SOCIALITY IN RABBITS

by

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ABSTRACT

Two populations of rabbits (Oryctolagus cuniculus) we: investigated to see whether polygynous, multi-male groups formed in the absence of large multi-entranced warrens. They did not. Rabbits neither gathered in space nor time. The small warrens were spread out evenly across homogeneou: patches and the females were well spaced out. Monogamy, distinguished by a battery of tests, was prevalent, with t more dominant males as 'mate' rabbits. That the polygyny frequently mentioned in the literature was a result of mal dominance and female defense was considered.

The genetic structure of each population was investigated by taking blood from rabbits and having it analysed electrophoretically and for immunoglobulins. A method for assessing relatedness between groups of pairs o animals was implemented, then validated and developed with Monte Carlo simulations. With the seven polymorphic allel obtained, no non-zero relatedness was found but it was sometimes possible to exclude high relatedness.

The bearing of sociality on vigilance during feeding was investigated. Although a rabbit's vigilance decreased as its 'mate' approached, the presence of other rabbits wa correlated with increased vigilance. It was concluded that the need for social vigilance outweighed the benefit of 'many eyes' watching for predators. This conclusion was tested by experiment, using stuffed animals as stimuli.

Rabbits increased their vigilance during grazing bout both by increasing the length and frequency of scans. Scar could be short or long: the probability of ending a scan decreased sharply at a certain point; a form of positive feedback. The durations of short 'maintenance' scans were dependent on chewlength (the amount of food in the mouth). This fitted a timesharing definition as supported by experiment. Long scans in response to a visible threat di not involve chewing.

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To my mother and father

CONTENTS

CHAPTER 1. INTRODUCTION

The adaptable rabbit

A fairly clear picture of the social life of rabbits (Oryctolagus cuniculus) has emerged from a number of studies made in Britain and Australia e.g. Southern (1948); Lockley (1954); Mykytowcyz (1958,1959,1960); Myers and Poole (1959,1961); Parer (1977); Cowan (1983) and others to which I shall be referring. The most striking feature of these studies is the variability of social structure and of reproductive strategy shown between rabbit populations.

There are rabbits in Europe from Portugal to western Poland, from the Shetland Isles to Sicily, from Norway to Hungary (Kopp 1965). They spread most dramatically on introduction to the Australian continent, at the rate of 70 miles per year (Mykytowcyz & Gambale 1965), settling in subalpine, subtropical, arid desert and mediterranean types of habitat (Myers 1970).

Rabbits adapt to these several habitats using different environmental cues such as rain or temperature to coincide breeding with the onset of better quality grass (Myers and Poole 1959; Myktowycz 1959; Poole 1960; Dunsmore 1974; Parer 1977). In England it is possibly photoperiod that instigates breeding (Poole 1960; Adams 1981; but see Sadleir 1969) although weather also plays a part (Lloyd 1970). The duration of the breeding season is shorter in subalpine areas than in mediterranean-type areas (Myers 1970), and increased in Britain after myxomatosis (Lloyd 1970).

Fecundity is also variable, being greater in those more favourable habitats with ample food and low rabbit density (Myers 1964; Stodart and Myers 1966; Lloyd 1970; Myers 1970).

Myxomatosis is a good example of the rabbit's speedy response to the environment. The British rabbit knew a 99% mortality rate when mxyomatosis was introduced in 1953 (Armour and Thompson 1955). Through the build-up of genetic resistance in the rabbit (and also through attenuation of the viral strains) this rate fell dramatically (Ross and Sanders 1977), e.g. the mortality rate from a particular strain of the virus fell from 90% to 21% in 10 years.

Rabbits have a variety of physiological features which enable them to make a flexible response to the environment. It is possible that duration of breeding season is under the control of the central nervous system, since rabbits appear to be physiologically capable of breeding all year round (Brambell 1944; Davies 1982). Opportunities for impregnation of does are increased by their having induced ovulation, i.e. ovulating in response to copulation (Denenberg, Zarrow and Ross 1969). Behavioural oestruses ensure that copulations occur at the optimum times such as post-partum (Myktowycz and Rowley 1958). Reabsorption of foetuses can be common in rabbit populations (Brambell 1942,1944) and Mykytowycz (1959) found it to be prevalent in crowded conditions. Their famous facility for reproduction provides a basis for fast genetic change in rabbit populations. Lloyd (1963) found average annual output of

does to be 29.5 young. Rabbits may be nocturnal or diurnal depending on the safety of the habitat and tameness of the animals (Gibb 1977). Even their digestive systems are adaptable: coecotrophy allows them to derive maximum benefit from poor quality grass by redigestion of their food (Harrison-Matthews 1968).

Behavioural flexibility can be seen in the variety of social structures of rabbit populations (Myers and Parker 1965). In this thesis, the social structure, mating system and distribution of rabbits and of warrens in two populations are described. These are all factors that vary between populations and their interdependences are considered. Sociality can be explained in evolutionary terms as being advantageous to all the individuals in a group (Bertram 1980) or as a form of altruism. Members may interact socially in order to benefit their relatives by kin selection (Hamilton 1964), or to gain future advantages for themselves by reciprocal altruism (Trivers 1971). Genetic analyses of the two rabbit populations were made to elucidate the relatednesses betwen socially interacting animals. Whether benefits were to be gained by sociality in these rabbits was investigated by looking in detail at the most vaunted advantage to sociality, that of corporate vigilance, for one population. Other factors influencing vigilance were also investigated in detail, particularly the interaction between feeding and vigilance behaviours.

How gregarious are rabbits?

The size, distribution and use of warrens all vary across rabbit populations (Myers and Parker 1965) e.g. in the arid areas of Australia, warrens appeared to be necessary for shelter, whereas in temperate climes there were more surface dwelling rabbits. Myers and Parker's thesis (1965) was that females liked to breed in company and that large warrens, of 50-60 entrances, were developed wherever the substrate allowed. They postulated that small warrens in homogeneous areas would at least be clumped. Mykytowycz and Gambale (1965) argued similarly, that gregariousness hindered their enclosed rabbits from constructing new warrens. They were thought to need an expansive area ahead of them to tempt them away from the 'magnetism' of the warren.

Cowan (1983) argued in the opposite manner for chalkland rabbits. He suggested that few new warrens were constructed in chalk since they were difficult to initiate. Reluctance to start fresh warrens was not caused by gregariousness; rather, having to share warrens imposed gregariousness upon the rabbits.

Coherent groups of rabbits have been noted as forming just before breeding begins, as the ill-defined ranges of individuals contract, and territorial behaviour intensifies (Myers and Poole 1959; Mykytowycz 1959). This group formation is a peaceful process in stable warrens, but is accompanied by intense fighting in less established groups (Mykytowycz 1960), or in high density populations (Myers and

Poole 1959). Once groups have been formed, there is little movement between them (Dunsmore 1974).

Myers and Poole (1959) described these groups as comprising two or three males and one to five females. They regarded the sexes as forming two distinct social units. The females drew together, around an old, dominant doe, confining their home-ranges about the warren. Female group-size was thought to be limited by the number of other does that a female could recognize. Similarly, the bucks contracted their home-ranges to produce male groups each of which overlapped with one or more female groups. It was thought that male group size was limited as only the most dominant bucks were likely to achieve matings.

Mykytowycz (1958) interpreted group-formation in a markedly different manner. He described pairings of oppositely-sexed rabbits that occurred down the hierarchies, with group-structure determined by rank. The dominant pair occupied the centre of the warren, subdominant animals were pushed to the periphery, and the lowest rankers became satellites. Garson (1982) suggested that when rabbit density was low, pairs were more likely to form than larger groups.

Parer (1977) found that if a rabbit group grew to two males and two females, and was spread over two warrens, it would divide into two groups. Similarly, Mykytowycz (1959) found his dominant pair of rabbits defending two warrens until the breeding season started when the subdominant pair took over the secondary warren.

Thus, three systems of sociality have been described. Rabbits may be attracted into single sex groups as Myers and Poole concluded. They may be attracted into groups of paired animals as Mykytowycz suggested. They may be attracted to warren-availability rather than to other rabbits, as Cowan hypothesized, and as Parer's findings supported, with groups separating to use more warrens. The greater numbers of rabbits that can be accommodated in large warrens might be being attracted to one another or to the warren. If to one another, then rabbits might be expected to clump together in space and time, even when not sharing a warren.

My studies at Walney and Oxford that took place in the breeding seasons when rabbits had settled into their breeding homeranges, sought to discover whether rabbits were attracted to one another. At both sites small single or double entranced warrens were the norm and if rabbits formed groups it could not have been to share warrens. Thus it was possible to test whether grouping occurred for reasons other than warren sharing. In Chapter 3 the distributions of warrens were inspected on both sites to see to see if rabbits dug warrens close to one another. Further tests in Chapter 3 describe the spatial and temporal distributions of rabbits out at particular moments in time to see whether the animals tended to clump together or to avoid one another.

Competition within the sexes

Rabbit distribution might be partly determined by individual relationships that make up the social structure i.e. by attraction and avoidance both between and within the sexes. Aggression between the sexes has seldom been observed in field studies e.g. (Mykytowycz 1958) although in enclosed circumstances it can be intense (Mykytowycz and Hesterman 1975). Aggression betwen same-sexed rabbits however, is commonplace.

Interactions between males appear to take two basic forms: aggression, characterized by fast chases and fighting; and assertion of dominance, characterized by less intense chasing and by 'displacement'. Displacement is when a subordinate moves out of the way of an approaching dominant animal (Lockley 1961).

Mykytowycz (1958) found that aggression was always demonstrated towards strange bucks, and bucks would team up to chase strangers off. Cowan (1983) described this as inter-group territorial aggression, advertized by paw-scraping and parallel running. This behaviour was not noted amongst sand-dune rabbits (Cowan and Garson 1985).

The literature unanimously asserts that there are strictly ordered male dominance hierarchies within rabbit groups. Cowan (1983) noted that dominance assertion occurred particularly in the presence of does, and several authors suggested that it determined access to does (Mykytowycz 1958; Myers and Poole 1959).

The nature of interactions between does is less clear-

cut. Although Mykytowycz (1958) found strict dominance hierarchies, in the larger groups described by Myers and Poole (1959) there were only partial hierarchies with a few does emerging as especially dominant.

Relationships within the sexes are described in Chapter 5 for both my dune and pasture-land populations. Attraction, avoidance and interaction between individuals were investigated. These data were used to consider whether does were attracted to one another as Myers and Poole (1959) suggested, and whether they had clear-cut dominance hierarchies. Dominance relationships were worked out for the bucks and related to the mating system as defined in Chapter 4. Further, in Chapter 5, relationships between the sexes are considered, in order to ascertain whether bucks or does were responsible for maintaining the mating system.

The mating system

'Since polygyny must always be advantageous to males, its presence or absence must depend primarily upon the advantages or disadvantages of the females' (Orians 1969). That only 5% of mammals are known to be monogamous (Wrangham 1983) has been ascribed to internal brooding which releases males from parental duties (Orians 1969). Rabbits would appear to be prime candidates for polygyny, with no overt paternal care.

As the numbers in a rabbit group increase, so the breeding-system becomes more polygynous. Southern (1948) compared his Oxford rabbit population to that of Lincke and

concluded that where rabbit populations were less dense, as at Lincke's site, the rabbits stayed in monogamous pairs, whereas the greater density of rabbits at Southern's Oxford site 'encouraged promiscuity'.

The consortship system was worked out for my two populations using attraction, avoidance and interaction data between individuals. This is set out in Chapter 4. It was assumed that consortships reflected the underlying mating system which, in turn, could be related to the levels of gregariousness found and to the distribution of warrens. Mechanisms by which polygyny may be maintained by males (following Emlen and Oring 1977) are considered in Chapter 5 in the light of the results.

Relatedness in rabbits

The underlying genetic relatedness between interacting individuals can be very instructive in elucidating social structure and the benefits of sociality (Foltz and Hoogland 1983; Wilkinson 1984). Interactions between same-sexed individuals could be influenced by their degree of relatedness as Bertram (1978) suggested for lions (Panthera leo). The relatedness between bucks was of particular interest: to discover whether the differential aggression shown by dominants towards strange bucks and to subordinate bucks might have been a form of nepotism. Alternatively, the migration system might have brought unrelated bucks into close proximity. This, and the relatednesses between neighbouring dominant bucks and between neighbouring does

are investigated in Chapter 9.

Chapter 9 describes the development of a new measure of relatedness, a measure between groups of pairs of animals with an estimate of its error. It uses data from polymorphic loci which were obtained by getting the rabbits' blood analysed for enzymic and IgG variations.

Relatednesses were also tested between consorting pairs to find out whether optimal outbreeding might be occurring (Bateson 1978) and to attempt to assess parentage of young. This would have shown whether consortships were a good indication of the mating system, and whether bucks, particularly, had differential breeding success.

Wariness in rabbits

In studying the social structures and levels of gregariousness in rabbit populations, it is worth considering whether rabbits benefit from the mooted advantages to group living. It could be that sociality would benefit rabbits; the increased corporate awareness of 'many eyes' decreasing the time each individual need spend in vigilance, and increasing the probability of a predator being spotted (Pulliam 1973). Conversely, groups with complex social structures formed of individually unique relationships, are likely to promote rivalry and competition which might result in increased individual vigilance in company.

In transient bird flocks, where feeding is paramount, there is often a simple relationship between vigilance and

numbers in the flock e.g. Powell (1974). A more complex relationship might be expected to obtain for mammals living in long-term proximity. Neither distance to burrow, number of neighbours out, nor the nature of the external stimulus terminating a feeding bout, affected either feedbout duration, eating or scanning rate in Garson's dune rabbits (pers comm).

The relationships between rabbits, as set out in Chapters 4 and 5 were used to investigate conspecifics' effects on vigilance in the Oxford population. In Chapter 7, classes of rabbits are looked at to see how individual vigilance was affected by the presence of and distance to other particular rabbits. Multiple regression techniques were employed to overcome the problems of spurious relationships occurring from highly correlated factors such as time of day and numbers of animals out. An experiment was run to complement the observational data.

Measures of vigilance

Bertram (1980) suggested for ostriches (*Struthio camelus*) that vigilance for predators, and vigilance for conspecifics might affect the rate of scanning and the proportion of time spent vigilant, respectively:

> "Improved scanning of the horizon for distant, slowly-moving ostriches is probably best achieved by increasing the length of each scan rather than by increasing their frequency".

In contrast, ostriches wary for predators should increase the rate of vigilance and not the scan-duration, since the predator would watch and wait for the ostrich's next feed

before attacking. This depends on the strategy used by the predator (Hart and Lendrem 1984).

In birds, feeding rate and scanning rate are independent (e.g. Caraco 1982). Feeding rate is the pecking rate between scans, and the headlifts it involves are distinct from true scans. The bird must lift its head in order to make discrete fresh attacks at new particles. In rabbits (as in ostriches) the head can be down, feeding for a period of time, when vision is obscured by grass during the feed. At the end of a feed the head goes up above grass level, making vigilance possible in the scan. Thus, for rabbits, the interpretation of rate of scanning is slightly equivocal, since it is also the rate of feeding!

The distributions of such feed and scan durations can throw light on the mechanisms of vigilance. Feed durations in ostriches were random (Bertram 1980) and Hart and Lendrem (1984) calculated this as being the best strategy for spotting predators. Scan durations in birds have usually been found to be constant e.g. Lendrem's (1983) blue tits (Parus caeruleus), but scans of house sparrows (Passer domesticus) did vary (McVean and Haddesley 1980).

In Chapter 6 the correlates of vigilance are set out for Oxford rabbits, showing in which ways proportion of time spent scanning, rate of scanning, durations of feeds, of scans, and of grazing bouts (which included scanning and feeding) were all related. Each of these measures was tested for effects against independent variables in Chapter 7. Also in Chapter 6, distributions of durations of feeds,

scans and grazing bouts were investigated. Scan durations were of particular interest since they were not constant and were likely to be affected by external stimuli as well as under the control of the internal state of the rabbit.

Sequencing of feeding and vigilance behaviours

Rabbits must be continually aware whilst above ground. In order to perform other behaviours than vigilance (e.g. feeding) they must pattern their behaviour sequences so as to distribute vigilance acts amongst the other behaviours. Since it is not possible to perform two mutually exclusive behaviours at the same time, there must be a mechanism for the rabbit 'deciding' (consciously or not) at each point in time, whether to feed or to scan. As McFarland (1985) pointed out, such decisions could be made by a stochastic process, or by one based on rules.

Tendencies to perform behaviours were described by Lorenz, Tinbergen and others as 'drives' with 'action-specific-energy' which had to be dissipated by the performance of those behaviours; although generalized energy was also considered possible (Manning 1967). The build-up of such energy explained how 'displacement' behaviours occurred. If the behaviour with greatest drive were thwarted, or two conflicting behaviours were equally matched such that both inhibited the other from expression, the excess energy would be used up in the performance of another, seemingly irrelevant behaviour (Tinbergen 1952). As Hinde (1970) describes, Andrew, and Van Iersol and Bol

showed, independently, that manipulating factors for the displacement behaviour affected the nature and intensity of that behaviour. Thus, instead of the allochthonous situation proposed by Kortland, with the displacement behaviour being energized by the flowing over of drive from the conflicting behaviours; displacement behaviours were autochthonous, driven by the levels of their own energies. The new proposition was that the displacement behaviour was disinhibited when the two behaviours with highest motivation mutually inhibited one another, and became unable to maintain inhibition over the third, displacement, behaviour.

The concepts of drives and energy were abandoned as inadequate and confusing (Hinde 1970; McFarland 1985). In 1966, McFarland explained displacement behaviours in terms of disinhibition mechanisms, showing why they should follow thwarted as well as conflicting behaviours (McFarland 1985). A mismatch between expectation and actual feedback, when a behaviour failed to be performed, caused a switch in attention, and the next-in-priority behaviour (the displacement behaviour) would be disinhibited. The displacement behaviour, being inappropriately performed, would also produce a mismatch with expectation, and so would be ineffectual and attention would quickly revert to the original behaviour.

McFarland showed in 1970 that the disinhibition hypothesis could be generalized to normal behaviour sequences in which neither thwarting nor conflict occurred. He created operational definitions of motivational

competition (McFarland 1985):

"A changeover due to competition can in practice be recognized when a change in the level of causal factors for a second-in-priority activity results in an alteration in the temporal position of the occurrence of that activity."

and of disinhibition:

"The time of occurrence of a disinhibited activity is independent of the level of causal factors relevant to that activity."

When a behaviour sequence occurs by disinhibition the animal is said to be timesharing, the sequence of activities being performed in a manner analagous to that used in computer timesharing. Timesharing can be recognized as a description of a behaviour sequence when the dominant controlling behaviour disinhibits the subdominant behaviour and then re-establishes itself by competition as its own motivational tendencies arise again.

Timesharing between two behaviours is usually looked at in respect of activities consisting of non-overlapping, exclusive actions (McFarland and Sibly 1975). In Chapter 8, I look at feeding and vigilance in a slightly different way. There is an action, 'chewing' which a rabbit can perform, combining feeding and vigilance. Chewing appears to be a 'permissive' behaviour which allows scanning to be slotted into the grazing sequence without impairing feeding. In Chapter 8, various experiments manipulated motivational levels of fear, and levels of availability of food, in order to investigate the interaction between feeding and vigilance. Whether high fear levels influenced the length of food selected and whether long food pieces affected the levels of vigilance were both studied. Timesharing is

considered as a useful definition for describing these behaviour sequences.

The social structure of two rabbit populations are described in Chapters 3-5. Particularly tested was whether rabbits were as gregarious as some other studies have assumed. Distributions of rabbits and of their warrens were studied, the mating system was investigated and relationships between same-sexed rabbits were worked out. Social structure was related to kinship levels as elucidated by blood-analysis in Chapter 9. The effects of conspecifics on vigilance levels during feeding were investigated by observation and experiment, described in Chapter 7. Chapters 6 and 8 look into the patterning of feeding and vigilance behaviours, and consider their interrelationships. Observational and experimental data were used.

CHAPTER 2. METHODS

Section 2a. The field sites

Two field-sites were eventually selected. Preliminary investigations at Beckley, Didcot and Hill End Camp, all near Oxford, revealed small rabbit populations that were difficult to observe or were heavily controlled. These sites were nevertheless used in the winter of 1980-81, to practise techniques. Devastation of the Beckley population by myxomatosis in March 1981 prompted a move to Walney Island, off Barrow-in-Furness in Cumbria, where Oxford University were to use the field station in the South Nature Reserve for a final summer. Permission for the use of this site came from the Cumbria Naturalist Trust. The two subsequent field seasons of 1981-1982 and 1982-1983 were carried out at Hill End Camp, a nature reserve near Oxford administered by the Oxfordshire County Council for use by local schools.

Walney

Walney 'Island' is connected to the mainland by a causeway, covered over at high tide. There is also easy access to the island by a man-made bridge. The site was a 2.3ha area of duneland with typical dune vegetation which fell into distinct patch types:

i) bare sand

ii) dune covered by marram grass (*Arenaria maritima*)

iii) plains of nettle (Urtica dioica), ragwort (Senecio jacobaea) and bracken (Pteridium aquilinum)

iv) dune covered by short turf grasses

A hide used by A. Hart to observe the herring gull (Larus argentatus) colony, was situated at the centre of the observed area. It was convenient to divide the area into four sections delimited by lines running at 45° to the North-South axis, and meeting at the hide. These Areas were North (0.6ha visible from the hide), South (0.4ha), West (0.9ha) and East (0.4ha). Marram grass was the rarest patch type, found only in East. Small patches of nettle, ragwort and fern were common in all Areas. Turfed dune covered the major parts of each Area, forming about 80% of the total surface area. Patches could be further characterized as occurring on sloping or flat dune.

Oxford

The site was of two fields abutting onto the Eynsham Road, five miles from the centre of Oxford. In the summer the pasture was grazed by bullocks.

The floral species present were surveyed and the fields were found to be of species-poor sward, dominated by Agrostis tenuis and Phleum grasses. Two species of Phleum were found, timothy (P.pratense) and catstail (P.nodosum). Other grasses present were yorkshire fog (Holcus lanatus), creeping fescue (Festuca rubra), cocksfoot (Dactylis glomerata) and perennial ryegrass (Lolium perenne).

Other plant species on the fields included spear

thistle (Cirsium vulgare), nettle (Urtica dioica), dandelion (Taraxacum officinale), marsh bedstraw (Gallium pelastra), red and white clovers (Trifolium pratense and T. repens), plantains, especially ribwort plantain (Plantago lanceolata), buttercup (Ranunculus), creeping cinquefoil (Potentilla reptans), selfheal (Prunella vulgaris), and ground ivy (Glechoma hederacea), as well as bryophytes. Hawthorn (Crataegus monogyna) hedges bounded the fields, and common ivy (Hedera helix) was found amongst them. Bramble (Rubus fruticosus) was very common in the hedges. By the roadside beyond the hedge, hogweed (Conium maculatum) grew in abundance. The hedges shielded banks of sand and mud where the rabbits constructed their burrows.

Mapping of study sites

Active warrens were identified before rabbit breeding commenced, by the presence of fur, faeces or freshly dug soil. Ferrets, used to catch the rabbits, revealed which holes were joined, by emerging from each entrance of contiguous tunnel-systems. A burrow-post was erected at the centre-point of the entrances to each warren. As more warrens appeared during the breeding season, so additional burrow-posts were erected.

At the end of the season at Walney, distances between each burrow-post and its nearest three were measured. These data were used directly for analyses of burrow distribution, described in Chapter 3. Sketch-maps were drawn to show the topographical relationships between posts and patch types.

Each Area was treated separately. Gridded maps were constructed from these data, with each post uniquely positioned by its distance and approximate direction from its neighbour posts (Figs 3.1-3.2). X Y coordinates were assigned to each post.

At Oxford, the fields were approximately rectangular and the hedges were used as the bases of a grid. Marker posts were set up every 4m, along the hedgerows and at right angles to it to a distance of 20m into the fields. Burrows, found only along the hedgerows, were assigned X Y coordinates (Fig 3.3), used in analyses in Chapter 3.

Environmental parameters

A weather station at the Walney site made frequent weather recordings. Since analysis of Walney data was limited, weather data were not used.

At Oxford, daily records were made of the highest temperature, the total precipitation and the highest wind-speed in each 24 hours. Measurements were taken at mid-day when cloud cover was also assessed in eighths of the sky clouded over. Weather parameters were used in the multiple regressions of Chapter 7, (variables TEMP, PPT, CLOUD, WIND).

Section 2b. Handling rabbits

Catching

A variety of techniques for catching rabbits (in order to tag them) were tested. At Beckley and Hill End Camp, experiments were done with projectile nets fired by elastic or by compressed air; and with long nets which were either released behind the grazing rabbits or else into which the rabbits were driven. Experiments at Walney with gull-traps and stop-snares were as unsuccessful as the rest of this battery of methods, by which, in total, one rabbit was caught. Other, less promising, methods such as catching rabbits in butterfly nets or creating traps in the burrows of grazing rabbits by stopping the burrows with brambles (R.C. Soriguer pers comm) were not attempted. Ferreting, and trapping with specialised traps proved to be very successful.

Ferreting was restricted to outside the breeding season, i.e. between October and January, because young in the nests were too vulnerable. Each entrance to a contiguous warren system was covered with a purse-net. This was lain loosely over the hole and pegged in firmly above it. A single ferret was introduced under a net and the ferreters retired out of sight and remained quiet. If the warren contained rabbits, one would normally emerge very rapidly and the purse-net tighten around it. Rabbit and net were put into a bag, a new net was put over the hole, and the ferret was re-introduced. The process continued until

all the rabbits had been cleared, at which stage the ferret refused to re-enter the warren, or passaged from entrance to entrance very quickly.

Ferreting was generally very successful with all rabbits being chased from a warren in about 20 mins (the warrens were small). Occasionally a rabbit would not come up or the ferret would succeed in damaging one. Ferrets could be instantaneously recalled from a warren by dangling fresh liver at the entrance. Of 80 rabbits caught by ferreting, I destroyed two that had been badly damaged; perhaps two more were killed or severely maimed underground.

No muzzles, lines or radio-collars were attached to the ferrets, since I had no trouble with their re-emergence. Ferreting was sometimes in complicated burrow systems or around tree-roots where lines were likely to snag or catch. Muzzles do not stay on very well. Naive ferrets worked the best, since they were least capable of seizing rabbits.

Ferreting tends to catch a female biassed sample (Cowan in press) and this was particularly noticeable at Oxford. The bucks probably laid up in the scrub more and used the warrens less than did the does. At Walney ferreting took place when there was no ground cover, so it is likely that all the rabbits were using the warrens.

Since ferreting could be used to catch only adults, it was complemented by trapping, which succeeded in catching only juveniles. Treadle traps were made up. These had rectangular, wire-mesh sides, roof and ground (480mm long)

with a square, open entrance (230x230mm). The door, a metal plate hinged to the top of the entrance, was held up to the roof by a rod attached to the treadle, a metal plate lying at a slight angle to the ground. When the rabbit's foot pressed on the treadle the rod released the spring-loaded door which sprang shut. At the back of the trap the mesh sides were attached to a plate-metal box (320mm long), by two catches. The rabbit could hide in the box until it was collected; trap-checks were made twice-daily. Juveniles were generally quiescent enough that the wire mesh part of the trap could be unclipped and lifted off and the rabbit picked up and put in a bag.

Traps were usually baited with oats, fruit or vegetables, although P. Garson (pers. comm.) experimented with baits and found them unnecessary; the inquisitiveness alone of a juvenile rabbit will take it into the trap. Trapping never damaged the animals, but Cowan (1983) noted that it caused a considerable depression in weight gain.

The breeding season of rabbits at Walney started later than at Oxford and ferreting was carried out in April 1981. Trapping continued from April to July. At Oxford, ferreting was done each winter from 1980 to 1983, always ending by February. Rabbits were trapped from May to August in 1982.

By May 1981, when observations at Walney commenced, 29 adult rabbits and one juvenile had been marked; a further six adults and 71 juveniles were tagged in the course of the season. Assuming that untagged rabbits were sighted as frequently as tagged ones, there were an estimated 60

untagged adults over the four Areas at Walney. Behavioural observations were concentrated on rabbits close to the hide where recognizable-rabbit density was greater.

At Oxford, 33 adults had been marked by May 1982; six juveniles were marked as the season progressed. (A further 17 adults and four juveniles were caught 1982/83). Only 11 adults were in view of the hide during the 1982 observation season. This allowed easy individual recognition of untagged rabbits by their distinguishing characteristics.

Processing rabbits

There were two main aims to catching the rabbits. These were to mark them for individual recognition, and to take a blood sample for kinship studies.

The bagged rabbits were taken to the field laboratory (a caravan at Walney, a garage at Oxford) and body measurements made. The rabbits were very docile as long as their eyes were kept covered. Rabbit and bag were weighed from a Pesola spring balance and the weight of the bag subtracted. A pair of callipers were used to measure the length of the left foot and that of the right ear. Such measures can be used to assess the general health of the animal. The rabbit was sexed by inspection of the genitalia. Although rabbits are easy to sex at birth (Adams, pers. comm.) the sexes quickly come to look similar. At about 200g body-weight, sexes can again be differentiated: the male's penis has grown out as a column whereas the female's vulva is split down to the base at the

rear end. The age of the rabbit was assessed as under or over nine months by feeling for apophyseal fusion in a hind leg (Watson and Tyndale-Biscoe 1953). Females were palpated to assess whether they were pregnant. Date and place of capture were recorded for each rabbit with the above measurements.

Blood can be taken quickly and easily from rabbits by cardiac puncture (W. Van der Loo, pers. comm.) but it was considered too high-risk a method for these small populations, so blood was taken from the ear.

Samples of up to 5ml of blood were taken from adult rabbits, up to 1ml from juveniles. Each sample was mixed with 0.2ml sodium citrate (an anti-coagulant composed of 8g disodium hydrogen citrate and 12g glucose, made up to 500ml with distilled water). The rabbit's head was held beneath a hot lamp and its ears warmed up. A small area on the back of the ear was shaved to expose the marginal vein running down the edge. Xylene was applied to the tip of the ear to encourage dilation of the vein. A nick was made across the vein with a fresh razor blade. Blood collected in a puddle at the shaved area and was sucked up into a needle and syringe. It was ensured that the blood mixed with the sodium citrate contained in the syringe. When sufficient blood had been taken the (carcinogenic) xylene was washed thoroughly from the tip of the ear with cold water. The nick in the vein was held closed with dry cotton wool until it ceased to let out blood. The blood sample was carefully dispensed into a labelled tube and put on ice for further

treatment within twelve hours.

Various methods of marking rabbits had been considered such as tattooing the inside of the ear, shaving or dying the fur, and freeze-branding. To enable quick recognition of visible rabbits these methods were not the best, radiotransmitters and betalights were unnecessary, and eartagging was the simplest solution (Wallage-Drees pers. comm; Cowan 1983).

Dalton's Rototags were used. Each was of two strips of plastic, 35x9x2mm, a male one sporting a spike at one end, 17mm long and 5mm in diameter, and a female one with a recipient hole. The tags were put into pinchers and positioned one each side of the rabbit's ear, the female tag on the outside. The male tag was quickly pinched through the ear above the cartilagenous ridge and to the outside of the artery. Female rabbits were tagged in the left ear and males in the right.

There were eleven different colours of Rototag, although only nine of these were easily enough distinguished to be used. There were 72 combinations of tag colour and position for each sex of rabbit.

For young rabbits under 500g in weight, Dalton's Minitags were used since Rototags were too large and heavy. Minitags were only 20x5x1mm with a spike on the male tag 7mm long and 2mm diameter. The colours were less bright and distinct than those of the Rototag so numbers were embossed on the male tags. These were very useful, particularly if only the male tag was visible. It would have been

advantageous to have had numbers embossed on Rototags as well.

Recaptured rabbits were simply re-measured. If they had been caught below and then above the critical weight, their Minitags were replaced with Rototags and their blood was taken a second time. This was because their immunoglobulins would have changed from maternal antibodies to their own type.

After processing, and when the nick in its vein had closed up, the rabbit was released. Rabbits were returned to the holes from whence they had been ferreted, (or if caught in traps, they would be taken to the hole nearest to the trap). The head of the rabbit was aimed well-down the hole, so that it would bolt down it, rather than off across the site.

Preliminary processing of blood

On return to the laboratory, the tubes of blood were centrifuged for ten minutes and the top layer of plasma drawn off from the red-blood cell layer and dispensed into two or three separate labelled tubes. One sample of plasma was to be used for immunoglobulin analyses, and the remaining one or two for electrophoretic analyses. For the latter, it was better to have more than one sample since thawing and refreezing, necessitated by different analyses, causes deterioration of the enzymes.

The red-blood cells were cleaned in phosphate buffered solution (PBS) which was added to them in the ratio of 5:1.

This was mixed by gentle shaking and the tubes were centrifuged for another ten minutes. The supernatant of dirty PBS was drawn off in a pipette, and the process repeated to leave clean red blood cells. An equal volume of distilled water was added to the red blood and the mixture vigorously shaken. Osmosis of the water into the cells caused them to lyse and a clear red blood solution resulted. This was decanted into one or two labelled tubes. The red blood was only to be used for electrophoretic analyses, and again, more than one sample per rabbit was preferable.

Plasma and red-blood samples were frozen immediately at -20°C (at Walney the freezer was less efficient and the temperature was -10°C). They could be stored in this state indefinitely.

Transporting the blood samples

It was essential, particularly for the electrophoretic analysis, that blood samples should be kept frozen. This was not a problem with the Oxford samples, as blood was processed at the Zoology Department. Dry ice was needed to transport blood from Walney to Oxford. This was kept cool in a thermos flask into which the blood samples were inserted.

The immunoglobulin analysis was done in Brussels, but fortunately it was less critical that the plasma should not thaw. It was carried across, well wrapped-up with dry ice, by travelling colleagues. Another method used was to freeze-dry the plasma samples. Cobalt chloride crystals

were added to the transporting box to absorb any moisture around the freeze-dried samples. The samples were reconstituted by adding water.

Details of the analyses of blood are given in Chapter 9.

Section 2c. Collecting behavioural data

Regime

Behavioural data were collected by observation at Walney, 25th April to 19th July 1981, and at Oxford, 3rd May to 27th August 1982. Experiments were carried out on the free-ranging rabbits at Oxford, 3rd May to 19th July 1983.

Different watching regimes were essayed at Walney:

April 25 - May 12:	Sporadic
May 13 - May 19:	Day divided into six three-hour blocks; alternate blocks watched, to cover all blocks in two days
May 20 - July 8:	Two watches per day:1400-1730hrs and 1900-2130hrs
July 9 - July 19:	One watch per day: 1700-2130.

The rationale behind these changes was that most rabbit activity occurred in the evenings, day-time watches yielded scanty data, and dawn was less productive than dusk. To minimize the disturbance caused to the rabbits by my movement to and from the hide, single, long hidewatches were made at the end of the season. In total, 294 observation hours were spread over 91 observation periods on 55 days; 29, 18, 29 and 15 observation periods for North, East, South and West respectively. One Area was watched during each period, and the same Area was not watched more than once a day.

Observation periods at Oxford were limited to evening watches of two-hours duration (1745-1945hrs). In the second week of the season, dawn watches were made instead (0530-0800) to check that conditions were not markedly different. In total 107 observation hours were spread over 55

observation periods on different days. The population was small enough that the whole site could be monitored during each observation period.

Instruments

Noctovist Mark II 8×30 binoculars were used to observe behaviour and assess distances. A Swift Mark II Zoomscope 60mm, 15×-60× telescope was employed to identify far-off rabbits or to monitor their behaviour. All data were recorded on a 'More' timed-event recorder (made by Observational Systems Inc. Seattle WA). This had six 'control' buttons for presenting and editing data on its display panel, and for dumping and loading data by interface with a cassette-recorder or computer. Continuous timed records of events were recorded on the numbered keys 0-9, in codes of varying numbers of digits: the end of a code was signalled by the 'break' key. Duration of an event was timed from the first key of a code to the first key of the next code. Eight latchswitches were used to record presence or absence of background parameters running concurrent to the main record. Each observation period was divided into sessions, started, ended, and labelled by session control keys. Data were held on the More until the battery was switched off, by which time data had been dumped onto cassette at Walney, for subsequent transfer to the PDP11 Digital computer at Oxford Zoology Department. Oxford data were dumped directly to computer.

Measures and Codes

The identities of eartagged rabbits were recorded as two-digit numbers (except from 7th July at Walney when numbers ran above 100 and the records had to be accordingly modified). Unrecognizable rabbits at both sites were recorded as adult (Code 98), subadult (Code 94) or juvenile (code 97) as assessed by their size and behaviour. For ease of reading I shall refer to these as A, S and J respectively. Throughout the thesis, identity-numbers for known does will be underlined, to distinguish them from bucks.

Rabbit lengths were used to estimate distances. The true distances between burrow-posts, obtained by measurement at Walney, were compared to the average estimated distances in rabbit lengths as made on three separate occasions. This showed the mean estimate of a rabbit length to be 40cm.

Positions of rabbits at Walney were recorded as the number of rabbit lengths from the nearest burrow post, in one of eight compass bearings set at 45° to one another. Positions were converted into X Y coordinates using one rabbit length equal to 40cm, and Pythagorus theorem to position them from the X Y coordinate of a burrow post.

Positions of rabbits at Oxford were read directly off the 4m grid. The grid was subdivided into tenths by eye, such that a rabbit could be positioned within 40cm (or one rabbit length).

Estimates of distance in single rabbit lengths were found to vary between occasions and deteriorated at larger

distances. Nevertheless, they were thought to be adequate to position a rabbit relative to a grid or burrow post, as the rabbit would never be far from one. However, the much larger distances between rabbits were also estimated, at speed, during behavioural observations. For these measures, distances were classified into broad ranges of numbers of estimated rabbit lengths (r), and distance codes were recorded:

Distance Code	r
0	0
1	1- 2
2	3- 5
3	6-10
4	11-15
5	16-30
6	31-50
7	>50

90 different rabbit behaviour patterns were identified. These were divided into Solitary behaviours such as feeding, which a rabbit did on its own, and Interaction behaviours such as chasing which involved another rabbit. Feeding and vigilance behaviours were categorized from the Solitary behaviours, and these, as well as Interaction behaviours, were used in analyses. They are described in the relevant chapters.

Rabbit identities, positions, distances and behaviours were recorded on the numbered keys. Various functions were tried out for the latchswitches. They were eventually (from the 6th June 1981) found to be most useful to encode the degree of cover of a subject animal (variable GRALEN in Chapter 7). The rabbit was, for each latchswitch:

'1' in short turf or on bare ground
'2' with its legs and lower body covered
'3' with its head and shoulders visible
'4' completely covered, visible by the tips of its ears

Latchswitches 5-8 were used for vegetation type at Walney and for weather and disturbance parameters at Oxford. The only ones of these to be used in analyses were for the Oxford data:

'5' human disturbance (variable DISTUR, Chapter 7)
'6' cow disturbance (variable COWS, Chapter 7)

Human disturbance was registered when walkers or slow cyclists passed by on the road, whistling or talking. Cow disturbance was registered if the bullocks came within 50m of the rabbits. They would sometimes chase rabbits.

Records

Scan samples were made every 30 minutes for the whole period at Walney and for the first fortnight at Oxford. The Area being watched at Walney, or the whole of the site within the field of vision at Oxford (Figs 3.1-3.3) were scanned and the position and identity of every rabbit seen, whether or not recognizable, were recorded. A scan-sample was a discrete session on the More and used only the numbered keys, to code at Walney in the form ABCDEFG, where AB were the two digits of the rabbit's number, CD the estimated number of rabbit lengths and E the direction of the rabbit from FG the burrow post. A mean of 5.9 scan samples (SD=3.5) were made in each Walney observation period. At Oxford HIJKLMNO were HI, the number of the rabbit, JKL, its X coordinate and MNO its Y coordinate.

Although the More timed these data, time was not used, and scans were taken as being instantaneous.

Focal animal samples, timed recordings of everything a rabbit did, were made at both sites. At Walney, such samples continued for 15 minutes or until the animal disappeared, whichever were the shorter. At Oxford they continued for as long as the subject were visible. Subjects were chosen at both sites as that one of the observable rabbits for which least data were currently available. A number of different recording methods of focal animal samples were tried out at Walney until May 24th, when one was found that yielded the most information with the least inaccuracy. All previous data were transformed to this format, which was the format used at Oxford. Each focal animal sample made up a More session and was labelled with the identity of the subject and the date and time of onset of the session. Every Solitary behaviour was recorded as a two-digit code. Every Interaction behaviour was recorded as a four digit code PQRS where PQ was the behaviour of the subject and RS the identity of the interactant. Every new position of the subject was recorded as the five-digit CDEFG at Walney (as above), or the six-digit JKLMNO at Oxford (as above). Every new distance to another rabbit was recorded as three digits: TUV where T was the distance class and UV the identity of the other rabbit. When positions, distances or the incidental behaviour of interactants (such as 'subject is approached by interactant') were being recorded, the ongoing behaviour of the rabbit was the one that

preceded these data. Other rabbits and interactants included unrecognizable rabbits, but the subject rabbit was always a known one.

At Oxford it was unnecessary to interrupt focal animal sampling with scan samples since the population was small enough that positions of rabbits, relative to one another, could be monitored. Thus the distance of every other rabbit to the focal animal was continuously recorded during the focal animal sample. The pilot study of behaviour sequences at Walney prompted much finer recording of longer sequences at Oxford, hence the change to longer focal animal samples. These Oxford samples were analysed for vigilance and feeding studies in Chapters 6 and 7. Interaction behaviour data from Oxford and Walney are described in Chapters 4 and 5. Scan-sample information was also required at these stages and 'scan-samples' were constructed from the Oxford data for the period after the first fortnight. Half-hourly points were taken from each observation evening and the identities of rabbits present and absent obtained from the focal animal data. This gave the absolute positions of the focal animal only.

CHAPTER 3. HOW GREGARIOUS ARE RABBITS?

Sociality is usually explained on the basis of ultimate functions including enhanced food finding, avoidance of predation, and increased ability to modify the environment. Alternatively, group-living might offer no advantages *per se*, but simply result from exploitation of a patchy resource. The rabbit is a good species in which to study the causation of group-living, since social structure is extremely variable. Cowan (1983) has suggested that group-living is not itself advantageous, but that it is the result of rabbits aggregating in areas of high warren availability.

In Sections 3a-3c, I investigate the spatial distribution of warrens and spatial and temporal distribution of their occupants chiefly at Walney but also at Oxford. Most of the warrens (interconnecting tunnel systems), at both sites, were very small with no more than two entrances. I shall refer to these as Burrows to distinguish them from larger multi-entranced warrens. The scale over which the distributions of rabbits and Burrows are measured is critical for tests of Cowan's hypothesis. It is trivially obvious that rabbits and their Burrows must be clumped in space since they have restrictive habitat requirements, while rabbits' emergence times must be clumped in time since they are primarily nocturnal (Stodart and Myers 1964). Therefore the hypothesis must be tested using scales of time and space which are biologically relevant. I have attempted to define these scales such that conditions

within them would be homogeneous, since this would eliminate the environmental causes of grouping. Furthermore, independent data points were needed for the analyses of rabbit distributions, and methods for obtaining these are described.

Section 3a. Burrow distribution

Methods

Burrow distributions were measured at two levels:
1) At the heterogeneous ecosystem level, namely over each of the four Areas of observed dune at Walney, and along the whole length of hedgerow at Oxford.
2) At the homogeneous patch level. At Walney, the homogeneous patch type chosen for analysis was the flat turfed-dune, since it was the most prevalent type and it contained only Burrows (the sloping turfed dune supported some larger warrens). Each patch was demarcated as the maximum rectangular area of flat turfed-dune that fitted in between other patch types and changes in topography (i.e. hills), and contained a minimum of six Burrows. Three such patches were found to the North, West and East; severally designated NPCH (of 300m^2), WPCH (750m^2), EPCH (997m^2). At Oxford homogeneous patches could not easily be defined, and analysis was not made at this level. Figs 3.1-3.3 show the distributions of warrens at each site, for Areas North, South, East and West at Walney, and for the Oxford site. The homogeneous patches are indicated for the relevant Areas.

