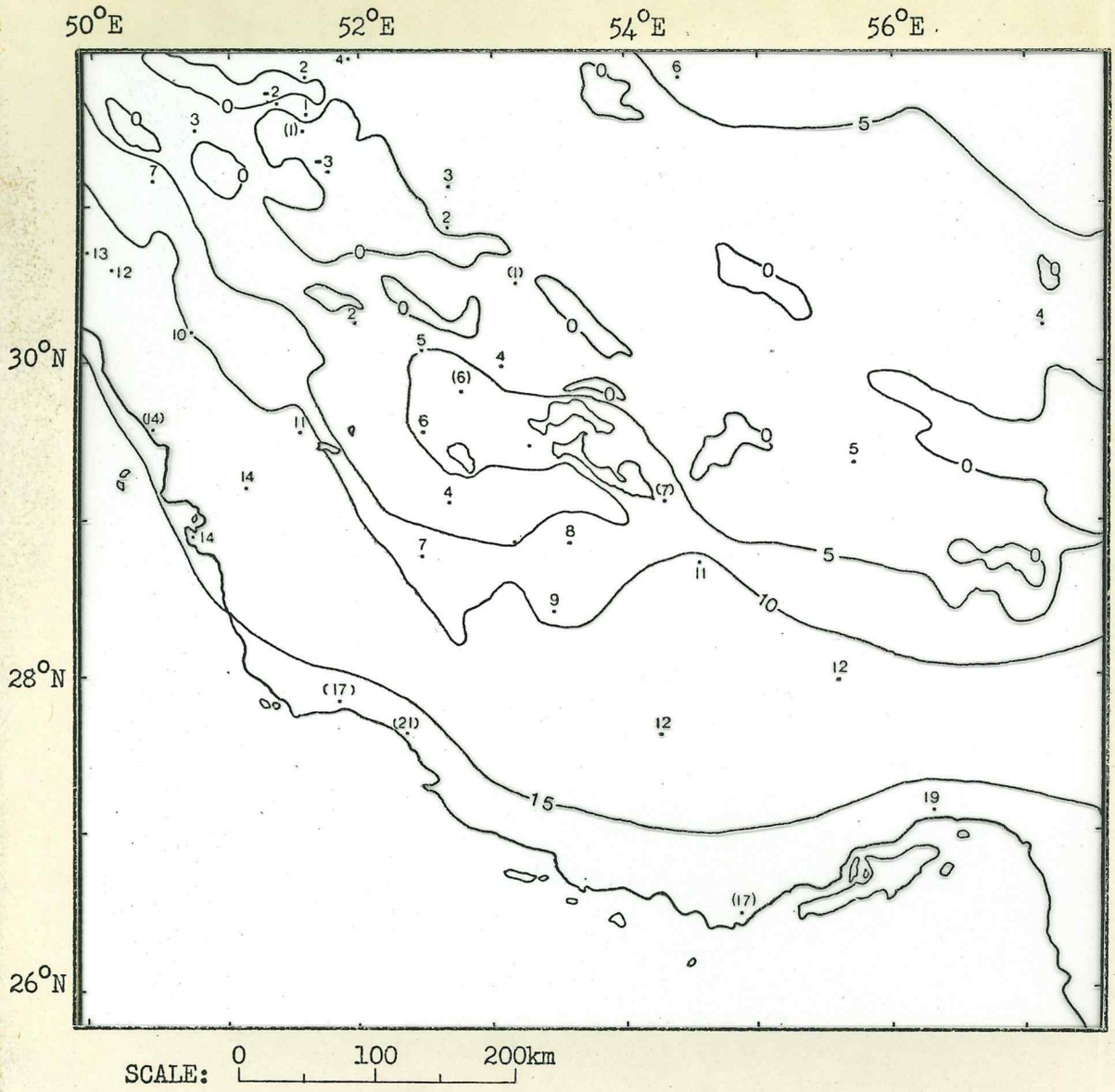
Isohyets with doubtful alignment.

Overlay 1. Mean annual precipitation (millimetres) in S. W. Iran.

(Based on Meteorological Year Books 1956-1968 published by the Iranian Meteorological Department, Tehran.)

MEAN MONTHLY TEMPERATURE - JANUARY

Overlay 2



KEY

13 Mean monthly temperature based on five or more years' data.

(15) Mean monthly temperature based on two-four years' data.

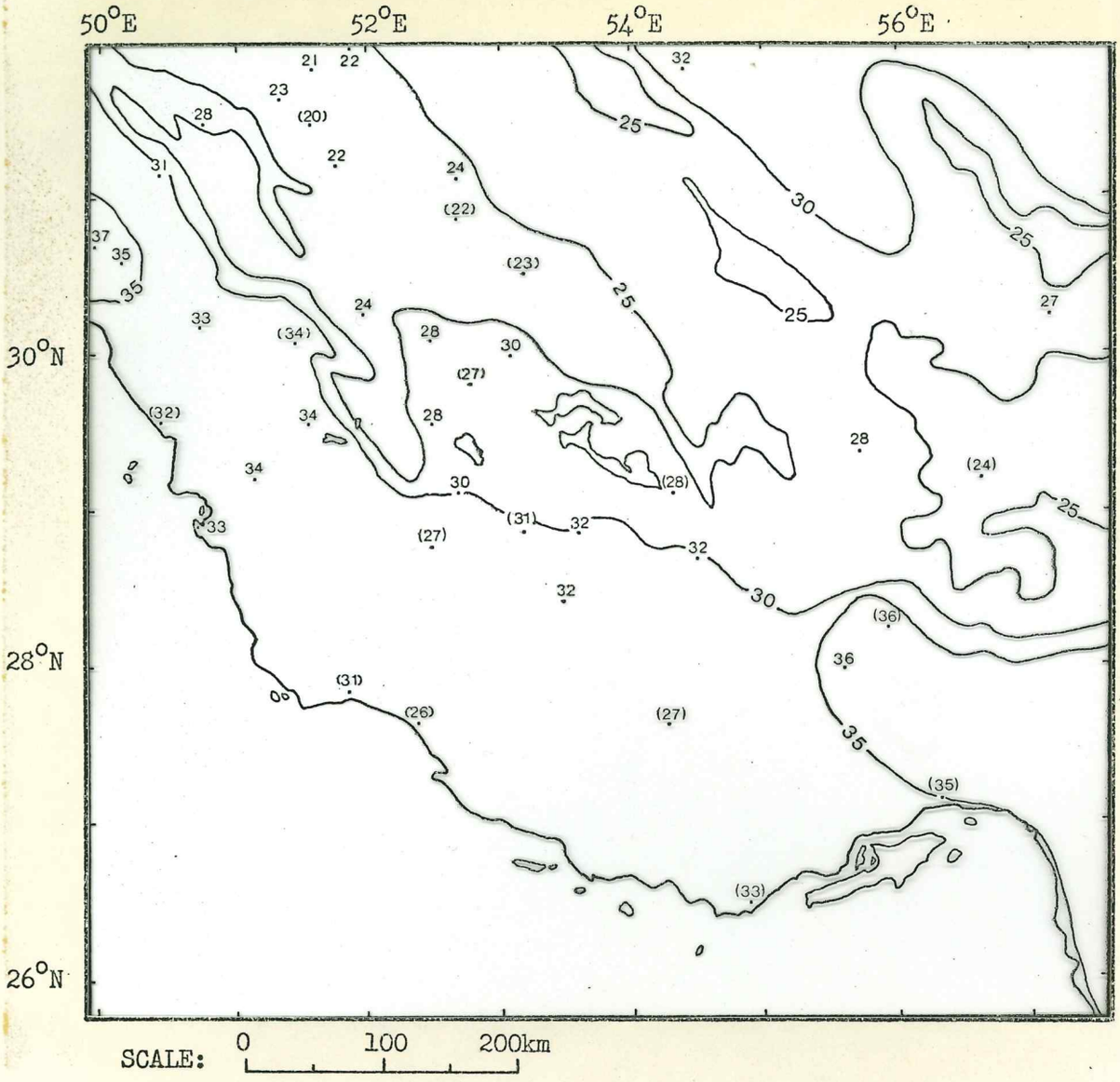
Isotherms drawn with reference to plotted values and the local relief.

Overlay 2. Mean monthly actual surface temperatures (°C) for January in S. W. Persia.

(Based on Meteorological Year Books 1956-1968 published by the Iranian Meteorological Department, Tehran.)

MEAN MONTHLY TEMPERATURE - JULY

Overlay 3



KEY

32 • Mean monthly temperature based on five or more years' data.

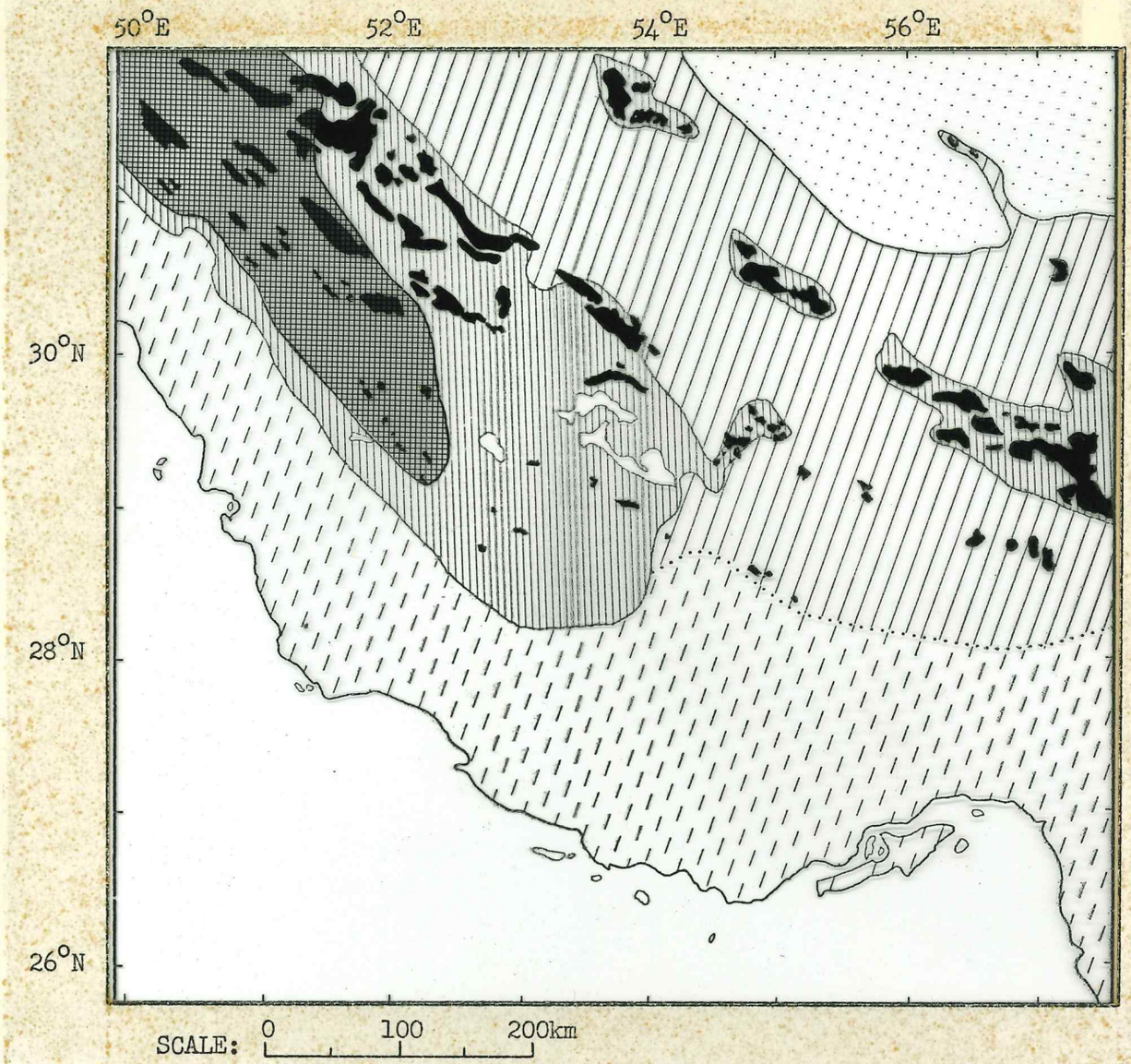
(28) • Mean monthly temperature based on two-four years' data.

Isotherms drawn with reference to plotted values and the local relief.

Overlay 3. Mean monthly actual surface temperatures (°C) for July in S. W. Persia.

(Based on Meteorological Year Books 1956-1968 published by the Iranian Meteorological Department, Tehran.)

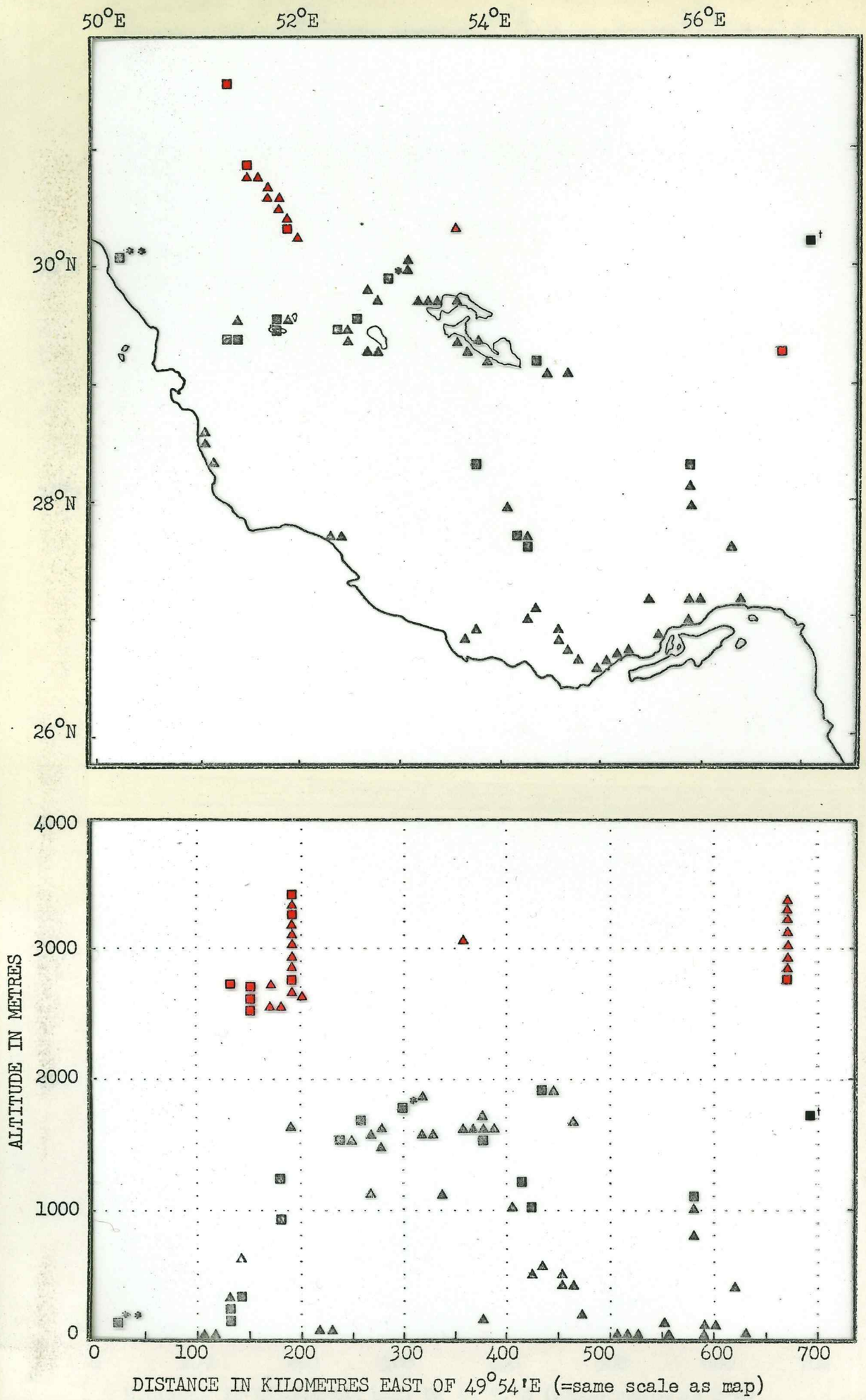
BIOCLIMATIC ZONES



KEY

- Montane zone (above 2,700m).
- Xerophilous forest (>400mm mean annual precipitation).
- Sub-steppe (200-400mm mean annual precipitation).
- Cold steppe (100-200mm mean annual precipitation) (mean temperature in January <10°C).
- Warm steppe (100-200mm mean annual precipitation) (mean temperature in January >10°C).
- Sub-desert (<100mm mean annual precipitation).

Overlay 4. Bioclimatic zones of S. W. Persia. (For summary of characteristics of each zone see table 2 and for method of delimitation see text pages 22 & 28.)

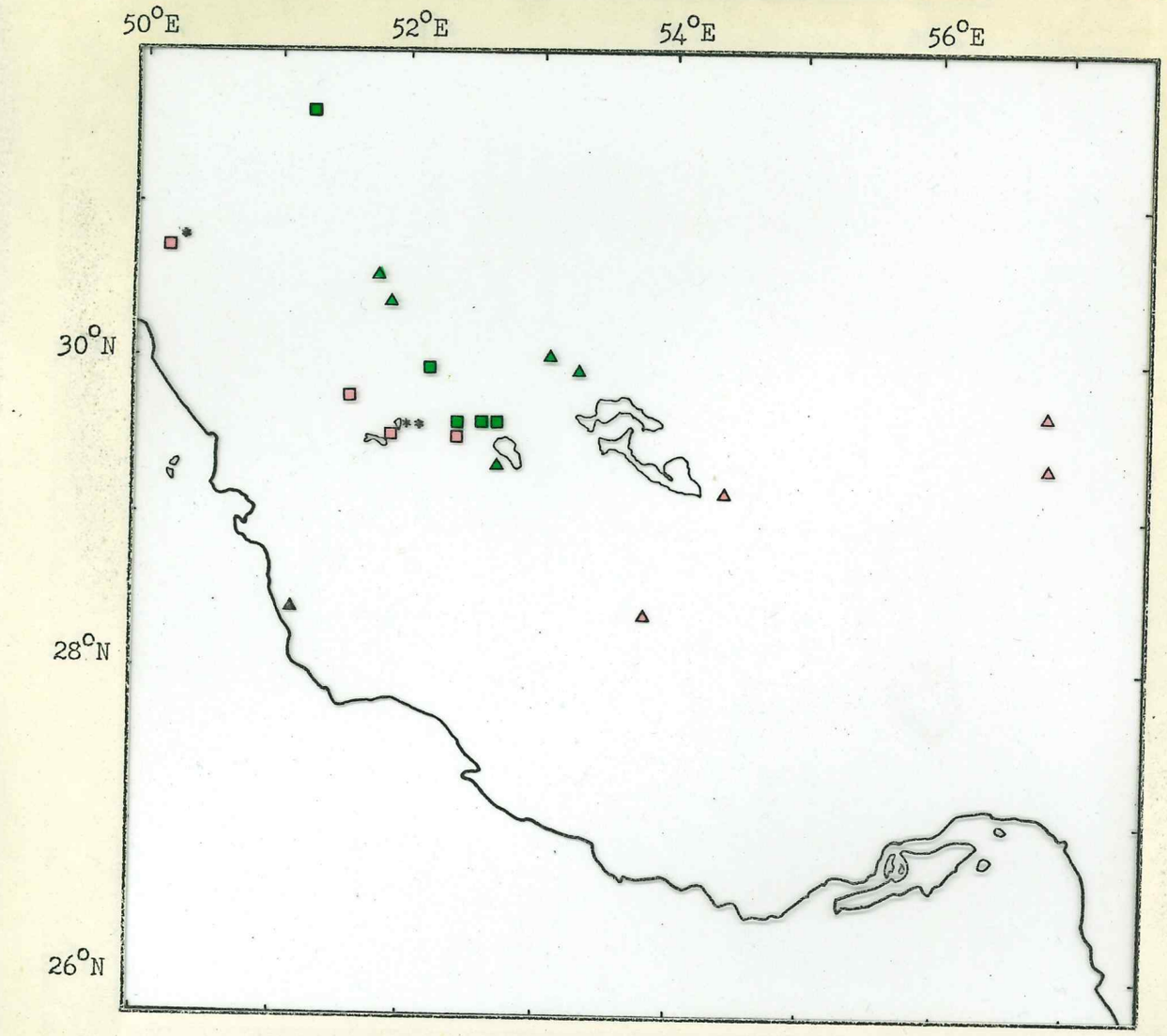


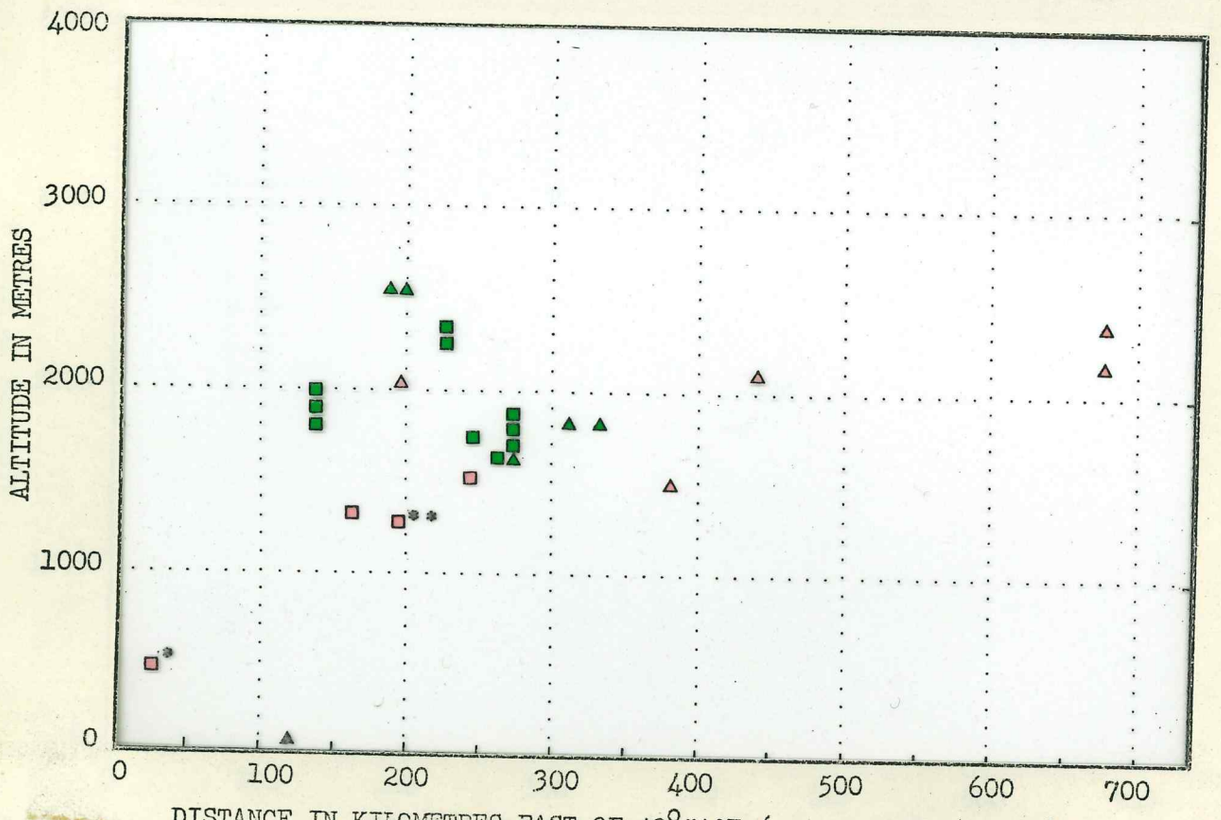
Overlay 5. Altitudinal and geographical distribution of breeding localities in S. W. Persia of O. alboniger and O. xanthoprymna.