Distributions of Burrows at Walney were compared with those expected from random distributions using the nearest neighbour technique (Clark and Evans, 1954). The ratio, R, of the observed mean nearest neighbour distance to the expected mean was calculated from the original data of

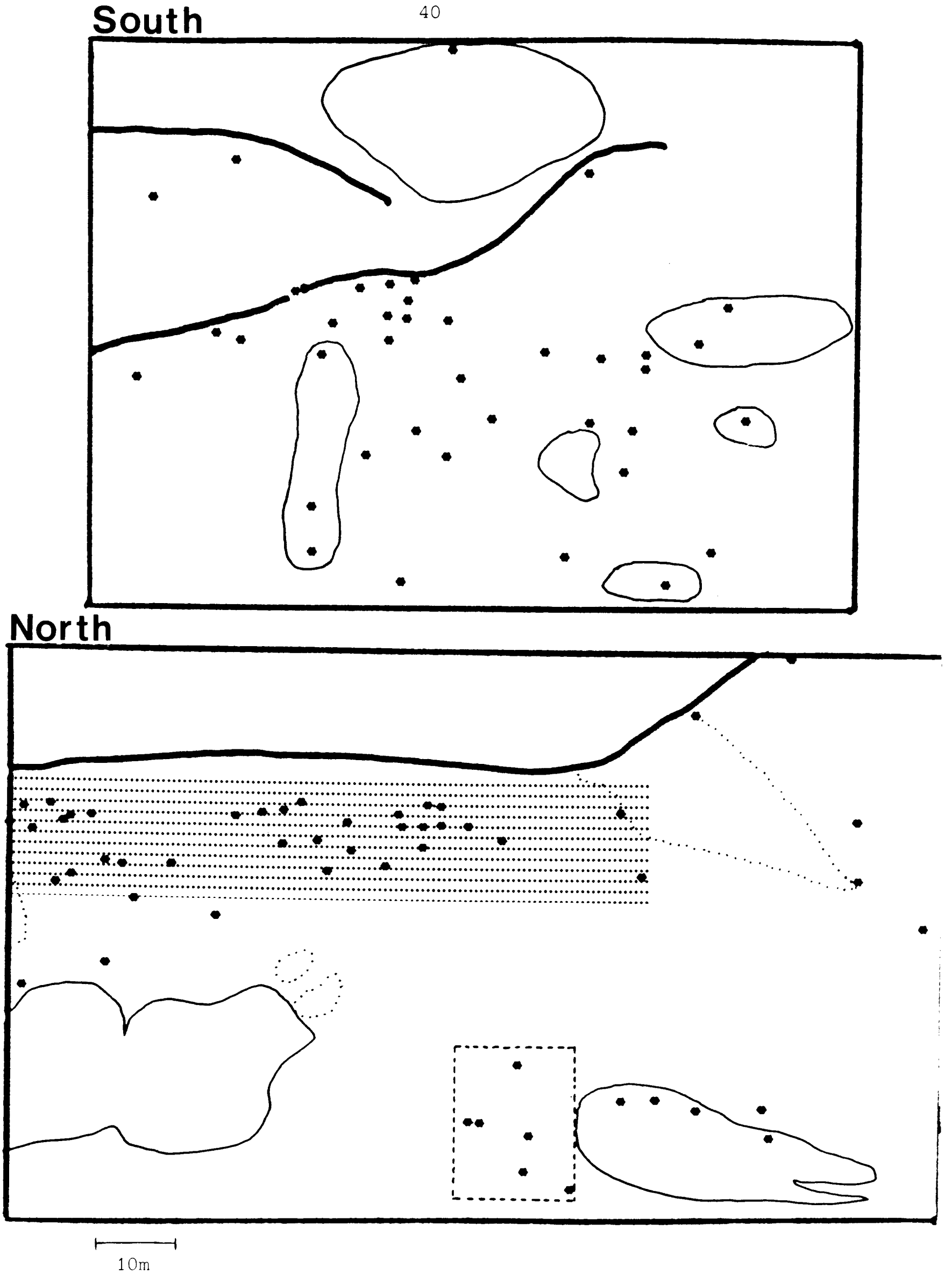

Fig 3.1. Positions of Burrows at Walney Areas South and North.
= Burrow. = hill ridge. = bracken patch. = sand patch.
= selected flat, homogeneous patch. = North Patch

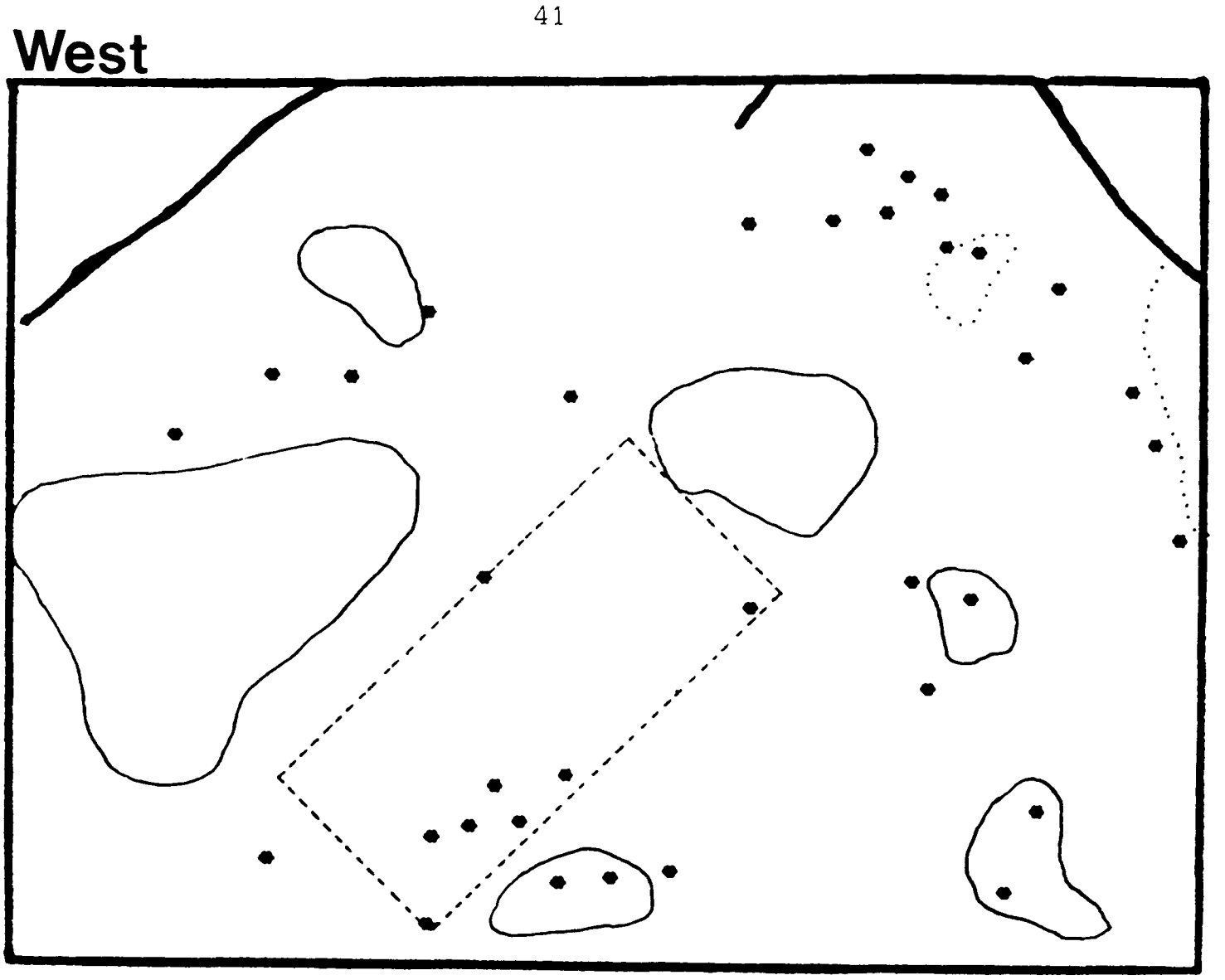

Fig 3.2. Positions of Burrows at Walney Areas West and East.
• = Burrow. ▬ = hill ridge. ⬭ = bracken patch. ⋰⋱ = sand patch.
▭ = selected flat, homogeneous patch.

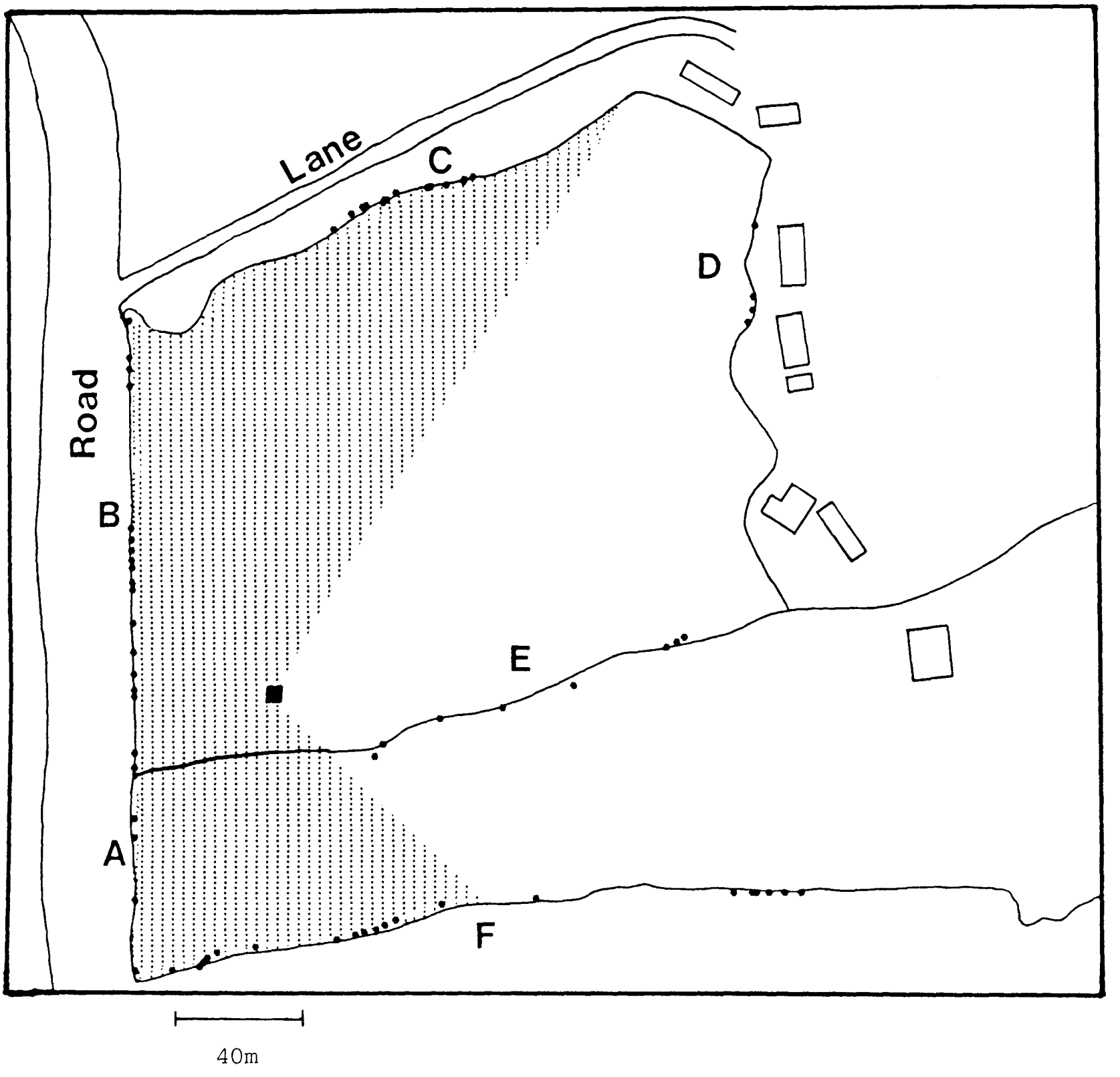

Fig 3.3. Positions of Burrows at Oxford.
• = Burrow. ▭ = building. ⌒ = ditches at field edge. ■ = hide. ⁞⁞⁞ = field of vision from the hide. A to F label regions of the ditches.

distances between closest posts, and the density of posts on the ground. The standardised deviate, c, gave the significance of the departure of R from unity. If R<1, c is negative and clumping is indicated, if R>1, c is positive, and overdispersal is indicated. Since the Burrows were effectively distributed along one dimension at Oxford, the analysis was done by counting numbers of Burrows in 20m samples of hedgerow, and comparing these to a Poisson distribution.

Results

Burrows were randomly distributed over the South, East and West Areas of dune at Walney. On Area North they were clumped in distribution. At the homogeneous patch level, Burrows were evenly distributed at very low significance levels for two patches, and almost to significance for the third. Table 3.1 describes these results. Burrows at Oxford were found to be clumped (P<0.01).

Table 3.1. Burrow distributions at Walney. Number of Burrows (N), total area (A), range of inter-Burrow distances for nearest neighbour Burrows, R, c and 2-tailed P for each large scale Area and for the three small scale patches.

	N	area(m2)	range(m)	R	c	P
Areas						
North	55	8840	1.5-14.6	0.747	-3.49	0.0003
South	39	5600	1.7-22.7	1.071	0.84	0.4010
East	24	4200	4.1-16.5	1.053	0.49	0.6242
West	35	5230	2.8-18.5	0.995	-0.05	0.9602
Patches						
NPCH	6	300	1.5- 8.2	1.381	1.78	0.0750
EPCH	11	997	4.1-16.5	1.681	4.32	0.0000
WPCH	8	750	3.2-20.0	1.650	3.52	0.0005

Section 3b. Temporal distribution of rabbits

Methods

Scan-samples were used for this analysis, which required that they be independent. Runs tests were done to test the null hypothesis that, within each evening, the serial distribution of a rabbit's presences (+) and absences (-) in scans was random. Separate tests were done for the most commonly seen adults at Walney: two females and four males from Area North.

The runs tests were done as exact tests for each rabbit, obtaining an expected E(T) and observed T number of consecutive +'s, with the variance V(T) (Cox, 1970). Summing across days for each rabbit, a normal standardised deviate c was obtained, such that

$$c = \frac{\Sigma T - \Sigma E(T)}{\sqrt{\Sigma V(T)}}$$

Table 3.2 details the results for each rabbit.

c-values were summarised across rabbits as $(\Sigma c/\sqrt{n})$, where n was the number of rabbits); this gave a highly

Table 3.2. Non independence of scan-samples. The identities (ID) of the six frequently observed rabbits (females underlined) with the N number of evenings on which the rabbit was present, and from which c-values were obtained (normal standardised deviates).

ID	N	c
6	15	1.83
47	15	1.93
4	15	3.55
7	11	1.47
8	11	-0.44
56	9	1.89

significant z-score of 4.44, serial dependence of presence/absence data being at the P<0.0001 level.

It was not possible to find the stage at which scans became independent for presence/absence data; abstracting further-apart scans and testing for independence might eventually fail to reveal lack of independence, but the cause of failure might be from too few data points. In consequence one data point, the data from a single scan sample, was used from each evening. It was assumed that each evening was independent, not least because before and after each observation period the rabbits scattered at my movement through the site.

For the temporal analysis it was impossible to define truly homogeneous stretches of time, composed of samples from different evenings, as environmental and social changes occurred with time of year. It was decided to use the same time each evening to approximate to homogeneity. Samples comprised counts of the numbers of all rabbits, tagged and untagged, present at 2030 hours for each Walney evening which encompassed such a scan; and at 1930 hours for the Oxford site. Only adult rabbits were used in this analysis. The appearance of new juveniles throughout the season would have added greater variance as the numbers of subjects increased.

These distributions of counts of rabbits for each respective Area and for Oxford were compared to Poisson distributions. The ratio I of the variance to the mean, was calculated. χ^2 was derived as I(N-1), where N was the

number of counts.

Results

The distribution of numbers of rabbits present at the same time on different evenings was random for each Walney Area as shown in Table 3.3. At Oxford the distribution of counts of rabbits showed an even spread, but there were too few rabbits to draw conclusions from these results. If a clumped distribution had resulted from these analyses, it would have indicated a preference for certain sizes of groups to occur, instead there seemed to be mutual independence of times spent out by rabbits.

Table 3.3. Rabbit distribution in time. Areas, number of evenings (N) over which data were analysed, range of numbers of animals present in counts, the values of I, χ^2 and 2-tailed P.

Areas	N	Range	I	χ^2	P
North	14	0-7	1.194	15.52	0.6595
South	15	2-10	1.041	14.58	0.8715
East	13	2-11	1.296	15.55	0.5328
West	6	0-9	1.800	9.00	0.2386
Oxford	**44**	**1-6**	**0.568**	**24.44**	**0.0130**

Section 3c. Spatial distribution of rabbits

Methods

Scan-samples were used to analyse spatial distribution of rabbits. Successive scans could not be used as independent data points, unless the positions of rabbits were independent from one scan to the next. The Walney data were tested to discover if a rabbit was closer in one scan to its position in the next than to its position in a scan on another evening.

A rabbit was randomly selected from those rabbits seen above ground in a randomly-chosen scan. If it was not present in the following scan (30mins later), the attempt was abandoned, and a different rabbit chosen. Otherwise, the distance between its position in the first and in the second scan was measured and paired with the distance between its position in the first scan and that in a third scan. This third scan was randomly chosen from the set of scans on other evenings in which that rabbit was present. Thirty-one such samples of pairs of distances were obtained from different tagged rabbits, and the two sets of samples were compared using a paired sample t-test.

The two samples were different in a one-tailed test at the $P<0.05$ level, ($t=-2.35$ and $Df=30$), showing that serial scans were not independent for rabbit positions.

Distributions of rabbits in space were analysed at Walney on North Dune, a homogeneous patch of sloping turf-covered dune, selected for being a large planar surface of

80m x 14m on which positions of rabbits could be accurately determined (Fig 3.1). Only one scan was used from each observation period. For each evening that Area North had been watched, all those scans in which more than three rabbits were present on North Dune were selected, and one scan was picked, at random, from these. Nearest neighbour analysis tested the distribution of rabbits (tagged or not) in these scans and c-values were obtained for each scan. A z-score summarised the c-values by summing c and dividing by $\sqrt{N}$, where N was the number of scans tested.

Analysis of spatial distributions of rabbits would have been trivial at Oxford where the separate pairs lived in separate Burrow systems and were evidently not grouping together (Fig 4.3).

Results

Data from 14 separate scans of North Dune were analysed for spatial distribution of rabbits; these produced a z-score:

$$\frac{\Sigma c}{\sqrt{N}} = 4.607$$

The rabbits were spatially spread out, overdispersed with $P<0.0001$.

Section 3d. Discussion

Clumping of Burrows on a large scale could reflect environmental heterogeneity. Rogers (1981) found concentrations of rabbits and warrens on particular homogeneous patch-types (the high grassland) rather than a spread across the whole dune system of his Camargue site. Rabbits and warrens on the Coto Donana were clustered into those areas where the dunes interdigitated with the moist feeding grounds (Rogers and Myers 1979). Similarly, the clumping of Burrows on Area North was likely to be due to heterogeneity.

However the even spacing of Burrows on the turfed dunes at Walney cannot be explained by environmental heterogeneity, unless this patchiness showed a similarly even spacing, which seems implausible. Note that heterogeneity within patches deemed to be homogeneous, and mistakenly counting different entrances to warrens as discrete Burrows, both work against the hypothesis of even spacing by introducing spurious clustering. One possible explanation for even Burrow spacing could be the avoidance of structural collapse. However the ranges of nearest neighbour distances between Burrows were large (Table 3.1) which suggests that engineering constraints did not enforce the observed Burrow distribution.

The random distribution of rabbits in time, obtained at Walney, indicated mutual independence of surface periods by rabbits. Note that the failure of the data to meet the

strict requirements of homogeneity ought to introduce spurious clustering and work against such results. At Oxford, **numbers of rabbits out were evenly distributed.** The Walney rabbits exhibited spatial avoidance as a group despite the fact that associations can be detected for certain dyads as described in Chapter 4.

Despite the theoretical advantages to group-living, rabbits did not form groups either in space or time. This lack of grouping could have been a maladaptive response to an environment to which the rabbits had not evolved. They may have had no mechanism for promoting beneficial social cohesion in areas where warrens did not bring them into close proximity. However, the rabbit originated in the Mediterranean area, which abounds with such dune-habitats e.g. Rogers and Myers (1979) and it is possible that the observed lack of grouping is an evolutionary adaptation to those environments where warrens need not, or cannot, be built.

It could be argued that a population of rabbits found at such high density as at Walney could be described as a single large group. This might be true to some extent, with rabbits obtaining such advantages of grouping as anti-predator protection. However the overdispersal of rabbits found here argues against a basically gregarious nature in rabbits.

In some habitats multi-entranced warrens occur which are associated with social groupings of rabbits larger than those discovered here (Myers and Poole, 1959; Cowan, 1983).

Two types of hypothesis are available to explain these variations. Firstly, multi-entranced warrens may be advantageous in some habitats but not in others, large social groups forming in consequence. Secondly, sociality may be favoured in these habitats with larger groups constructing larger warrens. These hypotheses are not exclusive.

Multi-entranced warrens may provide better protection against predators and weather. In addition it may be easier to extend existing warrens in heavy or hard substrates, rather than initiating a new Burrow (Cowan, 1983). At Walney and Oxford, multi-entranced warrens were probably difficult to construct, with soil depth being a likely limiting factor. At Oxford waterlogging probably precluded warrens in the open fields. Small warrens were constructed along the hedgerow-bank in the dryer parts of heaped-up sand, and around tree-trunks; elsewhere the banks appeared to be too damp and shallow to support more than single Burrows. Massive warrens occurred at Oxford high up on the hill behind this site, where waterlogging and soil depth would not have constrained digging. At Walney, soil depth was limited on the flat areas where shingle underlay the sand less than one metre down (A. Hart, pers. comm.), and only on the sloping dunes could warrens be developed. The instability of the sand might have prevented large warrens from developing.

Rabbits that did not share warrens at Walney and Oxford did not form groups above ground. Their Burrows were

spread evenly across the homogeneous areas and rabbits showed no tendency to cluster in space or time. That they did not, indicates that the tight social groups observed in other studies are a result of sociality being imposed upon the population because of co-habitation.

CHAPTER 4. THE MATING SYSTEM

Different mating systems have been described for different rabbit populations, varying from monogamy to polygyny. In this chapter, the mating systems at both my sites are described.

Copulations were rarely observed and would not by themselves prove exclusivity of mating. A number of methods were used together, to provide evidence of likely mates on the basis of consortships. In Sections 4a and 4b potential mate pools of animals sharing spatial and temporal ranges are delimited. Sections 4c and 4d investigate which of these potential mates interacted and whether any showed unusual degrees of proximity. Care was taken at each stage to ensure that data points used in analyses were independent.

Section 4a. Sharing of spatial ranges

Methods

Each recognizable individual's average position for each observation period was calculated as its mean X Y coordinate across scan-samples within the period. This was necessary because individuals' positions were not independent between half-hour samples as shown in Section 3c. By this method, a single data point summarised the information from non-independent scan-samples. The set of these means over the whole season defined the animal's homerange. Thus the homerange was a set of X Y coordinates, one for each observation period in which that animal had been observed.

The separation between home-ranges of each dyad of rabbits to be tested was investigated using discriminant function analysis. The two independent variables were the X and Y coordinates of the two individuals' home ranges, with the individual identity acting as the grouping factor. Both X and Y were 'forced' in so that the resultant F-statistic showed how great the separation between the two groups of points was. The probability for rejecting the null hypothesis that the two rabbits shared their home range was set at P=0.001; this conservative approach was used to avoid Type I errors.

The local population at both sites was taken as being those recognizable rabbits spotted in more than four scans. From this, dyads tested at Walney were each male with each

female within an Area. Spatiotemporal overlap was only feasible between rabbits living within an Area. At Oxford, dyads were each male with each female where their ranges at least abutted. Figs 4.1-4.3 for Walney and Oxford, show the identity of each rabbit, each positioned on the maps at the overall mean X Y coordinate taken across the set of points making up the rabbit's homerange.

Results

At Walney, there were 23 tagged adults in the local population. With the females underlined these were, North: 2,4,6,7,8,9,47,56; East: 10,11,12,22,23,25; South: 5,16,17,18,19,20,21,22; West: 2,13,26. The boundary-dwelling rabbits 2 and 22 were both included in two adjoining Areas. Analyses for rabbits sharing a spatial range with 56 were confined to the period after 12.6.81 when he was tagged. At Oxford the rabbits were 10,23,24,25,31,33,34,35,36,37,39. Analyses for all Oxford rabbits were confined to the 41 observation periods before July 30th when buck 36's disappearance caused change and upheaval in the social system.

Table 4.1 details the results of discriminant analyses between dyad ranges, where a high F and low P-level indicate greater range separation. At Walney the number of males with which each female shared her range varied from 0 to 5 (mean 2.2) and only one male (22) appeared to share his range with two females rather than one. However at Oxford most females (four out of five) shared their ranges with

Table 4.1. Extent of spatial range separation for male-female dyads. The first degree of freedom is always 2, the second Df is shown; F-value and P level obtained from discriminant function analyses between X Y coordinates of ranges; for the four Walney Areas, and Oxford. Females listed horizontally, males, vertically. **Underlining shows those rabbits with ranges not separable at the P=0.001 level.**

Walney North

Female:		2			6			47	
Male	Df	F	P	Df	F	P	Df	F	P
4	20	21.9	<0.001	31	1.0	0.402	31	59.7	<0.001
7	16	26.0	<0.001	28	21.3	<0.001	27	1.7	0.209
8	14	119.5	<0.001	26	81.4	<0.001	25	1.1	0.359
9	12	91.0	<0.001	24	230.2	<0.001	23	35.7	<0.001
56	12	45.1	<0.001	24	62.6	<0.001	21	0.5	0.604

Walney West

Female		2			26	
Male	Df	F	P	Df	F	P
13	13	12.6	<0.001	14	124.0	<0.001

Walney East

Female		11	
Male	Df	F	P
10	20	4.3	0.028
12	20	0.8	0.457
22	14	2.5	0.129
23	12	1.3	0.317
25	12	3.7	0.057

Walney South

Female		19	
Male	Df	F	P
5	22	11.6	<0.001
16	10	3.5	0.076
17	29	32.6	<0.001
18	20	1.0	0.418
20	10	1.4	0.323
21	28	48.2	<0.001
22	12	5.0	0.027

Oxford

Female		23			10			24	
Male	Df	F	P	Df	F	P	Df	F	P
25	24	0.3	>0.75	37	62.9	<0.001	30	67.6	<0.001
36	24	52.0	<0.001	39	0.8	0.475	32	1.5	0.241
39	19	13.7	<0.001	35	14.6	<0.001	28	21.5	<0.001
34		-		36	74.3	<0.001	29	57.4	<0.001
37		-		29	130.2	<0.001	22	155.7	<0.001

Oxford

Female		33	
Male	Df	F	P
36	23	24.4	<0.001
39	19	39.1	<0.001
34	33	0.0	>0.75
37	20	7.1	<0.005

Female		31	
Male	Df	F	P
35	12	0.1	>0.75

only one male, with the exception of 33 who shared hers with two. Only one of the six Oxford males (36) shared his home range with two females rather than one. Note that the 'potential mate pools' determined by these analyses will tend to be too large due to Type II errors (insufficient evidence to reject false null hypothesis). However the presence of untagged rabbits at Walney raises the possibility that the estimate for that site are in fact underestimates.

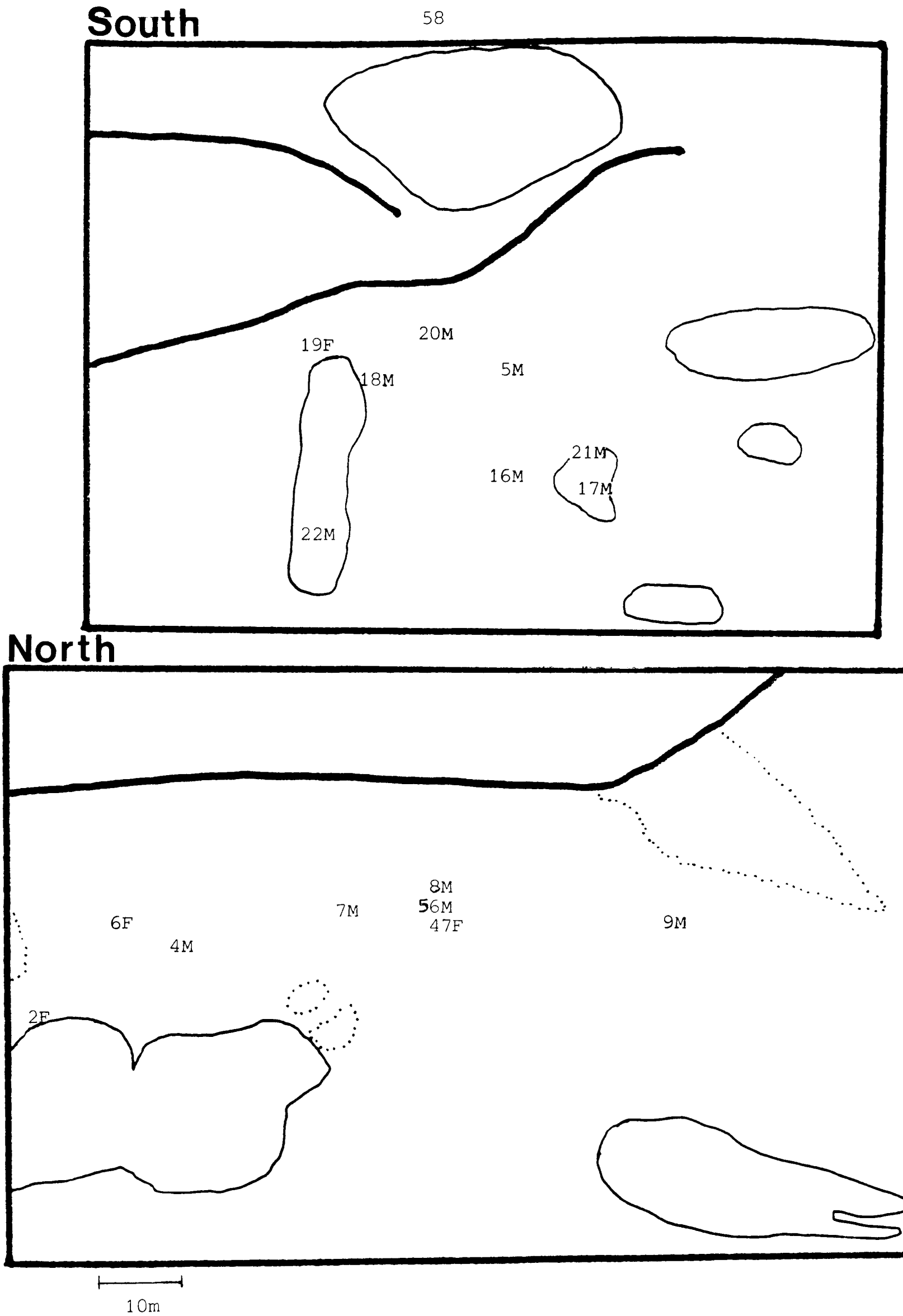

Fig 4.1. Mean position of adult tagged rabbits, Walney Areas South and North. '16' = rabbit identity. M = male. F = female. = hill ridge. = bracken patch. = sand patch.

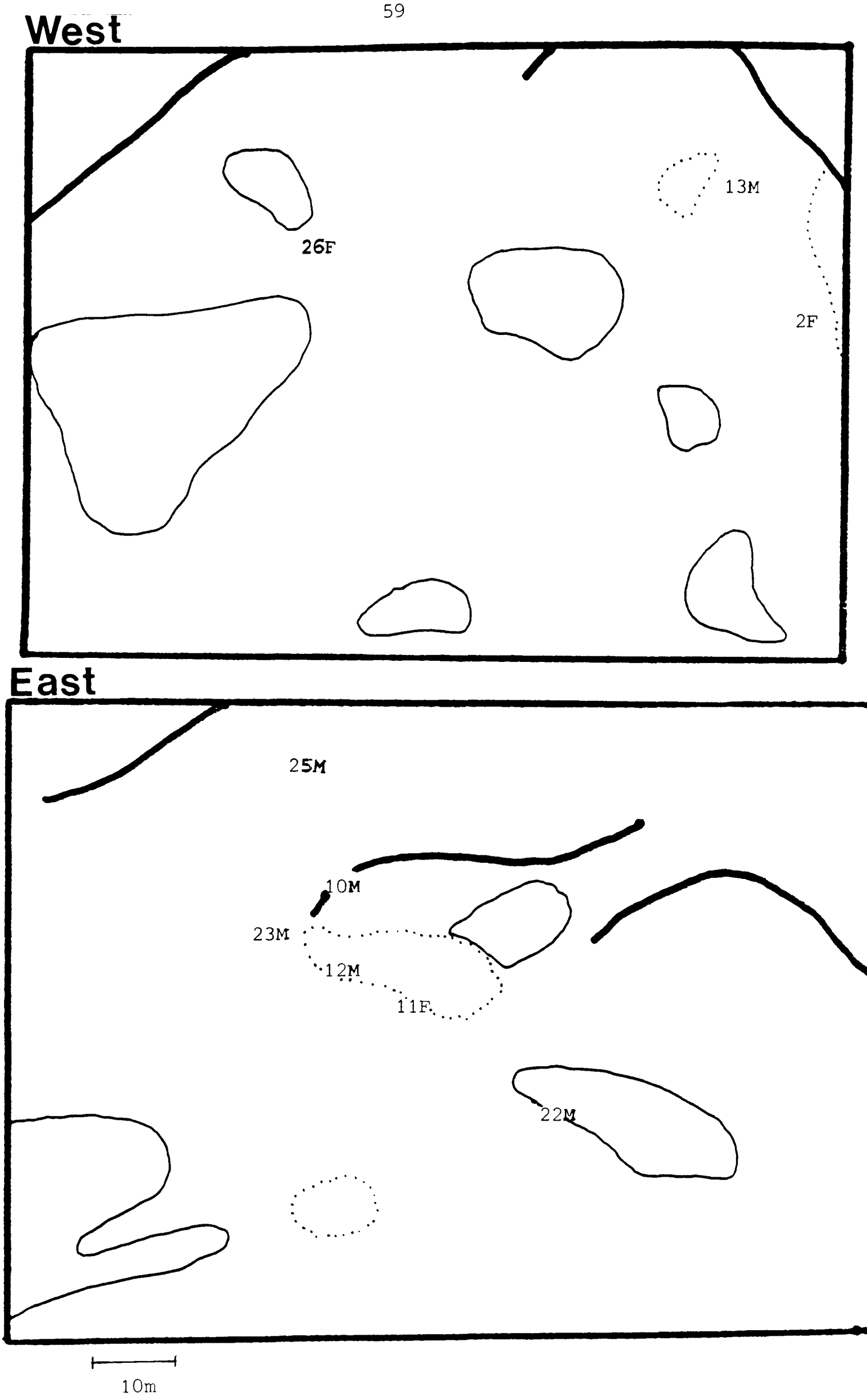

Fig 4.2. Mean positions of adult tagged rabbits, Walney Areas West and East. '26' = rabbit identity. M = male. F = female. = hill ridge. = bracken patch. = sand patch.

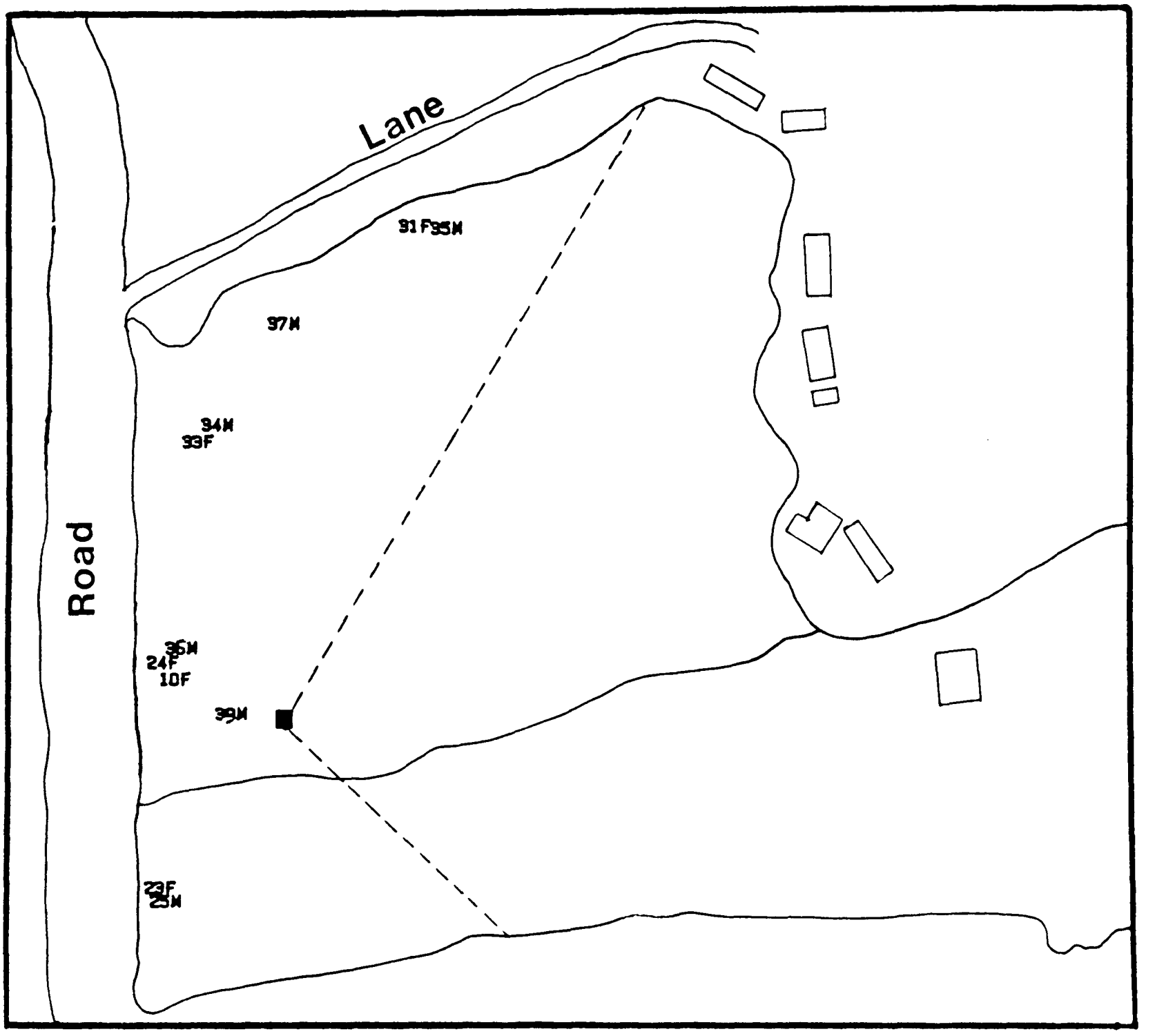

Fig 4.3. Mean positions of adult rabbits, Oxford.
'23' = rabbit identity. M = male. F = female.
▭ = building. = ditches at field edge.
■ = hide. - - - = limits of vision from hide.

Section 4b. Sharing of temporal ranges

Methods

These analyses were restricted to those dyads that could not be rejected as sharing the same spatial ranges at the 0.001 level. Two different methods were used to examine whether the members of such dyads tended to dissociate in time within and across evenings respectively. Data were restricted to those scans between the first and last scans that contained recognizable individuals. Both methods overcame the problem of the serial dependence of rabbit presence and absence data found in the Runs Test of Section 3b.

For within evening analysis, a 2×2 contingency table for each dyad, for each evening, was drawn up of their presence and absence data across scans.

	Rabbit 1 present	Rabbit 1 absent	
Rabbit 2 present	a	b	a+b=R
Rabbit 2 absent	c	d	
	a+c=A	b+d=B	

a+b+c+d=N

The exact test described by Cox (1970) was calculated for each contingency table as if independence held:

$$E(T;0) = BRN$$

$$Var(T;0) = \frac{ABR(N+R)}{N^2(N-1)}$$

T is the expected proportion of those occasions in which Rabbit 1 was absent that Rabbit 2 was present; the observed value of this is b. A statistic 'h' was calculated:

$$h = \frac{b-E(T;0)}{\sqrt{Var(T;0)}}$$

If independence of scan samples within evenings had held this statistic would have had zero mean and unit variance. Since it was known not to, the assumption was made that the non-independence within evenings was such that these statistics had zero mean but an unknown, common variance. If this variance turned out to be one, this would have suggested that independence had indeed held within evenings; whereas high values for this variance would have suggested great dependence between serial scans. But whichever was true, a t-test could be used to test the hypothesis that the mean was truly zero, using the estimated variance from the sample of evenings. If a rabbit was either present or absent throughout an evening the variance would be zero and no information could be obtained.

The null hypothesis was that h=0. t (for use in t-tests) was calculated as:

$$t = \frac{H-0}{\sqrt{(s^2/n)}}$$

where H was the mean of the h values, across the n evenings

of data for that dyad, and s^2 was the estimated variance of h. This t value had n-1 degrees of freedom, since the sample mean was estimated from the data.

The second method assessed association across evenings. Spearman rank correlations were run between the number of scans in which the first member of a dyad was seen on each evening and the number in which the second member was seen.

Results

Table 4.2. Temporal association. Each dyad is listed, female first, with the T, Df and 2-tailed P obtained from within evening analysis. Across-evening results give Spearman's rho, number of evenings (N), and 2-tailed P (or N.S. if P>0.05).

	Method 1			Method 2		
	Within evenings			Across evenings		
	t	Df	P	rho	N	P
Walney Dyads						
6 & 4	-1.305	12	N.S.	0.5135	29	<0.01
11 & 10	-0.103	6	N.S.	-0.0178	18	N.S.
11 & 12	-3.005	7	<0.05	0.6200	18	<0.01
11 & 22	-	-	-	-	-	-
11 & 23	-	-	-	0.2733	18	N.S.
11 & 25	-	-	-	-0.1779	18	N.S.
19 & 16	-0.574	4	N.S.	0.4671	29	<0.01
19 & 18	-4.273	3	<0.05	0.1199	29	N.S.
19 & 20	-3.732	1	N.S.	0.2396	29	N.S.
19 & 22	-	-	-	-0.1558	29	N.S.
47 & 7	0.694	7	N.S.	0.4035	21	<0.05
47 & 8	0.029	7	N.S.	0.2049	21	N.S.
47 & 56	-1.854	7	N.S.	0.5608	14	<0.01
Oxford dyads						
23 & 25	-5.243	3	<0.02	0.2064	41	N.S.
10 & 36	-2.661	17	<0.02	0.4521	41	<0.01
24 & 36	-1.805	17	<N.S.	0.3243	41	<0.05
33 & 37	0.000	1	N.S.	0.3873	41	<0.05
33 & 34	-5.386	7	<0.01	0.7014	41	<0.01
31 & 35	-4.189	3	<0.05	0.8241	41	<0.01

Table 4.2 shows that no dyads with shared spatial ranges were dissociating in time. However, many dyads showed significant temporal association (negative t values, or positive Spearman's rho). The 'potential mate pools' remain the same as from Section 4a.

For within evening analysis a negative value of t indicates association and a positive value indicates dissociation. This is because t is a measure of the difference of H from 0; and when H is greater than 0 (making t positive) it shows that the rabbits were not-together more often than expected; when less than 0 that they were not-together less often than expected.

Dissociation across evenings appears as a negative **Spearman's ρ, and association as a positive one.**

Section 4c. Interaction data

Methods

Table 4.3 lists 18 behaviours classified as Amatory Interaction behaviours (AIs). These were never observed between rabbits of the same sex. (Southern (1948) described rabbit behaviour patterns, and used the term 'Amatory Interactions', although the more specific classification here is my own).

Table 4.3. Amatory Interaction behaviour patterns.

Instigatory	Receiving
Touching Head	Touched on Head
Touching Body	Touched on Body
Licking	Licked
(this was usually about the ears and head)	
Soliciting allogrooming	Solicited to allogroom
(pushing the head beneath the other's, usually resulting in allogrooming)	
Attempting to mount	Attempted mounting of
Copulating	Copulated
Sniffing	Sniffed
Chinning	Chinned
(rubbing of chin-gland over the other's body; usually male to female)	

Mutual

Lying together in head contact
Huddling together in body contact

Amounts of its own total focal animal time that each recognizable adult rabbit spent in AIs with each other adult rabbit were summed; AIs with untagged interactants were pooled, for each subject.

Table 4.4. Durations of time spent in Amatory Interactions (AIs). Subject rabbits are listed, with their total focal animal observation times (Total Subject Time), and durations of time spent, within this, in AIs with each other rabbit. 'A' are untagged adults; known females are underlined.

Subject Rabbit	Object Rabbit	Total Subject Time	Time spent in AIs	% Time spent in AIs
Walney				
2	A	14052	9	0.06
6	4	11686	35	0.30
	A	"	20	0.17
11	12	15444	195	1.26
	A	"	40	0.26
19	18	7150	20	0.30
26	A	8153	31	0.38
47	56	6335	62	0.98
4	6	15892	51	0.32
	A	"	67	0.42
5	-	11686	0	0.00
7	47	8229	118	1.43
8	-	9088	0	0.00
9	-	5046	0	0.00
10	-	8168	0	0.00
12	11	10903	346	3.17
13	-	2810	0	0.00
16	-	895	0	0.00
17	A	23312	5	0.02
18	19	9720	25	0.26
20	-	1904	0	0.00
21	A	22912	314	1.37
22	A	5302	22	0.41
23	-	1224	0	0.00
25	-	1244	0	0.00
56	47	6841	176	2.57
Oxford				
10	36	42319	385	0.91
23	-	10023	0	0.00
24	36	20647	53	0.26
31	35	7021	104	1.48
33	34	14583	12	0.08
25	23	18185	24	0.13
34	33	20958	35	0.17
35	31	7903	38	0.00
36	10	41831	208	0.50
	24	"	96	0.23
37	-	6903	0	0.00
39	10	21609	8	0.04

Results

Table 4.4 summarises the AIs observed for each recognizable adult at Walney and Oxford. Note that the maximum proportion of time spent in AIs was only 3.2% (Rabbit 12, all with Rabbit 11).

At Walney nine of the 17 males had no AIs with any tagged or untagged rabbits. Three males and two of the six females had AIs with untagged individuals only. This left nine tagged adults which had AIs with one another. These rabbits not only confined their AIs to other tagged rabbits (56 to 47, 7 to 47, 47 to 56, 12 to 11, 18 to 19, 19 to 18); but also confined them to just one each (except 47 interacting with 7 and 56).

Despite the obfuscating presence of untagged rabbits the system could be seen not to be promiscuous. Monogamous consortships could be identified within the large available mate pools, although there was probably polygamy occurring to a limited extent.

At Oxford most rabbits had AIs with only one member of the opposite sex. Buck 37 had no AIs with 33 despite appearing to share her spatio-temporal range. 33 shared with 34 also, and with him she did have AI's. Although 36 had AIs with both 10 and 24, he devoted twice as much attention to 10.

Section 4d. Spatiotemporal association

Methods

Associations within dyads that had not been found to dissociate in space or time were tested using proximity data. A t-test compared the set of distances between two rabbits when both were present in a scan to the distances between the first rabbit in a scan from which the second rabbit was absent, and the second rabbit in a different scan from which the first was absent. For each data set, only one scan per evening was used, to preserve independence. For the second data set, scans were randomly matched. Dyads that were seldom together could not be analysed, since the data were too few.

Results

Table 4.5 summarises the information from earlier sections, on Amatory Interactions and on spatial and temporal range overlap; indicating if there was significant association for overlap in time. It also presents the results of proximity tests within dyads at Walney and Oxford.

Consorts (dyads showing Amatory Interactions) were found to associate, whereas non-consorts, although sharing spatio-temporal ranges, did not. Furthermore, ranking by P-levels the extent of spatial and temporal range overlap of each potential dyad for each female always ranked her chief male consort first (the one with which she had had most

AIs). 36 (at Oxford) was the only buck with two overlapping females. Doe 10, his chief consort, ranked higher than 24 for spatial and temporal overlap with the buck.

Table 4.5. Association by proximity and summary of spatio-temporal range overlap. Dyads (female first) that shared spatio-temporal ranges, prefixed '+' if they had Amatory Interactions; 1-tailed P level of association by proximity test; ranking of males for degree of temporal and spatial range overlap with each female: ranks asterisked if the temporal associations were significant *=P<0.05, **=P<0.01. Does 10 and 24 at Oxford ranked for degree of overlap with buck 36.

	P of assoc by pro-ximity	Rank of within evening assoc	Rank of across evening assoc	Rank of spatial range-sharing
Walney				
+ 6& 4	0.056	1	1*	1
+47&56	0.0035	1	1**	1
+47& 7	0.0045	3	2*	3
47& 8	0.25	2	3	2
11&10	0.180	2	2	2
+11&12	0.038	1*	1**	1
+19&18	0.025	1*	2	1
19&20	0.289	2	1	2
Oxford				
+23&25	0.005	1	1*	1
+31&35	0.006	1*	1**	1
+10&36	0.0002	1*	1**	1
+24&36	0.005	2	2*	2
+33&34	0.004	1**	1**	1
33&37	0.32	2	2*	2

Section 4e. Discussion

At Walney at least some individuals of both sexes shared their home ranges with more than one member of the opposite sex. Most bucks did not have Amatory Interactions with does and those that did interacted with only one or two females. Similarly does tended to have Amatory Interactions with only one or two males. Amatory Interactants kept company and could be shown to associate. There may be underestimates for the mate pools available to each sex due to small sample sizes and the presence of untagged individuals.

At Oxford most individuals had Amatory Interactions with only one individual of each sex although one male had them with two females. The only female to be spatially associated with two males was observed to have Amatory Interactions with only one. Again Amatory Interactants were shown to associate.

Thus at both sites the tendency appears to have been towards monogamy rather than polygyny, as judged by consortships. It might be that polygyny was untenable in these populations, where the Burrows were spread out and rabbits did not group. Neither resource-defence nor female-defence could easily be maintained.

Although it is often suggested that monogamy is unlikely to occur unless there is paternal investment (e.g. Trivers, 1972), this is not true if males are incapable of monopolising sufficient access to more than one female to

gain the benefits of polygyny. This is considered in more detail in the next chapter.

Male rabbits play no overt role in caring for their young. However, there is possibly covert paternal investment. Males appear to guard does (Cowan 1983), perhaps protecting them from the interference of other rabbits (although effort is apparently exerted in avoiding the 'mate' himself). Such interference might threaten the unborn litter of a pregnant doe if physiological responses to conspecifics resemble those found in other mammals.