Breeding records: Proven ■ ■ Probable ▲ ▲ O. alboniger / O. xanthoprymna

*Erard and Etchecopar 1970. **D. A. Scott pers. comm. †Blanford 1876.

O. FINSCHII, O. MONACHA AND O. PICATA IN THE BREEDING SEASON



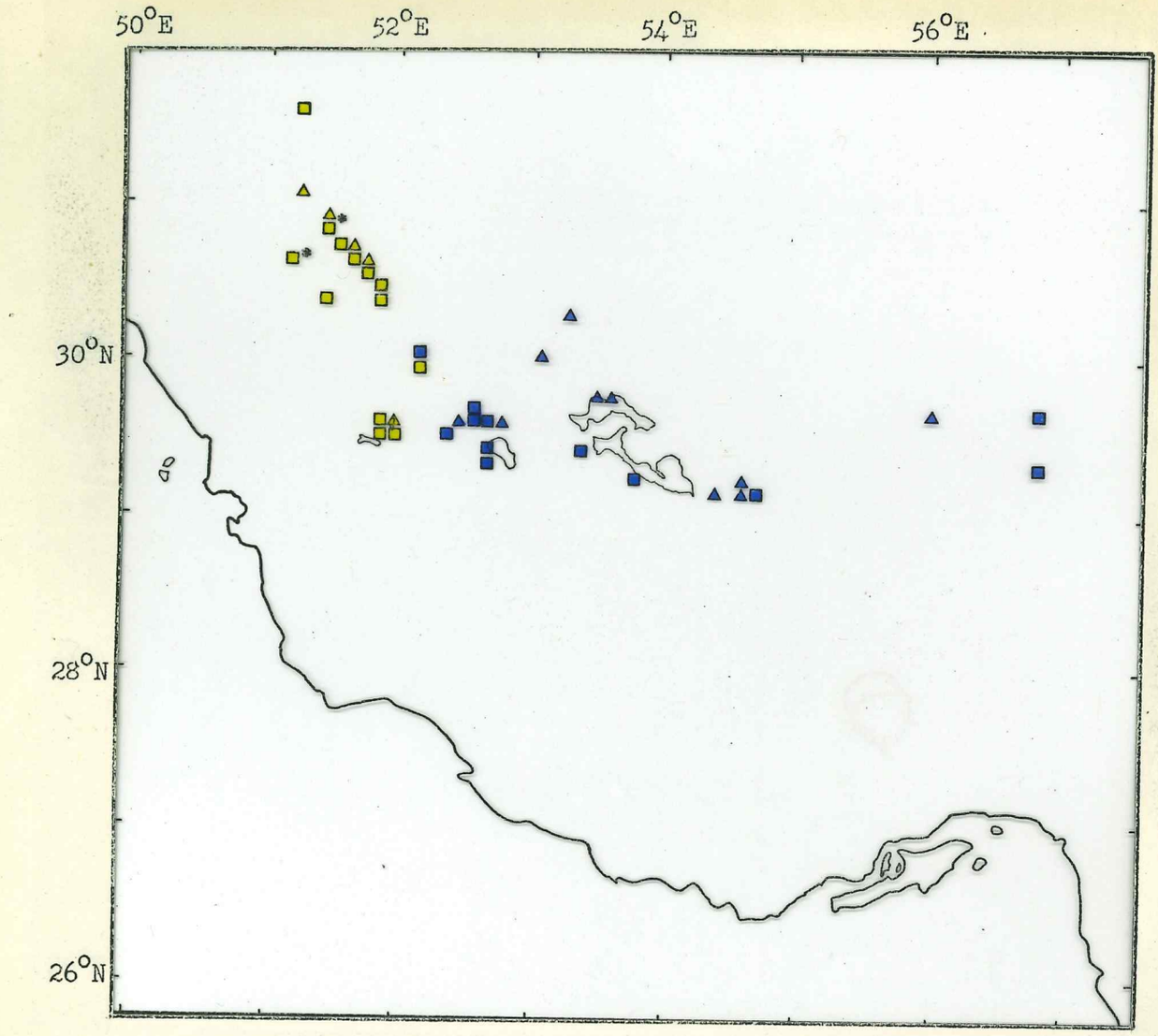


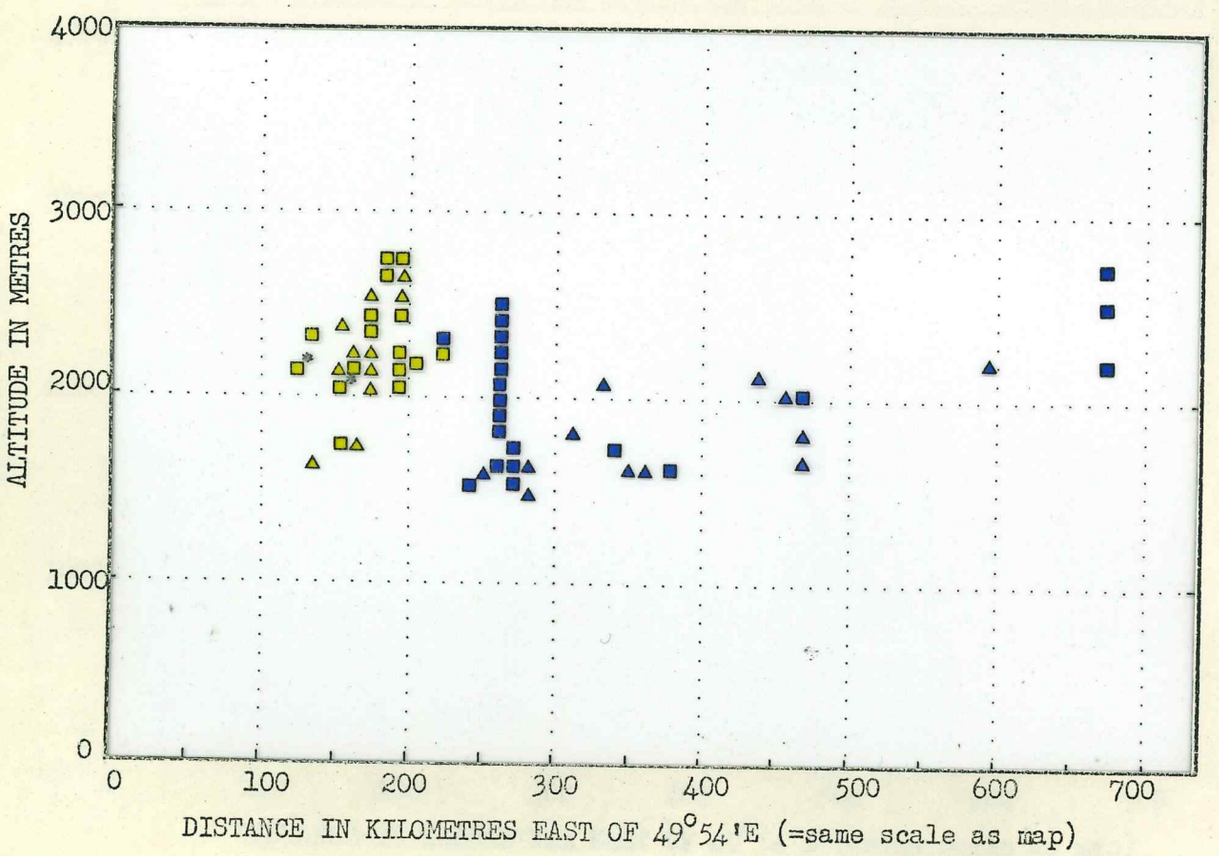
Overlay 6. Altitudinal and geographical distribution of breeding localities in S. W. Persia of O. finschii, O. monacha and O. picata.

Breeding records: Proven Probable

O. finschii
O. monacha
O. picata

*S. Cramp pers. comm. **D. A. Scott pers. comm.





Overlay 7. Altitudinal and geographical distribution of breeding localities in S. W. Persia of O. hispanica and O. lugens.

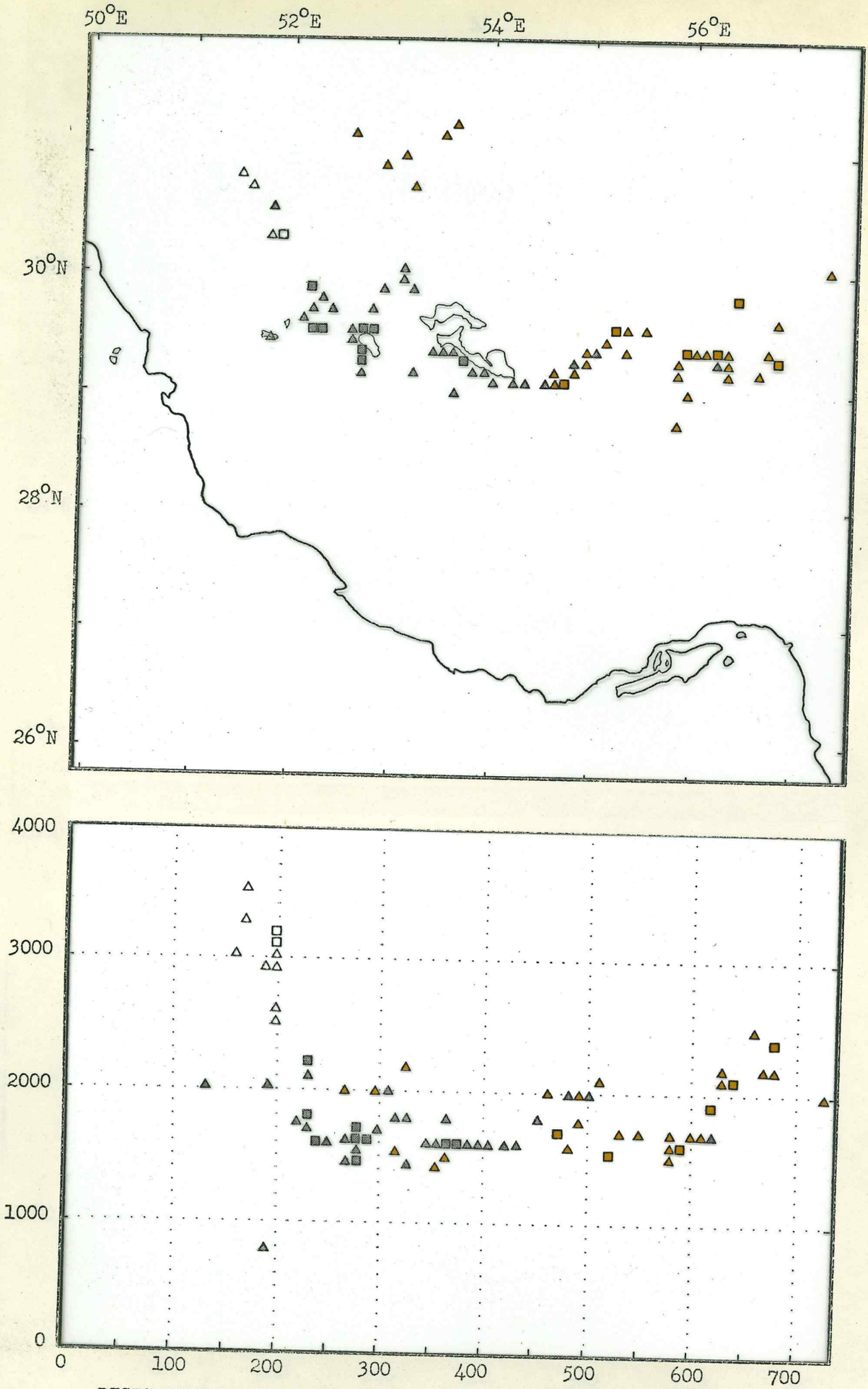
Breeding records:	Proven	Probable	
	□	△	O. hispanica
	■	▲	O. lugens

*Witherby 1903.