More direct paternal investment can be practised and bucks will show protective behaviour towards kitten rabbits. At Oxford I observed a screaming kitten being killed by a crow. The putative father made repeated attempts to drive the crow off, (but failed). Mykytowycz and Dudzinski (1972) showed that bucks would protect kittens from the aggression of does. Kittens frequently approach male rabbits which are usually responsive and non-aggressive towards them, perhaps fulfilling a protective role (Mykytowycz, 1959).

CHAPTER 5. BATTLES WITHIN THE SEXES

If rabbits fitted Emlen and Oring's (1977) model of mating systems then polygyny would have occurred on my sites if males had been able to

i) guard resources to attract females,
ii) maintain dominance hierarchies determining access to females, or
iii) guard females from other males

Competition between males is implicit in all these activities. It was investigated for my populations to see if territorial disputes as described by Cowan (1983) occurred; and to see whether dominance hierarchies could be identified (Mykytowycz 1958; Myers and Poole 1959).

Relationships betwen does can also permit or preclude polygyny. If they liked to breed in company as Myers and Parker (1965) suggested, this would facilitate their guarding by a single male. Their relationships are looked at here to ascertain whether females associated and to see whether they had dominance hierarchies, a matter of dispute in the literature.

The methods are basically those of the last chapter but put to different purpose. Spatiotemporal association is investigated in Sections 5a, 5b and 5d not only to assort same-sexed animals into potential interactants but also to discover whether avoidance was occurring, and whether, as

Hoogland (1979) suggested for black-tailed prairie dogs, the subordinates were limited in their times of emergence by the dominant animals. Interactions between same-sexed animals are looked at in Section 5c. Buck dominance hierarchies obtained from these data are related to the consortship system and to access to does. In Section 5f the reversal of dominance between two bucks is described.

In essence, polygamy can be precluded by within-sex competition, or by exclusive preference of a pair for one another. Amatory Interactions are analysed in greater detail in Section 5e to assess which member of a pair was most responsible for the bond. That animal that more often approaches the other may be the more responsible (Hinde 1983).

Section 5a. Sharing of spatial ranges by same-sexed rabbits

Methods

Discriminant function analyses between the X Y coordinates of individuals' homeranges were run as in Section 4a. Ranges were compared between the two rabbits of all same-sexed dyads, with abutting homeranges at Oxford, within an Area at Walney (excepting 4 and 9 at opposite ends of Area North). Figs 4.1-4.3 show where each animal's homerange mid-point was.

Results

Table 5.1 gives the results for the Walney and Oxford female dyads, Table 5.2 for male dyads. There was a large amount of overlap between the Walney bucks. There, each of the 17 recognizable males shared a range with 0-6 others, with a mean of 3.1, whereas at Oxford, only two of the six males shared. None of the six recognizable Walney does shared a range and of the five Oxford does, only two shared.

The presence of untagged animals at Walney prevent strong conclusions being drawn from these data. However, there is no reason to suppose that a disproportionate number of males were caught. At Oxford I found, like Cowan (in press) that ferreting caught a female-biassed sample. Of the six males in the local population, one was caught; of the five does, all were. If ferreting were impartial or female-biassed, then there was a strong male-biassed sex ratio for the Walney adults. Although more does must have

been present than were caught, the indication still remains that they were more dispersed than the males.

Table 5.1. Extent of spatial range separation for female dyads. Degrees of freedom, F-value and P-level obtained from discriminant function analyses between X Y coordinates of ranges; for those Walney does that inhabited the same Areas and for Oxford. **Underlining shows those rabbits with ranges not separable at the P=0.001 level.**

Walney

FemA		2			6	
FemB	Df	F	p	Df	F	p
6	19	17.6	<0.001	-		
47	17	69.6	<0.001	27	77.4	<0.001
26	18	113.6	<0.001	-		

Oxford

FemA		10			24	
FemB	Df	F	p	Df	F	p
23	34	55.9	<0.001	77	62.0	<0.001
10	-			42	2.7	0.08
33	33	51.5	<0.001	26	41.3	<0.001

Table 5.2. Extent of spatial range separation for male dyads. Degrees of freedom, F-value and P-level obtained from discriminant function analyses between X Y coordinates of ranges; for the three Walney Areas on which there were more than one male, and for Oxford. The first degree of freedom is always 2, the second is shown. Underlining shows those rabbits with ranges not separable at the P=0.001 level.

Walney Northn

MaleA		7			8			56	
MaleB	Df	F	p	Df	F	p	Df	F	p
4	29	14.7	<0.001	27	74.8	<0.001	16	32.2	<0.001
7		-		23	2.9	0.077	13	3.5	<0.1
8		-			-		17	0.2	<1.0
9	21	27.7	<0.001	19	26.4	<0.001	12	22.8	<0.001

Walney South

MaleA		5			16			17	
MaleB	Df	F	p	Df	F	p	Df	F	p
16	13	2.2	0.168		-			-	
17	31	7.8	0.003	19	0.8	0.484		-	
18	23	5.5	0.012	11	1.7	0.237	29	18.7	<0.001
20	13	0.7	<0.01	3	9.7	<0.05	19	3.2	0.067
21	33	8.9	<0.001	21	2.5	0.1	39	1.0	<0.5
22	15	24.9	<0.001	3	9.1	<0.1	21	20.2	<0.001

Walney South

MaleA		18			20			21	
MaleB	Df	F	p	Df	F	p	Df	F	p
20	11	0.6	0.578		-			-	
21	31	27.5	<0.001	21	6.3	0.008		-	
22	13	8.6	0.005	3	17.5	<0.025	23	58.3	<0.001

Walney East

MaleA		10			12			22	
MaleB	Df	F	p	Df	F	p	Df	F	p
12	17	2.5	0.115		-			-	
22	11	9.3	<0.005	11	5.1	<0.05		-	
23	9	0.5	<0.75	9	0.4	<0.75	3	146.9	<0.005
25	9	4.2	<0.1	9	4.1	<0.1	3	87.7	<0.005

Walney East

MaleA		23	
MaleB	Df	F	p
25	1	209.5	<0.05

Oxford

MaleA		36			39			37	
MaleB	Df	F	p	Df	F	p	Df	F	p
25	27	47.1	<0.001	23	14.0	<0.001		-	
36		-		25	7.5	<0.005	19	108.7	<0.001
34	26	41.0	<0.001	22	51.4	<0.001	22	10.0	<0.001
35		-			-		9	11.1	<0.001

Section 5b. Sharing of temporal ranges within the sexes

Methods

As in Section 4b, temporal analyses were made by two techniques for within and across observation sessions. All same-sexed dyads within an Area at Walney and over the whole Oxford site were tested.

Results

Table 5.3 shows the results for all females, Tables 5.4a and 5.4b show them for Walney and Oxford males respectively. Again, a negative t or a positive rho indicate a positive association.

Table 5.3. Temporal association between female dyads. Each dyad is listed, with the t, Df and 2-tailed P obtained from within-evening analysis. Across-evening results give Spearman's rho, the number of evenings (N), and 2-tailed P (or N.S. for P>0.05).

Dyad		Method 1 Within evenings			Method 2 Across evenings		
F1	F2	t	Df	P	rho	N	P
Walney North							
2	6	0.817	2	N.S.	-0.026	29	N.S.
2	47	-1.316	2	N.S.	0.0615	29	N.S.
6	47	2.650	10	<0.05	0.2349	29	N.S.
Walney West							
2	26	4.047	6	<0.01	0.3821	15	N.S.
Oxford							
10	23	4.482	4	<0.02	-0.0400	41	N.S.
10	24	-0.693	18	N.S.	0.4800	41	<0.01
10	31	-0.420	1	N.S.	-0.3570	41	<0.05
10	33	0.526	5	N.S.	-0.2015	41	N.S.
23	24	3.007	4	<0.05	-0.0029	41	N.S.
23	31	-	-1	-	-0.2022	41	N.S.
23	33	5.828	1	N.S.	-0.0308	41	N.S.
24	31	-0.172	1	N.S.	-0.1805	41	N.S.
24	33	-1.423	2	N.S.	-0.4098	41	<0.05
31	33	0.862	4	N.S.	0.5641	41	<0.01

Table 5.4a. Temporal association between Walney male dyads. Each dyad is listed, with the t, Df and 2-tailed P obtained from within-evening analysis. Across-evening results give Spearman's rho, the number of evenings, and 2-tailed P (or N.S. for P>0.05).

Dyad		Method 1 Within evenings			Method 2 Across evenings		
M1	M2	t	Df	P	rho	N	P
North							
4 &	7	1.292	10	N.S.	0.1130	29	N.S.
4 &	8	0.905	6	N.S.	0.1124	29	N.S.
4 &	9	1.127	6	N.S.	0.2104	29	N.S.
4 &	56	0.736	4	N.S.	0.1301	14	N.S.
7 &	8	-0.891	6	N.S.	0.3039	29	N.S.
7 &	9	-0.824	4	N.S.	-0.1521	29	N.S.
7 &	56	1.985	2	N.S.	-0.0681	14	N.S.
8 &	9	8.243	2	<0.02	-0.1735	29	N.S.
8 &	56	0.899	5	N.S.	-0.1977	14	N.S.
9 &	56	0.215	4	N.S.	0.3424	14	N.S.
South							
5 &	16	0.541	3	N.S.	-0.021	29	N.S.
5 &	17	0.619	11	N.S.	0.067	29	N.S.
5 &	18	0.101	6	N.S.	0.086	29	N.S.
5 &	20	0.000	1	N.S.	0.123	29	N.S.
5 &	21	1.993	9	N.S.	0.295	29	N.S.
5 &	22	0.000	1	N.S.	0.044	29	N.S.
16 &	17	0.745	4	N.S.	0.176	29	N.S.
16 &	18	5.828	1	N.S.	-0.113	29	N.S.
16 &	20	-	0	-	0.185	29	N.S.
16 &	21	8.469	3	<0.01	-0.115	29	N.S.
16 &	22	-	-1	-	-0.204	29	N.S.
17 &	18	0.746	8	N.S.	0.025	29	N.S.
17 &	20	-	0	-	-0.095	29	N.S.
17 &	21	1.434	14	N.S.	0.303	29	N.S.
17 &	22	3.070	2	N.S.	0.269	29	N.S.
18 &	20	-	0	-	-0.02	29	N.S.
18 &	21	0.140	6	N.S.	0.026	29	N.S.
18 &	22	-	0	-	-0.11	29	N.S.
20 &	21	-	0	-	-0.141	29	N.S.
20 &	22	-	-1	-	-0.109	20	N.S.
21 &	22	0.000	3	N.S.	0.135	29	N.S.
East							
10 &	12	0.996	5	N.S.	0.211	18	N.S.
10 &	22	-5.828	1	N.S.	-0.420	18	<0.05
10 &	23	-	0	-	0.160	18	N.S.
10 &	25	-	-1	-	-0.422	18	<0.05
12 &	22	-0.101	1	N.S.	-0.324	18	N.S.
12 &	23	-9.899	1	N.S.	0.168	18	N.S.
12 &	25	-	-1	-	-0.014	18	N.S.
22 &	23	-	-1	-	-0.219	18	N.S.
22 &	25	-	0	-	0.153	18	N.S.
23 &	25	-	-1	-	-0.125	18	N.S.

Table 5.4b. Temporal association between Oxford male dyads. Each dyad is listed, with the t, Df and 2-tailed P obtained from within-evening anlaysis. Across-evening results give Spearman's rho, the number of evenings (N), and 2-tailed P (or N.S. for P>0.05).

Dyad		Method 1 Within evenings			Method 2 Across evenings		
M1	M2	t	Df	P	rho	N	P
25 &	34	5.731	5	<0.01	-0.1652	41	N.S.
25 &	35	-	-1	-	-0.2339	41	N.S.
25 &	36	3.731	9	<0.01	-0.1613	41	N.S.
25 &	37	-	-1	-	-0.1613	41	N.S.
25 &	39	4.491	3	<0.05	0.0702	41	N.S.
34 &	35	0.424	4	N.S.	0.4522	41	<0.01
34 &	36	-0.395	4	N.S.	-0.5344	41	<0.01
34 &	37	-4.442	1	N.S.	0.3323	41	<0.05
34 &	39	1.739	3	N.S.	0.0901	41	N.S.
35 &	36	-	0	-	-0.2374	41	N.S.
35 &	37	0.225	1	N.S.	0.7161	41	<0.01
35 &	39	-	-1	-	-0.1844	41	N.S.
36 &	37	-	0	-	-0.0923	41	N.S.
36 &	39	-0.224	4	N.S.	-0.0253	41	N.S.
37 &	39	-	-1	-	-0.1272	41	N.S.

Care needed to be taken in the interpretation of these results. Since a number of comparisons were made, some would be expected to yield significant levels just by chance. Furthermore, the data were not independent in that two rabbits both dissociating with a third, will apparently be associating with one another.

There is some evidence that temporal exclusion between bucks occurred at Walney. The only significant results obtained for bucks were dissociations, found for four dyads. Also, for 20 of the 25 within-evening comparisons that gave a signed value to t, that sign was positive (indicating dissociation). The only significant results for does at Walney were also dissociations, found for two of the (four) tested dyads.

At Oxford there were both dissociations and associations between neighbouring bucks and between does. It is interesting to note that only one doe dyad shared a range, 10 and 24 at Oxford, and that these rabbits associated.

None of the within-evening comparisons at either site showed association for any same-sexed dyad: significant results were all dissociations. This contrasts with the association data between the sexes shown in the last chapter.

Section 5c. Within-sexes interaction data

Methods

There were only three within-sexes behavioural interactions observed: Chasing, Displacing and Leaping at. Chasing was one rabbit running after another. Displacing was one rabbit moving up to another, supplanting the second which moved away. Leaping at is self-explanatory. Each of these behaviours could be recorded as an instigating or receiving interaction for the focal animal e.g. chasing, or being chased. Both Chasing and Displacing were divided by eye, at the time of recording, into fast or slow. If fast, they were categorized (with Leaping at) as Aggression Interactions. If slow, they were categorized as Dominance Interactions. Aggression Interactions were taken to signify an aggressive relationship. Both Dominance and Aggression Interactions were often in one direction and, if so, defined which rabbit was 'dominant' over the other.

Data were obtained from all adult interactants, looking within the total observation times summed across both rabbits of a dyad. Durations of each rabbit aggressing against and dominating the other were summed using instigating and receiving interactions.

Table 5.5. Durations of time (s) spent in interactions between same-sexed rabbits. Rabbit 1 (R1); Rabbit 2 (R2). If identity of both were known: summed time across all observation periods of R1 and R2 (Total Time); summed duration across Total Time during which R1 aggressed against R2 (R1 aggress R2), dominated R2 (R1 domin R2); and during which R2 aggressed against R1 (R2 aggress R1), dominated R1 (R2 domin R1). For unrecognizable rabbits, R2 listed as A and durations summed across observation period of R1 only.

R1	R2	Total Time	R1 aggress R2	R1 domin R2	R2 aggress R1	R2 domin R1
Walney bucks						
4	A	15892	71	81	7	8
5	18	21406	14	0	66	0
5	A	11686	0	3	0	0
7	56	10545	0	0	8	0
8	56	13734	0	0	19	32
8	7	17317	0	0	21	24
10	12	19071	0	0	17	0
10	A	8168	12	28	0	7
12	A	10903	28	78	0	0
13	A	2810	24	29	0	0
17	18	33032	0	0	0	6
17	20	25216	0	0	6	0
17	21	46224	0	0	253	7
17	A	23312	0	86	16	27
18	A	9720	22	11	0	4
21	5	34598	0	4	0	0
21	A	22912	10	84	0	5
22	17	28614	0	8	0	8
22	A	5302	0	25	7	36
23	A	1224	11	0	0	8
56	A	6841	48	3	5	22
Oxford bucks						
25	39	18285	35	0	0	0
34	37	27861	30	57	0	0
34	A	20958	0	49	37	0
36	9	41831	11	6	0	0
36	39	63440	43	102	23	18
Walney does						
2	A	14052	0	0	0	35
6	A	17315	8	0	6	46
11	A	15444	0	17	6	135
19	A	7150	0	0	0	9
26	A	8153	0	0	19	12
47	A	12372	0	0	0	6
Oxford does						
10	24	62966	0	3	0	2
33	24	35230	0	4	0	0
33	A	24771	0	0	0	31

Results

Table 5.5 lists interactions between bucks and between does at both sites. The Oxford data do not include August 1982, when the social structure altered. Only one Aggression Interaction score between opposite-sexed rabbits was obtained, that of buck 34 displacing doe 33 fast for 11 seconds.

Aggression Interactions between known does were absent at both sites. At Walney alone, they occurred between does and unrecognizable rabbits that might have been does. Dominance Interactions between known does were practically absent, but does were greatly dominated by untagged rabbits, likely to have been male. Although the docility of the does was likely to have been because they were so spread apart, even 24 and 10, sharing a spatiotemporal range at Oxford, did not have Aggression Interactions (but see Section 5f).

Those bucks most closely associated in space were most aggressive to one another. Aggression Interactions between Walney bucks were only between those sharing spatiotemporal ranges, although Dominance Interactions occurred between non-sharing bucks. At Oxford, the highest levels of aggression were seen between 36 and 39, the only pair to share a range.

Clear-cut relationships between bucks could often be seen at Walney. In some cases, a buck always dominated in interactions with a particular other buck. Those bucks that were always dominant over at least one other buck were 56, 12, 18, 20, 21, 22 and 7 at Walney, 36, 25 and 34 at Oxford.

A very high score for instigating Aggression Interactions against untagged rabbits was obtained for buck 4 at Walney, from which it may be inferred that he had high dominance status.

From Chapter 4, chief Walney consorts to does were 56, 4, 12 and 18 at Walney, with 7 as a subsidiary consort. 21 consorted greatly with one or more untagged does. From the present chapter, it can be seen that each of these rabbits had high dominance status. 56, chief consort to 47, dominated 7, the subsidiary consort. At Oxford, the dominant animals 25, 34, and 36, were consorts to does, as was 35 that had no bucks to interact with. All Aggression Interactions at Oxford, and most at Walney, were between those males that had no or little access to the females, and males that acted as consorts to the females.

Section 5d. Proximity data

Methods

Proximity data within same-sexed dyads were analysed as in Section 4d, for all dyads that could be compared, within an Area at Walney, and over the whole visible area at Oxford. The test could not be done on those dyads which were never, or only once seen out in the same scans. For the Oxford dyads, measurements were fine enough to compare distances between close-living rabbits only. This was because relative distances, the largest category of which was 'over 50-rabbit lengths' had been recorded rather than absolute positions. (Scan-samples had been constructed from focal animal data, see Section 2c)

Results

Table 5.6 shows proximity data for bucks at Walney and Oxford and then for does.

There was only one significant result between Walney rabbits, for 7 and 56, that dissociated strongly despite sharing a spatiotemporal range. They were the only case of more than one recognizable buck consorting with a doe (47).

At Oxford, association was found between the subordinate 39 and each buck that he bordered with: 25, 36 and 34. 36 also associated with his two neighbours, 25 and 34. Doe 10 at Oxford, associated with both 23 and 24, that she bordered with and shared a range with respectively.

Table 5.6. Two-tailed P levels of association (+) or dissociation (-), followed by + or - for each testable dyad.

MALES	P	Assoc(+) Dissoc(-)	MALES	P	Assoc(+) Dissoc(-)
Walney South			Walney North		
5&17	0.533	+	4&7	0.441	-
5&18	0.994	-	4&8	0.839	-
5&21	0.771	-	4&9	0.990	+
17&18	0.994	+	4&56	0.818	-
17&21	0.669	+	7&8	0.083	+
18&21	0.645	+	7&9	0.850	+
21&22	0.350	-	7&56	<0.001	-
Oxford			8&56	0.153	-
34&36	0.009	+	9&56	0.600	-
25&36	<0.001	+	Walney East		
34&37	1.000	-	10&12	0.272	+
34&39	0.019	+			
25&39	0.034	+			
36&37	1.000	-			
35&37	0.121	-			
36&39	0.029	+			

FEMALES	P	Assoc(+) Dissoc(-)	FEMALES	P	Assoc(+) Dissoc(-)
Oxford			Walney North		
10&23	0.002	+	6&47	0.758	+
10&24	0.004	+			
10&33	0.320	+			
24&33	0.134	+			
23&24	1.000	-			

Section 5e. Maintenance of pair bond

Amatory Interaction behaviours of chief consorts (Chapter 4) were re-investigated to see whether bucks or does were most responsible for pair-bonding; and to see whether other potential mates were approached with similar intensity. This was to indicate whether the partner was the preferred consort or the 'default' consort.

Methods

The Amatory Interaction behaviour of a given rabbit could be instigatory, receiving or mutual as described in Table 4.3.

Table 5.7 divides the durations of behaviours into the two categories for Walney and Oxford rabbits. Interactions were summed across the observation periods of the subject rabbit only such that interactions by it with different rabbits were comparable.

Results

In every case, except that of female 26 at Walney, bucks were overwhelmingly more active than does in instigating Amatory Interactions. It was difficult to investigate whether the buck would act in a similar way to any doe that he had access to, since there were very few promiscuous relationships. Buck 36 at Oxford, the only buck to have had access to more than one tagged doe, showed marked preferentiality. From Chapter 4 it was seen that he

had most Amatory Interactions with doe 10; here we see that this occurred at his biassed instigation. At Walney, does 6, 11 and 47 instigated Amatory Interactions with their 'regular' consorts only (4, 12 and 56), although receiving attentions from other bucks.

Table 5.7. Direction of Amatory Interactions. Total durations of time (s) spent in Instigatory (Inst Time), Receiving (Rec Time) and Mutual (Mut Time) Amatory Interactions by each subject rabbit within its own focal animal observation time. Does are underlined.

Subject rabbit	Object rabbit	Inst Time	Rec Time	Mut Time
Walney				
4	6	46	0	5
4	A	57	10	0
7	47	112	0	6
12	11	332	14	0
18	19	15	10	0
21	A	286	28	0
56	47	32	33	111
6	4	15	20	0
6	A	0	20	0
11	12	19	176	0
11	A	0	40	0
19	18	0	20	0
26	A	26	5	0
47	56	0	62	0
Oxford				
25	23	24	0	0
34	33	35	0	0
35	31	38	0	0
36	10	178	4	26
36	24	89	7	0
39	10	8	0	0
10	36	12	223	150
23	25	0	16	21
24	36	0	51	2
31	35	0	76	28
33	34	4	32	4

Section 5f. Reversal of dominance

The disappearance at Oxford of buck 36 for the first two weeks of August proved an interesting 'natural experiment'. He had dominated the attentions of the two does 10 and 24 that shared a spatiotemporal range with one another and with him, and he had dominated the peripheral buck 39 in frequent aggressive chases.

Social set-up in 36's absence

There were not enough data from these days of 36's absence (3.8.81-16.8.81) to analyse spatiotemporal range-sharing by those animals left. What appeared to occur was that the peripheral buck 39 moved into 36's area and took up consortship with the two does. Table 5.8a shows the Amatory Interaction behaviour data for the whole of August.

Table 5.8a. Durations of time (s) spent in Amatory Interactions (AIs) at Oxford in August. Subject rabbits are listed, with their total focal animal observation times (Total Subject Time), and durations of time spent within this in AIs with each other rabbit. 'A' are untagged adults.

Subject rabbit	Object rabbit	Total Subject Time	Time spent in AIs	% Time spent in AIs
10	39	15866	67	0.42
23	25	1828	37	2.02
24	39	21522	67	0.31
33	34	10188	18	0.18
25	10	1716	18	1.04
34	10	11816	22	0.19
34	33	11816	22	0.19
34	A	11816	8	0.07
39	24	16681	6	0.04

39 was involved in a lot of Amatory Interactions with the two does, and like 36, concentrated most on 10 (relative to the amounts of time she and 24 were watched). Other changes were that the neighbouring males, 34 and 25, although continuing to interact with 33 and 23 respectively, also attended to doe 10.

The return of buck 36

Buck 36 returned on August 16th. That evening he remained in 39's old territory until 39 no longer attended the does, when he himself approached them. 39 returned to doe 10 and then chased 36 in a drawn out series of chases. 36 returned next on August 20th and was chased from the vicinity of 24 by 39. 36 then approached his old neighbour, 34, and 34 and 39 alternated between them in chasing 36 off. 39 remained in 36's old patch until at least August 27th when data-collection was terminated for that season.

The following April, 1982, 36 was again the buck present with 10 and 24. 39 was not recognised in 1982, though he may have been present; he had never been tagged and had been identified merely by a scratch in his ear.

Table 5.8b details the Dominance and Aggression interactions that occurred in August; this shows 39 as dominant to 36 (despite data being lost from the eventful August 20th). Aggression Interactions now occurred between the does, with 10 dominant to 24.

Table 5.8b. Durations of time (s) spent in interactions between bucks and between same-sexed rabbits. Rabbit 1 (R1); Rabbit 2 (R2). If identity of both were known: summed time across all observation periods of R1 and R2 (Total Time); summed duration across Total Time during which R1 aggressed against R2 (R1 aggress R2), dominated R2 (R1 domin R2); and during which R2 aggressed against R1 (R2 aggress R1), dominated R1 (R2 domin R1). For unrecognizable rabbits, R2 listed as A and durations summed across observation period of R1 only. (Does are underlined.)

R1	R2	Total Time	R1 aggress R2	R1 domin R2	R2 aggress R1	R2 domin R1
<u>10</u>	<u>24</u>	37388	40	18	0	2
25	9	1716	0	26	0	0
39	36	16802	41	0	0	0

Section 5g. Discussion

There was no spatiotemporal range-sharing between the does at either site except for 10 and 24 at Oxford. These does inhabited a sand-bank where there were two six-entranced warrens. The even spacing of rabbits supposed to be associated with small warrens (Chapter 3), can therefore chiefly be explained by the does spreading out across the warrens.

These tests do not show whether the does were avoiding one another, or whether they just had different preferences for times of emergence; although significant dissociations were found. There were barely any interactions noted between known does, presumably because they were too far separated; 10 and 24 were an exception and they did interact. Interestingly, 10, that asserted dominance over 24, was the more attractive to bucks.

Aggression between bucks was heightened by proximity, range-sharing bucks often chasing one another. Territorial defence as described by Cowan (1983) was not seen at all, nor were any fights seen. Since there were no coherent groups, neighbouring rabbits were likely to have formed relationships of mutual forbearance or dominance, and no inter-group rivalry would occur. Strange bucks alone would elicit serious aggression.

Dominance relationships between bucks were well defined at both sites, though they never went to hierarchies of more than three animals. At Walney, males tended to avoid one

another but at Oxford no such dissociation was apparent. There are possibly two strategies that subdominant males can use. At Walney, 7 consorted with 47 nearly as much as 56 did, despite being the subdominant. He achieved this by consorting in 56's absence, and keeping his distance in his presence, although they shared a spatiotemporal range. The alternative strategy, perhaps that of 39 at Oxford, is for the subdominant male to challenge the dominants. 39 associated with 36, and their relationship was not clear-cut, reflecting the imminent usurpation of 36.

Male dominance appeared to determine access to does at both sites. None of the bucks that were chief consorts to females, showed aggression towards one another, rather Aggression Interactions were limited to dyads where one of the bucks both had access to the female and dominated the other buck. The challenge from subdominant 39 was chiefly of 36, the only buck known to have had regular access to more than one doe. Although the obvious conclusion to be drawn is that dominant males can fight off other males from the females, it is likely too that added dominance is conferred on a male by his very status of consort. His access to a doe is a valuable resource to lose to another buck, whereas solitary bucks have no such resource to lose when attempting takeovers. This asymmetry of gains and losses in fights is likely to increase the aggressive dominance of a consort buck.

The separation of the does precluded the sequestering of more than one doe by a single male. This, with the

competition between males and the preferentiality by both sexes for their own 'mate' supported a monogamous mating system.

CHAPTER 6. THE NATURE OF VIGILANCE

A commonly cited functional cause of group-living is that vigilance can be reduced in larger groups (Pulliam 1973). This will be investigated in Chapter 7, but first, measurements of vigilance and potential underlying mechanisms are looked into. In birds, scanning occurs betwen bouts of pecking, but the peck-rate itself, within a bout, can be used as a measure of vigilance since increased peck-rate necessarily reduces vigilance, pecks themselves being discrete, stereotyped, almost instantaneous behaviours (Caraco 1982) like drinking (Dawkins and Dawkins 1973). In grazing mammals (and some birds) putting the head down into long herbage for protracted periods alternates with scanning. Thus an increased rate of feeding could increase or decrease overall vigilance depending on whether the increased rate was effected by smaller durations of feeds or of scans or of both (McVean and Haddesley 1980). The different measures of vigilance are correlated for rabbits in Section 6b to see how they are interrelated.

Further information on the nature of vigilance can be obtained by looking at the frequency distributions of duration of feeds (periods with the head down), and of scans, and of the grazing bouts in which they occur (Section 6c). This can throw light on the functional efficacy of scanning for averting predation and promoting feeding (Hart and Lendrem 1984), and on mechanistic causal factors. Various mechanisms have been described by which an animal

can avoid 'dithering' between two behaviours when the motivational tendencies of each are equal and the expression of a behaviour is determined by motivational competition (McFarland 1985). One such mechanism is positive feedback, whereby the motivational tendency to perform a behaviour is initially increased as the behaviour is performed (Houston and Sumida 1985). Wiepkema (1971) noted positive feedback occurring for feeding in mice, where subsequent feeding bouts increased in length. The method used here is rather different, looking at frequency distributions in Section 6c. These can show whether behaviours were of random duration, with an equal probability of a behaviour ending at any duration. Alternatively, it could be that the longer a behaviour continues, the longer in addition it will continue, i.e. the probability of ending the behaviour might decline with increased duration. This would be some evidence for positive feedback occurring.

An additional mechanism which may influence the patterning of scans and feeds within grazing bouts is investigated in a preliminary fashion in Section 6d. When feeding has the highest priority for an animal, it might become the dominant behaviour and the onset and termination for the subdominant scanning behaviour might be determined by pauses in the feeding. If the dominant behaviour dictates the pattern of the sequence in this way, timesharing is occurring (McFarland 1985). Natural pauses are occasioned in grazing bouts by 'chewing' when the rabbit has a mouthful to chew whilst it can scan. If feeding were

dominant it would be expected that the size of a mouthful would determine the duration of the scan. Either of two behaviours can be dominant, here vigilance or feeding, at any particular time (McFarland and Lloyd 1973).

Section 6a. General methods

Sessions of continuous data had been collected on the 11 Oxford rabbits (Chapter 2). A computer program was run through the data to extract durations of behaviour sequences. All the relevant Grazing Bout behaviours are listed in Table 6.1.

Table 6.1. Grazing Bout Behaviours

Scan behaviours

Non-Chews
1) Head up
2) Sitting up, whole body slightly raised (ears generally erect)
3) Standing up, front paws off ground (ears generally erect)
4) General alert, subject and all (or most) rabbits alert (usually standing up)

Undefined
1) Head up, probably chewing but mouth not visible

Chews
1) Head up and chewing non-protrusive fodder
2) Head up and chewing fodder which protrudes from mouth
3) Head up and moving whilst chewing

Feed behaviours

1) Head down, cropping at ground level
2) Head at body level cropping long grass
3) Standing up, head raised to crop tips of long grass

Other Grazing Bout Behaviours

1) General feeding, vigilance and feeding acts not differentiable
2) Stretch and/or yawn
3) Starts (body spasm, as if alarmed)
4) Hops short distance (2 or 3 hops)
5) Shaking ears
6) Scratching body

These definitions were used to define the following:

1). Grazing Bout. A sequence of behaviours beginning with a Chew (i.e. a Scan behaviour specific to grazing) or with a Feed, continuing through any of the Grazing Bout behaviours listed in Table 6.1, and terminating at the onset of a behaviour that was none of these. Bout duration was the sum of durations of all behaviours occurring within the Bout, excluding the durations of Other Grazing Bout Behaviours 2-6.

2) Scan. Successive Scan behaviours (Non-Chews, Chews and Undefineds), occurring within a Grazing Bout were summed to give the duration of a single Scan.

3) Feed. Successive Feed behaviours were summed to give the duration of a single Feed.

4) Chewlength. This measure was made in addition to the above. Within each single Scan that did not contain an Undefined, the durations of all Chews (even though not successive) were summed.

All of the data used in Section 6b and for the distributions of Grazing Bouts (Section 6c) are from Naturally-Ending Grazing Bouts only, i.e. from those that ended neither by the disappearance of the rabbit, nor by an interactive behaviour between it and another rabbit. Either of these endings might have truncated the bout prematurely.

Section 6b. Interrelationships between vigilance measures

Methods

Five parameters of feeding and vigilance were obtained from each Grazing Bout.

1) Grazing Bout duration (GRAZE)

2) Median Scan duration (MSCAN).

3) Median Feed duration (MFEED).

4) Proportion of bout spent scanning (PROP). Sum of Scan durations, divided by Grazing Bout duration and multiplied by 100 (for convenience).

5) Rate of scanning (RATE). Number of Scans divided by the Grazing Bout Duration and multiplied by 1000 (for convenience).

Kendals Rank Correlations were run between each of the five measures, over all of each rabbit's Naturally-Ending Grazing Bouts. Each τ value so obtained was converted into a z-score by the use of the formula

$$z = \frac{\tau}{\sqrt{(2(2N+5)/9N(N-1))}}$$

as described in Siegel (1956), where N is the number of Grazing Bouts. This is an acceptable procedure if N is greater than 10. An average z-score was obtained by adding the z-scores and dividing by $\sqrt{11}$, 11 being the number of rabbits. The probability level of this was looked up in normal tables.

Table 6.2. Correlations between each pair of parameters of feeding and vigilance expressed as z-scores for each rabbit, across N feeding bouts. Summary (Z) of z-scores:($(\Sigma z)/\sqrt{11}$), with overall P-level.

Rabbit	N	Mfeed & Mscan	Rate & Mscan	Prop & Mscan	Graze & Mscan	Rate & Mfeed
10	117	-1.380	-1.531	8.066	-0.436	-9.615
23	26	-1.141	-1.441	4.201	-0.093	-2.037
24	64	-2.468	-0.793	5.903	-1.055	-5.777
31	13	-0.583	-1.143	3.047	0.888	-3.215
33	45	0.217	-1.770	3.403	-0.072	-4.394
25	22	0.844	-3.142	2.749	0.630	-3.100
34	64	-0.895	-3.092	6.057	1.641	-6.089
35	24	0.052	-1.259	2.944	0.308	-3.074
36	72	-0.678	-2.691	6.295	1.497	-6.584
37	17	0.521	-2.258	1.672	0.502	-2.567
39	77	-0.685	-2.663	6.630	0.050	-7.334
Z		-1.87	-5.84	15.37	1.16	-16.22
P(2-tail)		0.061	<0.001	<0.001	0.246	<0.001

Rabbit	N	Prop & Mfeed	Graze & Mfeed	Prop & Rate	Graze & Rate	Graze & Prop
10	117	-7.726	3.486	5.027	-4.143	-2.086
23	26	-3.577	0.794	0.487	-1.109	-0.487
24	64	-5.599	1.375	2.304	-2.357	-0.209
31	13	-2.459	1.450	0.741	-1.916	-0.371
33	45	-3.565	2.055	3.187	-3.137	-0.658
25	22	-1.956	1.323	0.513	-2.309	0.255
34	64	-6.047	4.118	2.316	-6.47	-1.475
35	24	-2.050	1.725	0.448	-2.743	0.372
36	72	-5.183	3.665	2.606	-4.686	-0.518
37	17	-2.140	1.113	-0.412	-1.895	-0.659
39	77	-5.670	4.937	3.086	-6.325	-1.914
Z		-13.86	7.85	6.12	-11.18	-2.34
P(2-tail)		<0.001	<0.001	<0.001	<0.001	0.019

Results

Although it is true that multiple comparisons are always suspect when sifting through data for significant results, it was here known that certain dependencies must have occurred since the measures were all interrelated. The

aim was simply to sort out how the interrelationships worked. Table 6.2 gives the z-scores for each rabbit for each pair of parameters, and the summary across all rabbits.

Proportion of bout spent scanning and rate of scanning were positively correlated (bottom column 3); both reflecting increased vigilance. However, increased rate of scanning cut into both median Feed and median Scan (top columns 2 and 5), being negatively correlated with both. Thus, a high rate of scanning did not reflect pure increased vigilance, since it involved decreased Scan durations.

Grazing Bout duration was correlated with low vigilance both in respect of rate of scanning and of proportion of bout spent scanning (bottom columns 4 and 5). It was correlated positively with median Feed duration (bottom column 2). This suggests that long Grazing Bouts occurred when feeding held a high priority and priority for vigilance was low.

This is further borne out since the durations of median Feeds were negatively correlated with those of median Scans (although not quite to significance: top column 1). Thus it was not the case that after (or before) a long Feed, a long Scan was required to ensure safety. Rather, with increased priority for feeding, scanning was subsumed into the feeding effort. Similarly, rate of scanning, and proportion of bout spent scanning decreased with increased median Feed durations (top column 5 and bottom column 1).

Section 6c. Detection of positive feedback

Methods

Frequency histograms were drawn up of Naturally-Ending Grazing Bout, Scan and Feed durations for each rabbit over all of its observation periods. A Kruskal-Wallis program was written to test whether distributions for each parameter were the same across rabbits, and so could be pooled. The results of these tests were:

a) Scan durations. χ^2=82.83; df=10; p<0.001.

b) Grazing Bout durations. χ^2=30.62; df=10; p=0.0007.

Since the distributions of both these parameters were heterogeneous between rabbits, separate investigations of them had to be made for each rabbit. Feed durations were treated likewise since even if they had failed to show heterogeneity, it would have been suspected.

In order to test whether behaviours ended randomly, or whether positive feedback could be detected, the distributions were inspected to see whether the probability of the behaviour continuing increased with its duration.

Sophisticated statistical techniques for detecting a change in probability of a behaviour ending were investigated in depth. Multiple logisitic regression could have been performed if there had been adequate data. A logistic transform would convert the data into linear form and multiple regression could then be used to see whether a single straight line fitted the data better than two lines meeting at an angle. Iteration would have been used to try

out different positions for this angle. However, since it was not possible to pool data from the different rabbits, there were too few data for each analysis to make the logistic regression worthwhile. Instead, a simple graphical technique is presented.

For each distribution, for each rabbit, a log survivorship curve was derived from the frequency histogram. Frequencies were cumulated from the right hand side, and their $\log_{10}$ taken. If the process were random, there would be an equal probability of the behaviour terminating at each duration, and the log survivorship curve should appear as a straight line. If positive feedback were occurring, the probability of the behaviour terminating should decrease as duration increases and the log survivorship curve should curl round in a convex bend.

Results

In Figs 6.1-6.3, log survivorship curves of Grazing Bouts, Scans and Feeds are pictured for each rabbit. Grazing Bouts were on a different scale to Scans and Feeds since they were of longer durations and there were fewer of them.

Grazing Bouts. Since there were few data on Grazing Bouts, the patterns are not very clear. However there does appear to be an increase in probability of continuing a Bout at longer durations, showing itself as a convex bend at a fairly early stage (before 200s), in most of the graphs. These points may represent the stage at which the animal is

seriously going in for feeding, as opposed to small fill-in bouts.

Feeds. Although fairly straight, most of the Feeds log survivorship curves showed slight convex bending. This is strongest for 10 and 24, for both of which a good amount of data were collected. However the durations of Feeds do not depart greatly from randomness.

Scans. Being on the same scales, and with the same quantity of data, the Scan log cumulative frequency curves can be compared directly to those of Feeds to give a relative idea of curvature. All of the Scans graphs are convexly curved, and all show a particular bend between 20s and 50s. Thus, Scans particularly seem to work under two processes, being more likely to continue after a certain stage than they were before that stage. The next section tests these visual impressions more rigorously.

Positive feedback is definitely present in the case of Scans: the probability of ending a Scan decreases with longer Scan durations. There may be slight positive feedback occurring for Feed and Grazing Bout durations also, but it is not nearly so marked.

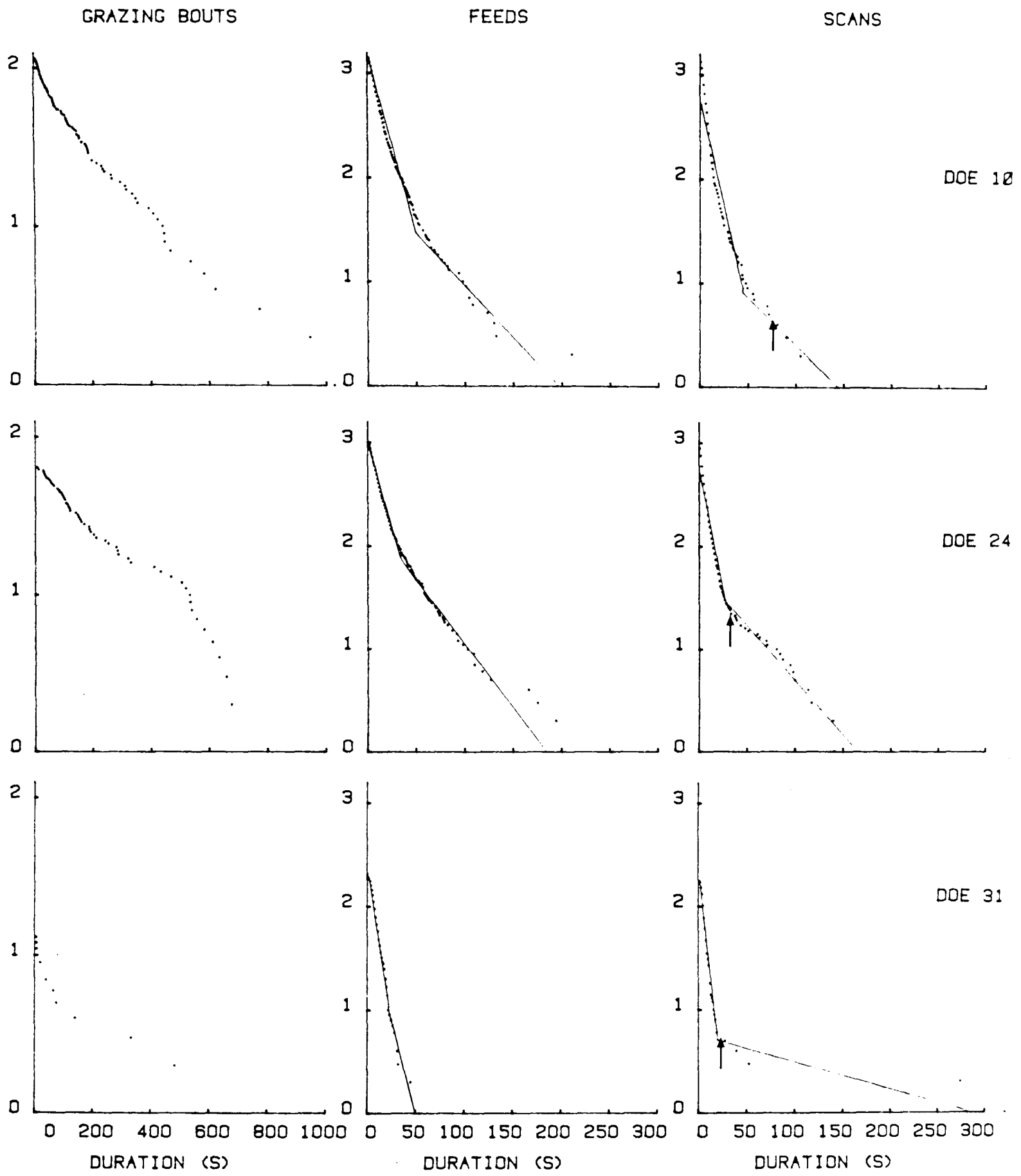

Fig 6.1. $Log_{(10)}$ cumulative frequency curves for Grazing Bout, Feed and Scan durations (s) for each rabbit. (Grazing Bout durations are on different scale to others). For Section 6d, Maximum Chewlength is arrowed in on Scans graph: best-fitting lines are drawn through points before and after position of arrow on Scans and Feeds graphs.

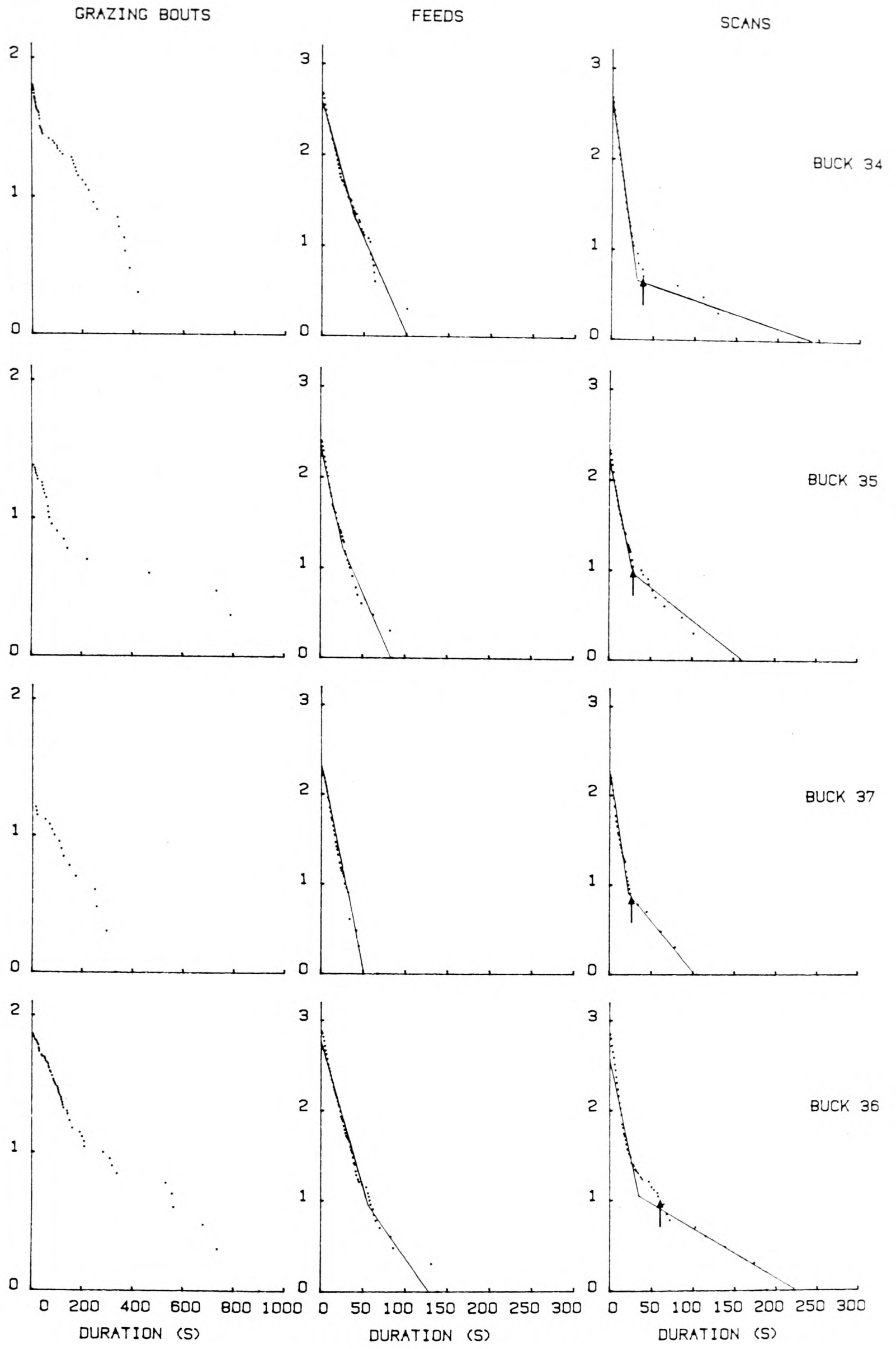

Fig 6.3. $\text{Log}_{(10)}$ cumulative frequency curves for Grazing Bout, Feed and Scan durations (s) for each rabbit. (Grazing Bout durations are on different scale to others.) For Section 6d, Maximum Chewlength is arrowed in on Scans graph: best-fitting lines are drawn through points before and after position of arrow on Scans and Feeds graphs.

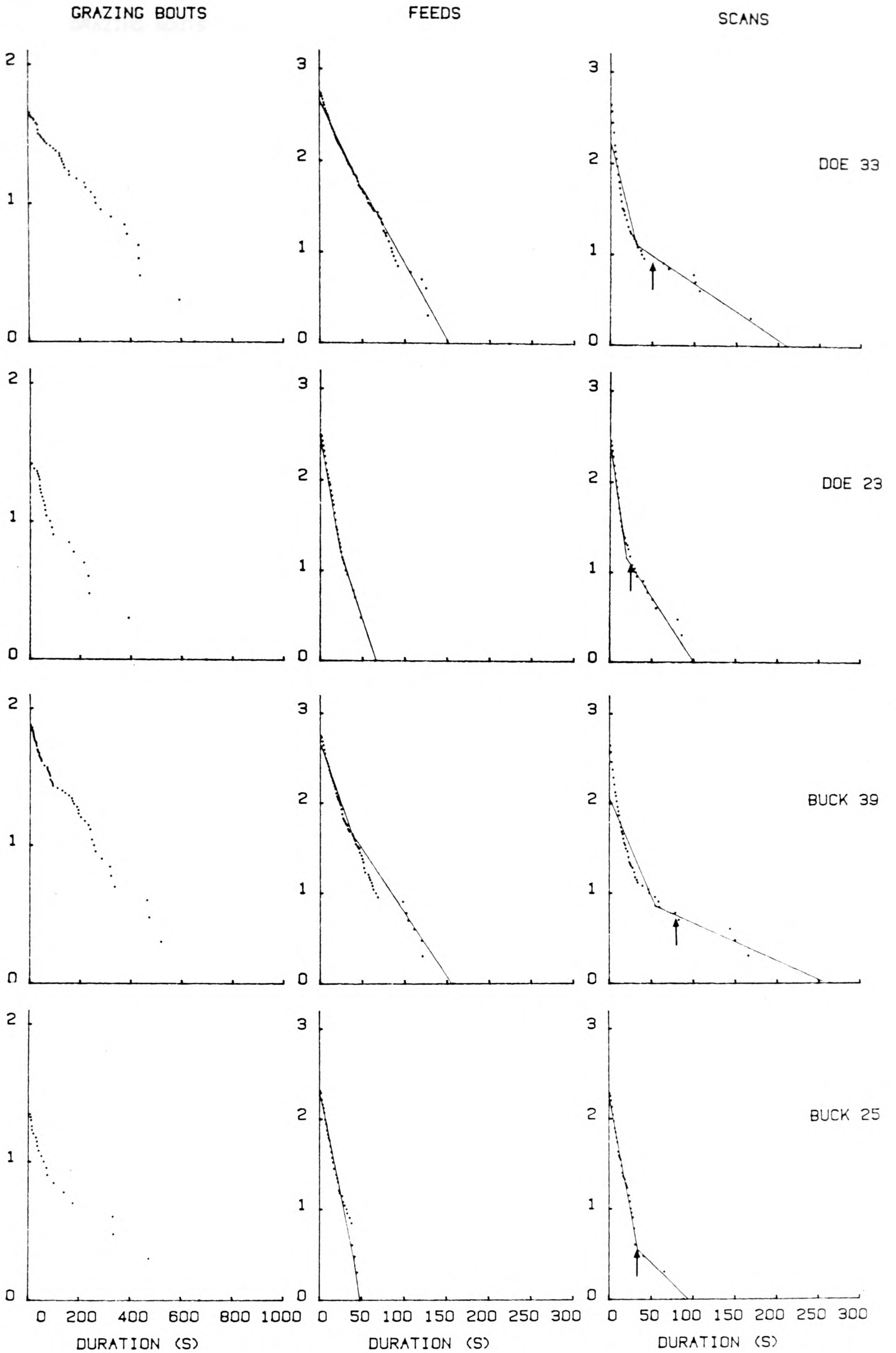

Fig 6.2. $Log_{(10)}$ cumulative frequency curves for Grazing Bout, Feed and Scan durations (s) for each rabbit. (Grazing Bout durations are on different scale to others). For Section 6d, Maximum Chewlength is arrowed in on Scans graph: best-fitting lines are drawn through points before and after position of arrow on Scans and Feeds graphs.

Section 6d. Effect of Chewlength

The point at which Scan durations decrease their probability of finishing may be related to Chewlength. As defined in Section 6a, Scans can include Non-Chews and Chews. The durations of Chews within a Scan add up to the Chewlength of that Scan. If timesharing were occurring, Scans would only be expected to last for a Chewlength, as long as feeding were dominant. Scans of longer duration than the time needed to chew a mouthful, necessitate taking time off feeding, and imply that feeding is no longer dominant. The Scan log survivorship curve might then be expected to bend at that duration of Scan which is the maximum Chewlength.

Methods

For each rabbit, the maximum Chewlength ever seen was taken, and was marked onto the Scan log survivorship curve (Figs 6.1-6.3). This provided the basis for the test required for Section 6c, as the point at which the bend might be expected. On each Scan graph one straight line was drawn through the points before the duration of maximum Chewlength and one through those after it, by getting equal numbers of points either side of the line. The two straight lines were extended until they met and the angle between them was measured; the set of angles was gathered across rabbits.

These angles could have been compared directly to

straight lines to see whether bends occurred. It was thought more interesting to compare them with angles drawn to the same points in the Feed graphs. The hypothesis was that Scan durations underwent change at these particular points. The point of maximum Chewlength would not be of any relevance to Feed behaviours so Feeds should not show so marked a change at these points. Thus the Scan angles were compared to angles obtained in the same manner from Feed graphs. Using Feeds as controls and making pairwise comparisons for rabbits (paired with themselves) controlled for the rabbit having a tendency to get stuck into any behaviour after a certain duration.

Results

Maximum Chewlength for each rabbit were as follows:

Rabbit	Max Chew-length (s)
10	72
23	24
24	32
31	22
33	48
25	31
34	37
35	28
36	59
37	24
39	83

In Figs 6.1-6.3, an arrow marks in the maximum Chewlength for each rabbit. The best fit lines onto points before and after this position are drawn in on both Scan and Feed graphs.

In some cases, notably for 10 and 39, the maximum

Chewlength was very long. For 10, that particular memorable chew was of a very large plantain leaf. Since such exceptional cases will sometimes be the maximum Chewlength, it is not surprising that maximum Chewlength frequently fell to the right of the bend in the graph. For bucks 25,34,35 and 37, and for does 24,23 and 31, the maximum Chewlengths were very close to the bends in the curves. For does 10 and 33 and bucks 36 and 39, they fell to the right of the bends.

The set of angles obtained from Feed and Scan graphs were as follows:

Rabbit	10	23	24	25	31	33	34	35	36	37	39
Feeds angle(°)	28	8	21	-6	6	4	9	12	19	0	14
Scans angle(°)	33	24	30	35	68	43	64	41	48	31	43

The difference between angles in Feeds and Scans was tested with a Wilcoxon matched-pairs test, which gave a 2-tailed $P<0.001$ with the Scan angles significantly greater than the Feeds. There was some positive feedback occurring for Feeds since all but two angles were greater than 0°, but it was not as impressive as that seen for Scans. A bend in the Scans graphs could be detected at the maximum Chewlength although it might have been detectable at other points also.

Section 6e. Discussion

Rabbits are well-built for vigilance. Smythe (1961), Hughes (1977) and Collewijn (1977) describe rabbits' visual capacity in the following manner. Their protrusive lateral eyes have a wide field of vision, and they can see 340° around them. Although the eyes usually move together, they are capable of independent movements. The head tends to follow the eyes, perhaps because the potential field of binocular vision is limited to just 20-30° in front and 35° above. Whether there is stereopsis is unknown, but rabbits are apparently neuronally capable of it. However, a rabbit cannot see at all up to 30cm directly in front and the two eyes cannot focus on the same thing unless it is at least 2m away. The rabbit has a blind spot of 1-2° and a yellow streak rather than a fovea.

To use sight to gauge distance to a predator, or to investigate nuances of social behaviour in other rabbits, would require orientation and observation. Of course, other sensory systems are likely to be of great importance, particularly hearing and smell. In my studies I have concentrated on consideration of visual detection since it would have required rather finer techniques to gauge the direction of pinna-pointing or the speed of nose-winking (Harrison-Matthews 1968) to assess intensity of use of these other important senses.

Rabbit wariness sometimes took the form of very alert postures, the animal standing up and scanning, possibly in

response to a specific external stimulus. There were also less alert postures: brief headlifts during feeding might have increased the rabbit's awareness and reflected its 'nervousness'. This might itself have been undirected as far as the rabbit was concerned, although it may have had a particular function unbeknownst to its performer. Thus vigilance can be conciously or unconciously directed at some ultimate goals, protecting the rabbit from specific threats of predation or competition.

The interdependencies of vigilance and feeding parameters indicate that either feeding or vigilance can take priority and depress the other. Thus Grazing Bout length was correlated to Feed duration, both these parameters rising together. Also, the negative correlation between Scanlength and Feed duration indicate that high motivational tendencies for scanning tended to depress feeding and vice versa.

This simple system of either feeding or vigilance taking priority does not fit for rate of scanning, which was correlated with both shortened Feed and Scan durations. Scanning rate was negatively correlated with Grazing Bout length and it seems likely that a high rate of scanning signified the impending termination of a Grazing Bout. A high rate of scanning, therefore, may indicate conflict between feeding and vigilance which is resolved by abandonment of both, and disinhibition of a quite different behaviour bout. (There is also a less significant negative correlation of Grazing Bout length with proportion of time

spent scanning but this is caused by the correlation between rate and proportion and not by increased Scan length). Thus, although both rate of scanning and proportion of time spent scanning are indicators of level of vigilance, it is likely that vigilance is increased by one or the other for different purposes.

That Feed duration and Scan length were (almost significantly) negatively correlated argues against any simple mechanism for feeding and vigilance with an inexorable build-up of motivational tendency for one whilst the other is being expressed. Early 'drive' models might have predicted such a system, and functional considerations might also predict that the longer it has been since a Scan occurred, the longer the animal would scan to make up for it. Since this was not found, it is more feasible to consider that many causal factors, in addition to time since last expression, determine an animal's 'motivational state space' (McFarland and Sibly 1972) and that one behaviour can take priority; here, either scanning or feeding.

Causal factors may be internal or external to the animal. In the case of scanning, external factors are bound to influence, and are likely to be responsible for the positive feedback observed in the longer Scans. Longer Scans must often be occasioned by external stimuli with the rabbit responding to a seen threat by increasing the Scanlength. The probability of ending a Feed is closer to random than that of ending a Scan, which might make headlifts less predictable to a predator (Hart and Lendrem

1984).

The probabilities of Scans ending appeared to change quite abruptly, and this point of change was, for 7 out of the 11 rabbits, at the maximum Chewlength (before it for the rest). This provides circumstantial support for feeding and vigilance behaviour sequences being patterned by a timesharing mechanism. As described above, motivational tendencies for either feeding or vigilance could take priority, and, at the extremes of priority, one or the other could become 'dominant'. (A dominant behaviour in timesharing terminology is the one that patterns the behaviour sequence). When feeding is dominant, scanning might be slotted into the chewing pauses. If a Scan exceeds maximum Chewlength it cannot be being slotted in, and feeding can be assumed not to be dominant. It is at this stage that Scans become more likely to continue. Again, functional considerations can be made, and confining Scans to the permissive Chews enables a rabbit to remain vigilant without sacrificing feeding time.

The possibility of timesharing occurring, with Scan durations being determined by Chewlength, is investigated further in Chapter 8, where experiments into the patterning of behaviour sequences are described. Next I return to a consideration of group-living and the external influences on vigilance.

CHAPTER 7. FACTORS INFLUENCING FEEDING AND VIGILANCE

Rabbits at Oxford did not form groups, but on those occasions that they were together, individuals might have gained from having to spend less time watching out for predators (Bertram 1978). Neither Cowan (1983) nor Garson (pers comm) found vigilance of rabbits to be influenced by the numbers of surrounding rabbits. This may have been because they were unable to separate out the different effects of particular individual rabbits on one another.

Individual rabbits are considered here, for the effects of external factors on vigilance within Grazing Bouts (as defined in Chapter 6). Limiting the investigation to Grazing Bouts removed one source of variation, which was that different behaviours might themselves incur different vigilance requirements. The definitions of Mscan, Mfeed, Prop, Rate and Graze are given in Section 6b. Social factors influencing these measures of vigilance were investigated in isolation as described in Section 7a. In Section 7b, multiple regression techniques were used to see what relative effects social influences had on vigilance. Section 7c describes an experiment to elucidate at what vigilance might be directed.

Section 7a. Social factors influencing vigilance

Mate-rabbits at Oxford were identified in Chapter 4. Social units basically consisted of a mated pair, with occasional 'hanger-on' satellite males (37 and 39), and one case of a bigamous male (36 with 10 and 24). Since no aggression was noted between the sexes, there was probably no competition within a mated-pair; thus individuals would not need to be wary of their mates. Consequently, proximity of the mate would not have lead to increased social vigilance, but indeed would decrease individual's vigilance for predators, for the usual arguments, in that two animals comprise a larger group than one. In contrast, non-mate rabbits, which effectively meant rabbits from different social units, might be associated with increased vigilance because of social interference. This would be most intense between competing, same-sexed rabbits, but also oppositely-sexed rabbits might be wary of one another, not having the established relationship of a mated pair.

Methods

The predictions made were that vigilance would be reduced in the presence of the mate and that it would be increased in the presence of a non-mate rabbit, whether that rabbit were of the opposite sex (providing a direct control to the mate rabbit) or of the same sex. Each non-mate rabbit was selected as that of the appropriate sex from those living closest to the subject.

Grazing Bouts, Feeds and Scans are defined in Section 6a. Whereas in Section 6b, measures of vigilance: Mfeed, Mscan, Prop, Rate, and Graze were calculated for each Grazing Bout, in this Section the unit from which a single measure was obtained was the Condition. The Conditions were:

1a) Mate Present
1b) Mate Absent
2a) Control same-sexed rabbit present
2b) Control same-sexed rabbit absent
3a) Control opposite-sexed rabbit present
3b) Control opposite-sexed rabbit present

Scans and Feeds that occurred within Grazing Bouts within each Condition were made into frequency histograms for each rabbit e.g. every time 10 scanned within a Grazing Bout when her mate, 36 was present, that Scan-duration was added to her Scans histogram for Condition 1a.

Four vigilance parameters were compared for each rabbit between each of the three pairs of Conditions using Wilcoxon signed rank tests. These parameters, prefixed C to define them as relating to a Condition rather than to a Grazing Bout, were:

CMscan. Median Scan duration for the Condition.
CMfeed. Median Feed duration for the Condition.
CProp. The total duration of Scans was summed up for the Condition, divided by the total duration of time spent in Grazing Bouts in that Condition (as in 3), and multiplied by 100.
CRate. The duration of time spent in Grazing Bout behaviours within a particular Condition was obtained by summing the durations of Scans and Feeds occurring within those Conditions. CRate was then calculated as the number of Scans occurring within that Condition, divided by the total duration, and multiplied by 1000.

Table 7.1. Grazing parameters with, (+) and without, (-) other rabbit present. Median scan duration, feed duration, rate, percentage time spent vigilant across all Grazing Bouts for each rabbit in conditions + or -; for different categories of other rabbit: mate, same-sexed rabbit, opposite-sexed rabbit. Each category ends with Wilcoxon's T, number of pairs (N), and 1-tailed probability level (P).

Subj	Othrab	CMscan		CMfeed		CRate		CProp	
Presence:		+	-	+	-	+	-	+	-
Doe	Mate								
33	34	3	4	12	9.5	53	54	22	36
31	35	5.5	5	8	7	61	93	41	48
23	25	5	5	7	7	60	67	33	49
10	36	5	4	8	8	53	60	35	38
24	36	4	4	9	7	49	66	38	38
Buck	Mate								
34	33	4	5	7	6	70	92	39	43
35	31	5	5	9	7	57	62	49	43
25	23	6	5	7	6	66	71	52	56
36	10	5	5	8	7	59	66	39	35
T		15		0		0		10	
N		5		7		9		8	
P		-		<0.01		<0.005		>0.05	
Doe	Doe2								
23	10	3	4	7	12	79	43	26	28
23	10	7	5	3	7	55	60	73	41
10	24	4	5	9.5	8	49	59	28	38
24	10	5	4	8	9	59	53	26	33
Buck	Buck2								
37	34	5	5	8	10	69	42	42	59
34	37	5	4	5	8	83	76	40	42
35	34	5	5	7	8	58	53	37	48
36	39	7	5	10	8	52	57	43	37
39	36	5	3	6	10	67	68	47	37
T		9		7.5		14		17.5	
N		7		9		9		9	
P		>0.05		>0.05		>0.05		>0.05	
Doe	Buck2								
33	36	2.5	4	7	12	76	44	24	29
10	34	5	5	10	9	42	57	34	35
Buck	Doe2								
34	10	5	4	9.5	6	79	77	50	38
37	33	5	5	8	8	51	62	46	50
39	24	5	4	6	8	63	68	52	39
T		7		6		6		6	
N		3		4		5		5	
P		-		-		-		-	

Results

Table 7.1 shows the results of these tests giving the values of parameters for each rabbit in each condition and the overall Wilcoxon T and resulting one-tailed P-levels. Results for both sexes were pooled but there were still not enough data points to adequately test vigilance in the presence of a non-mate oppositely-sexed rabbit (bottom section of table). There did not appear to be any tendency towards decreased vigilance however.

Vigilance in these rabbits was reduced when their mates were present: feed durations were longer and the rate of scanning during grazing decreased (top section of table). Proportions of time spent scanning increased (non-significantly) for all of the females when their mates were absent, but this was not the case for the males.

There were no significant effects on vigilance with the presence of a same-sexed control rabbit (middle section of table). Feed durations tended to become shorter, the opposite effect to that found when the mate was present.

Section 7b. Factors affecting feeding and vigilance

Spurious relationships between vigilance level and mate presence could have been obtained if both covaried with a third, truly causal, factor such as time of day. Further, the distance to other rabbits might be of greater importance than simply their presence or absence. In order to overcome these difficulties, multiple regressions were run, using the BMDP statistical package (BMDP 1979).

Methods

As described in Section 6b, all Grazing Bouts were abstracted from the data for the 11 rabbits and Mfeed, Mscan, Graze, Rate and Prop taken for each Bout. These were each used as dependent variables. Independent variables were the following external factors, measured for each Bout (see Chapter 2):

DATE: (decimalized)
TIME: (decimalized)
GRALEN: Ambient grasslength (1,2,3 or 4)
DISTUR: Presence or absence of disturbance
COWS: Presence of cows within 50m
TEMP: Highest temperature that 24hrs
PPT: Amount of precipitation that 24hrs
CLOUD: Degree of cloud cover (1,2,3,4,5,6,7 or 8)
WIND: Highest wind speed that 24hrs
M: Distance to mate rabbit (1,2,3,4,5,6,7 or 8 (=absent))
MATE: Presence or absence of mate rabbit (uses up variable due to M=8)
DCLO: Number of other rabbits, excluding mate, within 30 rabbit-lengths
DFAR: Number of other rabbits, excluding mate, over 30 rabbit-lengths away

Data used for multiple regressions were restricted to those from evening observations to avert a further source of variation (this lost only two week's data); to pre-August for 10 and 24 because of the complication of 36's disappearance; to those rabbits that had mates i.e. 10,23,24,31,33,25,34,35,36; and, for Graze, to Naturally-Ending Bouts. The identities of the rabbits were added as independent variables, to remove the effects of individual variation. Multiple regressions were first performed on all the data, and then for the females and males separately. These were all repeated in a second bout of regressions which divided up the social factors more finely. Instead of DCLO and DFAR, there were:

KIDCLO: No. subadults and juveniles within 30 rabbit-lengths
MACLO: " male adults " " " "
FEMCLO: " female adults " " " "
KIDFAR: No. subadults and juveniles over 30 rabbit-lengths
MAFAR: " male adults " " " "
FEMFAR: " female adults " " " "

where numbers excluded the mate rabbit.

If a parametric multiple regression is to be a valid test, the residuals must be distributed with equal variance all along the regression line. To check this, normal probability plots of the residuals were constructed. These were plots of the obtained residuals against the values the residuals would have taken had they been normally distributed. Thus, if the residuals are normally distributed, the plots will appear as straight lines passing diagonally through the origin.

Such plots were made of the untransformed data after multiple regression, and were found to be rather poor. It was necessary to transform the data. By trial and error, different transformations were made of the values of the dependent variables until the normal probability plots made straight lines. The transformations used were as follows:

Mscan	transformed to		$\frac{1}{(\text{Mscan} + 2)}$
Mfeed	"	"	Log_{10} (Mfeed)
Rate	"	"	Log_{10} (Rate)
Prop	"	"	Log_{10} (Prop + 30)
Graze	"	"	Log_{10} (Graze)

Results

Tables 7.2-7.4 summarise the significant results of the two bouts of regression runs. The BMDP outputs for the 30 multiple regressions, each with their normal probability plot of the residuals, are shown in Appendix I. Since the MScan transformation involved reciprocating the values, the sign had to be reversed to get the direction of the effect. This has been done for Tables 7.2-7.4. The first bout of regressions was of the small model with other rabbits simply grouped as DCLO and DFAR. The large model subdivided these into age and sex classes. In the small and large models, non-social factors gave similar results; Table 7.2 lists these as found from the small model only.

Table 7.2. Feeding and vigilance factors regressed on independent variables. Significant results for non-social factors; small model. * = P<0.05, ** = P<0.01, *** = P<0.001. Dependent variables for all rabbits, for bucks, and for does listed vertically, independent factors along the top.

	DATE	TIME	GRALEN	DISTUR	COWS	TEMP
ALL						
GRAZE	+	+	−	−**	−	+
MSCAN	+	−	+	+	+	−***
MFEED	+*	+***	−	−	−	+
RATE	−	−***	+	+	+	−
PROP	−	−**	+	+	+	−**
BUCKS						
GRAZE	+	+	−	−*	−	+
MSCAN	+	−	+	−	+	−
MFEED	+***	+**	+	−	−	+
RATE	−**	−***	−	+	+	−
PROP	−*	−**	+	+	+	−
DOES						
GRAZE	−	+	+	−*	−	+
MSCAN	+	−	−	+	+*	−*
MFEED	+	+*	−*	−	−	+
RATE	+	−**	+**	+	+	−*
PROP	+	−*	+	+	+	−

Of the non-social factors, time was the most important modifier of vigilance, with Feeds increasing and Rate and Prop decreasing highly significantly for both males and females as the evening progressed. Date had a similar strong effect on the same parameters but for males alone; vigilance decreasing with season. Disturbance served only to terminate Grazing Bouts for both sexes. It was the females that were most affected by cows, increasing their Scanlengths. Temperature had the odd effect of reducing Scanlength, and thus reducing Prop (and also Rate in females). Grasslength affected only females, that increased their Rate.

With multiple regressions, it is possible to get a large number of odd, uninterpretable results. These should be treated with cirumspection and only highly significant factors taken very seriously, since there are problems with multiple testing. What was important for this analysis was to remove the strong effects of time and date particularly, and to unravel the different social influences. Nevertheless, it has thrown up these interesting results for temperature, and shows that date affected male vigilance only.

Table 7.3. Feeding and vigilance factors regressed on independent variables. Significant results for social factors; small model. * = P<0.05, ** = P<0.01, *** = P<0.001. Dependent variables for all rabbits, for bucks, and for does listed vertically, independent factors along the top.

	M	DCLO	DFAR
ALL			
GRAZE	-	-	-
MSCAN	-	-	+
MFEED	-**	-**	-
RATE	+*	+*	+
PROP	+	+	+*
BUCKS			
GRAZE	-	-	-
MSCAN	-	+	+
MFEED	-*	-*	-
RATE	+*	+	+*
PROP	+	+**	+
DOES			
GRAZE	-	-*	-
MSCAN	+	-	+**
MFEED	-*	-*	-
RATE	+	+**	-
PROP	+	-	+**

The significant results for social factors from the small model are presented in Table 7.3. These bear out the results of Section 7a, in that the effect of the mate rabbit can be contrasted to that of other rabbits. The variable MATE (mate present or absent) never reached significance and it was distance to the mate (M) that was important. As this increased so did vigilance. In contrast, the more other rabbits there were about, both near and far, the greater the vigilance.

It is interesting to see which vigilance parameters were being affected. With distance to mate, the rate of scanning was increased by a decreased Feed duration; the effect was slightly stronger for males. Rabbits close-up affected males and females differently; both decreased their Feed durations, which for females meant a faster scanning rate, but for males, with slightly increased Scanlength, Prop was increased. For rabbits farther off, it was the females that increased Prop with increased Scanlength, and the males that had a higher rate of scanning.

From Table 7.4, it can be seen that the increased vigilance with non-mate rabbits about, was mostly due to the presence of females and subadult rabbits. With these fine divisions of other rabbits, the effects on males all became non-significant. It must be remembered that all of these measures were made during Grazing Bouts. Extremes of vigilance as were likely to occur between bucks preparing for chasing, might have been more common outside grazing. Also with these subdivisions, the data sets will have been

quite small, and the results less reliable. The results for distance to mate (M) are not repeated for the large model; they are similar to those in the small model, although not always reaching the same significance levels (see Appendix I for details).

Table 7.4. Feeding and vigilance factors regressed on independent variables. Significant results for social factors; large model. * = P<0.05, ** = P<0.01, *** = P<0.001. Dependent variables for all rabbits, for bucks, and for does listed vertically, independent factors along the top.

	FEMFAR	KIDFAR	FEMCLO	KIDCLO
ALL				
GRAZE	-	+	-	-
MSCAN	+	+	-	+
MFEED	-	-	-*	-
RATE	+	-	+	+
PROP	+**	+	+	+*
BUCKS				
GRAZE	+	+	+	-
MSCAN	+	-	+	+
MFEED	-	-	-	-
RATE	+	+	-	+
PROP	+	+	+	+
DOES				
GRAZE	+	-	-*	+
MSCAN	+	+*	-	+
MFEED	-*	+	-	-
RATE	+	-	+*	+
PROP	+**	+	+	+

In summary, even with date and time and other non-social factors taken into account, rate of scanning increased with distance to the mate. In contrast, the presence of other rabbits close by predicted increased vigilance. For does, the rate of scanning was high when

rabbits, particularly young but also other does, were close-by. The proportion of time spent scanning increased with more young and female rabbits far off. Bucks had a higher proportion of time spent vigilant when there were more rabbits close up, and a higher rate of vigilance with more far off.

Section 7c. Stuffed-animals experiment

Having found from observational data that the presence of non-mate rabbits increased a rabbit's vigilance, the next step was to see whether this effect could be elicited by experiment. Stuffed animals were used to see whether predators and conspecifics would both raise vigilance. A stuffed pheasant and an empty trolley were used as controls.

Methods

A 17-day experiment was run from dusk 26th June to dawn 12th July 1983, on rabbits at the Oxford site. Four treatments were presented to the rabbits:

1) Stuffed Fox
2) Stuffed Rabbit
3) Stuffed Pheasant
4) Empty Trolley

Only rabbits living close to the hide and therefore within 70m of the stimulus object were used for this experiment. Does 10 and 24 and buck 36 were the known adults from the previous field season. 76 was a battered looking male; he may have been one of bucks 34 or 39 from the previous year. 78 and 79 were large sub-adult rabbits, 77 a little younger, and 80 a kitten rabbit, all of unknown sex. These untagged rabbits were all individually recognizable.

The trolley itself was painted green, and its height did not exceed that of the surrounding grass. When a

stuffed animal was mounted on it, this would be apparent above the height of the grass. The sizes of the stimulus objects were unfortunately different, the Fox was largest, then Pheasant, then Rabbit.

The experiment was arranged as a Latin square, with one treatment presented each night. If F,R,P and T represent Stuffed Fox, Stuffed Rabbit, Stuffed Pheasant and Trolley treatments respectively, then the order was:

Replicates	Days	Treatments			
1	1- 4	R	F	T	P
2	5- 8	F	P	R	T
3	9-12	T	R	P	F
4	13-16	P	T	F	R

This particular Latin square was arranged such that every treatment followed every other treatment at some stage (Cochran and Cox 1957).

Each evening, the cows were herded into an adjoining field and fenced off with barbed wire. The trolley, attached to the hide by a string running through the grass and up to the hide-window through staples, was pulled out into the centre of the rabbits' area. The stimulus-object was mounted on to the trolley and I retired to the hide, waited until the rabbits emerged, and proceeded to collect data from each rabbit.

Since the evenings were quite variable in the amount of human disturbance, each treatment was repeated the following dawn. I arrived at about 0430 to set up the treatment again (the equipment was stored in the hide overnight). The cows were allowed back into the field after the dawn session. On

average, I retired to the hide at 1730 in the evening, or 0500 at dawn, and commenced data collection after 20mins.

Data were taken once for each rabbit during an observation session. When the rabbit was engaged in a Grazing Bout, and close to the stimulus object, data collection was initiated. For at least 60s, continuous observation and recording of the rabbit's Feeds and Scans were made in the usual way. The string to the trolley was then pulled in for 6s to bring in one metre of string, thus pulling the stimulus object forward a metre. The string was secured and the rabbits' grazing parameters observed and recorded for at least a further 60s. The procedure was repeated for each rabbit.

Feeding and vigilance parameters for the 60s which began 10s after the beginning of trolley-pulling, were used. Two sets of data were obtained: the number of Scans and the number of seconds spent scanning. To simplify the analysis, dawn data alone were used, because the data set was more complete and because dawns were less disturbed. The results were analysed using an ANOVA with partitions and with the missing data values accounted for.

Table 7.5. Numbers of seconds spent scanning. The number of seconds spent scanning per 60s is given for each rabbit in the first part of the Table. The 16 dawn periods go from left to right, with each four consecutive periods representing a complete set of treatments, which were repeated four times. The Anova follows.

	Days 1-16															
Rabbit																
10	43	10	45	19	8	19	34	12	25	26	14	10	11	15	32	6
24	25	60	8	27	36	33	37	15	12	52	12	10	24	7	60	4
78	30	22	20	8	15	20	20	13	15	31	30	17	2	27	28	60
36	16	40	16	14	11	50	26	37	15	44	1	19	19	9	25	35
77	43	37	27	25	15	0	16	45	3	24	0	23	16	3	11	4
76	-	60	31	-	-	16	12	11	0	42	16	13	17	16	15	6
79	29	60	-	9	40	-	-	28	10	22	-	26	12	-	-	37
80	-	-	17	55	12	52	22	20	2	31	24	14	24	10	16	27

ANOVA table of number of seconds spent scanning in 60s.

	Df	SS	MSq	VR	P
S=Between Subjects	7	954.84	136.41	0.61	N.S.
Within Subjects	109	24346.41	223.36		
R=Between Rows	3	2007.08	669.03	4.00	<0.05
C=Between Columns	3	1866.73	622.24	3.61	<0.05
T=Between Treatments	3	2062.44	687.48	3.05	0.05<p<0.1
(Rb-Fx x Tr-Ph)	1	1922.13	1922.13	12.27	<0.01
(Rb x Fx)	1	59.43	59.43	0.34	N.S.
(Ph x Tr)	1	80.89	80.89	0.23	N.S.
RxS	21	3512.75	167.27	0.98	N.S.
CxS	20	3702.75	185.14	1.09	N.S.
TxS	21	4733.18	225.39	1.33	N.S.
(Rb-Fx vs Tr-Ph)xS	7	1096.44	156.63	0.92	N.S.
(Rb vs Fx) xS	7	1211.32	173.05	1.02	N.S.
(Ph vs Tr)xS	7	2425.49	346.49	2.04	N.S.
Within squares	38	6461.49	170.04		
Total	116	25301.25			

Results

Table 7.5 shows the results for the amount of time spent scanning. The variance ratio for the treatments sum of squares fell just short of significance. It was reasonable however to test the three hypotheses: that treatments Fox and Rabbit raised vigilance relative to Trolley and Pheasant, that the Fox and Rabbit treatments did not differ, and that the control treatments did not differ. This was tested by means of orthogonal contrast.

a) Rabbit and Fox vs Trolley and Pheasant
b) Rabbit vs Fox
c) Pheasant vs Trolley.

The partition of the relevant sums of squares are shown in the table. It turned out that the first contrast (a) was highly significant (at the 0.01 level of significance) while the other two were not. This is despite the fact that the Pheasant was larger than the Rabbit; the Rabbit still caused the higher vigilance.

Table 7.6 gives the results for the number of scans in the 60s following the pulling of the stuffed animal; none of the effects were significant.

Table 7.6. Numbers of Scans. Number of scans in 60s is given for each rabbit. The 16 dawn periods go from left to right, with each four consecutive periods representing a complete set of treatments, which were repeated four times. The Anova follows.

	Days 1-16															
Rabbit																
10	6	2	2	4	3	4	4	4	5	5	3	5	2	5	3	2
24	4	1	2	4	5	4	5	4	4	3	3	4	8	2	1	1
78	3	4	3	3	5	5	7	3	5	4	4	2	2	7	6	1
36	4	5	4	3	3	2	5	5	3	6	1	3	2	3	4	3
77	5	3	5	5	4	0	6	4	2	7	0	6	5	1	4	2
76	-	1	4	-	-	4	4	4	0	2	4	5	5	4	3	2
79	3	1	-	3	5	-	-	3	1	5	-	7	2	-	-	7
80	-	-	2	2	2	2	5	4	2	3	3	3	6	1	5	5

ANOVA table of number of scans in 60s.

	Df	SS	MSq	VR	P
S=Between Subjects	7	7.19	1.03	0.35	N.S.
Within Subjects	109	319.58	2.93		
R=Between rows	3	8.21	2.74	1.57	N.S.
C=Between columns	3	2.34	0.78	0.23	N.S.
T=Between Treatments	3	13.14	4.38	1.27	N.S.
(Rb-Fx vs Tr-Ph)	1	9.70	9.70	1.64	N.S.
(Rb vs Fx)	1	3.44	3.44	3.56	N.S.
(Ph vs Tr)	1	0.00	0.00	0.00	N.S.
RxS	21	36.62	1.74	0.56	N.S.
CxS	20	68.39	3.42	1.10	N.S.
TxS	21	72.51	3.45	1.11	N.S.
(Rb-Fx vs Tr-Ph)xS	7	41.27	5.90	1.89	N.S.
(Rb vs Fx) xS	7	6.76	0.97	0.31	N.S.
(Ph vs Tr)xS	7	24.49	3.50	1.12	N.S.
Within squares	38	118.36	3.11		

Section 7d. Discussion

As expected, different classes of rabbits had different effects on the vigilance of conspecifics. For these rabbits, in the simplest of social units, with a buck and a doe, vigilance decreased with the mate closer. This might be caused by any of three factors:

i) Vigilance for predators might be reduced with the presence of the extra pair of eyes.
ii) Vigilance to avert harassment or to instigate interactions with other rabbits may be unnecessary in the presence of the mate.
iii) Animals might actively search out their mates.

The presence of conspecifics other than the mate increased vigilance in bucks and does, but particularly in the latter. Social vigilance could be accounted for by four factors:

a) That an animal was about to instigate an interaction with another.
b) That it was preparing to respond to such an interaction.
c) That it was watching out for predators on behalf of the others.
d) That it was keeping watch on rabbits to avoid or encourage their proximity.

The stuffed animals experiment supported the earlier conclusion that increased awareness for predators is not

always an advantage that pertains to sociality, since the presence of unknown rabbits (which the Rabbit Treatment in the experiment sought to imitate) caused increased vigilance.

The experiment also showed that it was the proportion of time spent scanning that was affected by the stuffed animals, and not the number of Scans. If a rabbit had something to watch, it watched it rather than just checking up on it with increased rate of vigilance. And of course, longer scans will also have the effect of decreasing the rate of scanning.

Vigilance for predators and for other rabbits could not be separated out as affecting rate and proportion of time spent scanning respectively. It is likely that both parameters will be affected by both factors: a higher rate occurring when the situation is likely to change quickly but there is no immediate problem to monitor; a higher proportion occurring when something is going on which the rabbit might watch in preparation for reacting to. These interpretations are interesting in the light of the multiple regression results: it is rate that is increased with distance to the mate, supporting the ideas that the rabbit is checking out for predators or for the mate itself (factors i and iii), though it has nothing particular to monitor. Social vigilance increases Prop for bucks with rabbits close-up, perhaps as they prepare to instigate social interactions, and increases Rate for does, perhaps as they prepare to ward off advances.

CHAPTER 8. INTERACTION BETWEEN FEEDING AND VIGILANCE

A further influence on the extent and occurrence of vigilance during Grazing Bouts will be the effects of the feeding behaviour itself. Once feeding has taken priority, and there is no pressing occasion for high vigilance, the necessary 'checking' vigilance might be wholly patterned by the occurrence and durations of Chews. These permissive activities allow scanning to occur without interrupting feeding. Sections 8a-8c investigate this with data from observation and experiment.

When there is a higher need for vigilance, Scans will lose their strong dependence on Chewlengths. If vigilance is not so vital that grazing must end, it may retain some relationship with Chewlength: it may be partly determined by it, or vigilance itself might influence Chewlength, causing the rabbit to select longer pieces of food to enable longer Scans. These possibilities are investigated by experiment in Sections 8d and 8e.

Section 8a. Chewlength and Scanlength

Methods

Observational data from the 11 Oxford rabbits (1982) were used to see whether Chewlength and Scan duration were related. Frequency histograms of three types of Scans were extracted for each rabbit using a computer program. Each Scan within a Grazing Bout could include Chews, Undefineds and Non-Chews (see Table 6.1). If there had been no indication as to whether there had been particular food-sizes in the mouth, or none as to whether chewing had even occurred, that Scan was omitted (i.e. if it comprised Non-Chews with Chews 3) and/or Undefineds). The remaining Scans could be divided into three types:

i) Non-Chew Scans were of Non-Chews only
ii) Short-Chew Scans included Chews 1) and could also contain Chews 3), Undefineds and Non-Chews.
iii) Long-Chew Scans included Chews 2) and could also contain the other Chews, Undefineds and Non-Chews.

Chew-Scans were defined as ii) and iii). For each rabbit, the number of, and the median duration of each Scan type was obtained. A Friedman two-way ANOVA was performed on the medians across the three Scan types.

Results

In Table 8.1, the median durations are set out for each rabbit for each Scan type. Note that by the method used, Scan types did not overlap, each count for a Scan type being exclusive to that type. The results were significant (N=11,

k=3, χ_r^2=13/95, Df=2 and P<0.001), with Long-Chew Scans being the longest, then Non-Chew Scans, then Short-Chew Scans. Although the Anova does not give significant difference levels between each group, Long- and Short-Chew Scans must have been significantly different, being at opposite poles.

Table 8.1. Median Scan durations for different Scan types. LC = Long-Chew Scans, SC = Short-Chew Scans, NC = Non-Chew Scans.

	Scan Type		
	LC	SC	NC
Rabbit			
10	6	4	4
23	7	4	5
24	6	3	5
25	10	4	9.5
31	1.5	5	5
33	6	3	4
34	8	4	4
35	9	5	8
36	6	3	4
37	8	5	7
39	5	3	4

Table 8.2. Frequency of occurrence of Non-chew (NC) and Chew-Scans (CS).

Rabbit	NC	CS
10	153	1161
23	57	206
24	168	707
25	26	162
31	23	129
33	103	316
34	99	353
35	45	151
36	118	567
37	20	138
39	85	357

In Table 8.2 the numbers of Non-chew Scans are compared with the total numbers of Chew-Scans. For each rabbit, Chew-Scans occured much more frequently, between three times and eight times as often as Non-Chew Scans.

Section 8b. Manipulating grasslength in the field

Observational data (Section 8a) showed that Scanlength and Chewlength were related. The following experiment was run to discover the direction of the dependence: available food-length was manipulated to see whether it affected vigilance. High ambient grasslength might have three effects: a) allowing lower vigilance by the greater cover; b) requiring higher vigilance for the decreased visibility; or c) allowing longer Scans by the provision of longer pieces of grass for extended Chew-Scans. In Section 7b, greater ambient grasslength was found (for does) to be correlated to higher rates of scanning and shorter feed durations; effect b) was occurring. This experiment was designed to find out whether effect c) also occurred.

Ideally, the rabbits would have been trained to feed from food piles, which could have been controlled. However, repeated efforts at Walney in 1981 and at Oxford in 1983 to attract the rabbits to grain, apple, carrot etc. met with no success (the cows and crows were more responsive).

Methods

The experiment was run in 1983, when nine rabbits were known to be regularly using a patch of grass 90x32m (some using some areas and others using other). These were the same rabbits used in the last experiment described in Section 7c. The area was divided up into 36 blocks, each 10x8m. One of three treatments was applied to each plot on

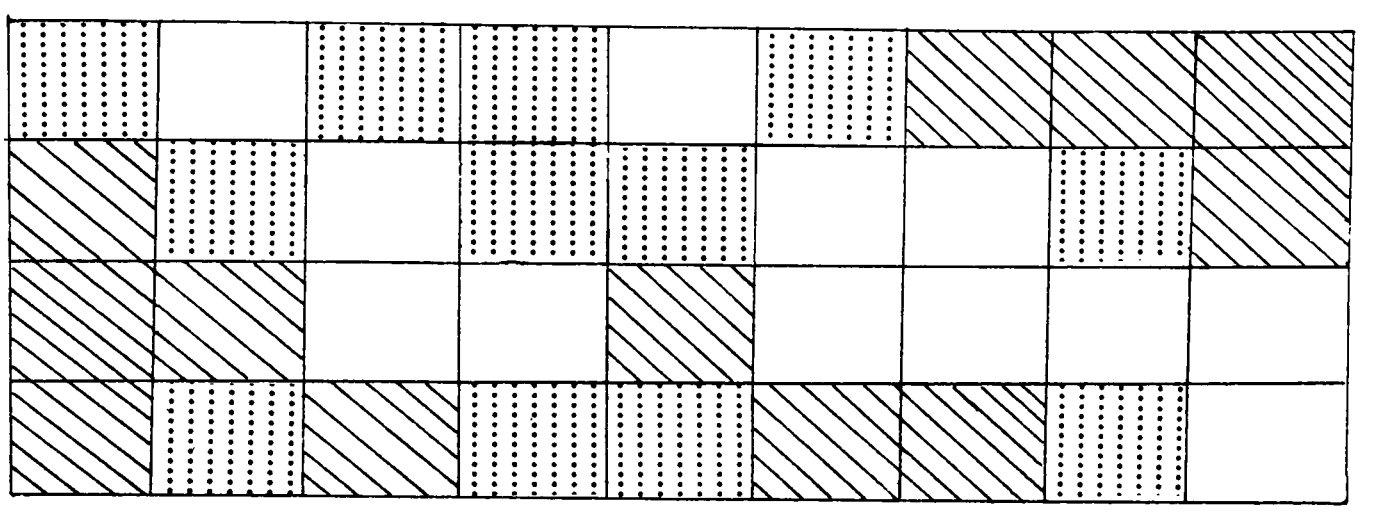

Fig 8.1. Grasslength experiment.
Randomised plots arranged with:

= short mown grass.

= short grass with cuttings left lying.

= long grass.

Each plot was 10 x 8m.

July 15th and on the morning of July 16th, as follows:

(i) Grass was mown, and the cuttings raked off (MOWN).
(ii) Grass was mown, and the cuttings left to lie (LAIN).
(iii)Grass was left long (UPRIGHT).

Those plots that were already of fairly short grass were randomly assigned to either (i) or (ii). If to ii), cuttings were sprinkled over them from Treatment i) plots that had been of long grass. The rest of the plots were randomly assigned to either (i), (ii) or (iii), to produce equal numbers of each plot type. The resulting arrangement is depicted in Fig 8.1.

Data were collected in two sessions: on the evening of July 16 (1700-2100), and the following dawn (0500-0900). Each of the nine rabbits was watched in each plot type (fortunately they all went into each one). The area was scanned for a rabbit grazing in a plot in which it had not previously been recorded, and a continuous record of its behaviour was made. Feeding and vigilance parameters described in Section 6a were extracted from these data. If the rabbit moved into another plot, or the Grazing Bout ended, before 60s was up, that record was abandoned and made on a later occasion.

The number of seconds that each rabbit spent in Scans during the first 60s of each record was obtained, and a two-way classification ANOVA was used to analyse these data. The different rabbits were the replication, and the plot

types were the different treatments. In addition, Newman-Kreuls test was run to find which of the differences were significant (Armitage 1971). This involved taking the within groups mean sum of squares (here the sum of squares of the replicates plus the error term divided by the sum of their degrees of freedom) to estimate the standard error (s) and calculate Q where

$$Q=\frac{\max(Y_i)-\min(Y_i)}{s/\sqrt{n}}$$

where Y are the mean values for treatment groups and n is the number of replicates in the group. The critical values of Q depend on the within groups degrees of freedom and the number of groups being compared.

Results

Table 8.3 gives the results and analysis and shows that all comparisons were significant. Long grass was available in both treatments LAIN and UPRIGHT, and a higher proportion of time was spent in vigilance in these two treatments than in MOWN. This increased proportion of time spent scanning was at least partly due to the availability of long pieces of grass for Chew-Scans. If it had been entirely due to decreased visibility then there would have been no difference between the MOWN and LAIN plots. Visibility may have been decreased on the LAIN plots as the lying grass had some bulk. However, the rabbits' eyes were still well above the level of the lying grass even when the rabbit was

cropping. Also vigilance tended to be higher in LAIN than in UPRIGHT despite the lower visibility in the latter. Interference with the area by the experimenter did not cause increased vigilance, since those plots least interfered with (UPRIGHT) were the places where vigilance was high. (Also the fields were mown periodically by the farmer, so the adult rabbits had experienced such an event before).

Table 8.3. Amount of time (s) spent scanning in different plot-types during 60s by each rabbit, with 2-way Anova.

	Rabbit								
	10	24	33	36	76	77	78	79	80
Plot type									
(i) MOWN	3	3	1	1	1	0	8	11	7
(ii) LAIN	34	18	17	13	23	29	20	39	13
(iii)UPRIGHT	17	22	22	13	11	21	13	13	16

Anova

Source of Variation	Df	SS	MS	F
Columns (replicates)	8	317.19	39.65	1.00
Rows (treatments)	2	1680.52	840.26	21.25
Error	16	632.81	39.55	
Total	26			

Vigilance levels in the three plot types differ with $P<0.001$ ($F=21.25$, $Df=2,16$).

Newman-Kreuls comparisons

Within groups Ssq=950; Df=24; Msq=39.58
$s/\sqrt{n}=\sqrt{(39.58/9)}=2.097$
Ordered means: (i) 3.889 (iii)16.444 (ii)22.889
Q(ii-i) = (22.889-3.889)/2.097 = 9.06; p<0.01
Q(ii-iii) = (22.889-16.444)/2.097 = 3.07; p<0.05
Q(iii-i) = (16.444-3.889)/2.097 = 5.99; p<0.01

Each group was significantly different from each other.