N.B. Where the two species bred in the same locality the symbols are placed side by side.

O. DESERTI, O. ISABELLINA AND O. OENANTHE IN THE BREEDING SEASON

Overlay 8



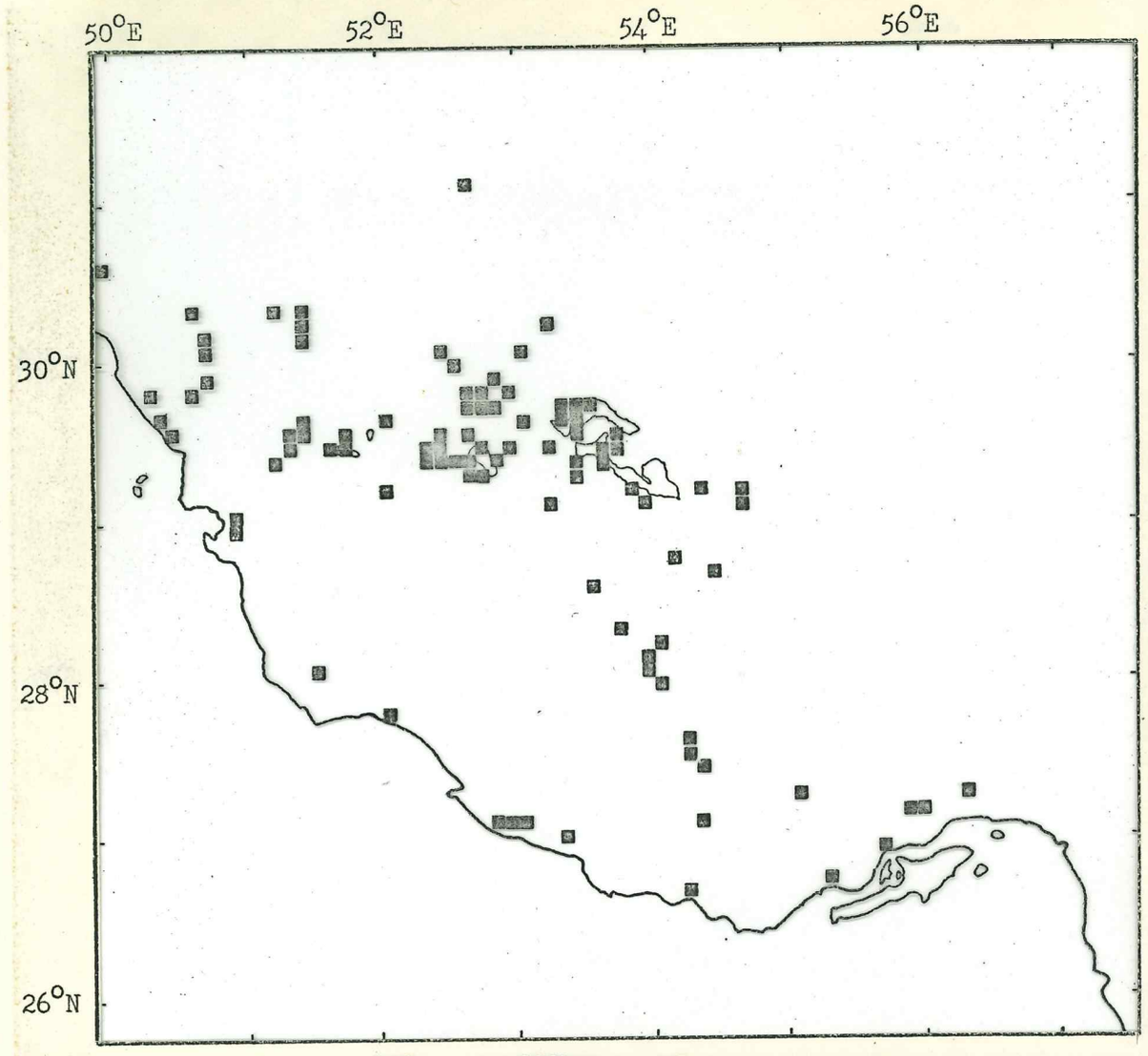
Overlay 8. Altitudinal and geographical distribution of breeding localities in S. W. Persia of wheatears inhabiting flat ground.