Section 8c. Ambient grasslength and reaction times

An experiment was run to determine whether rabbit-awareness was actually improved on those plots of Section 8b where the rabbits had shown greatest vigilance. The alternative hypothesis was that headlifts whilst chewing were simply more comfortable positions and subserved no vigilance function.

Methods

The experiment was conducted in four sessions, two dawn and two dusk sessions over two days, commencing with the dusk watch on July 17th 1983. The set-up with treatments and rabbit subjects, was the same as in Section 8b. Assistant human 'predators' were selected on the grounds of their willingness to perform. One woman assisted for the two dusk sessions, a different woman for the first dawn, and a man for the second dawn.

On arrival at the site I climbed up into the wooden hide and the assistant lay down in the grass beneath the hide, out of sight. The assistant was attached to me by a piece of string wrapped around his or her finger and passing up through the window of the hide to the main string-ball.

The area was scanned for a rabbit grazing in a plot type for which its response time had not yet been recorded. The number of the rabbit was recorded, as well as the plot type it was in. I then tugged on the communication string to alert the assistant. The assistant readied his or

herself, and, when prepared, gave an answering tug. A '1' was keyed into the recorder, signifying the start of the response time, as the assistant stood up and started walking toward the rabbit patch. I let out the string as the assistant walked at a predetermined pace along a specific path. When the rabbit exhibited a startle response, a '2' was recorded. The duration of time for which '1' had lasted was taken as the response time.

The startle response varied: sometimes the rabbit would run off, sometimes stop feeding and remain still, sometimes raise its head and keep it still. It was often difficult to ascertain whether the rabbit had observed the assistant and easier to tell in retrospect. If the rabbit settled back to feeding, that response time would be scrapped and recorded on a later occasion; if it ran off, then the response time was used.

When the rabbit responded, I tugged on the communication-string and the assistant returned to his or her starting position beneath the hide. I reeled the string in and waited for the rabbits to re-settle, before repeating the whole procedure.

Results

The response times and the Anova are shown in Table 8.4. The F-value between plot types was 1.09, not significant with Df=2,16. Thus, this experiment showed no differences in response times for rabbits reacting to a potential human predator, between the three plot types of

Table 8.4. Reaction times in different plot types for each rabbit; with 2-way Anova.

Response times in seconds

	Rabbit								
	10	24	33	36	76	77	78	79	80
Plot type									
(i) MOWN	30	14	13	46	25	10	16	6	11
(ii) LAIN	16	62	27	50	3	33	25	29	2
(iii)UPRIGHT	28	13	57	46	26	32	16	21	12

Anova

Source of Variation	Df	SS	MS	F
Columns (replicates)	8	2930.65	366.33	1.77
Rows (treatments)	2	451.56	225.78	1.09
Error	16	3316.46	207.28	
Total	26			

There was no difference in response times in the three plot types ($F=1.09$; $Df=2,16$; $p>0.25$)

mown grass, mown grass with the cuttings lying there, and long grass. This is either because there genuinely were no differences, or because the experiment was inadequate to show them up. There were faults in the experiment:

1) Each rabbit might have been tested anywhere in the experimental area as long as it was on the right plot type. Thus its distance from the hide could be 10-100m. In practice buck 36 ranged farthest, over 60m. The rabbits responded less quickly if the disturbance was further off, partly because they took longer to perceive it, but also because they would not respond to humans until they were fairly close. (I was able to approach within 20m of the rabbits before they took flight). Analysis could have taken account of distance to the hide, but this had not been recorded.

2) The actual startle response of the rabbit could be

equivocal. Although each response used led into a flight response, the rabbit may have spotted the danger earlier than was apparent.

3) This experiment was a rather gross test of whether Chew-Scans increased awareness. Response time in different plot types did not take account of what the rabbit was doing in the plot e.g. it might have been in a type (i) plot, having found a leaf with which to sit up and chew. Replications would have overcome this problem, but time and repetitions were limited as:

a) The rabbits might have either become overwary or else accommodated to the disturbance.

b) The grass cuttings were drying out to form hay which could not be compared directly to the fresh grass treatment.

The null hypothesis that Chew-Scans afforded no extra awareness was not properly tested here as the occurrence of Chew-Scans might have been affected by the particular conditions of the experiment. That reponse times were the same in each plot might have been due to the rabbits maintaining a minimum response time. With the continual presence of a human nearby, their vigilance might have been raised to the maximum possible whilst grazing. The following Section shows that the presence of a potential threat affects the occurrence of Chew-Scans.

Section 8d. Further analysis of Stuffed Animals experiment

During normal feeding, the durations of Scans are at least partly determined by Chewlength. When vigilance requirements are increased, but not so greatly as to terminate feeding, either of two effects might occur. Large mouthfuls might be selected by the rabbit to permit long Chew-Scans, or Non-Chew-Scans might become more frequent. The Stuffed Animals experiment (Section 7c) was designed to alter vigilance requirement, and was found to increase vigilance when either Fox or Rabbit treatment obtained. This Section re-analyses a small part of those data to see whether mouthful-size selection was influenced by treatment.

Methods

From the dawn data, the number of Non-Chew-Scans, Long-Chew-Scans and Short-Chew-Scans (Section 8a) in the 60s following the movement of the Stuffed Animal were obtained for each rabbit under each treatment. Counts were added for each rabbit over the four replicate days of a treatment. Long-Chew-Scans and Short-Chew-Scans were summed to give Total Chew-Scans, and these summed with Non-Chew-Scans to give Total Scans. The proportions of Total Chew-Scans that were Short-Chew-Scans, and of Total Scans that were Chew-Scans, were obtained for each rabbit and two comparisons were made, between:

1) Trolley and Fox
2) Trolley and Rabbit

For each rabbit the differences between proportions for each pair of treatments were calculated. Information was combined across rabbits using Cochran's method for combining 2x2 tables, as described in Armitage (1971). The mean difference D and standard error of this difference SE(D) was calculated across rabbits. A normal standardized deviate D/SE(D) was obtained to indicate the significance of the differences between treatments. Weights were given to rabbits.

Table 8.5. Frequencies of Scan types in different Conditions of experiment of Section 7c. NC = Non-Chew-Scans. LC = Long-Chew-Scans. SC = Short-Chew-Scans.

	TROLLEY			FOX			RABBIT		
	NC	LC	SC	NC	LC	SC	NC	LC	SC
Rabbit									
10	1	5	12	7	1	5	3	7	7
24	6	1	3	6	4	0	7	3	2
33	0	1	7	6	0	0	4	2	1
36	2	8	3	7	6	3	7	5	6
76	3	1	9	2	0	7	5	1	3
77	2	7	3	10	2	4	5	5	10
78	5	1	11	2	6	9	7	4	2
79	1	2	1	7	1	5	6	5	4
80	1	4	4	4	0	5	6	2	5

	Rabbit Condition compared to Trolley Condition	Fox Condition compared to Trolley Condition
Difference in proportions of Short-chew Scans to Total Chew Scans	D=-0.0451 SE(D)= 0.0833 D/SE(D)=-0.54 N.S.	D= 0.051 SE(D)= 0.0762 D/SE(D)=-0.67 N.S
Difference in proportions of Non-chew Scans to Total Scans	D= 0.2024 SE(D)= 0.0595 D/SE(D)= 3.39 P < 0.001	D= 0.2555 SE(D)= 0.0636 D/SE(D)= 4.02 P < 0.001

Results

Table 8.5 gives the counts of each Scan type under each relevant condition, for each rabbit, and shows the analysis. With both Rabbit and Fox treatment, there was a higher proportion of Non-chew Scans to Chew-Scans than in the control Trolley treatment. The proportions of Long-Chew-Scans to Short-Chew-Scans were not significantly different from the control. As suggested in the last Section, a manifest threat raises vigilance above the levels provided for by Chew-Scans. The number of Non-Chew-Scans increased as the need for vigilance was raised. Longer mouthfuls were not selected to permit longer Scans.

Section 8e. Feeding and vigilance in the laboratory

This experiment was devised to see whether vigilance requirements could be made to influence feeding behaviour. Rabbits presented with large pieces of food were expected to eat more, when afraid, than if offered small pieces. Long pieces would take longer to chew (which could be done whilst scanning), and would require less collection time, so releasing the rabbit for the needed vigilance.

Methods

The experiment was attempted on three rabbits: Belinda, a Dutch doe that normally lived free-ranging in an orchard; Solomon and Angel, a buck and doe from a zoo. Angel died of an intestinal worm infestation before the experiment got underway.

The food-type used was dandelion leaves, either chopped up small or presented intact. Solomon would not eat them, and was given either long peels of carrot or chopped peels. Vigilance level was manipulated by bringing a ferret into the room or not doing so. The procedure was to present the rabbit with 15g of short or of long food and to leave it with the rabbit for 90s. If in a 'Scare' Condition, the caged-ferret was brought into the test-room 45s before the food arrived and was left there throughout the test-run, out of sight. The Conditions were:

A Short Food, Scare
B Short Food, Non-scare
C Long Food, Scare
D Long Food, Non-Scare

When 90s was up, the remainders of the food (and the ferret if present), were removed. The food was weighed to see how much had been eaten.

It took almost one month of investigation to come up with this design. Previous designs had involved using two mixed food-types: cauliflower and dandelion leaves, but the latter deteriorated too fast relative to cauliflower leaves. In another design the long and short dandelions were mixed, to test the hypothesis that the proportions of different sized ones taken would alter under different Conditions. This method suffered from the complication of the long dandelion leaves being easier to pull out anyway, since they were more protrusive. The extent of ferret-exposure that the rabbit received had to be finely tuned such that the rabbit would continue to feed, and yet be nervous. Manipulations of hunger-levels were also tried out. Food deprivation made the rabbits too hungry so that they would ignore a slight predation threat. Finally, they were fed the night before, but food was removed an hour before testing and there was no re-provisioning until after the experiment.

Each rabbit was run, receiving each Condition each day for four days, the order arranged by a Latin square (Cox 1958):

	BELINDA				SOLOMON			
TIME:	10.00	11.30	13.00	14.30	10.00	11.30	13.00	14.30
Day 1	B	C	D	A	A	B	D	C
Day 2	D	A	B	C	B	D	C	A
Day 3	C	B	A	D	D	C	A	B
Day 4	A	D	C	B	C	A	B	D

Table 8.6. Quantities of food (g) eaten under different Conditions

	Belinda		Solomon	
	Scared	Not Scared	Scared	Not Scared
Short	3.00	5.25	0.50	10.00
	0.50	7.00	7.50	9.00
	0.00	6.25	11.00	10.00
	0.25	7.00	1.50	11.00
Long	5.25	5.75	5.00	9.50
	5.50	6.25	8.50	9.50
	4.50	5.75	9.00	7.50
	7.25	6.00	7.50	9.00

<u>Belinda</u>

Source of variation	Df	SS	MS
Between rows (Prey Length)	1	18.06	18.06
Between columns (Fear)	1	33.06	33.06
Interaction (Fear × Length)	1	26.27	26.27
Error	12	12.09	1.01
Total	15		

Variable	F	Df	P
Prey Length	17.9	1,12	<0.005
Fear Level	32.81	1,12	<0.001
Interaction	26.07	1,12	<0.001

<u>Solomon</u>

Source of Variation	Df	SS	MS
Between rows (Prey Length)	1	1.56	1.56
Between columns (Fear)	1	39.06	39.06
Interaction (Fear × Length)	1	12.25	12.25
Error	12	88.87	7.41
Total	15		

Variable	F	Df	P
Prey Length	0.21	1,12	>0.1
Fear Level	5.27	1,12	<0.05
Interaction	1.65	1,12	>0.10

Results

In Table 8.6, the amounts of food eaten under each Condition are given for both rabbits. The two rabbits' data were analysed separately, using two-way analyses of variance.

Both rabbits ate less when afraid, and Belinda showed a strong effect in the interaction term i.e. when she was afraid she would eat more long food than short food. This was over and above her tendency to eat more long than short food anyway. This might have been partly due to long pieces enabling chewing whilst scanning, but is also probably due to the longer pieces being more accessible and easily plucked without an extended Feed. Solomon's carrots collapsed and stuck together more, making them less accessible. But chiefly for him, feeding or vigilance appeared to be all-or-nothing; and rather than performing both in a bout, he would feed or be vigilant.

Section 8f. Discussion

These experiments show that aspects of feeding behaviour do affect vigilance. In normal feeding, the durations of Scans are related to, and indeed determined by the size of the mouthful that the rabbit has to chew. This was found from observational data and confirmed by experiment. The confounding factor of long mouthfuls being more available in long grass where vigilance is impaired but cover is increased, was controlled for in the experiment. Thus Chewlength, the duration of a pause from feeding with the head down, influences the duration of a Scan. If it wholly determined it, timesharing would provide an operational definition of the sequence of events, calling feeding the dominant behaviour since it determines the times of onset and termination of the subdominant scanning behaviour.

It may not always be that Chewlength itself is determined by feeding requirements. A rabbit wanting to scan may choose longer mouthfuls. It could collect more grass in its mouth for a protracted Scan, or just grab small pieces for frequent Scans. The implications for nutrition are interesting, with food selection not being wholly dependent on the quality of the foodstuff.

When vigilance behaviour is called upon, with the threat of stuffed animals, ferrets or perhaps humans, rabbits make little effort to use their scanning periods for chewing, and more Non-Chew-Scans occur.

There could then be a continuum between different grazing states. With feeding dominant, Scans are determined by Chewlengths. In the middle state both feeding and vigilance are called for and long pieces of food can be selected. In the state at the other end of the spectrum, vigilance becomes dominant and Non-Chew-Scans take precedence, feeding being slotted into periods when vigilance is not required. Beyond this, feeding will be completely abandoned. Belinda exemplified the middle state. This is a likely state to occur when, for example, a rabbit is about to initiate an interaction with another, and needs a high proportion of time spend scanning to assess the situation, but not a high rate of scanning, since the rabbit itself is in no immediate danger. Thus it has time to select or gather a large mouthful (see Section 7b).

CHAPTER 9. BLOOD

Blood had been taken from all caught rabbits for analysis to assess the genetic structure of the populations. It proved to be difficult to obtain pedigrees of rabbits by observational techniques, particularly since there was more than one study site. Blood data alone were therefore used.

Kinships were gauged between different classes of rabbits to see if these correlated with different behavioural relationships, such as between neighbouring dominant males, neighbouring females, subdominant and dominant males, mated pairs, adults and young (Section 9c). Two people undertook biochemical analyses of the blood, as described in Section 9b. Immunoglobulins were analysed by Dr Wessel Van der Loo, and electrophoretic analyses of blood enzymes was performed by Mr Peter King. Both of these sets of analyses revealed genetic polymorphisms of blood proteins, and the results were pooled to provide as many polymorphisms as possible.

Most studies of the genetic structuring of populations have looked within and between subpopulations to assess the degree of inbreeding e.g. Foltz and Hoogland (1983); Chesser (1983). These use Wrights F-statistic, or this as modified by Nei, or Rogers' measure of genetic distance (Rogers 1972; Nei 1977). The F-statistic looks at the variance in genetic similarity within and between groups. Rogers' measure compares sub-population means with one another as

$$D = L^{-1}\Sigma[0.5\Sigma(P_{ijx} - P_{ijy})^2]^{0.5}$$

where L is the number of loci; the first summation sign is between 1 and L; the second summation is over the alleles at the ith locus; P_{ijx} is the frequency of the jth allele at the ith locus in population X and P_{ijy} is the frequency of the jth allele at the ith locus in population Y; D is the measure of similarity.

Schwartz and Armitage (1983) adapted Rogers measure to obtain relatedness between individuals, such that P_{ijx} becomes the allelic frequency for individual X, and P_{ijy} that for individual Y. Arithmetic means were used to get the overall relatedness across loci, and means were taken across individuals to get average intra-population relatedness. These authors had also obtained pedigree information for their animals. They correlated known pedigrees against relatedness obtained from this genetic similarity method and found the two measures to be positively correlated, but the predictability of pedigree from genetic relatedness was low. They were working with eight polymorphic loci.

My requirement, to assess relatedness between particular pairs of individuals in two classes, e.g. the males and females of particular pairs, was not fulfilled by any of the above techniques. In general, the techniques concentrate on relatedness within groups versus relatedness between groups. Amalgamating males and females, for example, and comparing the relatedness within such a group

with the overall population relatedness would have been unsatisfactory, since it would not have given the average relatedness within dyads. The closest technique to the one I needed was the method of Schwartz and Armitage (1983) in averaging relatedness between pairs. However, they themselves found this method unreliable, and I had fewer polymorphic loci, only six at Oxford. Their technique suffered from the wasteful problem of not according extra weight to rare alleles, and from the fatal flaw of not providing a measure of the error of the obtained kinship coefficient.

Grafen and Roberts (in preparation) have developed a method of obtaining kinships from data on polymorphic loci, based on Hamilton's (1972) measure of relatedness. As this is not yet published, the essential theory is presented in Appendix II. The rationale and bases for the technique may be read in Grafen (1985). My contributions to this paper are the implementation and validation of the method, and some further explorations. These are described in Section 9a, and the results of applying the method to the rabbit data are the topic of Section 9c. Section 9b describes the results of biochemical analyses.

Section 9a. A new method of estimating relatedness

Implementation of the method

The method required that each rabbit's genotype be represented by a sequence of numbers. Each number in the sequence represented the frequency in the rabbit of each allele present in the population. For each allele in turn the rabbit was scored as 0, 0.5 or 1 and this frequency was subtracted from the mean population frequency for that allele. This gave a set of measures of the deviations of the rabbit's frequencies from the population means. The theory behind the method stated that a simple relationship holds between the sequences of numbers of two rabbits: each number in the second rabbit's sequence should on average be equal to the product of the degree of relatedness (β) between the rabbits and the corresponding number in the first rabbit's sequence. Knowing the sequences for both rabbits, it is therefore possible to derive an estimate (b) of the true relatedness between them by regression, the slope of the regression line being the coefficient of relatedness. In Appendix II the formulae used are fully described, some of the terms from there are used in the following.

To implement the method, a FORTRAN program was written that used the formulae described in Appendix II. It was so devised that it can readily be adapted to other animal populations of different gene frequencies and numbers of loci. The main program defines gene frequencies and number

of loci and reads genotypes from a data file for pairs of rabbit identities. Identities of each pair of X and Y rabbits are fed in interactively by the operator at the time of program running. The program works through the rabbits pair by pair. For each locus, one of three subroutines is called depending on whether the X rabbit is a homozygote, a heterozygote at a two-allelic locus, or a heterozygote at a locus with more than two alleles. Within each subroutine, the summary statistics n_{il} and d_{il} (for the ith pair of animals at the lth locus) are obtained (as shown in Appendix II). The main program combines these summaries across loci, and, if there are more than a single pair of animals, across pairs.

In addition to obtaining an estimate of relatedness and an estimate of the standard error of this, a method was developed to assess the power of the test for any particular population. This was achieved by Monte Carlo simulations. Large, artificial populations of animals of particular relatednesses were created using the same genetic frequencies at the same number of loci as found in the real population. The artificial populations were also created so that the statistical technique could be validated.

Genotypes of three artificial rabbit populations were generated to create populations of pairs of particular relatednesses. The actual gene frequencies found for the first five loci of the Oxford population were used. The first population, of 3000 unrelated animals was generated by randomly picking the two alleles at each locus for each

animal, with a probability for picking any particular allele being equal to the frequency of that allele in the population.

The second population was of sibs; each consecutive pair of unrelated rabbits from the first population were used as parents. There was an equal probability of taking either of the two alleles of each parent for each allele in each offspring. One pair of sibs was produced from each parent-pair (1500 pairs in all). The third population, of cousins, was produced by pairing each of a pair of sibs with a random member of the first, unrelated, population (actually sibs were paired with the two unrelated rabbits that followed their own parents in the unrelateds' file; 1499 cousin pairs were produced). Again, from each parent, there was an equal probability of either allele passing to the offspring. At each stage of these generations, different random numbers were used.

Each of the three populations was tested to ensure that they were as they should be. For the unrelateds, frequencies of homozygotes and heterozygotes were obtained for each locus, e.g. at locus 2 (a three-allelic locus):

	a1	a2	a3	Expected popln freq	Observed popln freq
a1	672	182	569	0.4681	0.472
a2	224	70	163	0.1383	0.1447
a3	513	159	448	0.3936	0.3833

A χ^2 test was done on the frequencies of allele combinations at each locus, and none was found to depart significantly from random. Expected and observed allele

population frequencies were similar at each locus.

For sibs and for cousins, the frequencies of combinations of genotypes were obtained, e.g. at locus 1 (a two-allelic locus):

		Sib2		
		a1a1	a1a2	a2a2
	a1a1	65	74	11
Sib1	a1a2	69	414	177
	a2a2	20	204	466

	a1	a2
Expected population frequencies	0.3298	0.6702
Observed population frequencies	0.3308	0.6692

Again expected and observed allele population frequencies were similar at each locus. The tables were inspected for symmetry and no striking deviations were observed.

These checks on the generated populations were important. Earlier checks had shown errors in the allelic frequencies. The errors were caused by the random number generator using the same numbers at each run. It was corrected by setting the generator to where it had left off at its last use.

Validation of the method

The method required an initial 'guess' at β, called ρ, to be made such that the standard error of b could be calculated. (No guessing is required in the fully developed method). For these validations, ρ was set to the true value of β (0.0 for unrelateds, 0.5 for sibs and 0.125 for cousins).

As noted above, different procedures are used when the X-rabbit is a homozygote, a heterozygote for a 2-allele locus, or a heterozygote at a locus with more than two alleles. These procedures were embodied in the three subroutines of the program that ran the method. Initially the method was tested on individual pairs; obtaining for each pair at each locus, an estimate (b) of β (from n_{il}/d_{il}), a theoretical sampling variance ($1/d_{il}$), which I shall call v^2 for the individual pairs case, and the true variance obtained as the square deviation of the obtained b from the known, true β, i.e. $(b-\beta)^2$. Within each subroutine, results were summed across rabbit-pairs for each combination of alleles, and a mean b, a sum of theoretical variances (Σv^2) and a sum of true variances ($\Sigma(b-\beta)^2$) obtained.

The simulation revealed a flaw in the method, producing marked deviations in the obtained values of mean b and Σv^2 from the true values of β and $(b-\beta)^2$. The error was detected in the third subroutine for heterozygotes at a locus with more than two alleles. It was corrected and the simulations were re-run to produce the results shown in Table 9.1. The estimates of b from each subroutine were now quite good, and the calculated variances matched the true variances.

The method was also tested on whole rabbit pairs (as opposed to individual loci). Mean values of b and their true mean square deviations from the known β were calculated across rabbit pairs. This was part of a different test

Table 9.1 Output from subroutines with X-rabbit as homozygote (Sub1), heterozygote at 2-allele locus (Sub2), heterozygote at locus with more than two alleles (Sub3). Values taken across rabbit-pairs for two loci (Locus 1 is 2-allelic, Locus 2 is 3-allelic) are mean b, sum of v^2 (calculated theoretical variances), and the sum of the true variances $(b-\beta)^2$. Results for unrelated, sib and cousin populations. b is found to be close to 0.0, 0.5 and 0.125 for the respective populations; Σv^2 is similar to $\Sigma(b-\beta)^2$.

Unrelateds

			X's alleles	N rabbits	Mean b	Σv^2	$\Sigma(b-\beta)^2$
Sub1	Locus	1	1 1	167	-0.077	41.09	39.50
	"	1	2 2	689	-0.050	700.07	697.60
	"	2	1 1	310	0.039	136.41	139.06
	"	2	2 2	40	0.043	3.21	3.81
	"	2	3 3	220	-0.049	71.40	73.71
Sub2	Locus	1	1 2	644	0.056	2456.93	2387.95
Sub3	Locus	2	1 2	210	0.024	77.26	82.91
	"	2	1 3	546	0.049	1613.13	1532.19
	"	2	2 3	174	-0.075	60.30	57.17

Sibs

			X's alleles	N rabbits	Mean b	Σv^2	$\Sigma(b-\beta)^2$
Sub1	Locus	1	1 1	150	0.523	37.20	31.56
	"	1	2 2	690	0.464	436.79	455.34
	"	2	1 1	328	0.550	113.16	110.26
	"	2	2 2	30	0.575	4.95	3.49
	"	2	3 3	206	0.460	59.18	64.60
Sub2	Locus	1	1 2	660	0.519	2053.48	1970.76
Sub3	Locus	2	1 2	207	0.519	79.33	84.36
	"	2	1 3	571	0.498	931.26	858.37
	"	2	2 3	158	0.609	54.60	48.30

Cousins

			X's alleles	N rabbits	Mean b	Σv^2	$\Sigma(b-\beta)^2$
Sub1	Locus	1	1 1	157	0.116	42.39	43.23
	"	1	2 2	676	0.045	637.98	651.49
	"	2	1 1	314	0.201	138.07	116.64
	"	2	2 2	24	0.081	3.00	2.68
	"	2	3 3	228	0.114	77.21	74.63
Sub2	Locus	1	1 2	666	0.184	2573.98	2588.02
Sub3	Locus	2	1 2	230	0.124	97.50	91.50
	"	2	1 3	528	0.019	1402.88	1621.37
	"	2	2 3	175	0.195	67.96	73.04

explained under 'Different measures of relatedness' and the results are shown in the first and second rows of data in Table 9.7, for each population. ρ was offered as equal to β and also as 0.0 (0.5 in the case of the unrelateds). These mean estimates of b were very good, even with ρ not equal to β. The method, therefore, worked for single pairs of rabbits, particularly when ρ is set equal to β. This is not empirically useful, but it does confirm the correctness of the statistical theory.

Validations were also made on groups of pairs of rabbits. To combine b across pairs of animals, an appropriate weighted average is used. Since it cannot be assumed that pairs making up a group will be of the same relatednesses, two variances need to be estimated. The first of these is s'^2 which measures the variance between pairs in their relatednesses. s^2, which is $\max\{0,s'^2\}$, is then incorporated into t^2, a final estimate of the variance of the estimate of β.

Initially, each population was treated as one large group of dyad-sets, to obtain b, t (the theoretical standard error of b), and s'^2. Since these populations were each purely composed of one sort of relatedness, s'^2 should come to 0. Results are shown in Table 9.2.

Each population was then tested, to produce the same variables from 150 groups (149 in the case of the cousins) of 10 pairs of rabbits from each population. Results were averaged across the groups (mean b; root of the mean theoretical variance of b: $\sqrt{(\Sigma t^2/N)}$; and the mean estimate

Table 9.2. Monte Carlo estimates of relatedness for single large groups of pairs of rabbits. Columns show the initial ρ put into the program, the obtained estimate of β, which is b, the variance between pairs s'^2, and the theoretical standard error t of b. In each case b is close to the true β and s'^2 is close to 0.0.

Population	Initial ρ	b	s'^2	t
Unrelateds	0.000	-0.002	0.005	0.009
Sibs	0.500	0.499	-0.003	0.009
Cousins	0.125	0.132	-0.005	0.009

of within group variance in β: $\Sigma s'^2/N$; where N is the number of groups). Results are in Table 9.3.

These validations showed that the formulae worked as expected, and that the computer program functioned correctly. The method produced good estimates of β with reasonable standard errors, and values of s'^2 close to 0.

Table 9.3. Mean Monte Carlo estimates of relatedness across many groups, each of 10 pairs of rabbits. Columns show the initial ρ put into the program, the mean obtained b across groups; $\Sigma s'^2$ the mean estimate of within group variance in β (true value is zero), and $\sqrt{(\Sigma t^2/N)}$, the root mean squared calculated theoretical variance.

Population	Number of groups	Initial ρ	Mean b	$\Sigma s'^2/N$	$\sqrt{(\Sigma t^2/N)}$
Unrelateds	150	0.000	-0.003	0.003	0.124
Sibs	150	0.500	0.498	-0.004	0.113
Cousins	149	0.125	0.133	-0.005	0.126

Development of the method

The weights for each point in the regression are known in terms of the unknown true value of β, and depend on this and on the values for the X-rabbit. These weights are essential for calculating the standard error of the estimate of β. Initially, we attempted to provide an estimate of β for the weights by iterating ρ (the supplied 'guess' at β) from 0. Thus an initial value for b was obtained using ρ=0, and this estimate was used in a second run of the program, with ρ=b.

Two parameters were calculated for each rabbit-pair over all their loci: b, and the variance v^2, calculated as $1/\Sigma d_{il}$. Mean b and mean v^2 were taken across the N rabbit pairs. The mean true variance around the known (β), i.e. $\Sigma(b - \beta)^2/N$ was also calculated.

The results for each population are shown in Table 9.4. This gave the initial impression that iterating once, (running the program twice), was quite successful. The estimated b was quite close to β in each case, and, although mean v^2 was quite low, it was fairly close to the true variance.

Table 9.4 Single iteration, feeding first obtained b back through program as ρ. ρ set initially at 0. For each of the N rabbit-pairs b, v^2 and $(b-\beta)^2$ were taken, and the means of these were obtained across N. The theoretical and true variances Σv^2 and $\Sigma(b-\beta)^2/N$ should match, and mean b should be close to the true β.

True relatedness	β	N	$\Sigma b/N$	$\Sigma v^2/N$	$\Sigma(b-\beta)^2/N$
Unrelateds	0.0	1500	0.0094	0.1364	0.1435
Sibs	0.5	1500	0.4866	0.1022	0.1173
Cousins	0.125	1499	0.1239	0.1331	0.1404

To extend this test, the technique was repeated with further iterations. This was to discover how many iterations were required for the values to settle down to a steady level. It was presumed that estimates would improve with further iterations, b coming closer to β, and its variance from β decreasing. The program was run on each pair up to 20 times. For each number of iterations, results were summed across rabbits to give $\Sigma(b - \beta)$ and $\Sigma(b - \beta)^2$. These results are shown in Table 9.5. They show that, contrary to our prior belief, a single iteration (running through twice) gave a worse estimate of β for the unrelateds and the sibs than did no iteration at all, though it gave the lowest variance for unrelateds and cousins. The values oscillate in an unexpected way, and do not greatly improve.

These simulations showed that an iterative procedure gave complicated and unhelpful results, and so efforts in this direction were dropped. A better method was decided upon for providing the program with an estimate of β. This was to run the program several times for a series of values of ρ. This is a sensible solution since if a value of b is to be rejected as an estimate of β, the weights should be calculated using that same value of b. It could not then be argued that the weights were wrong in calculating the standard error, since if they were wrong it is further proof that β is not at that value of b. For each value of ρ, b and the two standard error intervals (2t) are calculated. If ρ falls within two standard errors of b it cannot be rejected as a value for β.

Table 9.5 Multiple iteration, feeding last obtained b back through program as ρ. ρ set for first run at 0. Up to 20 runs through program (19 iterations). The sum of deviations of obtained b from β and the sum of squared deviations $\Sigma(b-\beta)^2$. $\Sigma(b-\beta)$ shows the accuracy of the estimated b which is better when closer to 0.0. $\Sigma(b-\beta)^2$ is the sum of true variances, best when lowest.

	1500 pairs Unrelateds		1500 pairs Sibs		1499 pairs Cousins	
Run	$\Sigma(b-\beta)$	$\Sigma(b-\beta)^2$	$\Sigma(b-\beta)$	$\Sigma(b-\beta)^2$	$\Sigma(b-\beta)$	$\Sigma(b-\beta)^2$
1	-5.24	225.03	-4.55	186.88	9.77	220.77
2	-14.05	215.29	-20.05	176.02	-1.67	210.49
3	-5.85	220.13	-8.16	174.82	8.41	215.05
4	-7.53	219.67	-9.70	175.53	7.09	214.76
5	-5.91	220.20	-9.39	174.92	8.21	214.99
6	-6.86	220.00	-9.10	175.33	7.81	214.95
7	-5.99	220.19	-8.49	174.96	8.15	214.97
8	-6.69	220.05	-9.00	175.29	7.95	214.97
9	-6.04	220.18	-8.52	174.97	8.14	214.97
10	-6.63	220.07	-8.98	175.27	7.98	214.98
11	-6.07	220.17	-8.53	174.98	8.13	214.96
12	-6.60	220.07	-8.97	175.27	8.00	214.98
13	-6.09	220.17	-8.54	174.98	8.12	214.96
14	-6.58	220.07	-8.96	175.26	8.00	214.98
15	-6.10	220.17	-8.54	174.98	8.12	214.96
16	-6.57	220.08	-8.96	175.26	8.01	214.98
17	-6.11	220.16	-8.55	174.98	8.11	214.96
18	-6.57	220.08	-8.96	175.26	8.01	214.98
19	-6.11	220.16	-8.65	174.98	8.11	214.96
20	-6.56	175.08	-8.96	175.26	8.01	214.98

Power of the method

This latest form of the method was tested on different randomly generated populations for two reasons. The statistical properties of the procedure needed checking because the distribution of the estimated b is not normal, and the distribution of the variance estimates is not χ^2. Therefore the two standard error confidence intervals were inspected from the simulated cases to see if they were

approximately 95% confidence intervals (testing the chance of rejecting the null hypothesis when it is in fact true). The simulations further revealed the power of the test for the particular populations. The actual probability of rejecting the null hypothesis (that that ρ was equal to β) when it was in fact false, was found for several values of ρ.

The evaluations were applied to cases with the same number of loci and the same allele frequencies as found in the two rabbit populations. The latest data from Oxford were used to create new artificial unrelated, sib and cousin populations. There were now six loci and the frequencies were slightly altered. Three such populations were also generated from the allelic frequencies at the seven polymorphic Walney loci.

Groups of pairs of rabbits to be tested from natural populations were unlikely to contain pairs all of identical relatednesses. The evaluations were therefore tested at a range of values of β. A program was written which created groups of ten rabbits in specified proportions of sibs to unrelateds. E.g. for a β of 0.3, each new pair added to the group had a 0.6 chance of being taken from the sibs population and a 0.4 chance of being taken from the unrelateds. As many groups were created as possible, the limit being set by the number of pairs in the population making up the higher proportion; the number of groups in each case is shown in the tables.

For each group, b and t^2 were obtained and two standard

errors were calculated (2t). If ρ fell within b±2t the group was scored as having 'succeeded'. Across groups, the mean b was obtained, with $\sqrt{(\Sigma t^2/N)}$ as the mean standard error. The number of groups that 'succeeded' was added up and the procedure repeated for a range of ρ's.

Table 9.6. Extent of the confidence intervals, and power of the method. True β is shown, with the number of groups (each of size 10), the percentage of groups for which the correct value of b was wrongly rejected, and the upper and lower ρs at which at least 50% of the bs were rightly rejected. The percentage of false negatives should be at 5%.

β	N groups	% false negatives	Lower ρ for 50% rejection	Upper ρ for 50% rejection
At Walney frequencies				
0.0	150	1.3	-	0.3
0.1	187	5.3	-	0.4
0.2	246	7.3	-	0.5
0.3	249	7.6	-	0.6
0.4	184	4.3	0.1	0.7
0.5	150	4.0	0.2	0.8
At Oxford frequencies				
0.3	249	9.6	0.0	0.6

Table 9.6 shows the results for each relatedness tested (from 0.0 - 0.5 with Walney frequencies, 0.3 with Oxford frequencies). The chance of rejecting the true value of β is given for each. This varied from 1.3% to 7.6%, being higher in those populations that contained a greater variance between sample pairs. The 'nominal value' is 5%, as these are two standard error confidence intervals. These deviations from the nominal value are unexpectedly great, and show the importance of doing simulations. Further

development of the method will be required, although it is still useful in this form. The distance from the true value of β at which there was at least a 50% chance of rejecting values for b are shown. These were 0.3 from the true value in each case. So the method provides useful, if not pinpoint, information in this situation.

Different measures of relatedness

The inbuilt asymmetry in this regression method is somewhat of a disadvantage. It means an arbitrary choice must be made as to which rabbit acts as the X and which the Y. This could turn to being an advantage in matters of altruism where a donor and a recipient can be defined. It was chiefly chosen as the method for its simplicity.

Various different measures of β were investigated, combining estimates made with each rabbit acting as the X rabbit in turn. Two estimates of b were made from each pair, using one rabbit as the X-rabbit first and then swapping them round. Since the statistical relationship between the two estimates was unknown, the estimates were plotted out graphically, correlating the two b's. Fig 9.1 shows the results of these correlations, which were good, a strong correlation being found for each population.

Further, various ways of combining the two estimates of b were investigated. For each pair, a one-way estimate of b was obtained, using the first rabbit as the X-rabbit; with this, a square deviation of b from the true, known mean was taken, $(b-\beta)^2$. Also a truncated one-way b was obtained: if

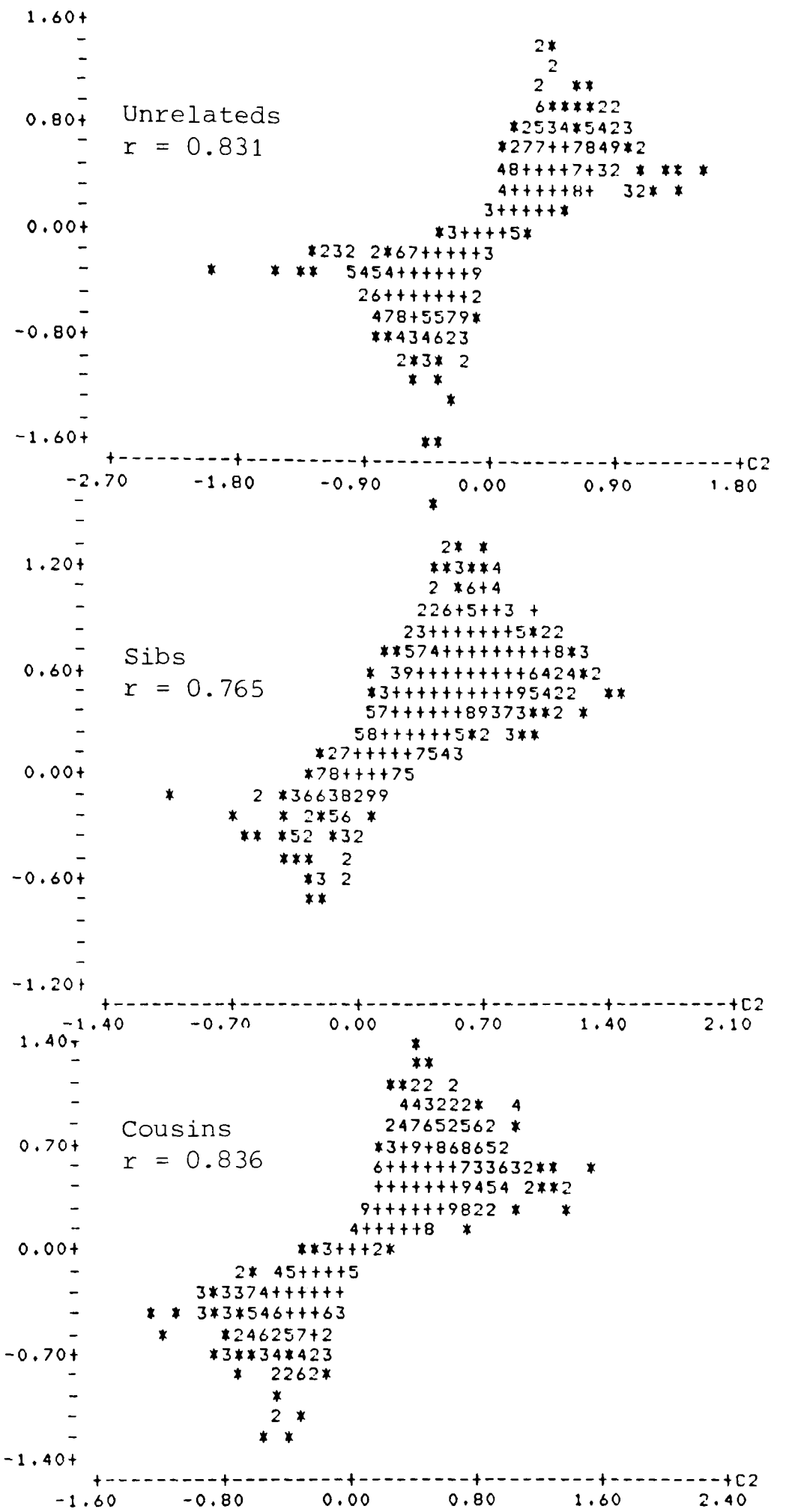

Fig 9.1. Correlations of estimates of β. X-axes are the values for b when calculated with the first rabbit as the X-rabbit. Y-axes are the values for b when calculated with the second rabbit as the X-rabbit. * = one point. '7' = number of points. + = more than nine points. Inserted ρ is equal to true value of β (0. for Unrelateds, 0.5 for Sibs, 0.125 for Cousins).

b>0, it was set to 0, and a square deviation obtained. Next, for each pair, the b with the other rabbit as the X-rabbit was obtained. The arithmetic mean and the geometric mean of the two b's were both taken. If one b was negative and the other positive, the geometric mean was set to 0. If both were negative, the negative square-root of the product of the b's was the geometric mean. The square deviations of both these estimates were taken from the true β. Truncated geometric means and arithmetic means, (setting all negative ones to 0) with their square deviations, were also taken. Results were averaged across rabbits to give mean estimates of b, and mean square deviations.

Results are shown in Table 9.7, for ρ set to 0 (0.5 for unrelateds) and also with ρ set to the true β for each population. The statistical theory behind combining estimates in these various ways was undeveloped, and standard errors of the estimates could not be calculated. However it is interesting to note that the geometrical mean gives the lowest mean square deviation in each population, and so would perhaps be the best combination to use if a symmetrical relationship were required.

Table 9.7. Results from different ways of combining asymmetric measures of relatedness. The initial ρ is shown, then each measure with the mean square deviation (MSQDEV) of its estimate from the true β. Measures shown are the usual one way estimate (b), a truncated b, the geometric mean (GM) of the two bs, one calculated with one rabbit as X, the second with the other as X, the truncated geometric mean, the arithmetic mean (AM), and the truncated arithmetic mean; where truncation meant setting negative estimates to 0. The estimates are made across single large groups of rabbit-pairs created from the five-allele population frequencies. Good results constituted a b close to β (0.0 for unrelateds, 0.5 for sibs, 0.125 for cousins), with a low mean square deviation showing the accuracy of this estimate.

	Unrelateds 1500 pairs		Sibs 1500 pairs		Cousins 1499 pairs	
ρ	0.0	0.5	0.0	0.5	0.0	0.125
b	-0.003	-0.006	0.497	0.495	0.132	0.131
MSQDEV	0.150	0.159	0.125	0.117	0.147	0.146
Truncb	0.151	0.153	0.513	0.511	0.227	0.226
MSQDEV	0.078	0.076	0.103	0.096	0.081	0.078
GM	-0.004	-0.003	0.488	0.489	0.128	0.130
MSQDEV	0.129	0.130	0.105	0.101	0.125	0.124
TruncGM	0.146	0.141	0.503	0.501	0.219	0.218
MSQDEV	0.068	0.066	0.086	0.086	0.067	0.067
AM	-0.007	-0.013	0.500	0.499	0.132	0.131
MSQDEV	0.142	0.147	0.110	0.104	0.136	0.135
TruncAM	0.151	0.149	0.516	0.513	0.227	0.226
MSQDEV	0.073	0.071	0.090	0.086	0.073	0.072

Final form of the method

In its final form, the method was performed on each group of rabbits 10 times. ρ was inserted for each run at 0.0, 0.1....0.9. No iterations were made. For each value of ρ, the following were calculated: b, the estimate of β; s'^2, the variance between pairs within the group; and 2t, the two standard errors, calculated using s'^2. These

results for the group were then investigated for each ρ. If ρ fell within $\pm 2t$ of b, it could not be excluded as a possible value of β. Confidence intervals were thus drawn up ranging from the lowest ρ which could not be excluded, to the highest. That b that fell closest to its value of ρ was recorded, as the best estimate of β.

The method differed slightly when the group was of a single pair only. Then, s'^2 must have been 0.0, since there was only one pair, and t was calculated simply as $1/\sqrt{\Sigma d_{il}}$ (see Appendix II). Again, each ρ was tested as for the multiple-pairs groups.

Section 9b. Biochemical analyses of blood

Samples of red blood cells and plasma from Walney, Oxford and Berkshire were taken to Mr Peter King, working in Professor Berry's laboratory at University College London. The Berkshire blood was from a sample of 29 rabbits, taken by Mike Harrison, an undergraduate at Oxford University. Mr King analysed the blood using electrophoresis for enzyme polymorphisms.

Plasma samples from Oxford and Walney only were sent to Dr Wessel Van der Loo, working at Brussels University. He analysed the samples for immunoglobulin allotypes.

Electrophoretic analysis

Protein molecules of different sizes and different electrical charge properties can be separated out by running a current across a gel (Smith 1968). Small samples of plasma or red blood are applied at the base of the gel and the end of the gel is left in contact with the buffer solution. Different alleles coding for the same enzyme have different phenotypic expression and produce morphs of the protein molecules that differ in their mobilities across a gel. Mr King used information from Richardson's (1980) work in which particular systems are described for their successes with different enzymes. Results for each enzyme and the systems used were as follow.

Transferrin TRF. Plasma samples were run on a Tris-citrate gel with a borate electrode buffer. A minority of samples

were found to be two banded. Resolution was not good, many samples producing bands that were extremely ragged or trailing backwards. Therefore, they were run again on a Tris-glycine buffer pH 8.5. The rarer type on this corresponded to the two banded samples on the other system.

The standard interpretation made of TRF is to call the rarer (two band) type a heterozygote for the normal fast form and a slow form. However this was far from obvious from the Tris-glycine gels. Thus animals were scored as 'f' and 's' for the rarer type (two bands on the gels), so as not to imply any genetic model. The transferrin locus was not used in the analyses of kinship.

Esterases. These were run on TEB buffer pH 8.6. Starting from the anodal end of the gel:

EST-4 was invariant.

EST-5 was present in most samples, generally very weakly but sometimes more strongly. It was invariant, and its presence was due to plasma contamination of the red cells.

EST-2 was very strong but there was not a single variant.

EST-3 was very weak, except on the fluorescent stain.

EST-1 was obviously varying.

For EST-1 the majority of animals had a slow band only. Some had a fast band, generally much stronger. Of these animals some had a second faint band in the position of the usual slow band and the remainder showed nothing there. These morphs were coded as 11 (slow, slow), 12 (slow, fast) and 22 (fast, fast), corresponding to the B, AB and A bands of Richardson.

Carbonic anhydrase CAR-2. This was run on Phosphate buffer pH 6.5. It gave very good results, running cathodally at this pH. Two alleles were found. The band closer to the origin was coded 2 (fast) and the one further away from it 1 (slow). Almost all the samples were scorable. 22 and 11 correspond to F and S of Richardson.

Phosphogluconate dehydrogenase PGD. This was run on Phosphate pH 6.5 and gave results good enough to be relied upon. Three alleles were found: fast (3), medium (2) and slow (1). The medium version is Richardson's '1', the fast one is his '2' and the slow form his '3'. This enzyme moved a very long way on the gel.

MPI. For this enzyme, the slow allele was in fact a composite of two alleles, medium and slow, of similar mobility. However it was very difficult to tell a fast-medium heterozygote from a fast-slow heterozygote, and as medium was a rare allele it was lumped in with slow. (Medium-slow heterozygotes were very easy to distinguish but there were only two of these, so they are included in the slow-slow homozygote category.) Codes are 2 (fast) and 1 (slow).

Other Enzymes. Diaphorase DIA would not show up on any gels. A minimum of 20 samples from each of Walney and Oxford were run for the following enzymes. Peptidases (PEP) came up at two loci. One had no variants, the other had just one animal as a possible heterozygote. PGM had only one locus which had no variants. Guanine deaminase (GDA), NP and GPI did not vary.

Immunoglobulin analysis

The immunoglobulins are a class of proteins found in the globulin fraction of the serum; they are antibodies. In each molecule there are one or more pairs of parts, each part bearing a heavy and a light chain $(H_2L_2)_n$. There are antigenic sites on the molecule which can be serologically detected. These reveal which allotypes are present, allotypes being variants of the molecule that are inherited as alternatives. E.g. the variable region of the molecule, which runs along the light chain and encompasses some of the heavy chain, has areas on it that are coded for by separate gene groups. (Smith 1968).

Wild rabbit populations show extensive IgG polymorphisms, the same as those found in domestic rabbits. Markers of codominant alleles exist on the variable, hinge and Fc regions of the heavy chain (loci a, d and e); and on the constant region of the light chain (locus b) (Van der Loo 1982). Dr Van der Loo was able to score rabbits for polymorphisms at these loci giving variants of b (b41, b42, b5, b6, b9), a (a1, a2, a3), d (d11, d12), and e (e14,15).

Up to 400g in weight, a baby rabbit's blood contains the IgG immunoglobulins of the mother. At 200g these score very strongly, causing marked agglutination in the test. Above this weight, immunoglobulins originally coded for by the mother's genotype fade away as the baby's own genotype starts to express. If rabbits were caught when very young as well as when adult, very useful information about their genotype would be available. It would be possible to

ascertain the combination of these alleles for both mother and father, ascribing to the father those parts of the rabbit's genotype that could not be ascribed to the mother. Unfortunately, it was rarely the case that a rabbit was caught more than once. Our method for assessing relatedness was limited to using data on the rabbit's own genotype; therefore very young rabbits could not be scored.

Results of immunoglobulin analysis. There is usually strong linkage between alleles d and e and this was found at both my sites, along with other linkage disequilibria, effectively meaning fewer polymorphisms.

At Walney, only b41 and b5 were present on the light chain. They were unlinked, with a crossing-over frequency of 0.5. For the heavy chain, a, d, and e were always linked. This meant there were only three haplotypes (combinations of alleles) on the heavy chain:

a1 d12 e15 (designated 1)

a2 d12 e14 (designated 2)

a3 d11 e15 (designated 3)

Effectively, for these rabbits, only six combinations could occur, with either b4 or b5 (designated 1 and 2) combining with a 1, 2 or 3 heavy chain. These are thought of as two varying loci, B with two variants, and A with three, since if two or more alleles were always linked, they are better regarded as a single variable.

The Oxford population showed similar limitations to

Walney, with three heavy chain haplotypes:

a1 d12 e15 (designated 1)

a1 d12 e14 (designated 2)

a3 d12 e15 (designated 3)

There was no a2 in the population, and a3 and e15 were always linked. With b4, b5 and b9 present in the light chain, nine combinations were possible. Again, there were effectively two loci: A with three variants, B with three also.

Population frequencies of polymorphisms

Table 9.8 gives the frequencies of the different alleles as found from electrophoretic and immunoglobulin analyses. Various interesting population properties of the polymorphisms were recognized. Dr Van der Loo was surprised at the strength of the linkage disequilibrium on the immunoglobulins, and at the high levels of b5 found at Walney.

The electrophoretic results were also quite interesting from the population genetics point of view. The island sample, Walney, seemed to be the most heterozygous, contrary to expectation. It was the only place with the PGD slow allele present. It also had the highest frequency of the CAR-2 fast allele (around 50%). For ADA all three populations were very distinct: the slow allele was absent at Walney, and fast was more common than medium there.

Table 9.8. Allele frequencies at Walney and Oxford of enzymic alleles and allotypes. Name of locus; number of rabbits scored for it; then for each allele: code number; number of times it was observed (scoring 1 in a heterozygote and 2 in a homozygote); and population frequency. Results are from 102 rabbits at Walney, 57 at Oxford; 29 from Berkshire.

Locus	N rabbits scored	Allele code	Counts of allele	Allele frequency
Walney				
CAR-2	101	1	103	0.5099
		2	99	0.4901
PGD	93	1	38	0.2043
		2	148	0.7957
ADA	94	1	52	0.2766
		2	136	0.7234
EST-1	97	1	159	0.8196
		2	35	0.1804
MPI	82	1	35	0.2134
		2	129	0.7866
A	79	1	23	0.1456
		2	26	0.1646
		3	109	0.6899
B	87	1	25	0.1437
		2	149	0.8563
Oxford				
CAR-2	57	1	80	0.7018
		2	34	0.2982
ADA	57	1	52	0.4561
		2	16	0.1404
		3	46	0.4035
EST-1	57	1	79	0.6930
		2	35	0.3070
MPI	44	1	38	0.4318
		2	50	0.5682
A	39	1	51	0.6538
		2	15	0.1923
		3	12	0.1538
B	40	1	27	0.3375
		2	31	0.3875
		3	22	0.2750
Berkshire				
CAR-2	29	1	45	0.7759
		2	13	0.2241
ADA	29	1	10	0.1724
		2	37	0.6379
		3	11	0.1896
EST-1	29	1	43	0.7414
		2	15	0.2586

At Oxford both the slow and the fast allele were common and the medium one was infrequent; at Berkshire the situation was different again, with medium being abundant, and both the others rather scarce. However, MPI was polymorphic at both Walney and Oxford, but the frequency of the rarer (slow) allele was much higher at Oxford.

Some wild rabbit populations in Australia have been found to have a null allele at the EST-1 locus in addition to the A and B alleles found in laboratory rabbits (Richardson 1980 following Daly). A null allele is one without phenotypic expression. If it is present in a population, homozygotes for it will appear with no bands on the gel. There will be a homozygote excess because A or B heterozygotes with the null allele will appear as A or B homozygotes.

At Oxford all rabbits showed EST-1 bands, so if the null allele was present, it was at a very low frequency, never appearing in a homozygote. At Walney, four of the tested animals were not scored for EST-1. They may have been null allele homozygotes; alternatively the samples could have been just too poor to score. All Oxford rabbits were scored for all electrophoretically-detected alleles. The Walney samples were older, and had been more roughly treated; in addition to the missing EST-1 scores, eight rabbits were unscored for PGD and nine for ADA.

In Table 9.9 each allele is inspected from each site to see if there was any homozygote excess. Since this was a multiple test over 37 alleles, at the 5% probability level

Table 9.9 Homozygosity at each site. The observed count of homozygotes for each allele at each site is shown, with the expected number (calculated as squared frequency of allele in the population, times number of rabbits scored for that locus), and the χ^2 with the P level for 1 Df, where significant.

Locus	Allele	Obs (N) homoz	Exp (N) homoz	χ^2	P
Walney					
CAR-2	1	23	26.26	0.40	N.S.
	2	21	24.26	0.44	N.S.
PGD	1	3	3.88	0.20	N.S.
	2	58	58.88	0.01	N.S.
ADA	1	7	7.19	0.01	N.S.
	2	49	49.19	0.00	N.S.
EST-1	1	69	65.16	0.23	N.S.
	2	7	3.16	4.67	<0.05
MPI	1	4	3.73	0.02	N.S.
	2	51	50.74	0.00	N.S.
A	1	0	1.67	1.67	N.S.
	2	5	2.14	3.82	N.S.
	3	38	36.60	0.05	N.S.
B	1	2	1.80	0.02	N.S.
	2	64	63.79	0.00	N.S.
Oxford					
CAR-2	1	27	28.07	0.04	N.S.
	2	4	5.07	0.23	N.S.
ADA	1	11	11.85	0.06	N.S.
	2	0	1.12	1.12	N.S.
	3	7	9.28	0.56	N.S.
EST-1	1	32	27.37	0.78	N.S.
	2	10	5.37	3.99	<0.05
MPI	1	7	8.20	0.18	N.S.
	2	13	14.21	1.10	N.S.
A	1	14	18.81	1.30	N.S.
	2	0	1.42	1.42	N.S.
	3	1	0.92	0.01	N.S.
B	1	4	4.56	0.07	N.S.
	2	7	6.01	0.16	N.S.
	3	3	3.02	0.00	N.S.
Berkshire					
CAR-2	1	17	17.46	0.01	N.S.
	2	1	1.46	0.15	N.S.
ADA	1	0	0.86	0.86	N.S.
	2	13	11.80	0.12	N.S.
	3	2	1.04	0.89	N.S.
EST-1	1	15	15.94	0.06	N.S.
	2	1	1.94	0.46	N.S.

for testing, 1.85 alleles should, by chance alone, have shown homozygote excess. Two did: Est-1 at Oxford and at Walney. However, it is rather suspect that the same alleles were in excess at both sites (although the Berkshire value was as expected).

Although there was a possibility of a null allele being present at my sites, it must either have been at a low frequency, or not have existed at all. Therefore EST-1 is included in the calculations of relatedness. Any error brought about if the null allele were present will be small, especially as EST-1 is only one of the six or seven loci used.

Inbreeding

It was an assumption of the regression method of Section 9a that no inbreeding occurs with respect to the local population (Section 9a). This was tested for the Oxford and Walney populations by seeing whether there was an excess of homozygosity. As Table 9.9 shows, there were few allelic excess homozygosities, so overall homozygote excess was not expected. The numbers of observed and expected homozygotes were obtained for each locus, from the allele frequencies as $N(f_1^2 + f_2^2 + f_3^2 + \ldots + f_n^2)$ where f_i is the frequency up to n of each allele at a locus, and N is the number of rabbits.

A z-score was obtained from the expected and observed numbers of homozygotes at each locus at each site to see if the numbers exceeded those expected by chance. z_i was

obtained as:

$$z_i = \sqrt{[(O_i - E_i)^2/E_i]},$$

returning the sign of (O - E). These were summed and divided by $\sqrt{n}$ to give $\Sigma z_i/\sqrt{n}$ as a final z-score. (O is observed and E expected numbers of homozygotes, n is the number of loci tested). The z-scores were not significant, -0.049 and -0.3764 at Walney and Oxford respectively. It therefore seemed safe to assume there was no excess homozygosity or inbreeding and so the method could be proceeded with.

Section 9c. Relatedness between rabbits

In Appendix III genotypes of each rabbit successfully scored are given. The method in Section 9a was used on these data. As the method was basically a regression, it was not possible to use the same rabbit more than once as a Y-rabbit in a group of pairs, since this would raise problems of independence. However, rabbits could be repeated without any problem as X-rabbits. Since the asymmetry of the method was meaningless in this case, there being no idea of 'donors' and recipients', which rabbit would be X and which Y was decided by which rabbits would need to be repeated in the group. Further, rabbits tested were only those from which blood had been successfully obtained. Thus many calculations were made for Walney rabbits only, as only one of the Oxford bucks was of known genotype.

There were four questions being asked about relatedness between rabbits.

1) Was there inbreeding? This question was addressed in the last Section by looking for (and failing to find) excessive homozygosity. A further check was now made by looking at relatedness between those consorting pairs defined in Chapter 5: (47 and 56, 47 and 7, 11 and 12, 6 and 4) at Walney, (23 and 25) at Oxford.

2) How were neighbouring males related? Figs 4.1-4.3 show

the mean range positions of the Walney and Oxford rabbits. From these were calculated the nearest male neighbours of known genotype for each buck. (The four Walney Areas were joined up to form a square around the hide, and neighbours across Area boundaries were included.) Relatedness was tested between (13 and 4, 4 and 7, 7 and 56, 56 and 8, 8 and 9, 9 and 23, 23 and 25, 25 and 10, 10 and 12, 12 and 22, 22 and 5, 5 and 21, 21 and 17) at Walney. Neighbouring males could be broken up into two major subgroups: neighbouring dominant males that were consorts to females and so in a less competitive position than pairs in the second group, which was of dominant and subdominant males. The first group was therefore of (4 and 56, 56 and 12, 12 and 21); the second of (56 and 7, 12 and 10, 21 and 5, 22 and 17, 17 and 21, 8 and 56, 7 and 8), both groups from Walney. Since it was possible that the dissociating bucks found by any of the techniques in Chapter 5 might bear a particular relatedness, it was tested for (8 and 9, 10 and 22, 10 and 25, 7 and 56), at Walney. (No associating males were found at Walney).

3) How were neighbouring females related? Nearest neighbour females of known genotype at Walney were (2 and 6, 6 and 47, 47 and 11, 26 and 2), and at Oxford were (23 and 10, 10 and 24, 24 and 33, 33 and 31, 31 and 16). (Although 16 was not visible from the hide and not used for Chapter 5 analyses, she was known to live, with a male, along the hedge from 31). The same divisions can be made as for the males, with neighbouring dominants that consorted with males (the same

group as above for Walney), (23 and 10, 10 and 33, 33 and 31, 31 and 16) for Oxford; and a second group of dominant and subdominant does (10 and 24) at Oxford. Next, dissociators and associators were tested; Walney dissociators were (6 and 47, 2 and 26), (there were no associators). Oxford dissociators were (33 and 24, 31 and 10), and associators were (10 and 23, 23 and 24, 24 and 10, 31 and 33).

4) The final interesting consideration was to do with success in breeding. Bucks and does were tested for their relatedness to the young of the year to ascertain which adults were the most strongly related to the young, and so the most likely to have sired or given birth to them. All Walney adults were tested: each adult was measured against all the young of the year, and then against only the young local to that adult's Area. (22 and 2 were both on the edges of Areas and so were tested over both Areas in each case). The age, sex, locality and genotype of each rabbit is given in Appendix III. Figs 9.2-9.5 are maps of Walney and Oxford and show where the young of 1981 for Walney and 1982 for Oxford were trapped.

At Oxford, behavioural data were available for a small number of rabbits only. Analysis was therefore limited to assessing the most likely parents of the five babies 38, 40, 41, 42 and 43 born during the 1982 season. In a way this was a test of the method since the location of the babies

made it strongly probable that 38 was born of 31 and 35, and the rest fathered by either 34,36 or 39 (but no data were available on these bucks' genotypes), and mothered by 10 or 24. Thus 38 is tested against 31 and against 16 and 33, the neighbouring does. 40,41,42, and 43 are tested against 10 and 24, as well as neighbouring does 33 and 23, and against the neighbouring buck 25, as well as 9 that wandered in from time to time, though neither of these were likely fathers.

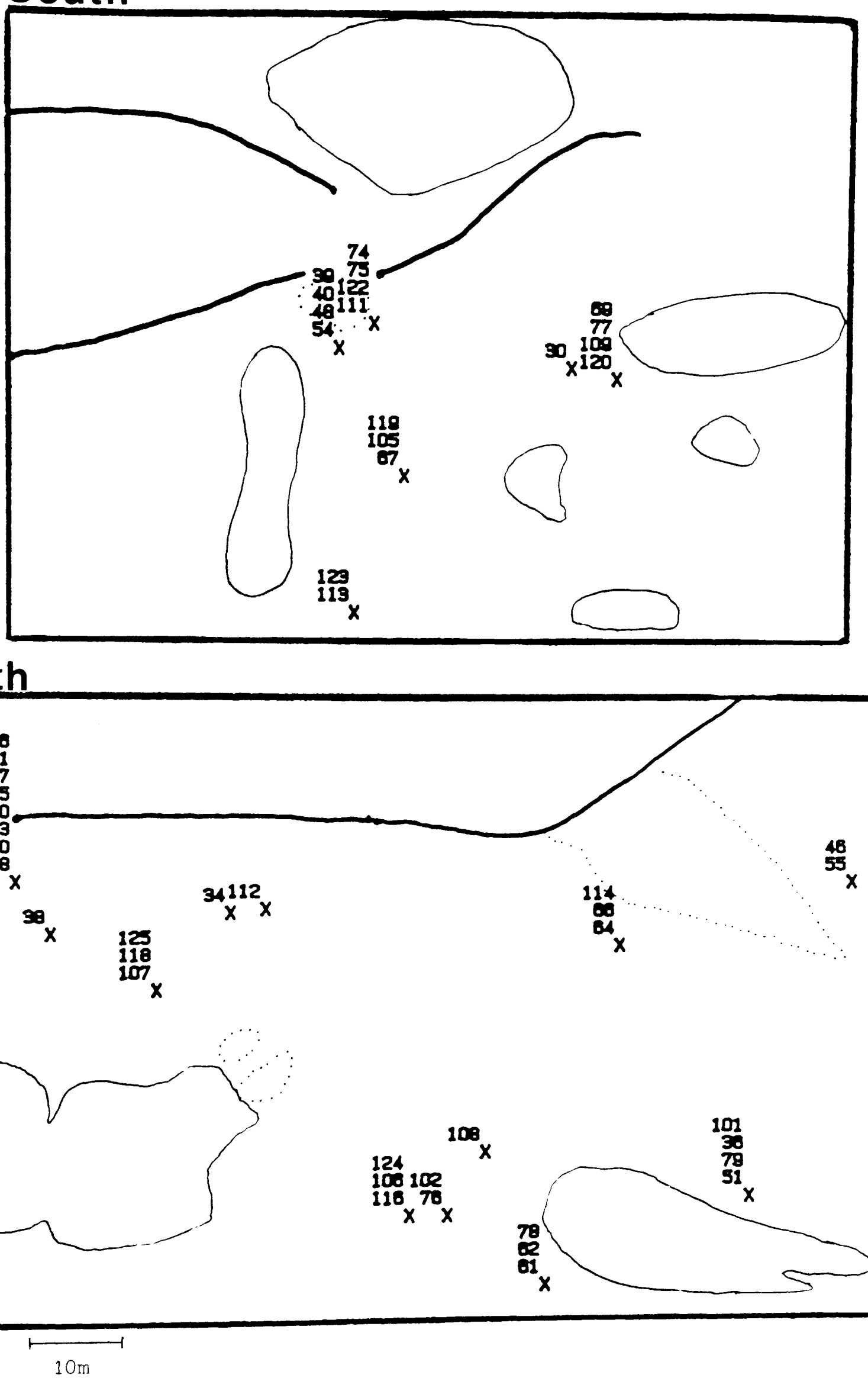

Fig 9.2. Trapping points of juveniles, Walney Areas South and North. X = position of trap. '123' = juvenile identity. = hill ridge. = bracken patch. = sand patch.

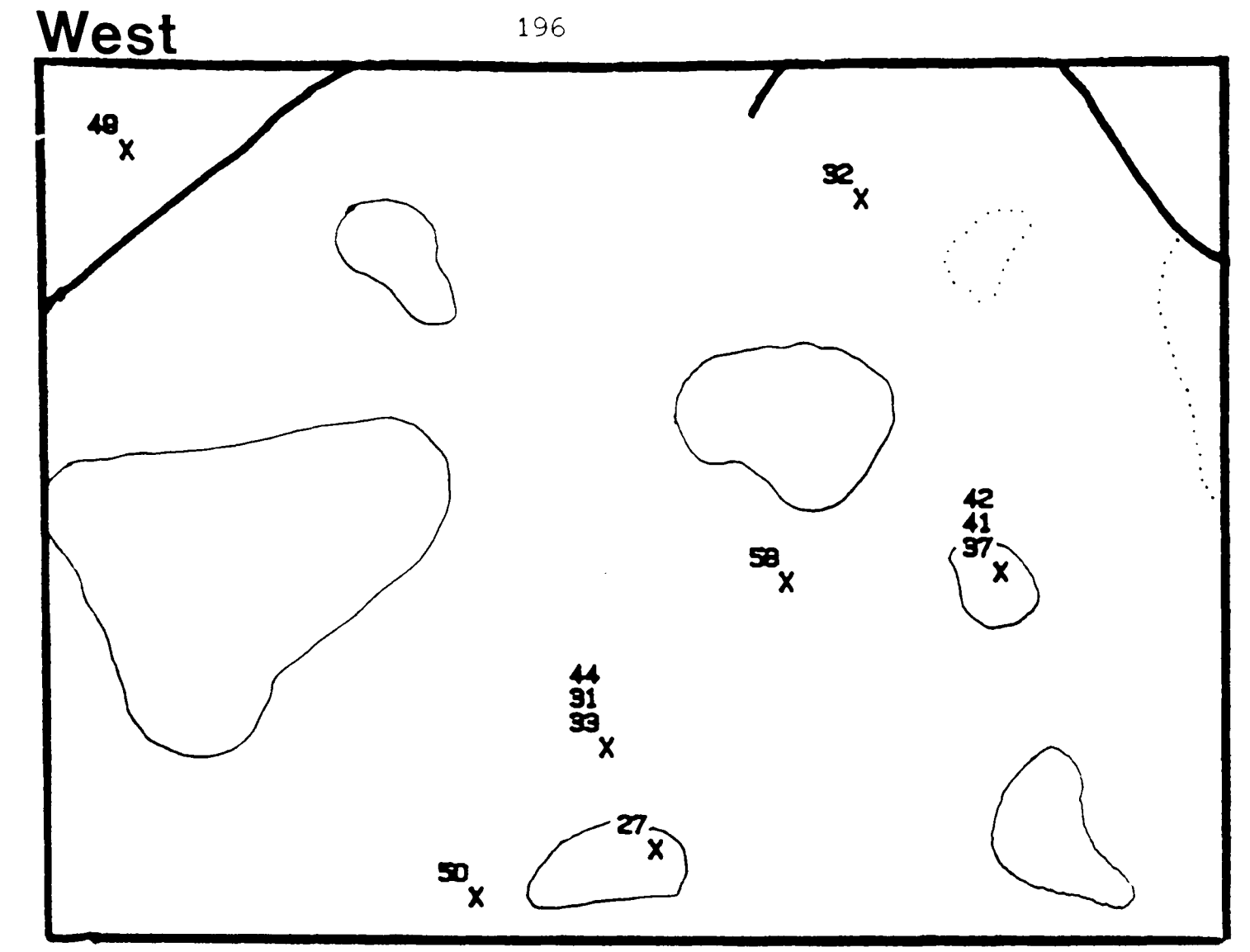

Fig 9.3. Trapping points of juveniles, Walney Areas West and East. X = position of trap: '33' = juvenile identity. = hill ridge. = bracken patch. = sand patch.

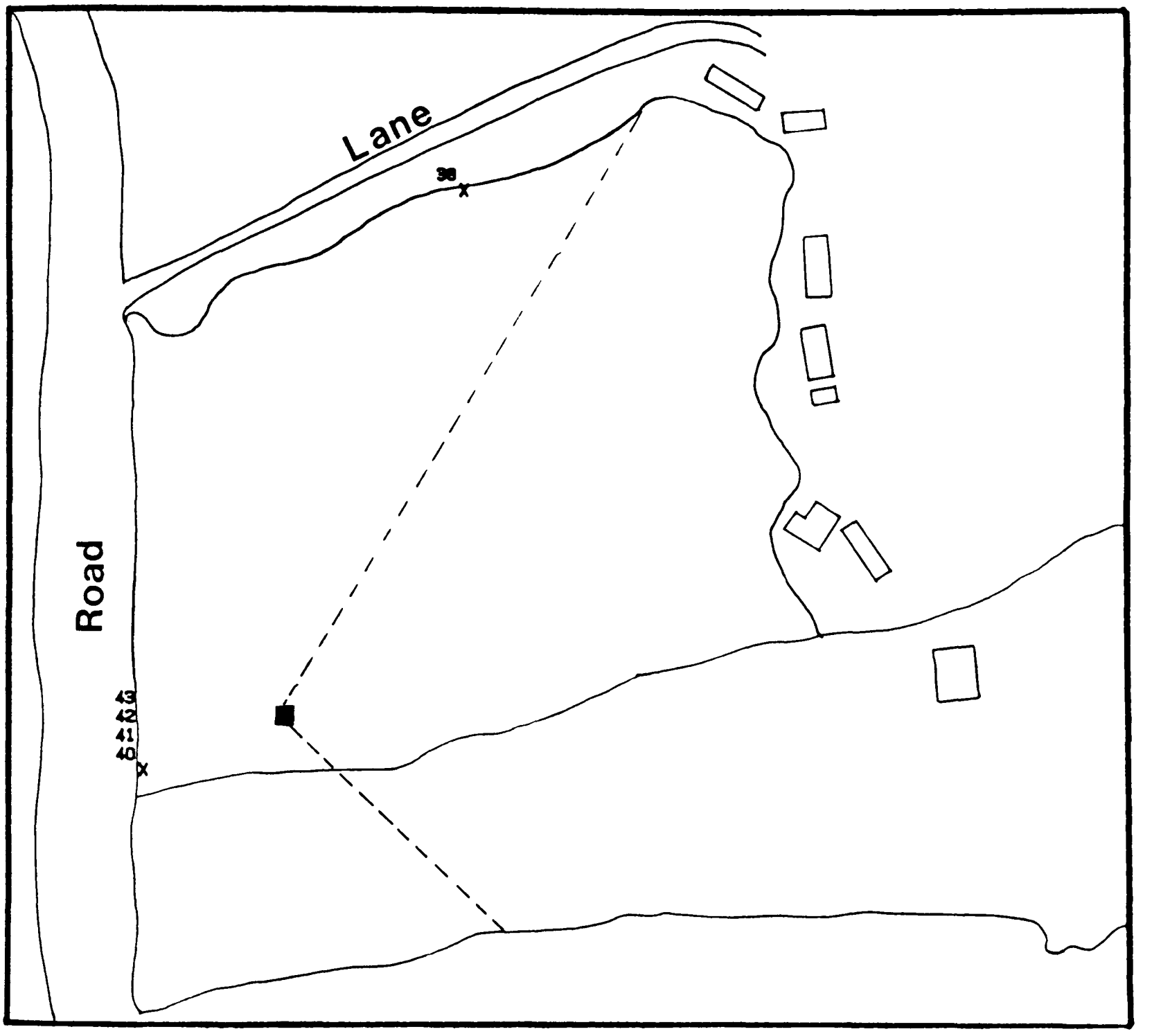

Fig 9.4. Trapping points of juveniles, 1982, Oxford.
X = position of trap. '43' = juvenile identity.
= building. = ditches at field edge.
= hide. = limits of vision from hide.

Table 9.10 Relatedness of different categories of pairs. Category is given followed by the two standard error confidence limits (set to 0.0 if negative), then the b which fell nearest to its offered ρ (set to 0.0. if negative).

Category	2SE confidence limits	b
1) PAIRS		
Walney consorting pairs	0.0 - 0.8	0.25
Oxford " "	0.0 - 0.6	0.01
2) MALES (WALNEY ONLY)		
Nearest neighbours	0.0 - 0.0	0.00
" neighbouring dominants	0.0 - 0.9	0.21
Dominants and subordinates	0.0 - 0.4	0.03
Dissociators	0.0 - 0.0	0.00
3) FEMALES		
Walney nearest neighbours	0.0 - 0.3	0.00
Oxford nearest neighbours	0.0 - 0.6	0.39
Oxford neighbouring dominants	0.0 - 0.7	0.46
" dominants and subordinates	0.0 - 0.7	0.33
Walney dissociators	0.0 - 0.4	0.00
Oxford dissociators	0.0 - 0.4	0.00
" associators	0.0 - 0.5	0.17

4a) OXFORD ADULTS WITH YOUNG

Adult	Young	2SE confidence limits	b
Females			
16	38	0.0 - 0.8	0.47
31	38	0.0 - 0.9	0.70
33	38	0.0 - 0.4	0.00
23	40,41,42,43	0.0 - 0.0	0.00
10	40,41,42,43	0.0 - 0.4	0.11
24	40,41,42,43	0.0 - 0.5	0.16
33	40,41,42,43	0.0 - 0.5	0.04
Males			
9	40,41,42,43	0.0 - 0.3	0.10
25	40,41,42,43	0.0 - 0.4	0.08

Continued....

Table 9.10 (Continued) Relatedness of different categories of pairs. Category is given followed by the two standard error confidence limits (set to 0.0 if negative), then the b which fell nearest to the offered ρ.

4b) WALNEY ADULTS WITH YOUNG

Adult	WHOLE AREA 2SE confidence limits	WHOLE AREA b	LOCAL AREA 2SE confidence limits	LOCAL AREA b
Females				
North				
2	0.0 - 0.0	0.00	0.0 - 0.0	0.00
6	0.0 - 0.0	0.00	0.0 - 0.0	0.00
47	0.0 - 0.0	0.00	0.0 - 0.0	0.00
106	0.0 - 0.0	0.00	0.0 - 0.2	0.08
East				
11	0.0 - 0.2	0.09	0.0 - 0.4	0.02
29	0.0 - 0.0	0.00	0.0 - 0.3	0.04
71	0.0 - 0.0	0.00	0.0 - 0.2	0.02
West				
2	0.0 - 0.0	0.00	0.0 - 0.4	0.19
26	0.0 - 0.1	0.00	0.0 - 0.3	0.00
28	0.0 - 0.1	0.03	0.0 - 0.3	0.00
57	0.0 - 0.2	0.07	0.0 - 0.4	0.16
60	0.0 - 0.0	0.00	0.0 - 0.4	0.12
North and West				
2	0.0 - 0.0	0.00	0.0 - 0.1	0.00
Males				
North				
1	0.0 - 0.1	0.03	0.1 - 0.2	0.16
3	0.0 - 0.1	0.00	0.0 - 0.0	0.00
4	0.0 - 0.0	0.00	0.0 - 0.1	0.00
7	0.0 - 0.0	0.00	0.0 - 0.1	0.00
8	0.0 - 0.1	0.01	0.0 - 0.0	0.00
9	0.0 - 0.1	0.00	0.0 - 0.1	0.00
56	0.0 - 0.0	0.00	0.0 - 0.1	0.08
East				
10	0.0 - 0.0	0.00	0.0 - 0.2	0.03
12	0.0 - 0.0	0.00	0.0 - 0.0	0.00
22	0.0 - 0.1	0.01	0.0 - 0.3	0.02
23	0.0 - 0.2	0.04	0.0 - 0.1	0.00
25	0.0 - 0.0	0.00	0.0 - 0.2	0.02
South				
5	0.0 - 0.1	0.05	0.2 - 0.5	0.37
21	0.0 - 0.1	0.02	0.0 - 0.4	0.18
22	0.0 - 0.1	0.01	0.0 - 0.2	0.00
West				
13	0.0 - 0.0	0.00	0.0 - 0.0	0.00
14	0.0 - 0.1	0.01	0.0 - 0.3	0.13
15	0.0 - 0.0	0.00	0.0 - 0.2	0.01
63	0.0 - 0.0	0.00	0.0 - 0.2	0.00
East and South				
22	0.0 - 0.1	0.01	0.0 - 0.1	0.00

Results

The results are summarized in Table 9.10. The range of relatednesses (b's) that fell within two standard errors of their respective ρ is given for each set, as well as that b which came closest to its respective ρ (set to 0.0 if negative).

The results showed barely any evidence for non-zero relatedness between adults, or between adults and young. Between adults, the confidence limits were usually very large.

Some of the results, though not showing significant relatedness were quite interesting. Nearest neighbour Walney bucks were completely unrelated, as were bucks that dissociated. The standard errors showed a possibility that neighbouring dominant rabbits were related, and the obtained b for these was quite high. This contrasted with the lower b and smaller confidence limits for dominants and subordinates.

The estimates of β obtained for neighbouring Oxford does were quite high, especially for associating and neighbouring does, although again, zero relatedness could not be excluded.

The results for adults with young at Walney were not very informative. Confidence limits for relatedness became larger as smaller samples of more local young were used. However the estimates of β were all very low, and non-zero relatedness was found in only two cases, for bucks 1 and 5 (of North and South respectively).

Results for Oxford does with young were more interesting, showing 31 to be the most likely mother for 38 (according to the b's). Confidence intervals show that 10, the dominant doe at the warren from which 40, 41, 42 and 43 emerged, could not have been mother to them all, since she was less than 0.5 related to them as a group. She might nevertheless have been mother to some of them. 24, the subdominant at the same warren, had a higher possibility of relatedness to the young, and only doe 33 could be completely discounted as a potential mother.

Section 9d. Discussion

The most interesting and reliable results obtained here showed that nearest neighbour bucks were unrelated. An aim of investigating this was to see whether the slow chasing and displacement behaviours, categorized as Dominance Interactions (Section 5c), were manifestations of a tolerant relationship between a dominant buck and his subdominant relative. Alternatively, the gentle nature of the interactions may have been despite the non-relatedness of the intruding subdominant, which the dominant attempted to keep at bay to the best of his ability. It appeared that the latter could have been the case, with an unrelated subdominant insinuating himself into the territory and into proximity with the doe. Such results are supported by the literature which shows that young bucks usually migrate from their natal warren (e.g. Dunsmore 1974). Neighbouring dominant bucks, that were more spaced apart than nearest neighbour bucks, were possibly related. At Walney, where rabbit density was very high, the distance between dominant bucks might have been the distance bucks would tend to migrate i.e. not very far. Also, if dominants were older and of more similar age, they are more likely to be related than a random pair. That dominant bucks appeared to be related supports Mykytowycz (1960) theory, that dominance runs in families; though whether it is heritable or environmental is another question.

Walney does were unrelated, but there were few of these

and they were widely spaced apart. The Oxford does, in contrast, showed the possibility of quite high relatednesses. It was likely that in this low density population with few areas apparently able to support warrens, nearby warrens were likely to fill up with related does.

Animals found from behavioural observation to dissociate were never related, whereas those that associated at Oxford might have been somewhat related. Associating rabbits were often likely to be close neighbours, and dissociating rabbits could have been dissociating by chance rather than by inclination. Nevertheless, such dissociations may have been purposeful avoidance of non-kin; or it may have represented genetically, or culturally heritable differences in habit e.g. emerging at different times of day.

Analyses of relatedness required a reasonable a priori understanding of possible relationships. Thus attempting to relate offspring en masse to different rabbits was unrewarding at Walney. Whereas knowing that 38 at Oxford was probably the offspring of 31, and having that supported by the genetic evidence, allowed greater faith to be put in the results concerning 10 and 24 and the four offspring from their warren. The results from this group were quite exciting. As 10 was the dominant doe (Chapter 5) I had assumed that the offspring from the warren were more likely to be hers than 24s. The results led me to check the genotypes of each kitten against each potential mother,

excluding maternity where neither of the kitten's alleles at any one locus could have come from the doe. 10 could not have been the mother of 40 or of 42, whereas 24 could have been mother of all four kittens, and must have been mother of 40 as neither of the neighbouring does, 33 and 23, could have been. Although these are the results from only a few offspring, they led me to consider dominance in does in a different way. Dominance in bucks appears to determine access to does and can be related to breeding success (Mykytowycz and Fullagar 1973). 10s attractiveness to males, which I had considered to be an aspect of her dominance status, might rather reflect her lack of success in breeding. Males finding her in a non-pregnant state would have been more attracted to her than to a breeding doe.

The statistical technique used here would be marvellously useful in more constrained populations with group-living occurring around localized warrens. It could be ascertained which does were producing most young and whether subdominants suffered reduced productivity when co-habiting with a dominant doe. Daly (1981) compared gene frequencies for three polymorphic loci (Car, Ada and Pgd), between three areas each containing several groups of rabbits, and found some genetic structuring between these subpopulations. She also looked at success in paternity by inspecting genotypes to see which offspring could not have come from particular males (as I have done above for local Oxford does). Where groups of rabbits contained dominant

and subordinate males, the dominants could not have sired 26% of the young in the group, the subordinates could not have sired 37%; 7% of the young could not have been sired by any of the group males.

CHAPTER 10. DISCUSSION

In contrast to some other populations, rabbits at Walney and Oxford did not form social groups of several adults. If social structure is under the control of evolutionary processes, then it should be optimally adapted to the environment, unless under some constraint, such as a timelag in evolution, a lack of available variation, or the animals' observing sub-optimal but adequate rules of thumb (Dawkins 1982). Whether or not rabbits 'should' be social in terms of the ultimate fitness of individuals is considered in Section 10a, from the literature. Group-living holds advantages and disadvantages in terms of predation, feeding, competition and disease, or may be occasioned by a neutral process of 'local enhancement'.

The lack of sociality at my sites may have been due to the absence of large warrens. Grouping rabbits might gather by local enhancement, with warrens acting as 'social catalysts'. The warrens on my sites were small and spaced out over homogeneous areas and the rabbits were also dispersed. This indicates that there is no underlying sociality that will cause gregariousness in the absence of cohabitation. Other studies on grouping in rabbits and on the attraction of warrens and the limitations on warren size are discussed in Section 10b.

A potential disadvantage of group-living is social competition. The does at both my sites lived apart, and seldom interacted, but the bucks spent much time maintaining

dominance relationships and keeping out intruders. Other rabbit studies describe aggression within the sexes, and the importance of dominance for males and females (Section 10c).

Dominance hierarchies were found to determine access to does on both my sites, and monogamy was found to be prevalent. This latter finding contrasts with the studies on grouping rabbits. The spacing out of the does probably made it impossible for bucks to sequester more than one doe. This constraint on polygyny is discussed in Section 10d, with other aspects of the breeding system.

Relatednesses between individuals were estimated in Chapter 9 from biochemical data. The development and validation of a new method for calculating relatedness were described. Very few non-zero relatednesses were discovered and, although this was partly because there were not enough data, in some cases, high relatedness could be excluded. This might have indeed reflected a social structure wherein unrelated rabbits came together in different social relationships. The migration system is responsible for the particular geographical distributions of animals of different kinships, and migration and relatedness are discussed in the Section 10e.

Group-living is particularly beneficial to many species in that it allows decreased individual vigilance for predators (Section 10a). In the Oxford rabbits, vigilance was decreased in the presence of the mate rabbit only, the presence of other rabbits was accompanied by increased vigilance. Other factors were also found to influence

vigilance, and the relationship between feeding and vigilance was investigated in depth. These aspects of vigilance are discussed in the light of other studies on the measures of vigilance, and in terms of the timesharing mechanism which they appeared to fit (Section 10f).

Section 10a. 'Should' rabbits be social?

Feeding

Group-living can increase the efficiency of foraging (Alexander 1974), and is important for learning and food finding in birds. By 'social facilitation' of feeding, woodpigeons develop search images for food (Murton 1971). Some birds, e.g. rooks (Corvus frugilegus), herons (Ardea herodius), and great tits (Parus major), use one another to find food (Murton 1971; Krebs 1974; Krebs, MacRoberts and Cullen 1972, also Zahavi 1971, Ward and Zahavi 1973). Food-finding is unlikely to be a relevant factor for rabbits, although Appleby (1980) considered this to be the function of the 'displacement behaviour' in red deer (Cervus elaphus) (which is similar to that found in rabbits described in Chapter 5).

There can be disadvantages to feeding in large groups. Barnard, Thompson and Stephens (1982) and Barnard and Stephens (1981) studied mixed flocks of lapwings (Vanellus vanellus), gulls (Larus ridibundus) and plovers (Pluvialis apricaria). Although for some of these species feeding was enhanced in larger groups, the enhancement depended on the ratios in which numbers of birds of each species were present, since some sub-groups interfered with the feeding of others. This effect can be thought of as paralleling that which might occur in groups of socially stratified animals, such as rabbits. Animals of different age, sex or social status might get differential benefits from the

presence of the rest of the group.

Although birds feeding in flocks can avoid depleting areas they have already been over and so make better search paths (Cody, 1974) rabbits in larger groups are more likely to suffer depleted food supply around the burrows (Farrow 1916). This is important for rabbit kittens which eat close to the warrens and do not move far from cover (Simonetti and Fuentes 1982). Competition for food in high density populations can lead to starvation (Mykytowycz 1961; Cowan and Garson 1985).

The selfish herd

Hamilton (1971) pointed out that individual animals are less likely to be taken by a predator if they are in a group; greater numbers reduce the chance of each member of 'the selfish herd' being taken. Predation on rabbits can be very high, and may sometimes control their populations (Myktowycz and Gambale 1965; Gibb 1977). They may be taken from the air; by ground predators; or underground. Avian predators are chiefly a risk to juveniles, which flee from birds (Dunnet 1957; Lockley 1961; Bell 1980; Stodart and Myers 1964; Myktowycz 1961). Cats (Felis spp), foxes (Vulpes vulpes) and humans will hunt rabbits above ground, putting the more peripheral subordinate animals to greater risk (Dunnet 1957; Myktowycz and Gambale 1965). Although badgers (Meles meles) and foxes are likely to catch only kittens by digging up the warrens, mustelids are an underground threat to adults as well (Cowan in press).

Conspicuousness

A small aggregation is more conspicuous than a single animal. The anti-predator gains will only outweigh this disadvantage in large groups (Vine 1973). Treisman (1975) suggested that grouping is only beneficial to individuals if the predator were likely to make just a single kill, or if the group was capable of defence and evasion. There is some evidence that larger groups of rabbits attract more predators. Large numbers of kittens appeared to attract birds in Mykytowycz and Gambale's (1965) study. In Parer's (1977) study, predation increased as cats, particularly, learnt about those warrens that produced young in sequential months.

Thus, for groups of rabbits, individuals will have a smaller probability of being taken by a single predator, but predators will be more attracted to the vicinity. Socially dominant animals might benefit, being central to the group and living in the better warrens, but subordinates might do worse.

Raising the alarm

Groups can avoid predation by confusing their predators, a suggested function for 'stotting' behaviour in Thomson's gazelles (Gazella thomsoni) and for shoaling in fish; although Schaller found that prey confused one another (Bertram 1978). Groups may also benefit from alarm calling, a risky activity to the performer, often best explained by

nepotism. Black-tailed prairie dogs (Cynomys ludovicianus) were more likely to give warning calls if there were more of their own relatives in the group. (Hoogland 1983).

Rabbits may warn one another of danger. Lockley (1954) suggested that does stamped and raised their scuts (white underside to the tail) to alert their young. Other functions have been suggested for a white scut though: Guthrie's (1971) hypothesis was that rump patches were used by animals to signal insubordination and invite mounting by dominants. Dominant bucks will mount subordinates under caged conditions (Myktowycz and Hesterman 1975; Black-Cleworth and Verberne 1975), but this has not been reported for wild rabbits. Myktowycz and Hesterman (1975) considered that the stamp might serve a social function, since it occurred after copulation, after winning a fight, and after returning to the buck's own territory.

Rabbits probably get ample warning of danger by observing escape reactions or scanning-postures in other rabbits. This was found to be true of pigeons (Columba livia) that, when electrically-shocked, were followed into the air by the rest of the flock. In contrast, those that flew off naturally, were not followed (Davis 1975).

Vigilance

Pulliam (1973) postulated that the selfish herd effect was inadequate to prevent peripheral animals, which are at greatest risk, from peeling away from the group. He proposed, and formalized with a mathematical model, that

'many eyes' not only enhance predator detection, but also allow individuals to scan less. This is the most frequently and most easily tested explanation for group-living.

Several studies on birds (starlings (Sturnus vulgaris), house sparrows (Passer domesticus), curlews (Numenius arquata), ostriches (Struthio camelus), juncos (Junco spp), Barbary doves (Streptopelia risoria)) show that individuals have lower levels of vigilance in larger flocks (Powell 1974; Barnard 1980; Abramson 1980; Bertram 1980; Caraco, Martindale and Pulliam 1980; Lendrem 1984). Furthermore, vigilance is higher with increased predation risk (Powell 1974; Barnard 1980; Lendrem 1984). Larger groups are better able to spot predators; Powell (1974) showed that larger starling flocks had shorter response times to a model hawk. Similar results have been obtained for mammals: when black-tailed prairie dogs were out at greater density, individual vigilance was lower; this was not due merely to the higher vigilance of newly-emerged animals since those that emerged when many animals were out had low vigilance straight away (Hoogland 1979). Nevertheless, the effect might have been confounded with time of day: less vigilance might be needed later in the day for reasons other than that many animals had emerged.

Pulliam, Pyke and Caraco (1982) applied the game theoretical approach to juncos to discover how animals could co-operate in vigilance without cheating occurring. They concluded that some vigilance would have to be expended on ensuring that the other animals were doing their fair share

of vigilance! Bertram (1980) could find no evidence for ostriches watching one another to ensure co-operative vigilance: they were more vigilant when alone, and their vigilance with a companion was not affected by the vigilance of that companion.

There are two other reasons why conspecifics should be watched, and these have opposite effects. Vigilance might be greater in smaller groups that are searching for more animals to join as suggested for ostriches, curlews, rooks, shelducks (Tadorna tadorna) and African antelopes (Bertram 1980; Abramson 1980; Feare, Dunnet and Patterson 1974; Patterson and Makepeace 1979; Underwood 1982). Alternatively, vigilance might be greater in larger groups since there are more animals to interfere with or to be interfered with by, as suggested for turnstones (Arenaria interpres) (Metcalfe 1984b). Larger groups can actually be worse at detecting predators; response time to a model hawk dropped suddenly as group size in wild doves (Streptopelia senegalensis) increased to over 15 birds, since squabbling was so great (Siegfried and Underhill 1975). Lazarus found response time was slower in larger flocks of Quelea, probably because of confusion (Lendrem 1982).

Vigilance was lower in larger prairie-dog (Cynomys spp) breeding groups, irrespective of numbers of animals out (Hoogland 1979). Cowan (1983) obtained a similar result for rabbits: as the size of a rabbit breeding group increased, so the rate of scanning during feeding decreased. He followed Hoogland in concluding that larger breeding groups

contained a higher proportion of subordinate animals, and that the greater intensity of feeding in such groups reflected the feeding strategies of subordinates. With their time above ground constrained and wasted by the attentions of dominant animals, subordinates were forced to reduce vigilance in order to have time to feed. This interpretation is supported by the 24-hour watches of Mykytowycz and Rowley (1958) which revealed that rabbits grazed all night with the dominant bucks staying out longest and the juvenile bucks and pregnant females grazing the most. Lockley (1961) similarly found that does were more intent on grazing than were bucks.

Local enhancement

Alexander (1974) pointed out that grouping can occur just to exploit a localized resource, e.g. Kummer (1968) found that Papio hamadryas baboons came together to sleep on the cliffs in large assemblages which broke up again into small groups for feeding.

The group itself can be an attractant, as it signals information about an area. Model geese with their heads up in vigilant posture were aversive to wild geese (Branta bernicla), whereas the models with heads down attracted wild geese to land (Inglis and Isaacson 1978). Armitage (1981) suggested that ground squirrels (Spermophilus spp) used the presence of conspecifics as a signal that an area was productive.

Cowan's (1983) hypothesis, that rabbits group to

exploit the limited resource of warrens, intimates no positive advantage to group-living. Nevertheless, in a group, rabbits might build larger, more effective warrens and so gain from the company. They could further protect themselves from the environment by huddling together for warmth, a system which greatly enhanced the survival of deermice (Peromyscus maniculatus) in refrigerators (Sealander 1952).

Competition and disease

Groups might benefit individuals, increasing success in competition with other groups (Bertram 1978). Defence between groups, with patrolling, marking and fighting at the borders was seen in Cowan's (1983) rabbit study.

Alexander (1974) suggested that competition for food and mates could arise within groups, although social order would ameliorate these, eliminating aggressive competition and reducing the further threats of parasitism and disease. Cowan (1983) found higher levels of coccidiosis in the young of crowded warrens. Myxomatosis, spread by physical contact and by the rabbit flea (Spilopsyllus cuniculus) is transmitted more rapidly in dense populations (Fenner and Ratcliffe 1965), especially in shared warrens (Williams 1971). It is rumoured that after myxomatosis, the rabbit altered its lifestyle to living predominantly above ground, shunning the warrens where cross-infection of the disease was more likely (Times newspaper 11.5.1963).

Section 10b. Are warrens social catalysts?