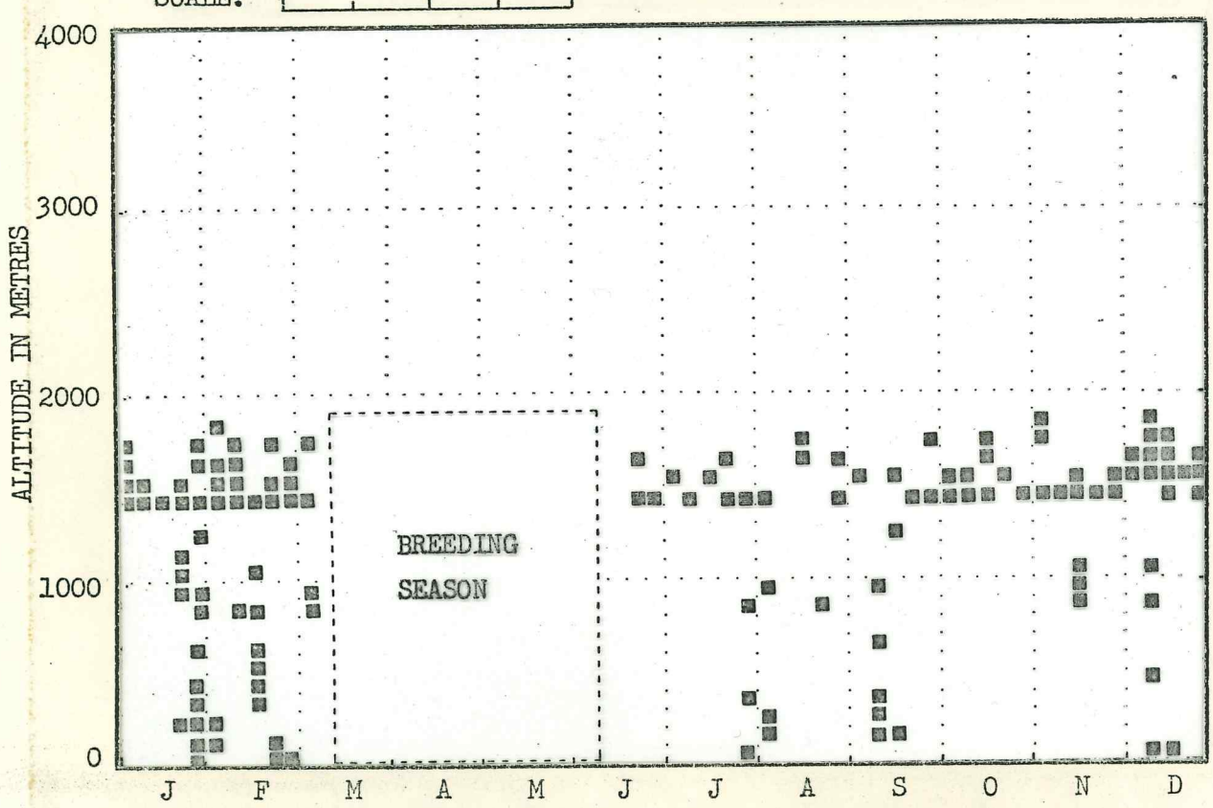
Breeding records: Proven Probable

- ■ ▲ O. deserti
- ■ ▲ O. isabellina
- □ △ O. oenanthe

N. B. Where more than one species bred in the same locality the symbols are placed side by side.

O. ALBONIGER OUTSIDE THE BREEDING SEASON

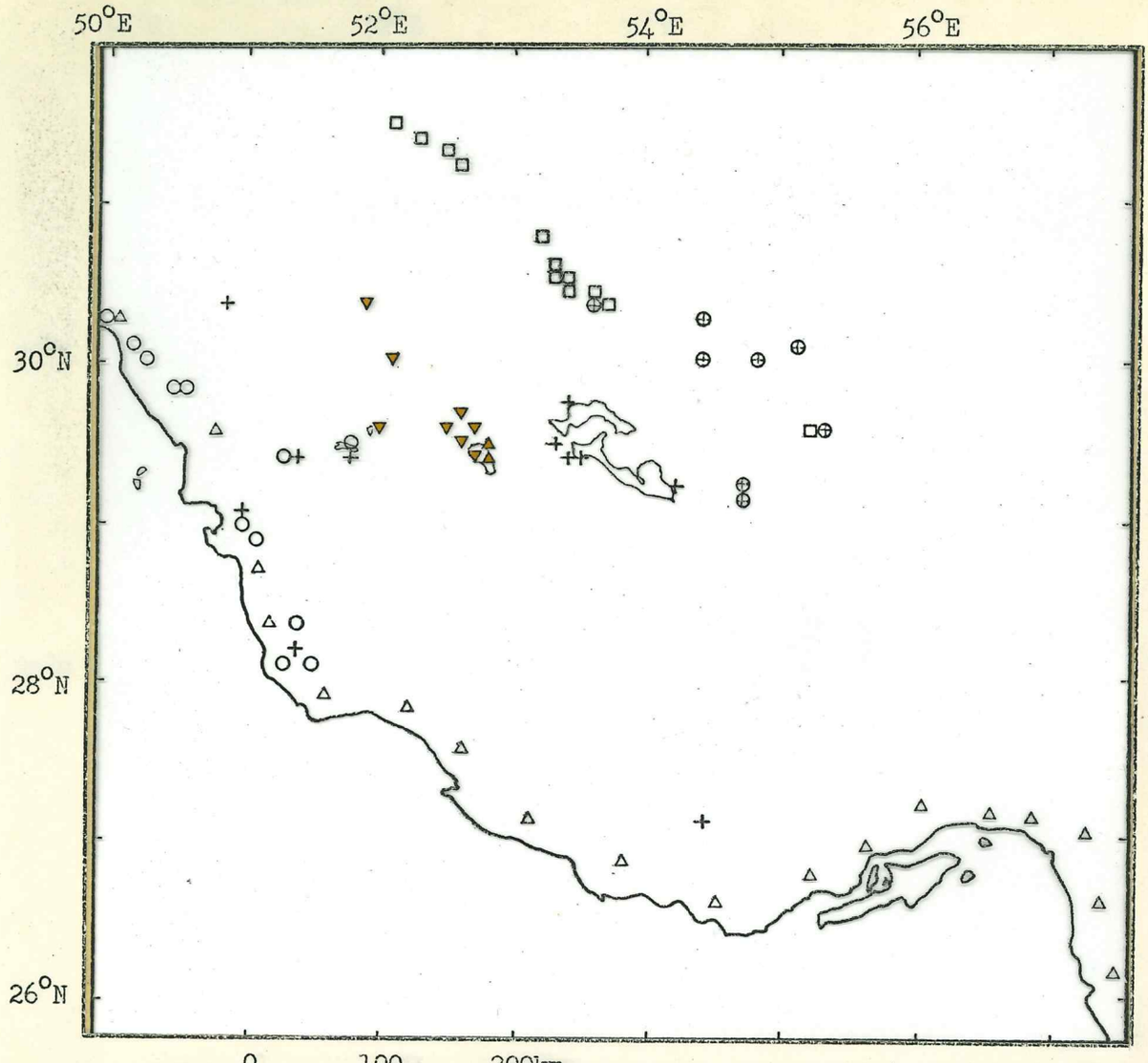


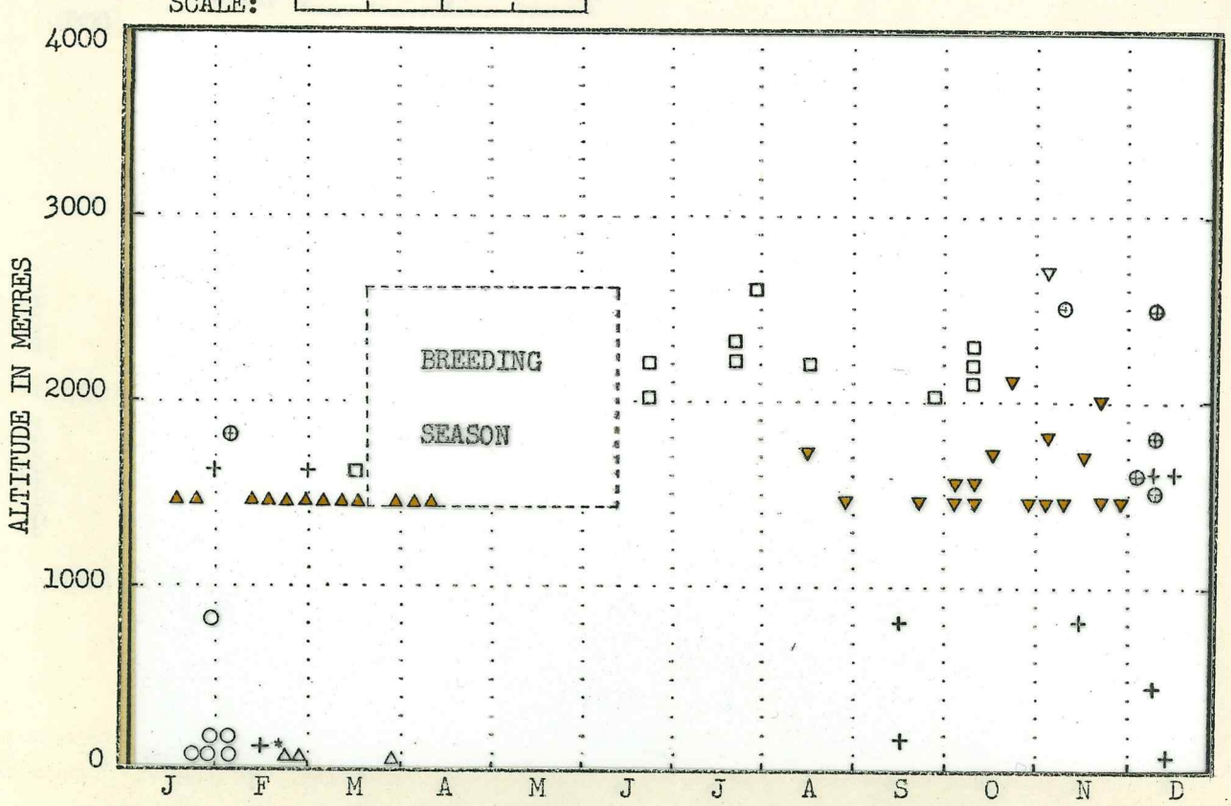


Overlay 9. Localities, altitudes and dates of records of O. alboniger in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

■ resident.

N. B. Eight of the above records were contributed by D. A. Scott.



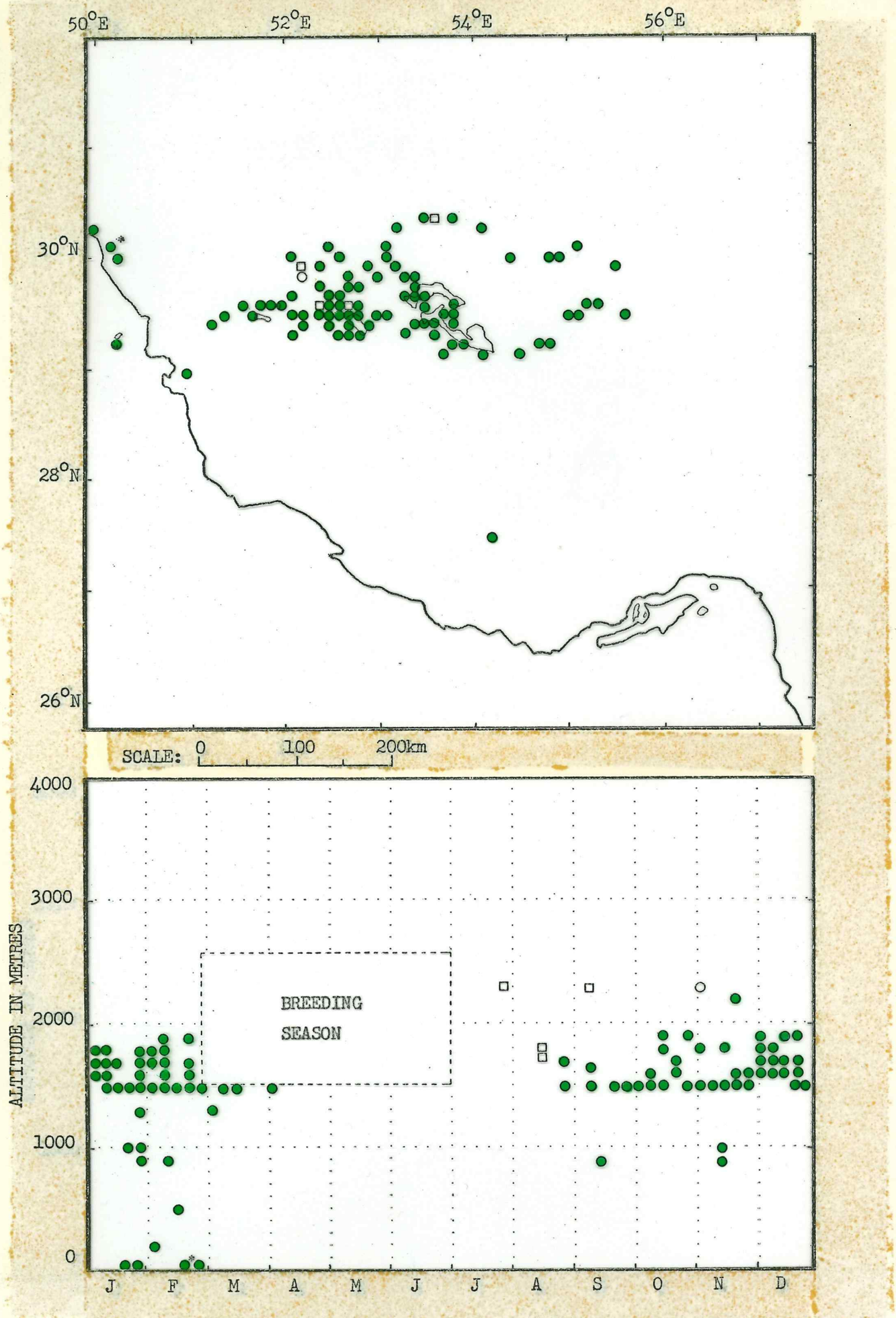


Overlay 10. Localities, altitudes and dates of records of O. deserti in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

- □ probably summer visitor/?migrant.
- ○ probably winter visitor/?migrant.
- \+ winter visitor/migrant.
- ⊕ winter visitor/resident/migrant.
- ▲ spring migrant.
- △ probably spring migrant/? winter visitor.
- ▼ autumn migrant.

*The records of probable spring migrants in February on the coastal plain were contributed by D. A. Scott.