Grouping in rabbits

In this study rabbits lived in small, single or double entranced burrows, spread over the dunes at Walney and around the hedgerows at Oxford. Parer's (1977) site resembled mine in that the modal number of warren-entrances was one; more than 15 entrances being extremely rare. My findings for social structure were similar to his, with adults grouping only into male/female pairs. This contrasts with the studies of Myers and Poole (1959) and Cowan (1983), in which the rabbits formed groups comprising several adults of each sex. At these sites the warrens were larger e.g. Myers and Poole's rabbits lived in big warrens with up to 50 entrances. That I found no coherent groups in the absence of large warrens supports the hypothesis that rabbits do not group for any evolutionarily advantageous reason, but in order to exploit the limited resource of warren-availability.

In a trivial sense, rabbits clustered in space and time at my sites, confined to their habitat requirements and emerging at similar times of day. Their burrows were constructed near one another. However, within such large-scale confines, rabbits apparently did not group, but spaced themselves and their burrows apart (at Walney), emerging above ground independently of one another. At Oxford, the burrows were clustered, probably because of the heterogeneity of the hedgerow.

The argument of Myers and Parker (1965), that does prefer to breed together and will build warrens close to one another is refuted by my results. Their findings of apparent gregariousness in does may be explained by does gathering to share warren space. Warrens themselves might appear to be clumped due to the clumped nature of suitable warren-sites. At Walney, recognizable does were spread widely apart and even avoided one another in time. At Oxford, does were widely dispersed, despite the clustering of burrows, and only in one case did two does live close together.

Mykytowycz (1973; 1974; 1975) considered the promotion of group cohesion to be the vital function of the rabbit pheromones secreted from the chin, inguinal and anal glands. The pheromones promoted a group identity, were used to delimit a group territory, and imprinted juveniles onto the group odour. However, pheromones were also thought to be used to signal social status, and this use alone would be adequate to explain the need for such chemicals (Mykytowycz and Fullagar 1973; Bell 1980).

Warren attraction

It is quite feasible that the warren itself is enough of an attraction to draw rabbits together. Success in breeding is largely dependent on the standard of the nest-site and there is some evidence that large warrens are better than small ones.

When breeding outside of warrens, purpose-built

breeding-stops are constructed by does. These are blind-ending single-entranced tunnels, which the doe covers over after each visit she makes (Myers and Poole 1961). Nests are made in the stop, and lined with the doe's own fur for warmth (Denenberg, Zarrow and Ross 1969). Lloyd and McCowan (1968) found such stops on Skokholm and noted that the does visited them for only a few minutes, once every 24 hours.

Breeding-stops are inferior to warrens as havens for young. Predation on their nests can be heavy. Badgers and foxes burrow directly down to the nests, or follow the tunnel along (Lloyd and McCowan 1968). The only threat to deeper warrens are mustelids. Myers and Parker (1965) found some fox-predation of warrens in sandy soils, but on Parer's site (1977) the deep sandy warrens were safe from this; foxes concentrated on the surrounding clay areas.

Breeding-stops are very susceptible to waterlogging, and the drowning of their occupants (Myers 1958; Lloyd and McCowan 1968). Mykytowycz and Gambale (1965) found that added to problems of predation and flooding, the young that emerged from stops had no adequate shelter to which to return; they would attempt to attach themselves to neighbouring warrens.

Rabbits themselves exhibit interest in and a high evaluation of warrens, particularly for breeding. Myers and Schneider (1966) described a doe insinuating herself into the main warren and dropping her litter there. She succeeded in feeding her young by entering the warren whilst

the other rabbits were grazing. Female aggression to other females and to young is generally over access to burrows (e.g. Mykytowycz 1960). The only aggression seen on my sites between known does, was between the two that shared a warren.

Limitations on warren size

Parer (1977) suggested that warren-size was limited on his site by the males suppressing the others from digging. Dominant males might have preferred smaller warrens where they could maintain control over fewer animals. Also, having fewer kittens around would be less likely to attract predators. The bucks' predilection for defaecating on freshly dug soil was suggested as a mechanism to inhibit further excavation.

Myers and Parker's (1965) survey across Australian sites showed that mean warren size varied with the type of substrate. It was largest in heavy soils, and smallest in sandy soils. Overall, small warrens were the most common with modal numbers of one to four entrances per warren, across many sites.

The most likely explanation for the lack of large warrens on my sites is that the substrate would not support them. It seems to be true that large warrens will develop where the substrate allows, inertia preventing rabbits from developing fresh warrens (Mykytowycz and Gambale 1965; Cowan 1983). It could be that any doe attempting to initiate a new warren would do worse than by staying and extending an

existing habitation. That cohabiting causes sociality is better supported by my results than to conclude that sociality encourages cohabitation. If the latter were true, the gregarious rabbits would be expected to gather together even when unable to share warrens.

Section 10c. Social competition

Aggression between does

There are reasons why does should avoid one another. Although usually quite tolerant, they can be aggressive to one another (Myers and Poole 1961) especially over burrows (Mykytowycz 1960; Mykytowycz and Hesterman 1975). Cowan (1983) found that female dominance peaceably determined access to burrows, although fighting also occurred, especially during nest-building. The greater proximity of does sharing warrens on chalk-land might explain the higher rates of aggression found in these than in dune rabbits (Cowan and Garson 1985). Myers and Poole (1959) implied that aggression between does was sometimes over bucks, though Lockley (1961) noted no 'sexual jealousy' by does.

At both my sites, the does were spread out, and whether this was engineered by the bucks, a fortuitous result of the spread of warrens, or effected by avoidance between females, it appeared to result in very little aggression between does.

Aggression between bucks

The functions of interactions between bucks are on the one hand to exclude strange bucks from the territory of the resident by fierce aggression and on the other hand to establish a hierarchy amongst co-resident bucks. Such a hierarchy would determine access to a limited resource. Unlike red deer (Appleby 1980) and experimental birds

(Krebs, MacRoberts and Cullen 1972) dominant bucks seldom feed after displacing a subordinate, thus food-finding is unlikely to be the function of the hierarchy.

Much more importantly, dominance hierarchies determine which males will have access to does. Mykytowycz (1958) described the pairing off of equally matched individuals taken from a male and a female dominance hierarchy, although the dominant male could always oust subordinates from other females. Myers and Poole (1959) described a more polygynous system, and assumed that the dominant male was siring all of the progeny; the secondary male only achieving matings by moving off with a doe to form a splinter group.

At both my sites there was a clear relationship between male dominance and the consortship system. The dominant bucks associated closely with females. The subordinates very rarely had access, and then only when the dominants were absent.

Doe-dominance and breeding success

Dominance is an indicator of breeding success. It is the dominant rabbits that breed in the driest, deepest warrens and produce the most, and fittest kittens (Mykytowycz 1959; Mykytowycz and Gambale 1965). Although higher productivity might be partly due to the better warrens, dominants' might boast genetic superiority. They breed earliest and their young achieve highest growth rates, feeding on the better grass (Mykytowycz 1960; Gibb 1977). Mykytowycz (1960) found dominant does to produce dominant

offspring, which Myers and Poole (1959) did not. The greater success of dominant does in breeding might be partly due to age: learning over successive broods increased the breeding success of domestic does (Ross, Sawin, Zarrow and Denenberg 1963).

Dominance status in does might also affect the physiology of reproduction. Brambell (1942,1944) compared the numbers of corpora lutea to the numbers of embryos in the reproductive tracts of shot does and found that up to 60% of whole litters had been lost by reabsorption, and 10% of ova released in the surviving litters had also been lost. These losses usually occurred after implantation and once the placenta had been well established. Neither Southern (Brambell 1944) nor Lloyd (1963) found such high levels of intrauterine mortality in their populations. 50% of embryos appeared to be being reabsorbed in Mykytowycz's (1960) study; he suggested that this was due to stress in the subordinate does caused by overcrowding.

Chapais and Schulman (1983) reviewed breeding success in female primates in relation to dominance, and found that harassment from dominant females induced stress in subordinates which bred less well as a result. Bertram (1978) suggested that the inhibition of dwarf mongoose (Helogale undulata), wild dog (Lycaon pictus) and wolf (Canis lupus) subordinate females such that only one dominant female breeds, occurs because a) a single female produces enough young to utilize the group's resources b) subordinates would not succeed living outside the group c)

the group is compact enough that the dominant can control subordinates and d) there is high relatedness between females such that kin selection might obviate the detrimental consequences of suppressed breeding.

Cowan (1983) found that average female lifetime reproductive success was greatest in rabbit warrens inhabited by a single doe. He concluded that group-living was disadvantageous to does. However, he did find that average productivity increased as group size increased from two does. These results could be explained if the dominant doe suppressed breeding in subordinates, bringing down the average productivity of a warren. As the group grew, so her influence over each subordinate waned, increasing average productivity. Cowan explains his results relative to burrow-availability. In any case, his work indicated that does have nothing to gain from gregariousness, a conclusion supported by my findings that they do not gather together when their habitations are separate.

Overt and covert hierarchies

Dunbar (1983) found that subordinate Papio hamadryas and Theropithecus gelada baboon females failed to ovulate when harassed by dominant females. Although unaware of it at first, he eventually realized that there was a very strict hierarchy amongst the females, but that it was subtle and covert. This idea of covert hierarchies is very interesting. Gaston (1977) found a strict order of dominance in jungle babblers (Turdoides striatus), which was

so well-defined that it needed no re-affirmation. Since there were no dominance struggles it was quite difficult to see the cryptic hierarchy. He suggested that obligate group dwellers that had been such for a long period of evolutionary time, would have strong, cryptic hierarchies. The overt dominance hierarchies in buck rabbits, constantly in need of re-affirmation, reflect their opportunistic social systems which sometimes involve group-living, sometimes not.

Section 10d. The breeding system

The literature suggests that as more rabbits come together the social system changes from non-grouping, monogamous rabbits to groups with female-biassed sex ratios and possible polygyny. At Parer's site (1977), the rabbits lived in monogamous pairs with solitary bucks in addition. Myers and Schneider (1964) found two males and two females in most warrens, these small groups occasionally sporting satellite males. Groups of two males and two females were the norm on Cowan's site (Cowan 1983). The large groups described by Myers and Poole (1959) comprised two or three males to four or five females.

Mate choice

Since there is no overt paternal care in rabbits, female choice of a male might be chiefly for his genes: to achieve genetic compatability (Lenington 1983); optimal outbreeding (Bateson 1978), and perhaps also to choose the 'fittest' male to produce fitter offspring. The male dominance hierarchy determines which males have access to females. This may provide females with the 'best choice' in genetic terms (Trivers 1972).

Pregnant does are very eager to dig, and can build breeding stops overnight (Myers 1958). Bucks also dig, but in less concentrated fashion, leaving structures which the does sometimes enlarge (Mykytowycz 1959). Since food is not defended by rabbits (Bell 1980) and burrows are constructed

chiefly by does, it is unlikely that bucks defend any resource which might initially attract does. However, if a non-transient bond were formed between a buck and doe, advantages other than the purely genetic might accrue to the doe by pairing with a strong buck. Such a buck might protect the doe, and the resources that she had acquired, from interference and usurpation by conspecifics.

Unless a buck can achieve access to several does, mate-choice is as critical for him as for does. He might also 'look' for genetic fitness in terms of a strong, healthy, compatible, dominant doe that would breed early. He might also be attracted to the resources that she had built up.

Prerequisites for polygyny

With access to females determined by male dominance hierarchies, polygyny requires that a male maintain his status. However, dominance hierarchies in bucks are location dependent. Mykytowycz and Hesterman (1975) and Mykytowycz (1975) showed that a buck familiar with an experimental cage, or in a cage impregnated with his own secretions, would usually win in contest with a second buck. Even a kitten would defend its home territory, unless the intruder were much older (Dudzinski, Mykytowycz and Gambale 1977). In the field, bucks are dominant in their own groups only, acting as subordinates elsewhere (Myers and Poole 1959; Cowan 1983).

Further, successful polygyny could only occur if the buck were able to dominate the attentions of all of 'his'

does over all of their periods of receptivity (Emlen and Oring 1977). This could be a considerable task in rabbit populations, with more than one male in a group. Mykytowycz and Rowley (1958) described courtship and mating sequences that continued right through the night. The doe continually breaks away and initiates tight circles as the buck attempts to remount (Rowley and Mollison 1955). It is a full ten hours after stimulation, that induced ovulation takes place (Denenberg, Zarrow and Ross 1969; Adams 1982) and presumably any buck achieving a mating within or soon after that time, has a chance of fertilizing eggs. Behavioural oestruses in does, which might require their guarding by bucks, occur quite often. Myers and Poole (1958) observed seven-day cycles of attractiveness in wild does. The does would solicit male attention, and copulate (except on rainy days!). Garson (1982) suggested that does were synchronously receptive which gave subordinate males access to mates (Cowan and Garson 1985).

As Trivers saw it, that sex providing the least parental investment will compete most strongly for the other sex. There might be sperm competition in the female tract, infanticide, or induced abortion brought about by the Bruce effect (Trivers 1972). The intra-uterine reabsorption seen in rabbits, which is affected by rabbit density, may, as suggested earlier, be a manifestation of competition between does, or it may be one of competition between bucks, bringing the doe back into oestrus. Hughes and Myers (1966) described 6-7 day cycles of attractiveness in domestic does

during pseudopregnancy. They suggested such behavioural oestruses coincided with particularly difficult stages in pregnancy: implantation and placentation occurring on the 6th and 12th days, and reabsorption of foetuses peaking on the 7th and 14th days. Cannibalism, noted only in domestic populations and probably an aberration (Sawin and Crary 1953), might otherwise be another demonstration of competition for siring offspring.

Monogamy at Oxford and Walney

The mating-systems at both Walney and Oxford tended towards monogamy. This was despite the large potential mate pools, particularly for the females, at Walney. At both sites the spacing-out of the does was the most likely explanation with the bucks unable to sequester more than one doe (following Emlen and Oring 1977). Male dominance hierarchies were found (usually only two tiers deep) which determined access to these does and precluded polyandry. The literature indicates that male dominance hierarchies are location dependent, and that does would require considerable attention to ensure exclusivity of mating. Polygyny might be achieved when does are clustered together, and this might explain (as Myers and Poole (1959) suggested) why there are relatively few males in large groups.

Section 10e. Kinships

That vigilance was increased with non-mate rabbits present could have been due to the animals watching other rabbits in order to avert or to initiate social interference. Alternatively, adults might have increased their vigilance in the presence of others in order to protect them, particularly to protect young and relatives. Relatedness between adults depends on dispersal. If animals were more closely related they might be expected to exhibit less competition and more cooperation.

Relatedness

Data on genetic polymorphisms were obtained by enzymic and immunoglobulin analyses and used to assess relatedness between individuals. Such studies have been done on other animals, some using regression methods to estimate relatedness. Craig and Crozier (1979); and Pearson (1982; 1983) used regression to investigate relatedness between nests of ants. However, none of the available methods compared relatedness between several dyads in a class of social relationship. A new regression method was developed and validated in Chapter 9 for use in this way, providing estimates of the standard error of the estimate of relatedness.

Knowing half of the genealogy of an animal gets the analysis a long way. This helped Foltz (1981) to find evidence for long-term monogamy in the oldfield mouse

(Peromyscus polionotus), McCracken and Bradbury (1981) to reveal the social organization of the polygynous bat (Phyllostomus hastatus) and Wilkinson (1984) to discover that altruism in vampire bats (Desmodus rotundus) was based on reciprocity. I attempted to reveal differential breeding success between dominant and subordinate bucks by relating each buck to all of the young, and to local young only. However, relatedness on such a large scale was found to be very low. Paternal exclusion, without knowing the genotype of the mother, would not have exluded enough bucks.

Some useful information was obtained from assessing relatedness between rabbits. A subordinate doe at Oxford was found to contribute greatly to the genetic constitution of the offspring in her shared warren. Subordinate and dominant males at Walney were found to be unrelated, whereas neighbouring dominant bucks at Walney and neighbouring does at Oxford showed the possibility of being quite highly related. These distributions of individuals were determined by the migration system.

Migration

Where groups of breeding rabbits have been described, their cohesion has been found to break down outside the breeding season (Mykytowycz and Gambale 1965). There are natal and breeding migrations, and bucks, particularly, move 100-300m (Myers and Poole 1959; Mykytowycz 1960; Dunsmore 1974; Gibb 1977; Parer 1977; Cowan 1983). Does also move, especially from crowded warrens, and Cowan (1983) estimated

that 46% of his does were breeding in non-natal warrens. Lockley (1954) described how the final litters of a season were tolerated in the warren, and immigrants were accepted in this 'neutral' season. When breeding recommenced, hostility took hold, and migrations occurred. Animals migrated after suffering aggression from the more dominant animals and losing access to the warrens (Myers and Poole 1959; Mykytowycz 1960).

Natal migration is also caused by the aggression of adults, particularly does, towards juveniles (Myers and Poole 1961; Mykytowycz and Dudzinski 1972; Dudzinski, Mykytowycz and Gambale 1977; Cowan 1983). They are aggressive to strange young kittens, recognising their own young by pheromones (Mykytowycz 1959; Muller-Schwarz 1974; Mykytowcycz 1974, Mykytowycz and Ward 1971). However, they also attack their own young, turfing them out of their natal warren to make room for subsequent litters (Mykytowycz and Rowley 1958).

Section 10f. Influences on vigilance

Wariness for conspecifics

Unlike Garson (pers comm) and Cowan (1983) who found no effects on vigilance of numbers of conspecifics out, I was able to detect effects by looking at subclasses of animals. The advantage to group living of reducing vigilance did not pertain to the Oxford rabbits except in the case of the 'mate' rabbit. The presence of other conspecifics did not reduce vigilance but the converse: the more females and young there were present, the greater the vigilance of bucks and does. An experiment run to test the effects of conspecifics on vigilance using stuffed animals bore out the observations in that vigilance was increased in the presence of both Rabbit and Fox, but not of Pheasant.

Wariness for mate

Pair bonds were noted at both my sites, and at Oxford, where vigilance was investigated, the 'mate' rabbit was found to have a unique effect on vigilance. Increased distance to the mate was a predictor of increased vigilance. This might be due to any of several factors (see Section 10a). It might be that the rabbit watched out in order to spot its mate when it was far off. This could be interpreted as a form of 'sexual jealousy' and mate-guarding, or as an attempt by the rabbit of avoiding being alone. Wariness could then be decreased with the mate's presence which protected against predators (by the usual

arguments for grouping), or guaranteed less interference from conspecifics. The reasons that obtained for males and for females might have differed.

Miscellaneous factors

Factors other than predator risk and conspecific competition influence feeding and vigilance. The feeding rate of house sparrows was affected by food density and temperature (Barnard 1980); reaction times of mixed-species bird flocks were shorter on warm, long days when feeding took a low priority (Thompson and Barnard 1983); vigilance in great tits increased as satiety increased (Cowie, Houston, Kacelnik, Krebs and Tarpy 1981). Lendrem (1984) found that presenting a Barbary dove with a choice of seeds reduced the feeding rate. Southern (1948) observed that rabbits fed more intensely, with more rabbits above ground, just before thunderstorms. In my Oxford rabbits, time of day was the most vital factor, vigilance decreasing as the evening progressed. Date was also important for bucks; vigilance decreased with the season. Scans were shorter on warmer days.

Measures of vigilance

The need to perform both feeding and vigilance is interesting in its own right, quite apart from the insight that it gives into sociality. I had hoped that investigating the nature of vigilance and the interrelationships between different measures might

elucidate the social parameters, but there were no clear-cut conclusions to be drawn. Lendrem's (1982) analyses of Barbary doves feeding used proportions of time spent scanning, and the rates of scanning. These rates were both the instantaneous rates of feeding, which were the pecking rates inbetween true scans, and the absolute rates of feeding, which were the peck rates overall. Response time is an unreliable measure since it is difficult to distinguish detection time from reaction time. For the rabbits, although proportion of time spent scanning was correlated with rate of scanning, they each correlated in opposite ways with median scanlength (positively and negatively respectively). This indicated that there were two distinct means of increasing vigilance, which might be employed in different ways for different purposes. Metcalfe (1984a) discovered a complicated relationship between vigilance (which he considered to be primarily for predators) and feeding. Purple sandpipers (Calidris maritima) increased their vigilance by increasing their rate of scanning, but turnstones did so chiefly by increasing scanlengths. He suggested that this was because turnstones had longer handling times for their prey, which precluded frequent scans. Further, he found in both species that scanlength increased after the maximum rate of scanning had been reached (Metcalfe 1984b).

Hart and Lendrem (1984) emphasised the advisability of looking at distributions of scan and feed durations. They criticised the simplifying assumption in Pulliam's (1973)

model, that scans were instantaneous, and constructed a model using interscan intervals from which they calculated the probability of a scan occurring. A Markov chain analysis of the probabilities of a peck following a peck or of a scan following a peck was done on juncos by Caraco (1982). He found that the constant I, the probability of a sequence of pecks ending, decreased as a linear regression with increasing group size. At each group size, I stayed constant regardless of the length of the sequence of pecks and scans, giving a geometric distribution. A flock size of four was the exception, with I increasing after each consecutive peck. For the rabbits, it was possible to look at distributions of durations of scans and feeds. Whereas the probability of a scan ending decreased with duration of that scan, feed durations were closer to random. The sharp decrease in probability for scanlengths finishing might have been due to a changeover between modes of vigilance, with average scanlength increasing and so increasing the proportion, but not the rate of scanning. Such an increase might be occasioned by external stimuli.

Timesharing

Experiments were run to discover the interdependence of chewlength and scanning and to see whether the temporal patterning of behaviour sequences fitted the timesharing hypothesis.

To some extent, scanlength is dependent on 'chewlength' the quantity of food in a rabbit's mouth as it begins a

scan. The original observational data showed that longer scans coincided with longer chewlengths. Further, the change to long scans occurred for at least half of the rabbits at the maximum chewlength point. Such correlations might have been due to two causes. Long chewlengths could have been chosen when the rabbit wanted to increase vigilance, or increased vigilance might have resulted from long chewlengths. Both effects could occur and, with vigilance or feeding respectively dominant, both effects could fit a timesharing mechanism. Subdominant behaviours are slotted into periods when the dominant behaviour is resting from expression.

The conditions under which such subtle effects occurred were difficult to emulate in experiment. For only one rabbit was it possible to manipulate fear in a fine enough way that fear interacted with food length to determine feeding success. Others of the experiments allowed feeding to remain dominant, under which conditions the availability of long grass to chew produced longer scans. Manipulating fear levels in the field indicated that grasslength ceases to be important under conditions of high vigilance-requirement. With a high vigilance requirement, longer grass was not selected to permit longer scans. Rather, chewing was completely abandoned. Nevertheless, it is still possible that long chewlengths could be chosen to enhance vigilance, but this is likely to be in non-threatening situations. I first suspected such an effect whilst observing a dominant buck making its way towards a

subdominant, tearing swiftly at long stalks en route, and chewing these up whilst standing up on hind legs and looking out. He eventually reached the subdominant and chased it off.

Thus, whereas scanlength may be affected by chewlength when feeding is dominant and there is no immediate call for great vigilance, when such occasion arises, chewing is abandoned and feeding is sacrificed to high vigilance.

In conclusion, rabbits that live in small warrens do not form large groups. This may reflect a basically asocial nature in rabbits, their often observed gregariousness resulting from cohabitation. Small social units were found, formed from monogamous pairs. Polygyny may have been precluded in these spaced-out rabbits since the males could not securely sequester more than one doe. Although vigilance during feeding may be reduced for a rabbit by the presence of its 'mate', non-mate rabbits caused increased vigilance, perhaps because of social interference. Rate of scanning and proportion of time spent vigilant could not simply be divided into vigilance for predators and vigilance for conspecifics. Polymorphisms revealed by biochemical analyses of blood were used to estimate relatedness between animals by a new method. The most accurate, interesting result from this was that close neighbour dominant and subordinate bucks could not have been closely related. An interesting controlling factor was found for scanning during

feeding. The duration of scans was sometimes found to be dependent on chewlength, when feeding was said to be dominant. At other times, a greater need for vigilance would produce more scans devoid of chewing.

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APPENDIX I

Multiple regression outputs from BMDP

The following 30 pages are the multiple regression outputs summarised in Section 7b. There are six outputs for each of the five dependent parameters which were Rate, Prop, MScan (here written UP), MFeed (DOWN), Graze (LENGTH). Each of the five parameters appear in turn.

For each parameter, the regressions were run in two bouts: the first three outputs are of the small model, with other rabbits classed as DCLO and DFAR. The second three are of the large model, with other rabbits further divided into male adult, female adult or juvenile (as visible on the left-hand listing of independent variables).

Each set of three outputs was run for all rabbits (with independent variables R1-R8 representing the rabbit identities); for does only (with doe identities R5-R8); for bucks only (with R1-R3).

Normal probability plots are shown with the results.

DEPENDENT VARIABLE. . . . . 4 RATES
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

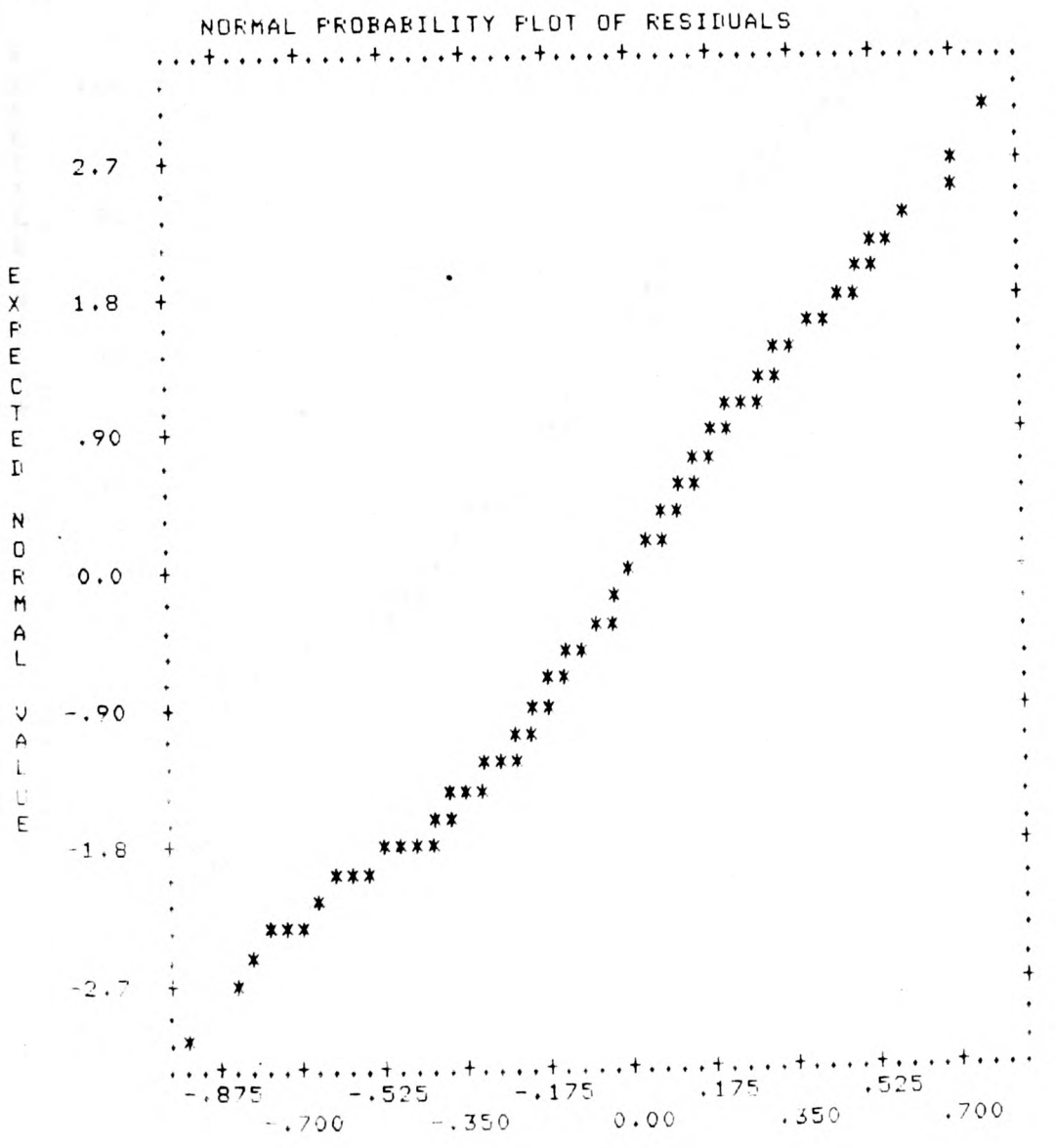
MULTIPLE R 0.4263 STD. ERROR OF EST. 0.2521
MULTIPLE R-SQUARE 0.1818

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	6.5232	21	0.3106	4.887	0.0000
RESIDUAL	29.3645	462	0.0636		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		3.13113					
DATE	6	-0.61247E-03	0.47249E-03	-0.074	-1.296	0.1955	0.53721
TIME	8	-0.13086E-02	0.29879E-03	-0.213	-4.380	0.0000	0.75158
GRALEN	11	0.02322	0.01193	0.089	1.946	0.0522	0.84458
DISTUR	12	0.07284	0.04952	0.064	1.471	0.1420	0.92131
R1	49	0.04145	0.04912	0.056	0.844	0.3992	0.40259
R2	50	0.14460	0.05150	0.190	2.808	0.0052	0.38658
R3	51	-0.03684	0.06343	-0.035	-0.581	0.5617	0.48647
R4	52	0.17361	0.09082	0.091	1.912	0.0565	0.78684
R5	53	0.00115	0.04611	0.002	0.025	0.9801	0.35167
R6	54	0.04456	0.05944	0.043	0.750	0.4538	0.52645
R7	55	0.03982	0.07285	0.032	0.547	0.5849	0.52502
R8	56	-0.04107	0.05245	-0.054	-0.783	0.4340	0.37271
DFAR	59	0.02741	0.01824	0.080	1.503	0.1336	0.63230
MATE	57	0.03762	0.04026	0.068	0.934	0.3506	0.33908
M	58	0.01615	0.00694	0.165	2.329	0.0203	0.35230
COWS	15	0.06741	0.04561	0.068	1.478	0.1401	0.83270
TEMP	44	-0.00330	0.00401	-0.057	-0.823	0.4107	0.37232
PPT	45	0.00154	0.00339	0.022	0.454	0.6502	0.76967
CLOUD	46	0.05658	0.03958	0.080	1.429	0.1535	0.57094
WIND	47	-0.00198	0.00303	-0.031	-0.653	0.5141	0.76198
DCLO	61	0.03474	0.01729	0.092	2.009	0.0451	0.83905

ALL



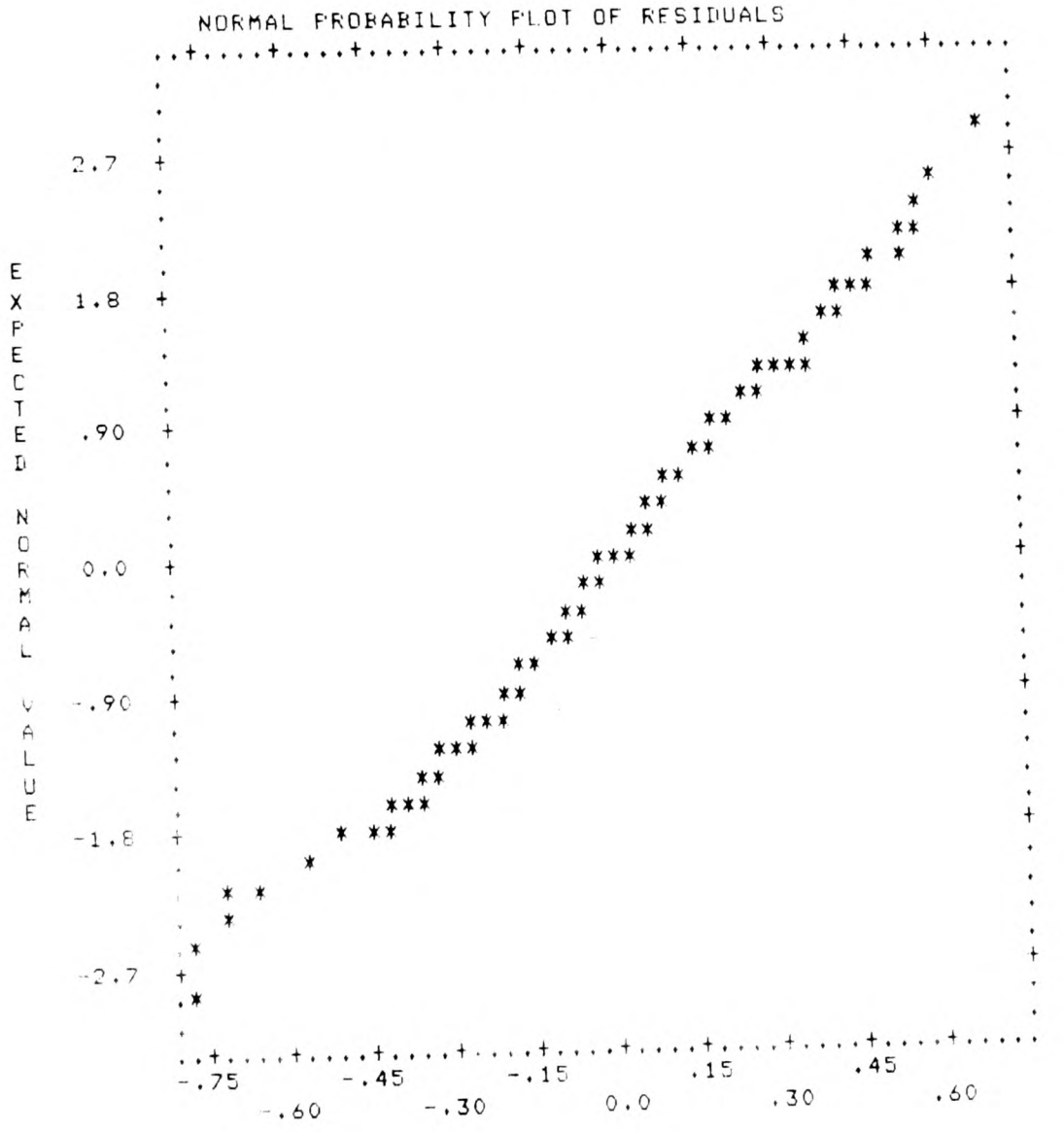
DEPENDENT VARIABLE. . . . . 4 RATES
TOLERANCE 0.0100

MULTIPLE R 0.4202 STD. ERROR OF EST. 0.2523
MULTIPLE R-SQUARE 0.1766

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	3.6869	17	0.2169	3.406	0.0000
RESIDUAL	17.1909	270	0.0637		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		2.80274					
DATE	6	0.79877E-03	0.71927E-03	0.093	1.111	0.2678	0.43045
TIME	8	-0.11602E-02	0.39411E-03	-0.195	-2.944	0.0035	0.69552
GRALEN	11	0.04795	0.01512	0.186	3.172	0.0017	0.89046
DISTUR	12	0.04784	0.05507	0.050	0.869	0.3858	0.91970
R1	49						VARIABLE NOT USED
R2	50						VARIABLE NOT USED
R3	51						VARIABLE NOT USED
R4	52						VARIABLE NOT USED
R5	53	-0.01655	0.04779	-0.030	-0.346	0.7294	0.41005
R6	54	0.03480	0.06225	0.043	0.559	0.5766	0.50953
R7	55	-0.01881	0.08128	-0.019	-0.231	0.8172	0.43806
R8	56	-0.10326	0.05812	-0.167	-1.777	0.0767	0.34591
DFAR	59	-0.00379	0.03065	-0.008	-0.124	0.9017	0.75816
MATE	57	0.01865	0.05876	0.034	0.317	0.7512	0.26541
M	58	0.01857	0.00993	0.197	1.870	0.0626	0.27345
COWS	15	0.07671	0.05978	0.080	1.283	0.2005	0.78040
TEMP	44	-0.01058	0.00531	-0.179	-1.991	0.0475	0.37755
PPT	45	-0.00570	0.00562	-0.061	-1.014	0.3115	0.84883
CLOUD	46	0.02721	0.05161	0.036	0.527	0.5985	0.65342
WIND	47	-0.22514E-03	0.34589E-02	-0.004	-0.065	0.9482	0.71962
NCLD	61	0.06056	0.02138	0.174	2.833	0.0050	0.80398



DEPENDENT VARIABLE. . . . . 4 RATES
TOLERANCE 0.0100

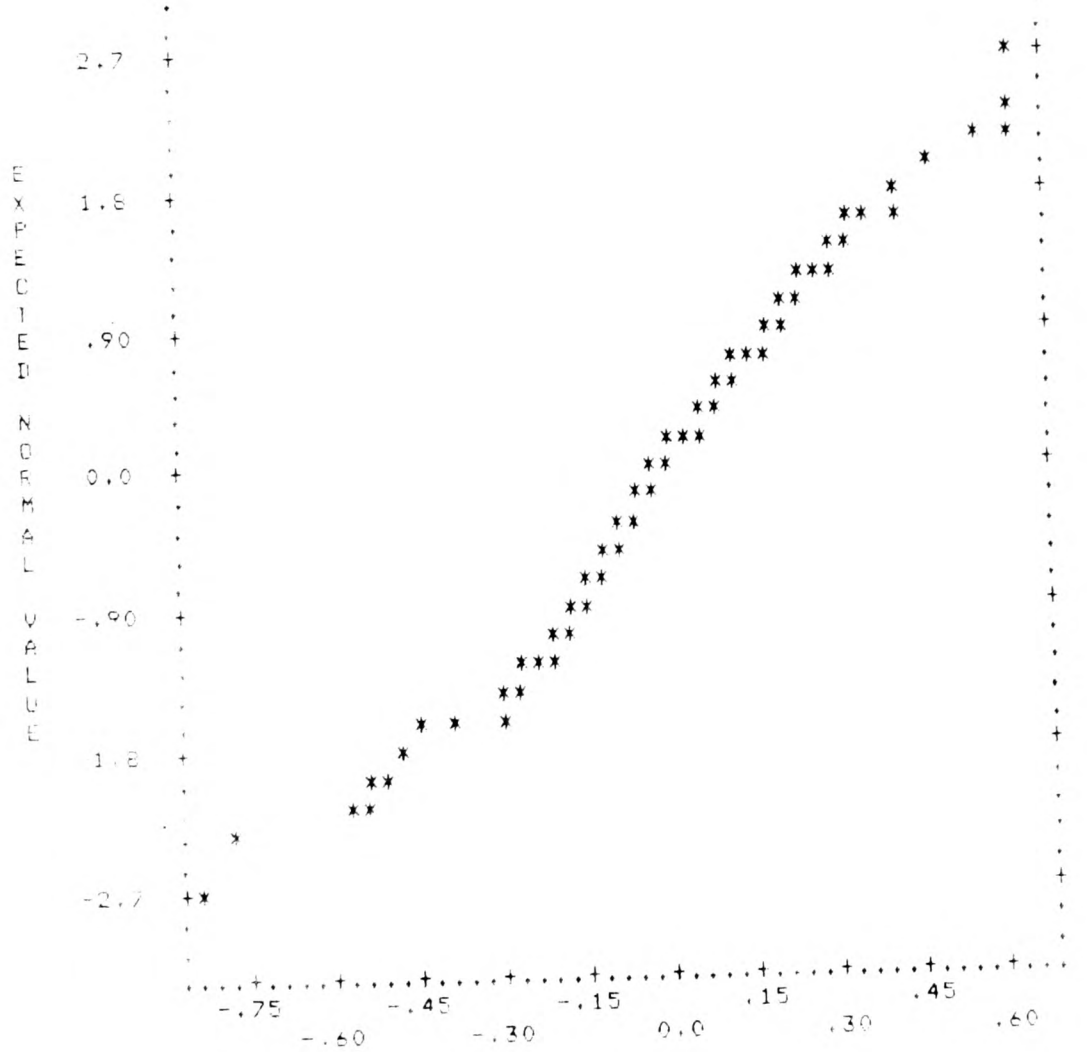
MULTIPLE R 0.5396 STD. ERROR OF EST. 0.2398
MULTIPLE R-SQUARE 0.2911

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	4.2283	16	0.2643	4.594	0.0000
RESIDUAL	10.2959	179	0.0575		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		4.75089					
DATE	6	-0.22420E-02	0.67936E-03	-0.290	-3.300	0.0012	0.51465
TIME	8	-0.22741E-02	0.54574E-03	-0.355	-4.167	0.0000	0.51485
GRALEN	11	-0.02561	0.01923	-0.098	-1.331	0.1848	0.72547
DISTUR	12	0.20214	0.11211	0.117	1.803	0.0741	0.93044
R1	49	-0.06004	0.09136	-0.108	-0.657	0.5119	0.14577
R2	50	-0.01082	0.08924	-0.019	-0.121	0.9037	0.17[illegible]
R3	51	-0.16202	0.10539	-0.228	-1.537	0.1260	0.19024
R4	52						VARIABLE NOT USED
R5	53						VARIABLE NOT USED
R6	54						VARIABLE NOT USED
R7	55						VARIABLE NOT USED
R8	56						VARIABLE NOT USED
DFAR	59	0.06171	0.02409	0.227	2.562	0.0112	0.50328
MATE	57	0.03226	0.05726	0.057	0.563	0.5739	0.38089
M	58	0.02265	0.01059	0.220	2.139	0.0338	0.37364
COWS	15	0.09533	0.07374	0.093	1.293	0.1978	0.76360
TEMP	44	-0.00499	0.00723	-0.089	-0.690	0.4910	0.23795
PPT	45	0.00458	0.00481	0.083	0.953	0.3419	0.52062
CLOUD	46	0.04741	0.06418	0.072	0.739	0.4610	0.41809
WIND	47	-0.00191	0.00727	-0.020	-0.263	0.7930	0.66106
DCLO	61	0.00212	0.03220	0.005	0.066	0.9476	0.69337

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 4 RATES
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

MULTIPLE R 0.4332 STD. ERROR OF EST. 0.2535
MULTIPLE R-SQUARE 0.1877

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	6.6967	25	0.2679	4.168	0.0000
RESIDUAL	28.9842	451	0.0643		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		3.19552					
DATE	6	-0.43141E-03	0.49939E-03	-0.051	-0.864	0.3881	0.50797
TIME	8	-0.13778E-02	0.31168E-03	-0.224	-4.421	0.0000	0.70370
GRALEN	11	0.02244	0.01214	0.086	1.849	0.0651	0.83259
DISTUR	12	0.06605	0.05013	0.059	1.317	0.1883	0.90963
R1	49	0.03098	0.05033	0.042	0.616	0.5384	0.38892
R2	50	0.12721	0.05574	0.164	2.282	0.0229	0.35042
R3	51	-0.05396	0.06669	-0.051	-0.809	0.4189	0.44550
R4	52	0.15092	0.09284	0.079	1.626	0.1047	0.76158
R5	53	-0.01394	0.04839	-0.021	-0.288	0.7735	0.32427
R6	54	0.02398	0.06206	0.023	0.386	0.6993	0.48898
R7	55	0.02220	0.07463	0.018	0.297	0.7663	0.50623
R8	56	-0.05233	0.05577	-0.068	-0.938	0.3486	0.34589
MAFAR	59	0.03720	0.03840	0.054	0.969	0.3332	0.57955
FEMFAR	60	0.04173	0.03454	0.070	1.208	0.2276	0.53559
KIDFAR	61	-0.03427	0.04517	-0.035	-0.759	0.4484	0.83807
MATE	57	0.03323	0.04246	0.059	0.783	0.4343	0.31295
M	58	0.01844	0.00722	0.188	2.555	0.0109	0.33194
COWS	15	0.07161	0.04627	0.073	1.548	0.1224	0.81913
TEMP	44	-0.00421	0.00411	-0.072	-1.023	0.3069	0.36312
PPT	45	0.51910E-03	0.35260E-02	0.007	0.147	0.8830	0.71921
CLOUD	46	0.06446	0.04077	0.090	1.581	0.1146	0.55595
WIND	47	-0.00209	0.00314	-0.033	-0.665	0.5061	0.74067
MACLO	63	0.05257	0.05611	0.047	0.937	0.3493	0.72610
FEMCLO	64	0.01493	0.03302	0.024	0.452	0.6514	0.64643
KIDCLO	65	0.04757	0.02622	0.083	1.814	0.0703	0.97076

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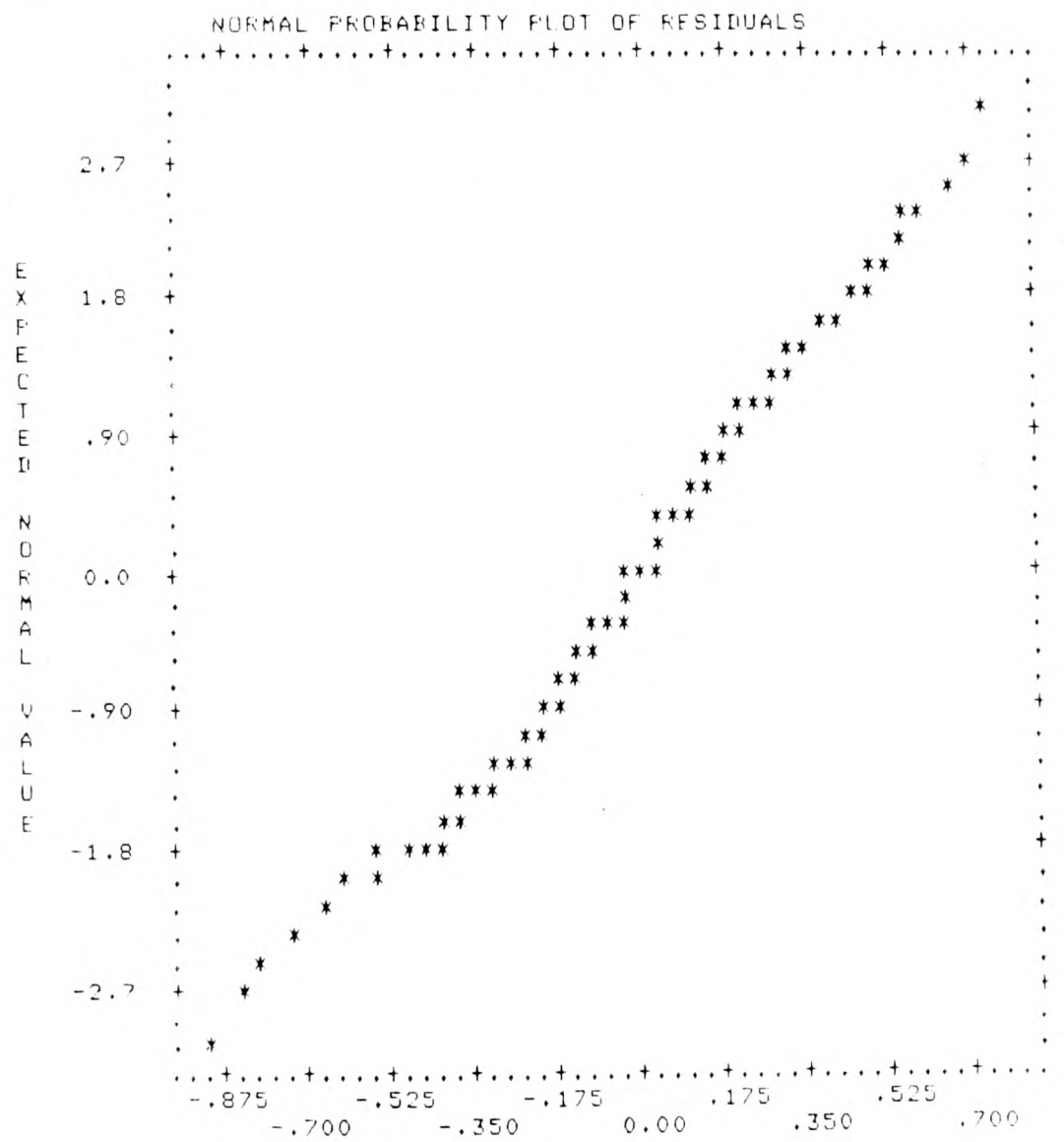