O. FINSCHII OUTSIDE THE BREEDING SEASON

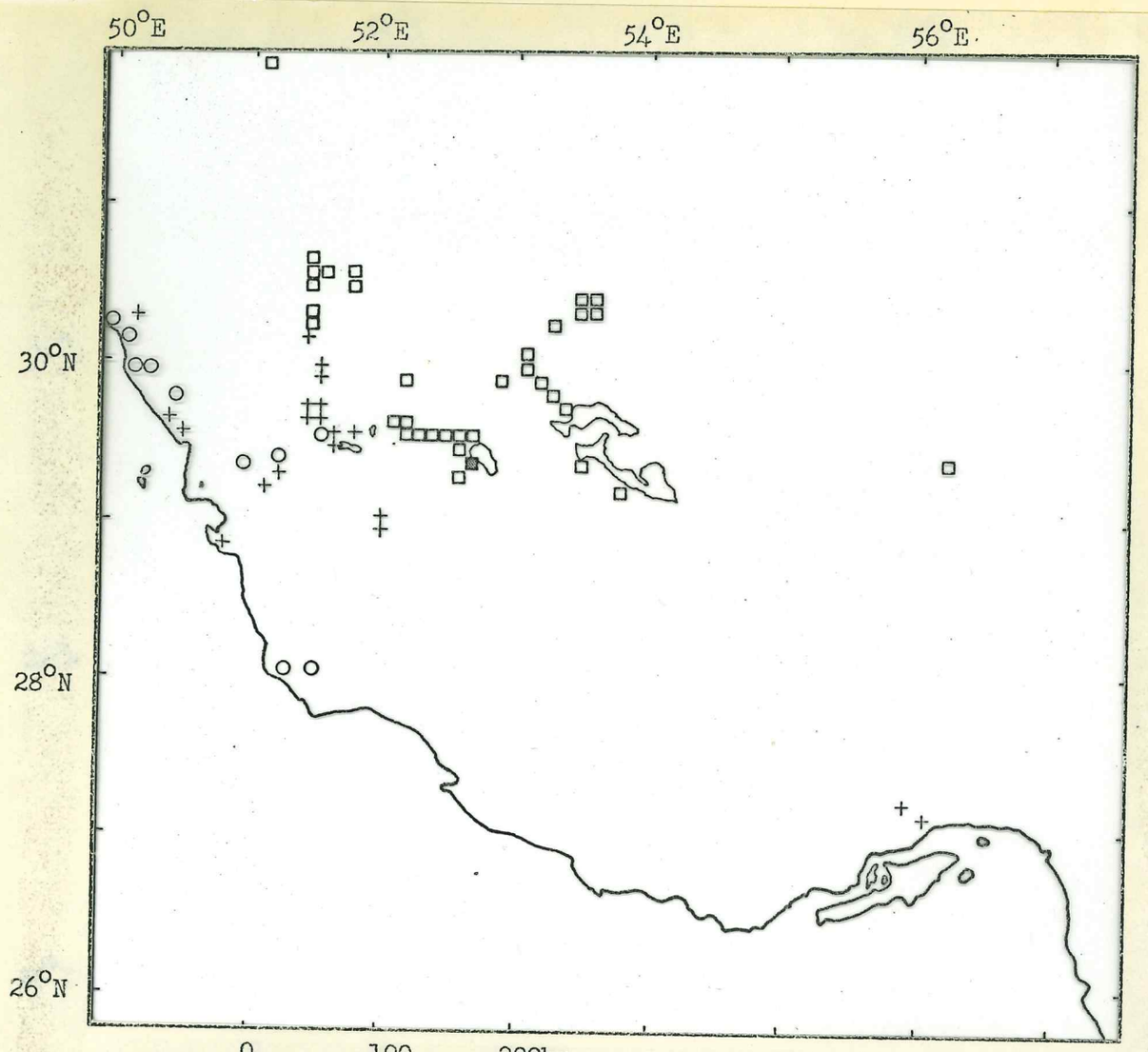


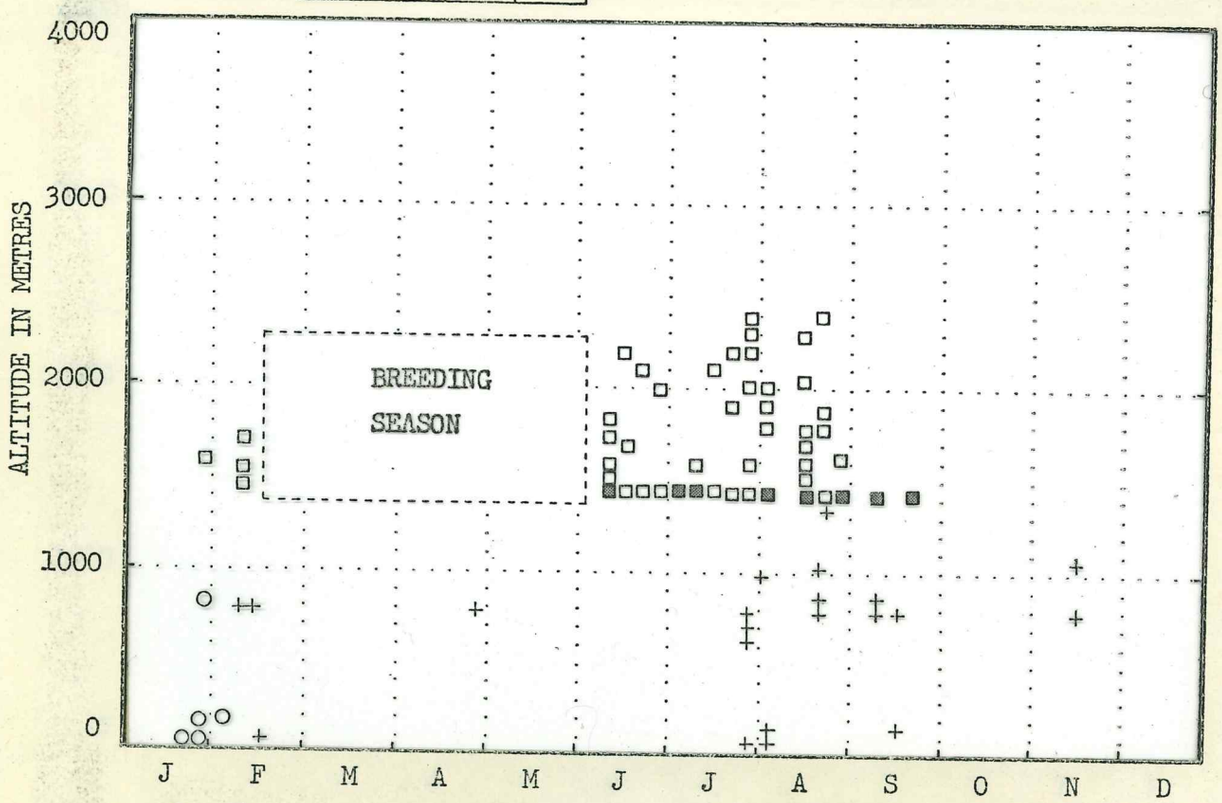
Overlay 11. Localities, altitudes and dates of records of O. finschii in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

□ summer visitor/resident. ○ summer visitor/resident/winter visitor.

● winter visitor (probably includes a few residents and migrants).

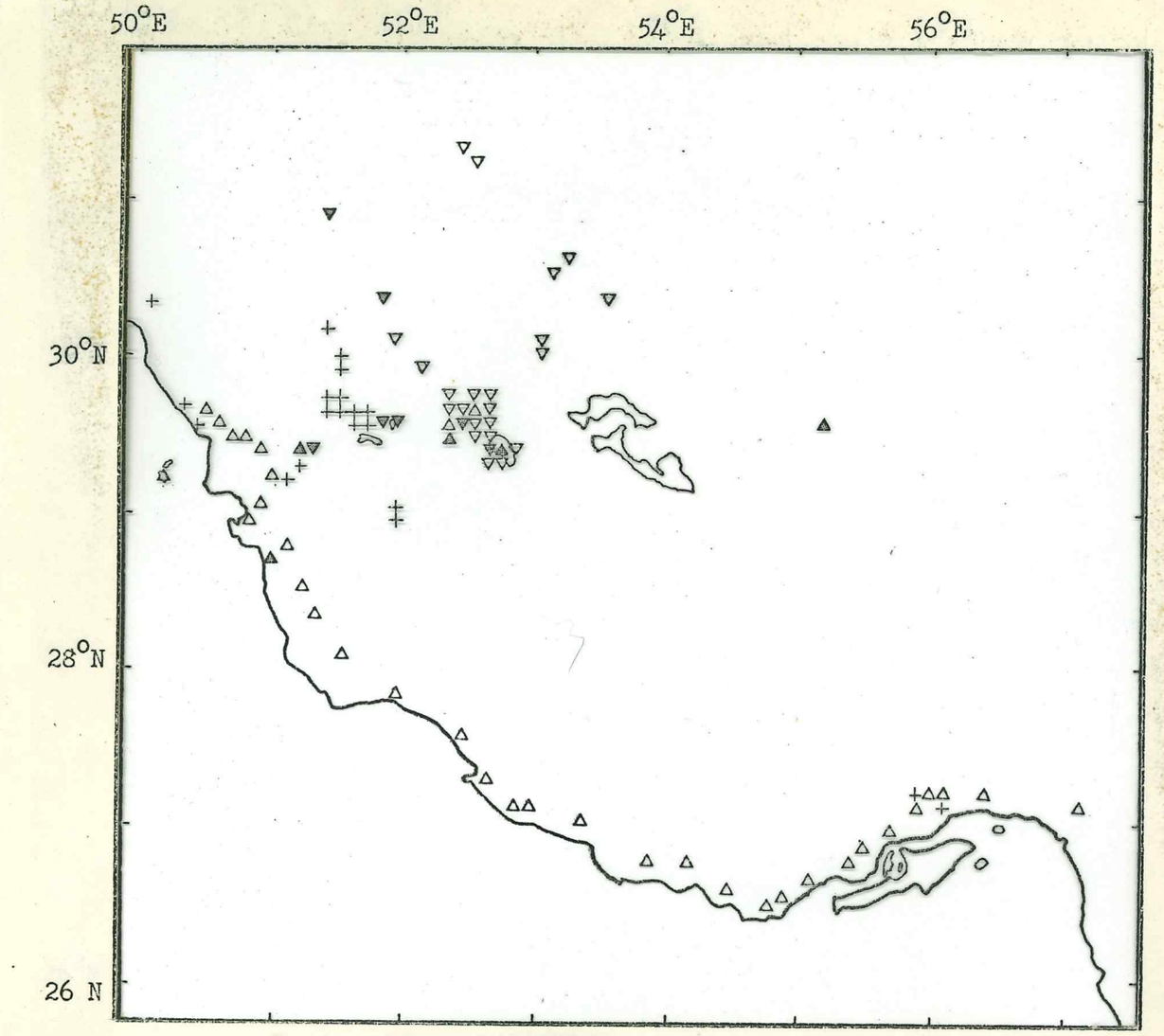
*D. A. Scott pers. comm.

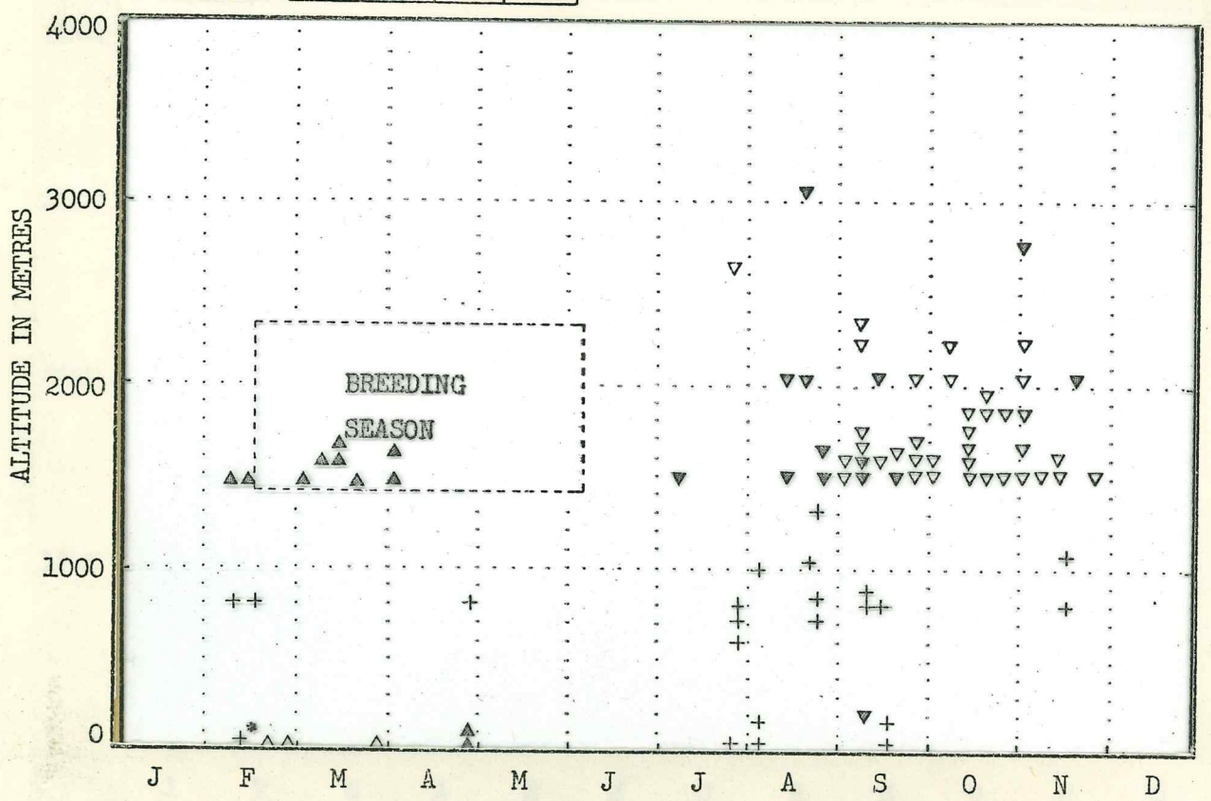




Overlay 12. O. isabellina: localities, altitudes and dates of records in S. W. Persia of winter visitors and of summer visitors outside the breeding season.

- ■ summer visitor.
- □ probably summer visitor/?migrant.
- \+ winter visitor/migrant.
- ● winter visitor.
- ○ probably winter visitor/?migrant.



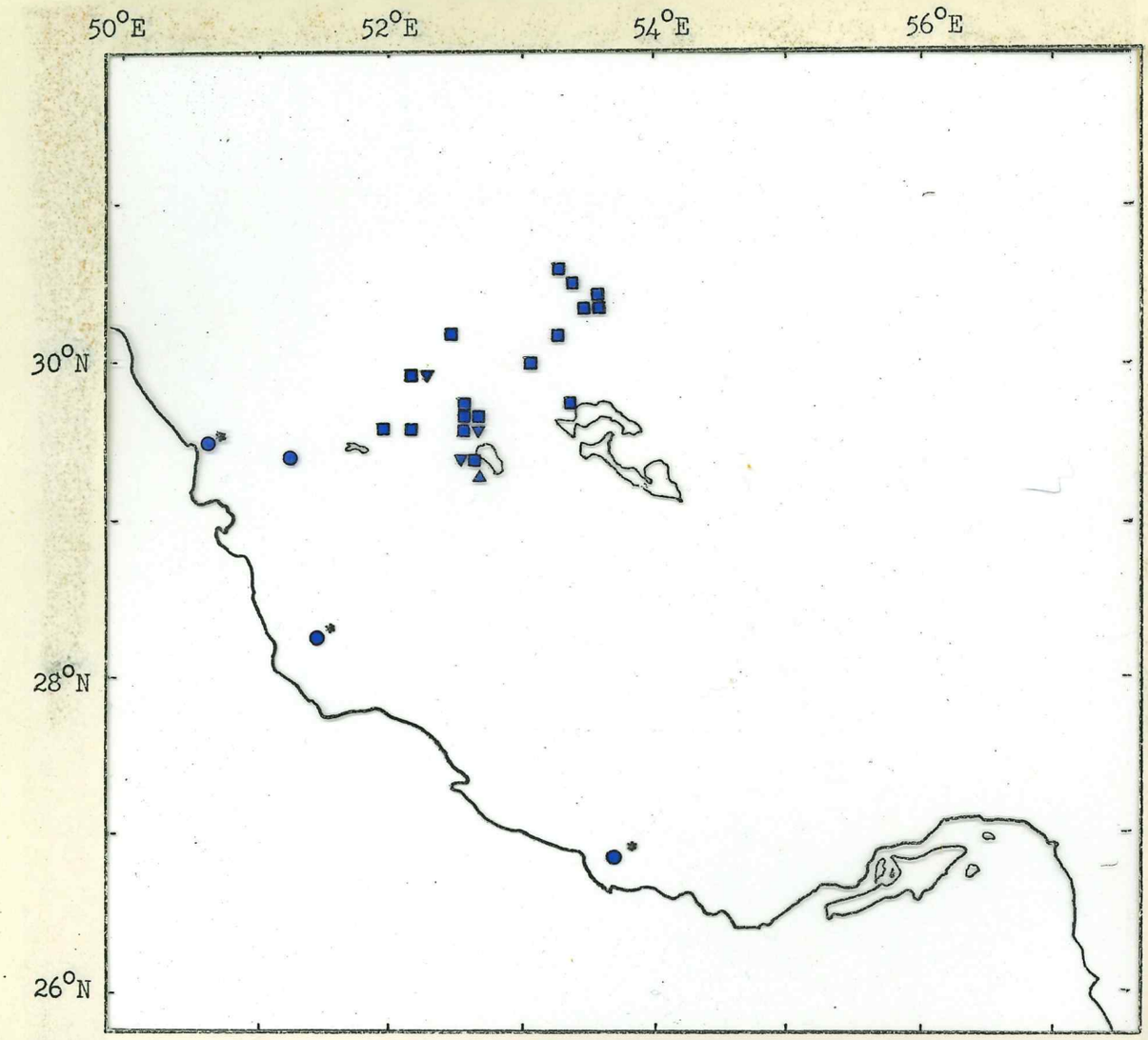


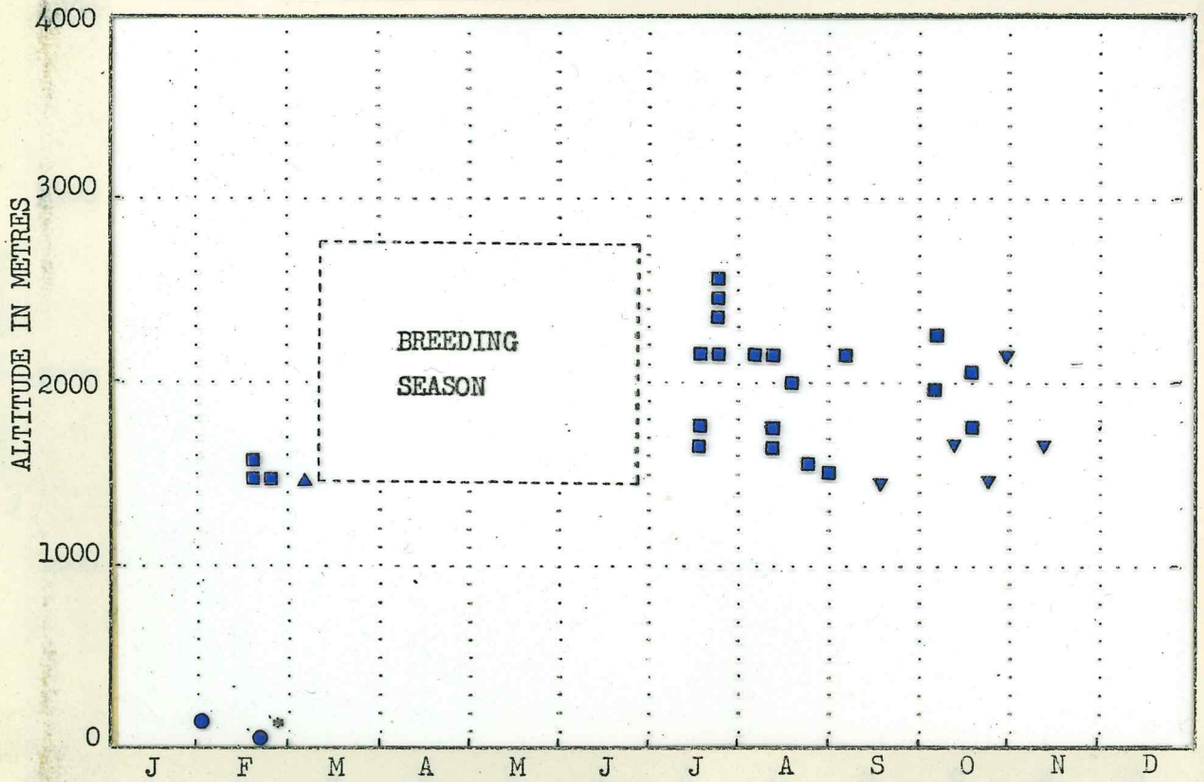
Overlay 13. Localities, altitudes and dates of records of migrant O. isabellina in S. W. Persia.

▲ spring migrant. △ probably spring migrant/?winter visitor.
▼ autumn migrant. ▽ probably autumn migrant/?summer visitor.
\+ migrant/?winter visitor.

*The records of probable spring migrants in February on the coastal plain were contributed by D. A. Scott.

O. LUGENS OUTSIDE THE BREEDING SEASON



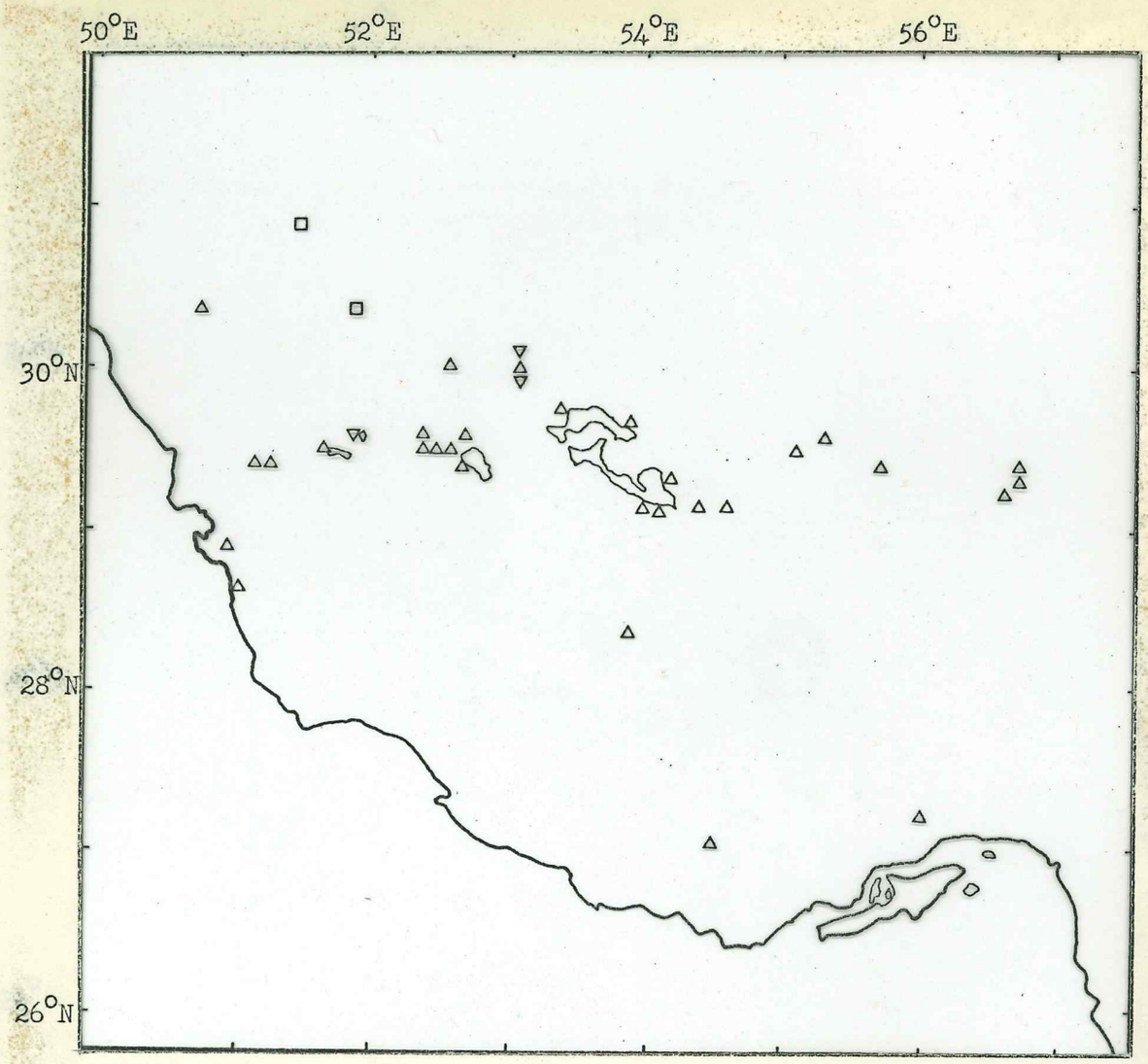


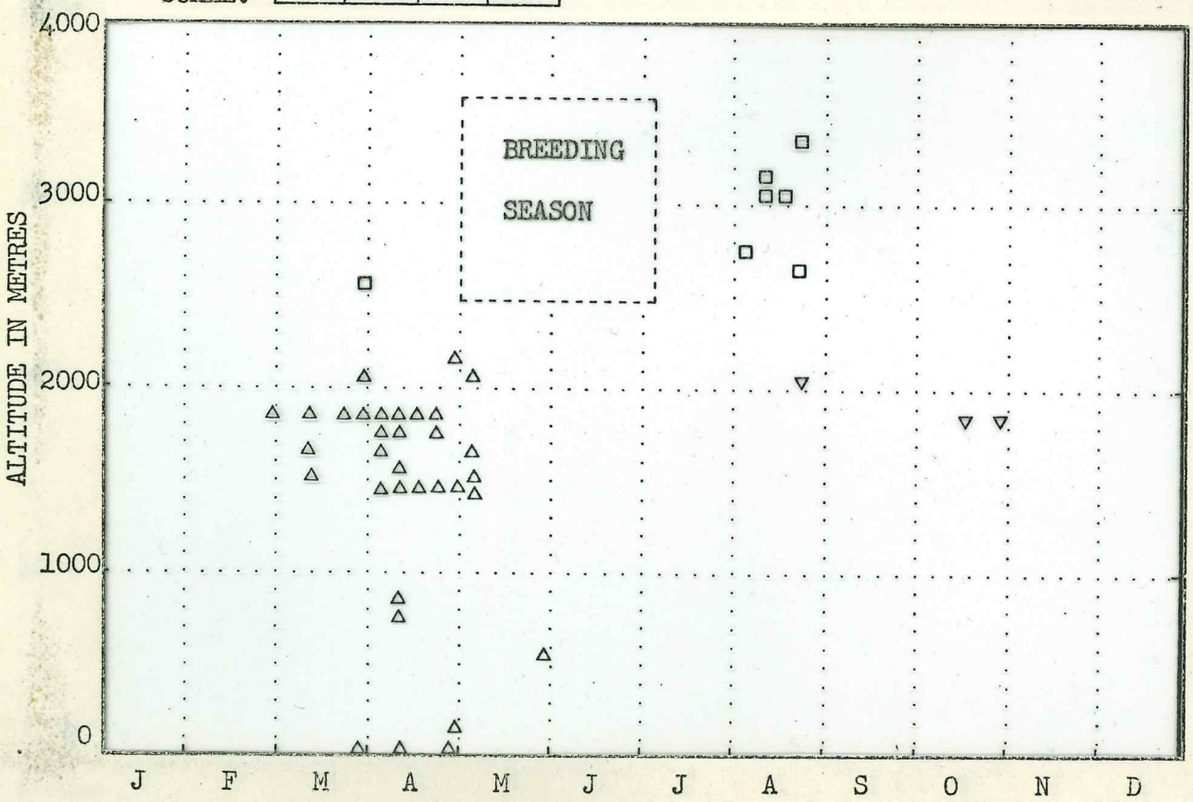
Overlay 14. Localities, altitudes and dates of records of O. lugens in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

■ summer visitor.
● winter visitor/migrant.
▲ spring migrant.
▼ autumn migrant.

*D. A. Scott pers. comm.

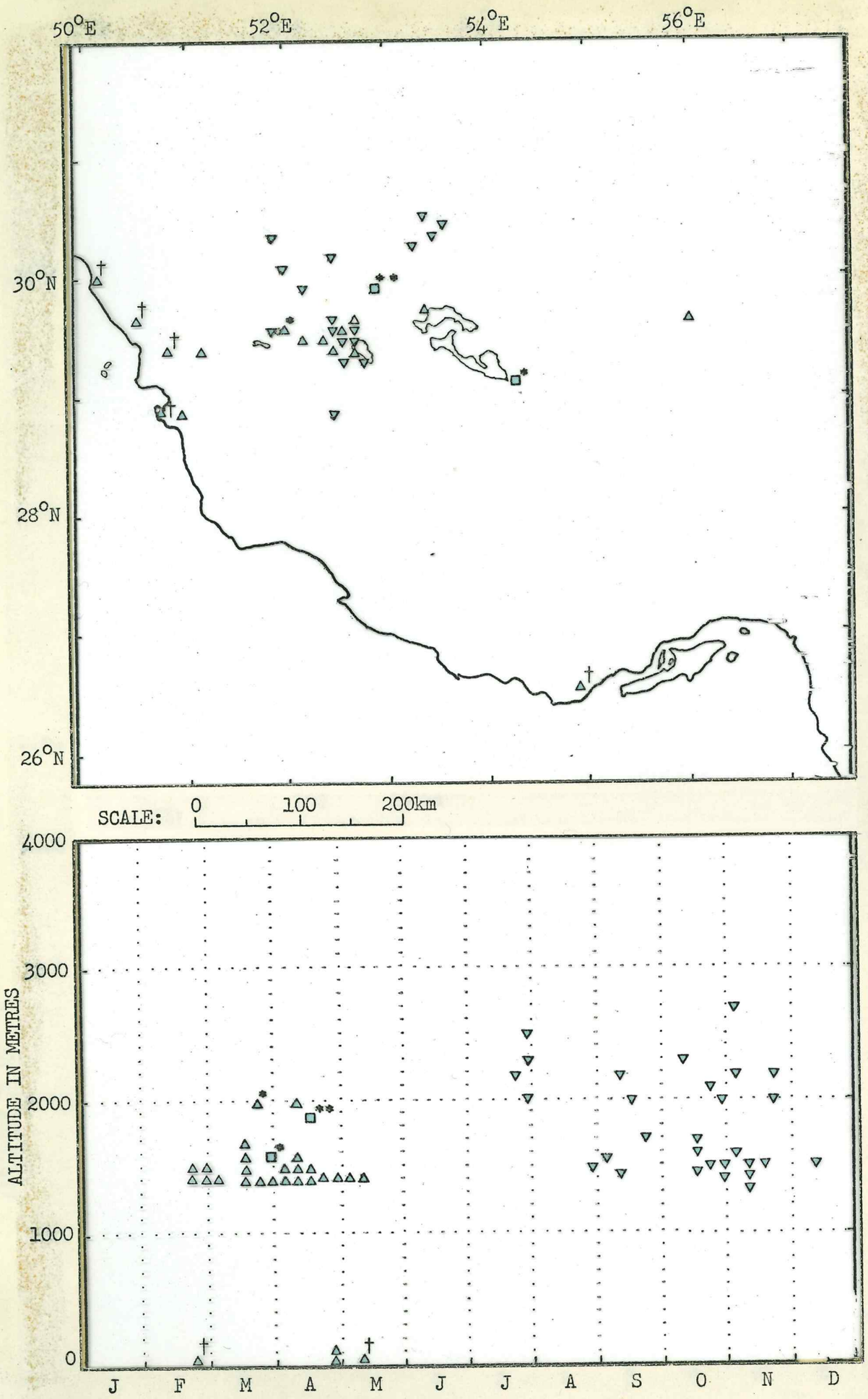
O. OENANTHE OUTSIDE THE BREEDING SEASON





Overlay 15. Localities, altitudes and dates of records of O. oenanthe in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

□ summer visitor. △ spring migrant. ▽ autumn migrant.



Overlay 16. Localities, altitudes and dates of records of O. pleschanka in S. W. Persia.

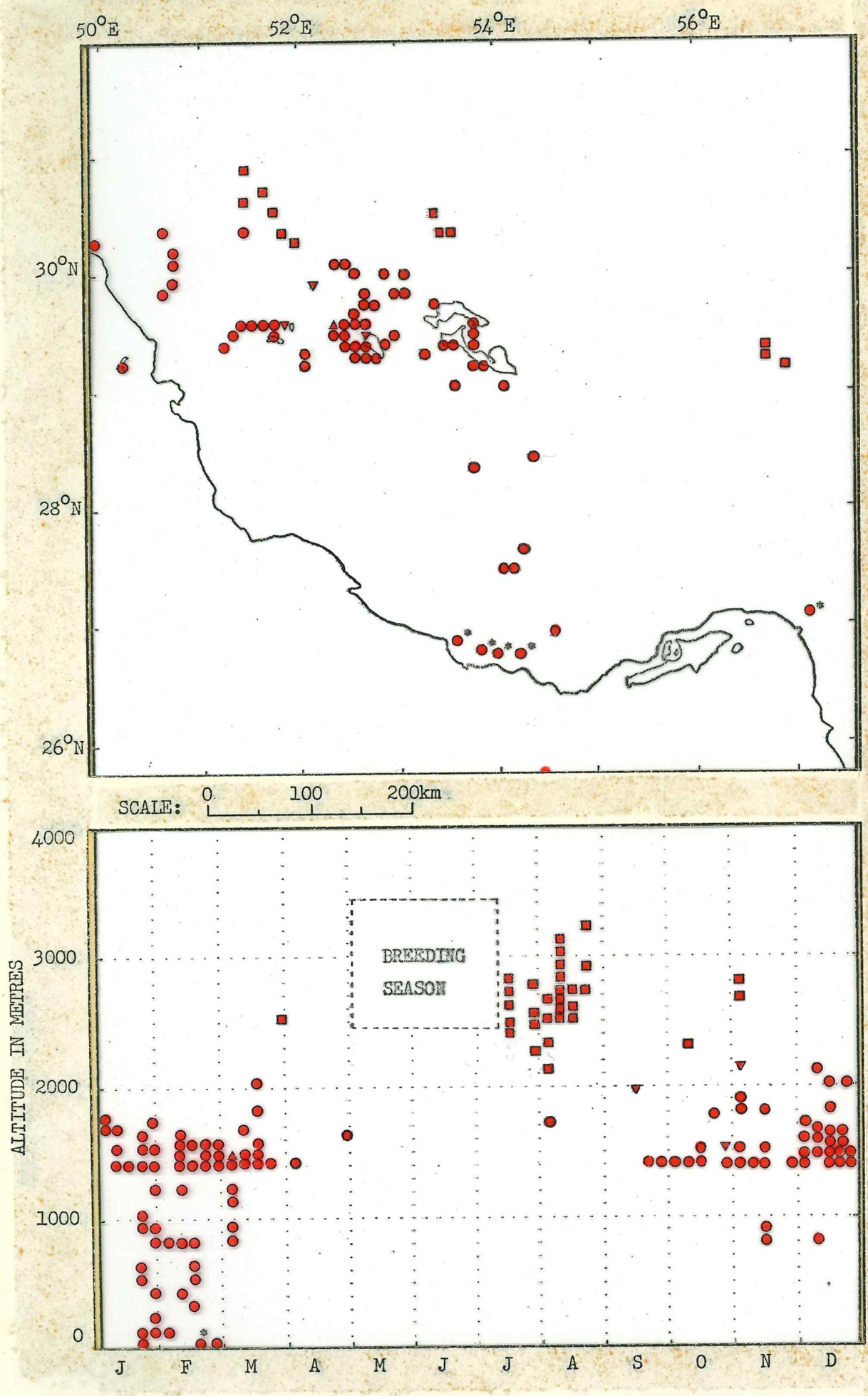
△ spring migrant. □ breeding. ▽ autumn migrant.

*Vaurie 1949.

**Erard and Etchecopar 1970.

†D. A. Scott pers. comm.

O. XANTHOPRYMNA OUTSIDE THE BREEDING SEASON



Overlay 17. Localities, altitudes and dates of records of O. xanthoprymna in S. W. Persia outside the breeding season and off the breeding grounds during the breeding season.

■ summer visitor.
● winter visitor.
▲ spring migrant.
▼ autumn migrant.

* D. A. Scott pers. comm.