DEPENDENT VARIABLE. . . . . 4 RATES
TOLERANCE 0.0100

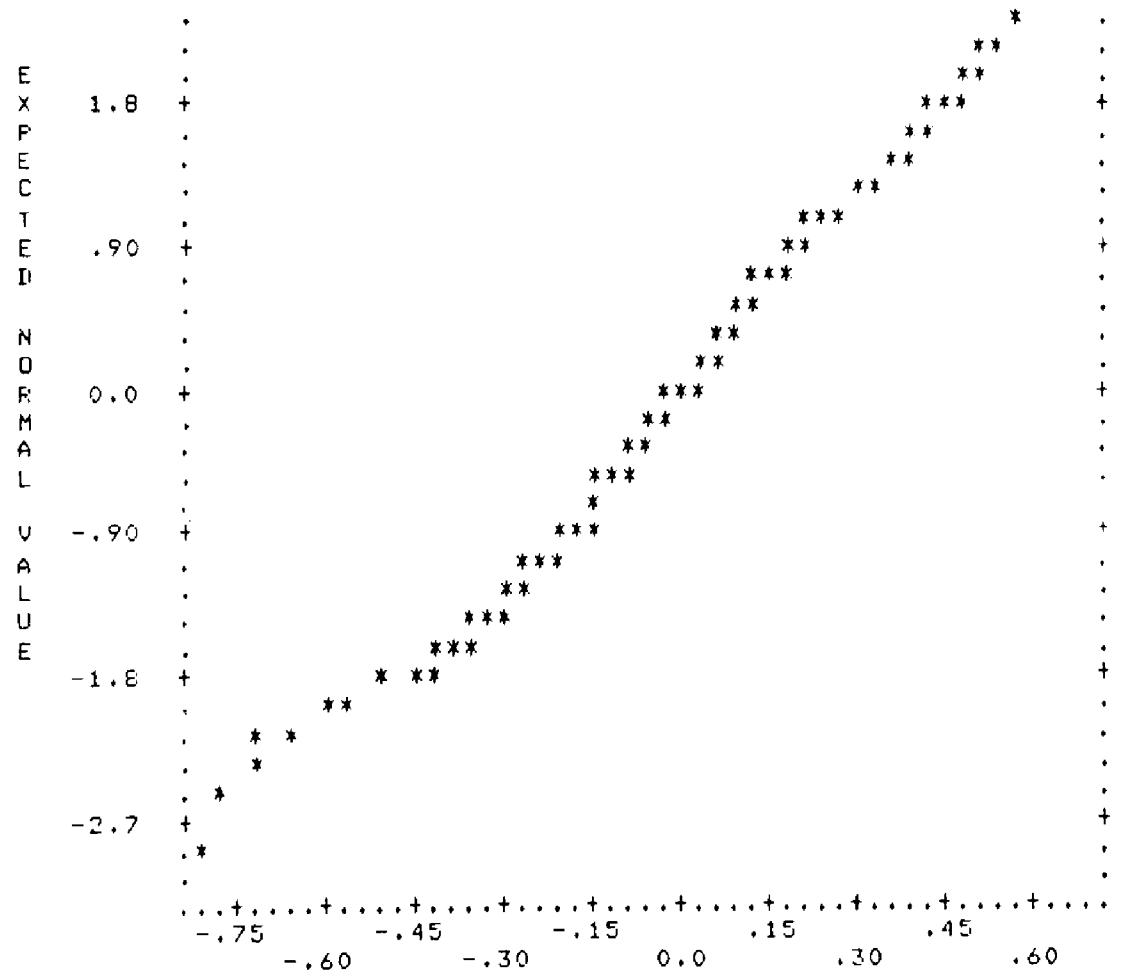
MULTIPLE R 0.4299 STD. ERROR OF EST. 0.2539
MULTIPLE R-SQUARE 0.1848

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	3.8442	21	0.1831	2.840	0.0001
RESIDUAL	16.9544	263	0.0645		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		2.92991					
DATE	6	0.82865E-03	0.75693E-03	0.096	1.095	0.2746	0.40376
TIME	8	-0.12959E-02	0.40961E-03	-0.218	-3.164	0.0017	0.65242
GRALEN	11	0.04667	0.01534	0.180	3.042	0.0026	0.88326
DISTUR	12	0.05445	0.05603	0.057	0.972	0.3321	0.90042
R1	49						VARIABLE NOT USE
R2	50						VARIABLE NOT USE
R3	51						VARIABLE NOT USE
R4	52						VARIABLE NOT USE
R5	53	-0.00856	0.05156	-0.015	-0.166	0.8682	0.35898
R6	54	0.04139	0.06683	0.051	0.619	0.5362	0.44835
R7	55	-0.01227	0.08317	-0.013	-0.148	0.8828	0.42405
R8	56	-0.09508	0.06237	-0.152	-1.525	0.1286	0.31386
MAFAR	59	-0.04486	0.07723	-0.040	-0.581	0.5618	0.64099
FEMFAR	60	0.06605	0.06202	0.076	1.065	0.2878	0.61502
KIDFAR	61	-0.05831	0.05868	-0.061	-0.994	0.3212	0.81899
MATE	57	0.04478	0.06284	0.081	0.713	0.4767	0.23870
M	58	0.01709	0.01013	0.181	1.686	0.0929	0.26959
COWS	15	0.07447	0.06189	0.078	1.203	0.2300	0.73798
TEMP	44	-0.01050	0.00551	-0.176	-1.905	0.0579	0.36473
PPT	45	-0.00635	0.00568	-0.068	-1.118	0.2647	0.84004
CLOUD	46	0.02097	0.05459	0.028	0.384	0.7013	0.59559
WIND	47	0.00112	0.00373	0.021	0.301	0.7640	0.63972
MACLO	63	0.00979	0.07766	0.009	0.126	0.8998	0.60274
FEMCLO	64	0.09926	0.04856	0.165	2.044	0.0419	0.47788
KIDCLO	65	0.05784	0.03143	0.111	1.840	0.0669	0.85039

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 4 RATES
TOLERANCE 0.0100

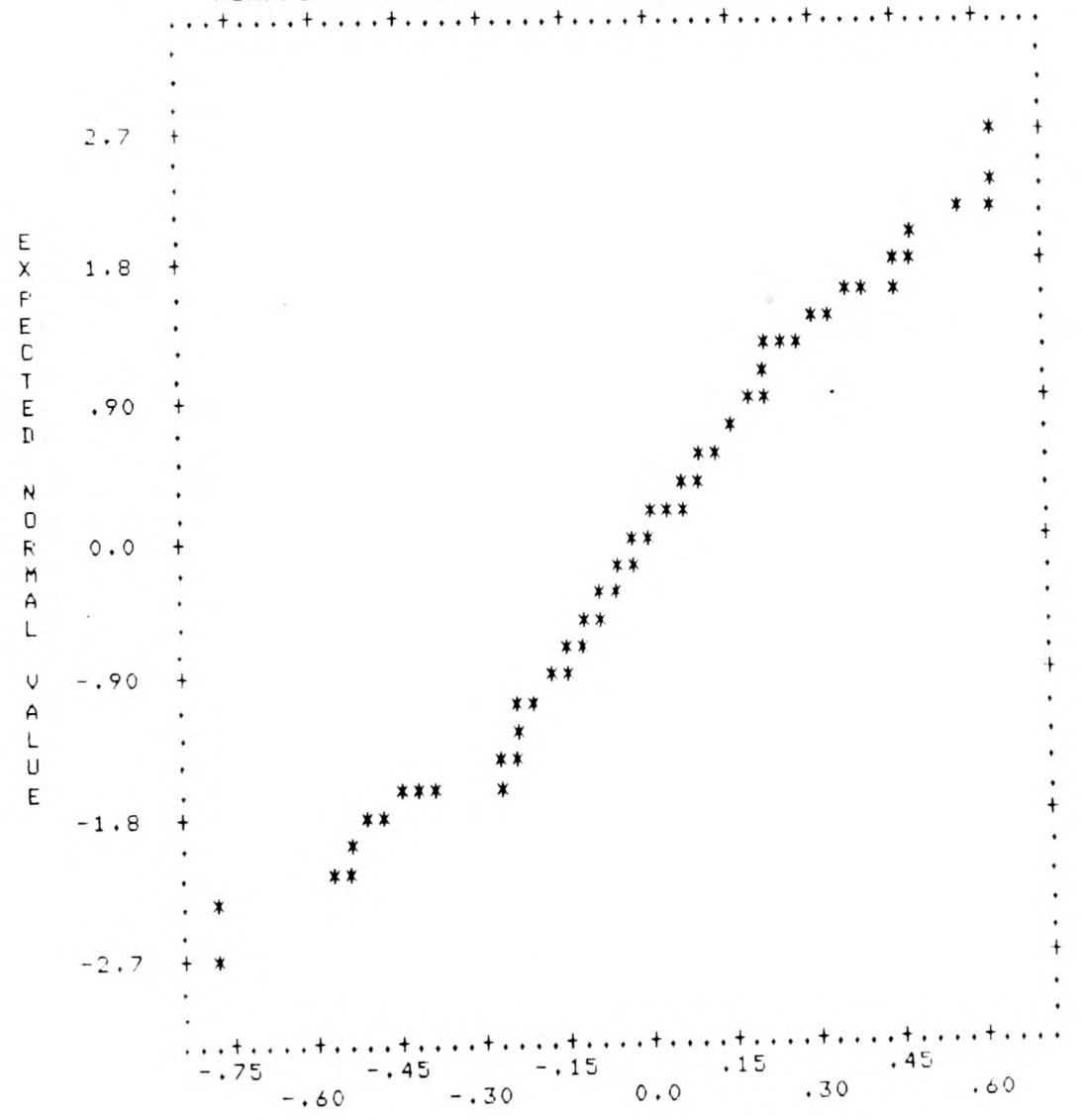
MULTIPLE R 0.5426 STD. ERROR OF EST. 0.2441
MULTIPLE R-SQUARE 0.2944

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	4.2513	20	0.2126	3.567	0.0000
RESIDUAL	10.1911	171	0.0596		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		4.68301					
DATE	6	-0.23954E-02	0.85255E-03	-0.302	-2.810	0.0055	0.35831
TIME	8	-0.21907E-02	0.58029E-03	-0.339	-3.775	0.0002	0.51285
GRALEN	11	-0.02397	0.02009	-0.092	-1.193	0.2344	0.69585
DISTUR	12	0.19989	0.11499	0.116	1.738	0.0840	0.92553
R1	49	-0.06929	0.09615	-0.124	-0.721	0.4721	0.13921
R2	50	-0.01420	0.09161	-0.025	-0.155	0.8770	0.16065
R3	51	-0.18208	0.11086	-0.256	-1.642	0.1023	0.16944
R4	52						VARIABLE NOT USE
R5	53						VARIABLE NOT USE
R6	54						VARIABLE NOT USE
R7	55						VARIABLE NOT USE
R8	56						VARIABLE NOT USE
MAFAR	59	0.05217	0.04548	0.102	1.147	0.2529	0.52047
FEMFAR	60	0.06517	0.04468	0.143	1.459	0.1465	0.43107
KIDFAR	61	0.08571	0.08496	0.086	1.009	0.3145	0.56295
MATE	57	0.02347	0.06359	0.042	0.369	0.7125	0.32412
M	58	0.02509	0.01161	0.244	2.161	0.0321	0.32374
COWS	15	0.09867	0.07867	0.097	1.254	0.2115	0.69644
TEMP	44	-0.00555	0.00779	-0.099	-0.712	0.4772	0.21214
PPT	45	0.00455	0.00534	0.083	0.851	0.3960	0.43730
CLOUD	46	0.04783	0.06757	0.071	0.708	0.4800	0.40926
WIND	47	-0.00110	0.00815	-0.011	-0.136	0.8924	0.60272
MACLO	63	-0.01762	0.09062	-0.015	-0.194	0.8461	0.69990
FEMCLO	64	-0.01804	0.05556	-0.028	-0.325	0.7457	0.56801
KIDCLO	65	0.03244	0.05221	0.047	0.621	0.5352	0.71732

NORMAL PROBABILITY PLOT OF RESIDUALS



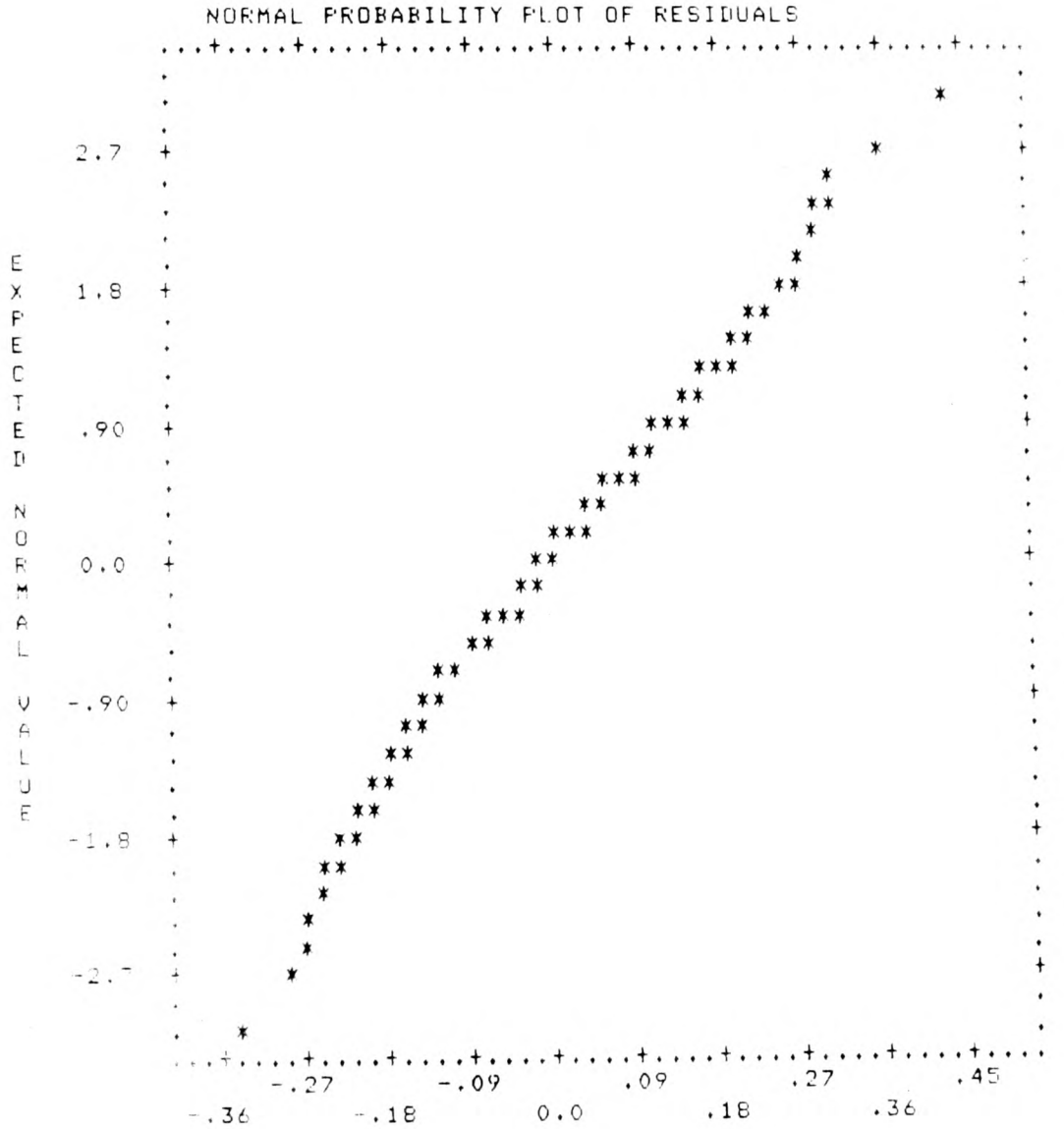
DEPENDENT VARIABLE. . . . . 5 PROPS
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

MULTIPLE R 0.4034 STD. ERROR OF EST. 0.1384
MULTIPLE R-SQUARE 0.1627

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	1.7186	21	0.0818	4.275	0.0000
RESIDUAL	8.8432	462	0.0191		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		2.46551					
DATE	6	-0.31148E-03	0.25929E-03	-0.070	-1.201	0.2303	0.53121
TIME	8	-0.48089E-03	0.16397E-03	-0.144	-2.933	0.0035	0.75159
GRALEN	11	0.00901	0.00655	0.064	1.376	0.1696	0.24455
DISTUR	12	0.03865	0.02717	0.063	1.422	0.1556	0.92121
R1	49	-0.00556	0.02696	-0.014	-0.206	0.8365	0.40258
R2	50	0.02438	0.02826	0.059	0.863	0.3887	0.38658
R3	51	0.00486	0.03481	0.009	0.140	0.8891	0.48647
R4	52	0.08161	0.04984	0.079	1.637	0.1022	0.78884
R5	53	-0.02360	0.02531	-0.067	-0.933	0.3514	0.35167
R6	54	0.01749	0.03262	0.031	0.536	0.5921	0.52645
R7	55	-0.02423	0.03998	-0.036	-0.606	0.5447	0.52502
R8	56	-0.07966	0.02878	-0.193	-2.768	0.0059	0.37271
DFAR	59	0.02145	0.01001	0.115	2.144	0.0326	0.63230
MATE	57	0.00185	0.02210	0.006	0.084	0.9333	0.33908
M	58	0.00645	0.00381	0.121	1.694	0.0910	0.35230
COWS	15	0.04173	0.02503	0.078	1.667	0.0961	0.83100
TEMP	44	-0.00654	0.00220	-0.207	-2.973	0.0031	0.30232
PPT	45	0.00108	0.00186	0.028	0.583	0.5605	0.76967
CLOUD	46	0.00960	0.02172	0.025	0.442	0.6588	0.57094
WIND	47	-0.00102	0.00166	-0.030	-0.612	0.5410	0.76198
DCLO	61	0.01572	0.00949	0.077	1.657	0.0983	0.83905



DEPENDENT VARIABLE. . . . . 5 PROPS
TOLERANCE 0.0100

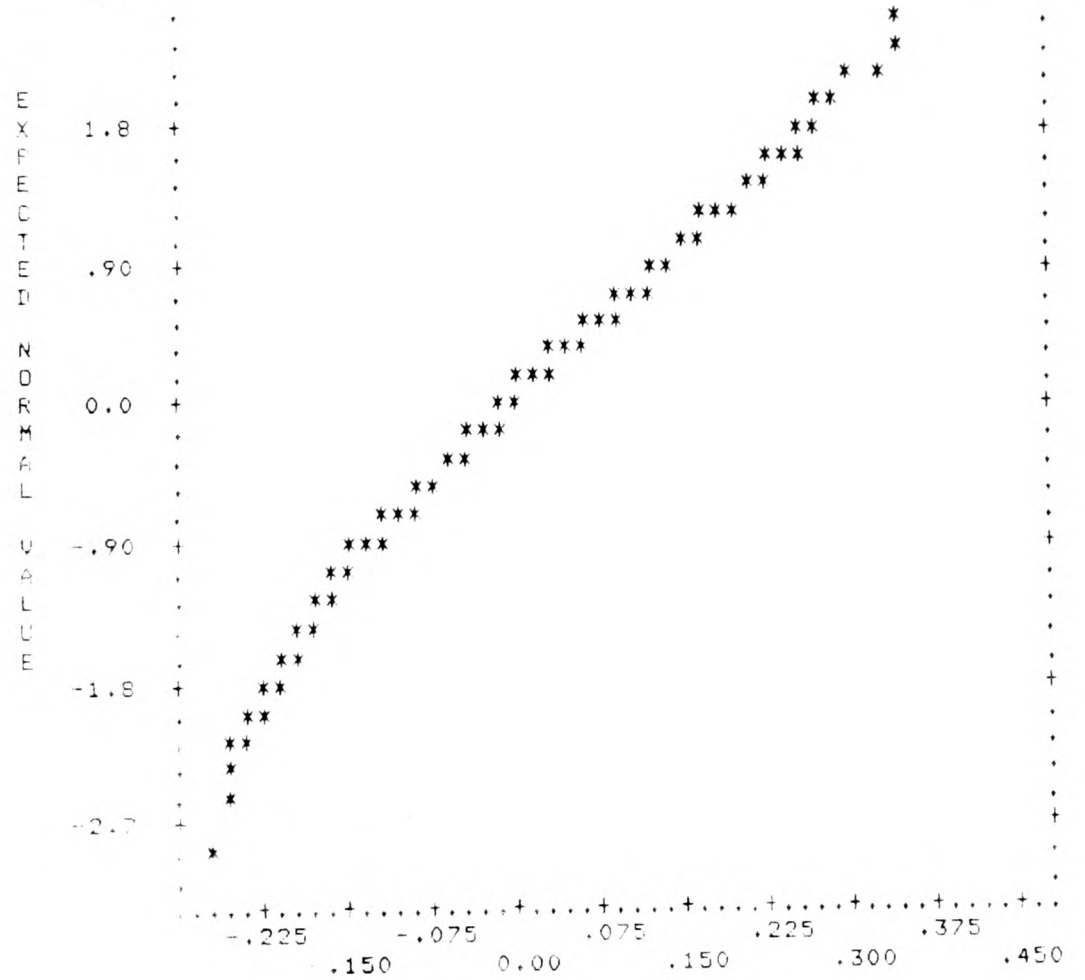
MULTIPLE R 0.4078 STD. ERROR OF EST. 0.1403
MULTIPLE R-SQUARE 0.1663

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	1.0597	17	0.0623	3.167	0.0000
RESIDUAL	5.3141	270	0.0197		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		2.40166					
DATE	6	0.24984E-03	0.39991E-03	0.053	0.625	0.5327	0.43045
TIME	8	-0.54630E-03	0.21912E-03	-0.166	-2.493	0.0133	0.59554
GRALEN	11	0.00853	0.00840	0.060	1.014	0.3113	0.85404
DISTUR	12	0.04857	0.03062	0.092	1.586	0.1138	0.73187
R1	49						VARIABLE NOT US
R2	50						VARIABLE NOT US
R3	51						VARIABLE NOT USE
R4	52						VARIABLE NOT US
R5	53	-0.00470	0.02657	-0.015	-0.177	0.8597	0.41005
R6	54	0.03210	0.03461	0.072	0.928	0.3544	0.50953
R7	55	0.01755	0.04519	0.033	0.388	0.6981	0.43806
R8	56	-0.05201	0.03231	-0.152	-1.610	0.1087	0.34591
DFAR	59	0.04473	0.01704	0.168	2.625	0.0092	0.75817
MATE	57	-0.01482	0.03267	-0.049	-0.454	0.6504	0.26541
M	58	0.01025	0.00552	0.197	1.856	0.0645	0.27345
COWS	15	0.06242	0.03324	0.118	1.878	0.0614	0.78040
TEMP	44	-0.00541	0.00295	-0.166	-1.831	0.0681	0.37755
PPT	45	0.29078E-03	0.31228E-02	0.006	0.093	0.9259	0.84883
CLOUD	46	0.00465	0.02869	0.011	0.162	0.8713	0.65342
WIND	47	-0.00329	0.00192	-0.112	-1.713	0.0879	0.71961
DCLO	61	-0.00173	0.01188	-0.009	-0.146	0.8842	0.80398

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 5 PROPS
TOLERANCE 0.0100

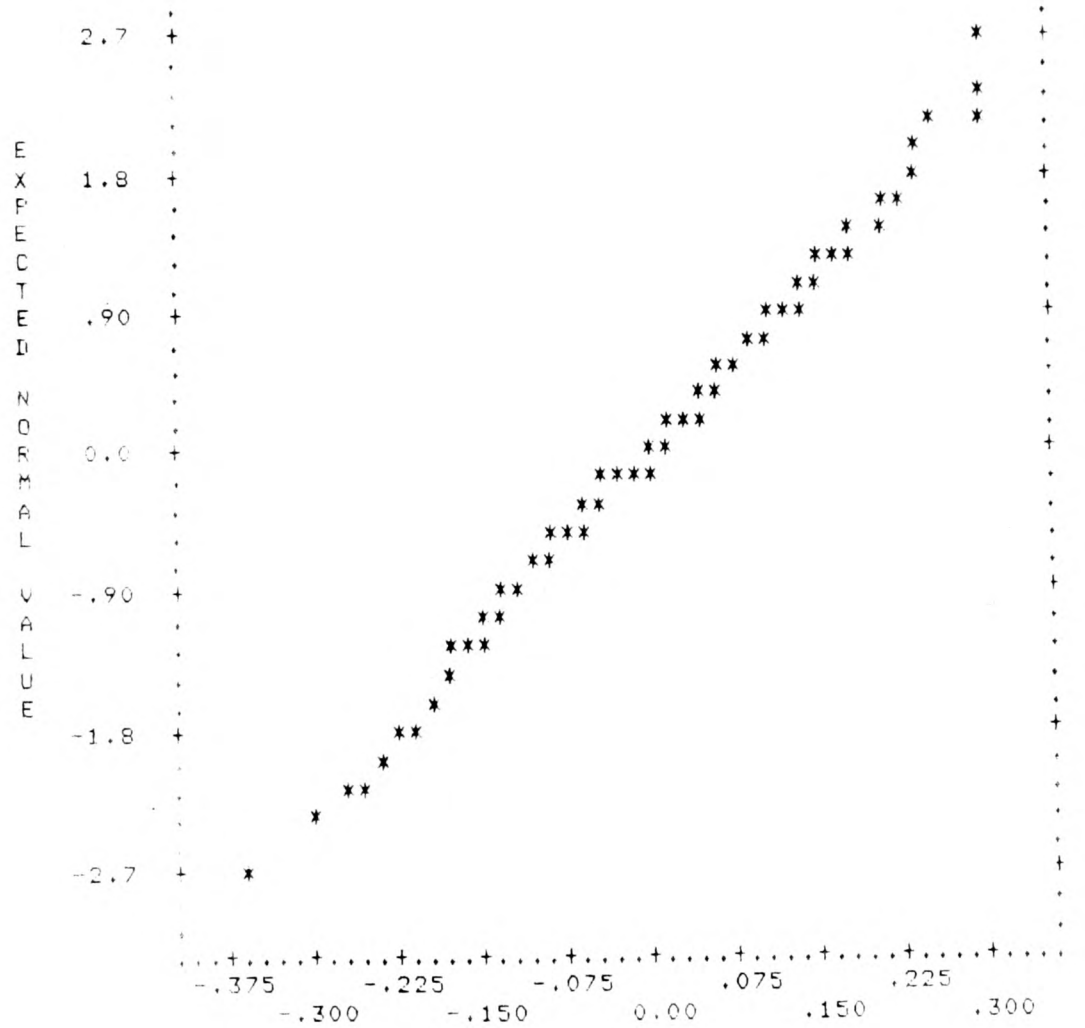
MULTIPLE R 0.4467 STD. ERROR OF EST. 0.1338
MULTIPLE R-SQUARE 0.1995

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	0.7985	16	0.0499	2.788	0.0005
RESIDUAL	3.2037	179	0.0179		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		2.93805					
DATE	6	-0.88047E-03	0.37896E-03	-0.217	-2.323	0.0213	0.51405
TIME	8	-0.80317E-03	0.30442E-03	-0.239	-2.638	0.0091	0.54693
GRALEN	11	0.35253E-03	0.10729E-01	0.003	0.033	0.9738	0.72023
DISTUR	12	0.01691	0.06254	0.019	0.270	0.7871	0.83419
R1	49	-0.04618	0.02847	-0.158	-1.622	0.1065	0.47028
R2	50						VARIABLE NOT USE
R3	51	-0.01830	0.03694	-0.049	-0.495	0.6210	0.45609
R4	52	0.06370	0.04978	0.098	1.280	0.2023	0.76112
R5	53						VARIABLE NOT USE
R6	54						VARIABLE NOT USE
R7	55						VARIABLE NOT USE
R8	56						VARIABLE NOT USE
DFAR	59	0.02201	0.01344	0.154	1.638	0.1031	0.50328
MATE	57	-0.00201	0.03194	-0.007	-0.063	0.9500	0.38089
M	58	0.00291	0.00591	0.054	0.492	0.6233	0.37364
COWS	15	0.05552	0.04113	0.103	1.350	0.1788	0.76340
TEMP	44	-0.00563	0.00403	-0.191	-1.397	0.1642	0.23795
PPT	45	0.00328	0.00268	0.113	1.221	0.2236	0.52062
CLOUD	46	0.00689	0.03580	0.020	0.192	0.8476	0.41808
WIND	47	0.00310	0.00406	0.063	0.763	0.4464	0.66106
DCLO	61	0.05151	0.01796	0.230	2.868	0.0046	0.69337

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 5 PROPS
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

MULTIPLE R 0.4265 STD. ERROR OF EST. 0.1378
MULTIPLE R-SQUARE 0.1819

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	1.9052	25	0.0762	4.011	0.0000
RESIDUAL	8.5698	451	0.0190		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		2.45088					
DATE	6	-0.44417E-03	0.27155E-03	-0.098	-1.636	0.1026	0.56707
TIME	8	-0.47350E-03	0.16948E-03	-0.142	-2.794	0.0055	0.70376
GRALEN	11	0.00959	0.00660	0.068	1.453	0.1469	0.83259
DISTUR	12	0.03844	0.02726	0.063	1.410	0.1592	0.90962
R1	49	-0.66468E-03	0.27365E-01	-0.002	-0.024	0.9806	0.38892
R2	50	0.05060	0.03031	0.120	1.669	0.0957	0.35042
R3	51	0.02484	0.03627	0.044	0.685	0.4938	0.44550
R4	52	0.09778	0.05048	0.095	1.937	0.0534	0.76158
R5	53	-0.00850	0.02631	-0.024	-0.323	0.7468	0.32427
R6	54	0.03040	0.03374	0.055	0.901	0.3681	0.48898
R7	55	-0.01063	0.04058	-0.016	-0.262	0.7934	0.50623
R8	56	-0.06173	0.03033	-0.147	-2.035	0.0424	0.34589
MAFAR	59	-0.02175	0.02088	-0.058	-1.041	0.2982	0.57955
FEMFAR	60	0.05193	0.01878	0.161	2.764	0.0059	0.53559
KIDFAR	61	0.03174	0.02456	0.060	1.292	0.1970	0.83807
MATE	57	0.00117	0.02309	0.004	0.050	0.9598	0.31295
M	58	0.00672	0.00392	0.127	1.713	0.0874	0.33184
COWS	15	0.04176	0.02516	0.078	1.660	0.0977	0.81913
TEMP	44	-0.00613	0.00224	-0.194	-2.740	0.0064	0.36312
PPT	45	0.00172	0.00192	0.045	0.898	0.3697	0.71921
CLOUD	46	0.01282	0.02217	0.033	0.578	0.5633	0.55595
WIND	47	-0.65730E-03	0.17060E-02	-0.019	-0.385	0.7002	0.74067
MACLO	63	-0.02097	0.03051	-0.034	-0.687	0.4922	0.72610
FEMCLO	64	0.01707	0.01795	0.050	0.951	0.3422	0.64642
KIDCLO	65	0.03348	0.01426	0.107	2.348	0.0193	0.87076

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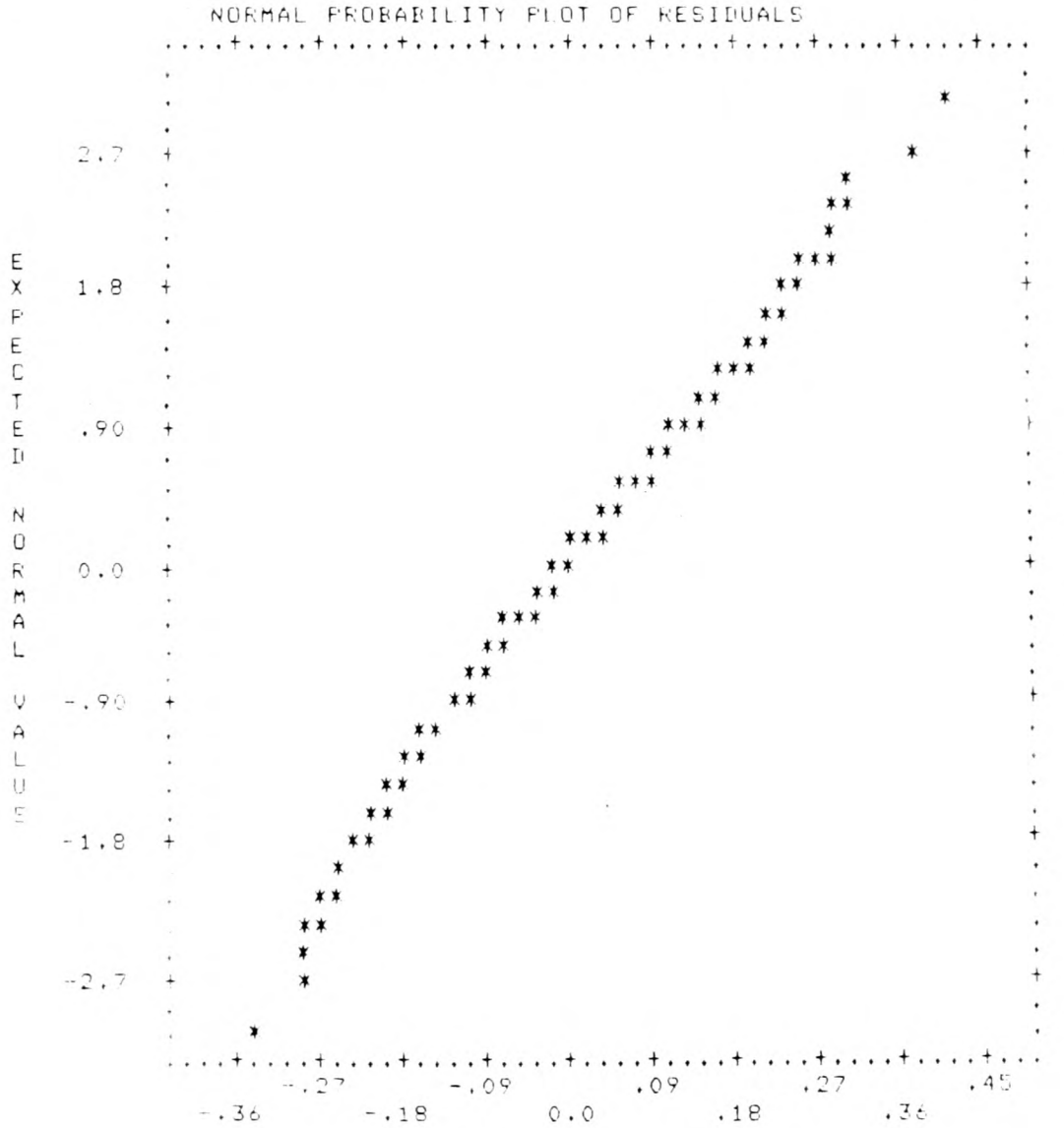
ALL



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DEPENDENT VARIABLE. . . . . 5 PROPS
TOLERANCE 0.0100

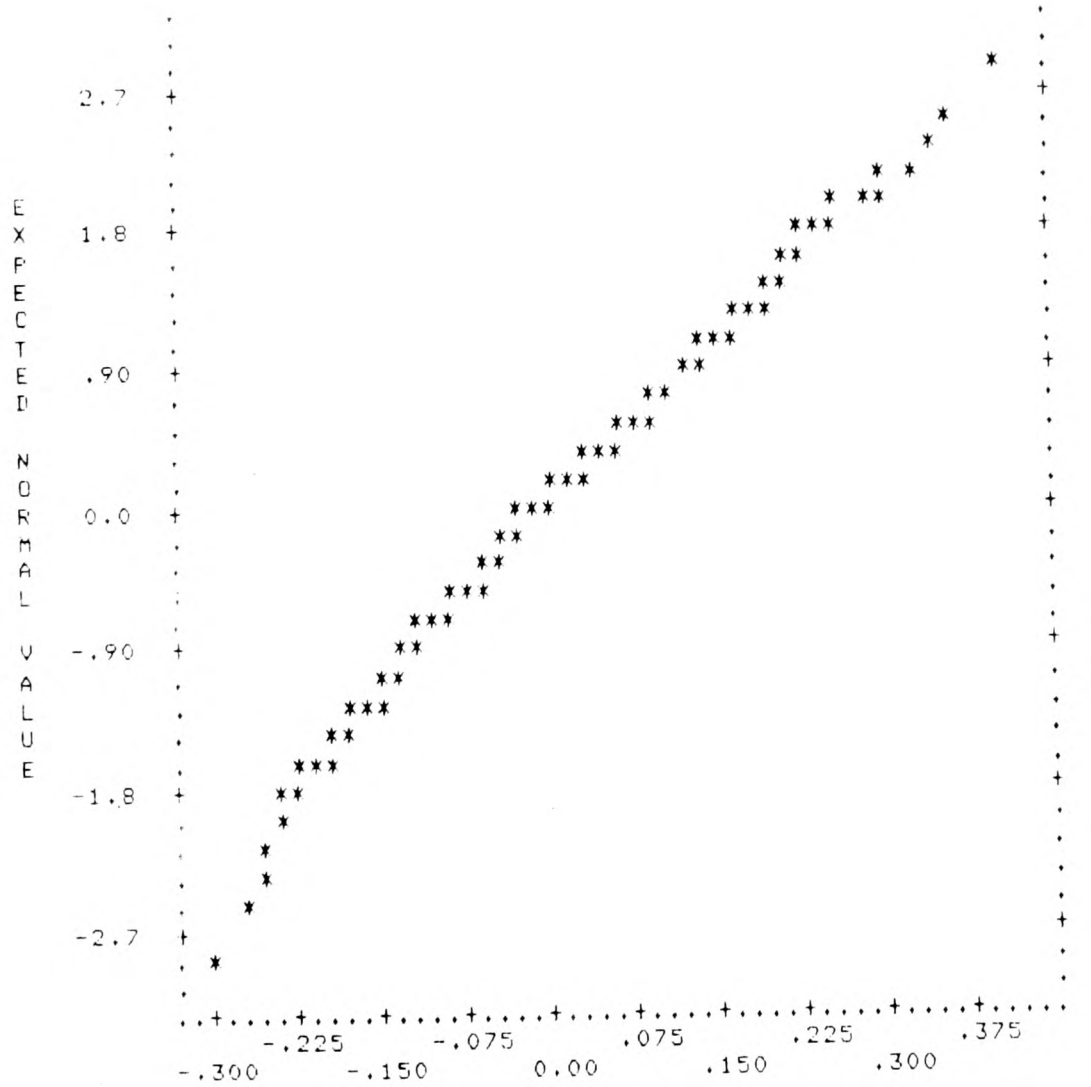
MULTIPLE R 0.4576 STD. ERROR OF EST. 0.1382
MULTIPLE R-SQUARE 0.2094

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	1.3303	21	0.0633	3.317	0.0000
RESIDUAL	5.0230	263	0.0191		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		2.31561					
DATE	6	-0.10307E-03	0.41200E-03	-0.022	-0.250	0.8027	0.40376
TIME	8	-0.46658E-03	0.22295E-03	-0.142	-2.093	0.0373	0.65242
GRALEN	11	0.01066	0.00835	0.074	1.277	0.2028	0.88320
DISTUR	12	0.05042	0.03050	0.096	1.653	0.0994	0.90042
R1	49						VARIABLE NOT USE
R2	50						VARIABLE NOT USE
R3	51						VARIABLE NOT USE
R4	52						VARIABLE NOT USE
R5	53	0.02490	0.02807	0.081	0.887	0.3758	0.35898
R6	54	0.05708	0.03637	0.128	1.569	0.1178	0.44835
R7	55	0.04543	0.04527	0.084	1.004	0.3165	0.42405
R8	56	-0.01378	0.03395	-0.040	-0.406	0.6851	0.31386
MAFAR	59	-0.05818	0.04203	-0.095	-1.384	0.1675	0.64099
FEMFAR	60	0.08858	0.03376	0.183	2.624	0.0092	0.61502
KIDFAR	61	0.06233	0.03194	0.118	1.952	0.0520	0.81899
MATE	57	0.00119	0.03420	0.004	0.035	0.9723	0.23870
M	58	0.00809	0.00552	0.155	1.467	0.1436	0.26859
COWS	15	0.06058	0.03369	0.115	1.799	0.0732	0.73798
TEMP	44	-0.00373	0.00300	-0.113	-1.242	0.2152	0.36473
PPT	45	0.21320E-03	0.30935E-02	0.004	0.069	0.9451	0.84004
CLOUD	46	-0.00349	0.02971	-0.008	-0.117	0.9066	0.59559
WIND	47	-0.00245	0.00203	-0.083	-1.207	0.2285	0.63972
MACLO	63	-0.08063	0.04227	-0.135	-1.907	0.0576	0.60274
FEMCLO	64	0.01193	0.02643	0.036	0.452	0.6520	0.47788
KIDCLO	65	0.02912	0.01711	0.101	1.702	0.0899	0.85039

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 5 PROPS
TOLERANCE 0.0100

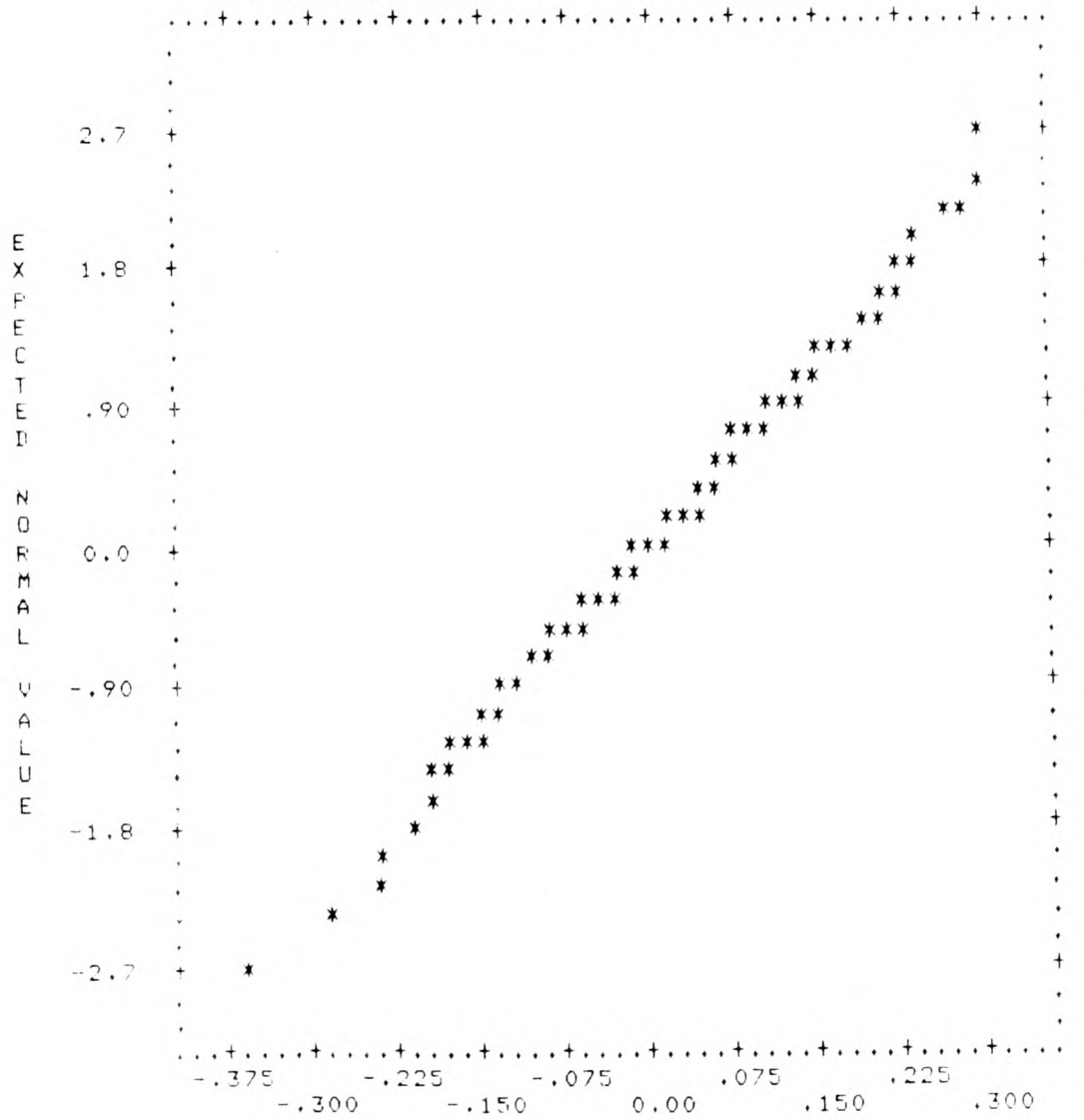
MULTIPLE R 0.4602 STD. ERROR OF EST. 0.1346
MULTIPLE R-SQUARE 0.2118

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	0.8329	20	0.0416	2.298	0.0022
RESIDUAL	3.0994	171	0.0181		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		2.99289					
DATE	6	-0.77638E-03	0.47016E-03	-0.187	-1.651	0.1005	0.35831
TIME	8	-0.87362E-03	0.32002E-03	-0.259	-2.730	0.0070	0.51285
GRALEN	11	-0.86964E-03	0.11078E-01	-0.006	-0.079	0.9375	0.69585
DISTUR	12	0.01377	0.06341	0.015	0.217	0.8284	0.92553
R1	49	-0.05091	0.03062	-0.175	-1.663	0.0982	0.41738
R2	50						VARIABLE NOT USE
R3	51	-0.01465	0.03880	-0.040	-0.378	0.7062	0.42075
R4	52	0.05634	0.05052	0.087	1.115	0.2664	0.74913
R5	53						VARIABLE NOT USE
R6	54						VARIABLE NOT USE
R7	55						VARIABLE NOT USE
R8	56						VARIABLE NOT USE
MAFAR	59	0.00982	0.02508	0.037	0.392	0.6959	0.52047
FEMFAR	60	0.03631	0.02464	0.152	1.473	0.1425	0.43107
KIDFAR	61	0.00215	0.04685	0.004	0.046	0.9635	0.56295
MATE	57	-0.01191	0.03507	-0.041	-0.340	0.7345	0.32412
M	58	0.00429	0.00640	0.080	0.671	0.5034	0.32374
COWS	15	0.04728	0.04338	0.089	1.090	0.2773	0.69644
TEMP	44	-0.00556	0.00430	-0.191	-1.294	0.1973	0.21214
PPT	45	0.00294	0.00295	0.102	0.997	0.3200	0.43730
CLOUD	46	0.01784	0.03726	0.051	0.479	0.6327	0.40926
WIND	47	0.00322	0.00449	0.063	0.717	0.4742	0.60272
MACLO	63	0.05432	0.04997	0.088	1.087	0.2785	0.69990
FEMCLO	64	0.05494	0.03064	0.162	1.793	0.0747	0.56801
KIDCLO	65	0.05100	0.02879	0.142	1.771	0.0783	0.71732

NORMAL PROBABILITY PLOT OF RESIDUALS



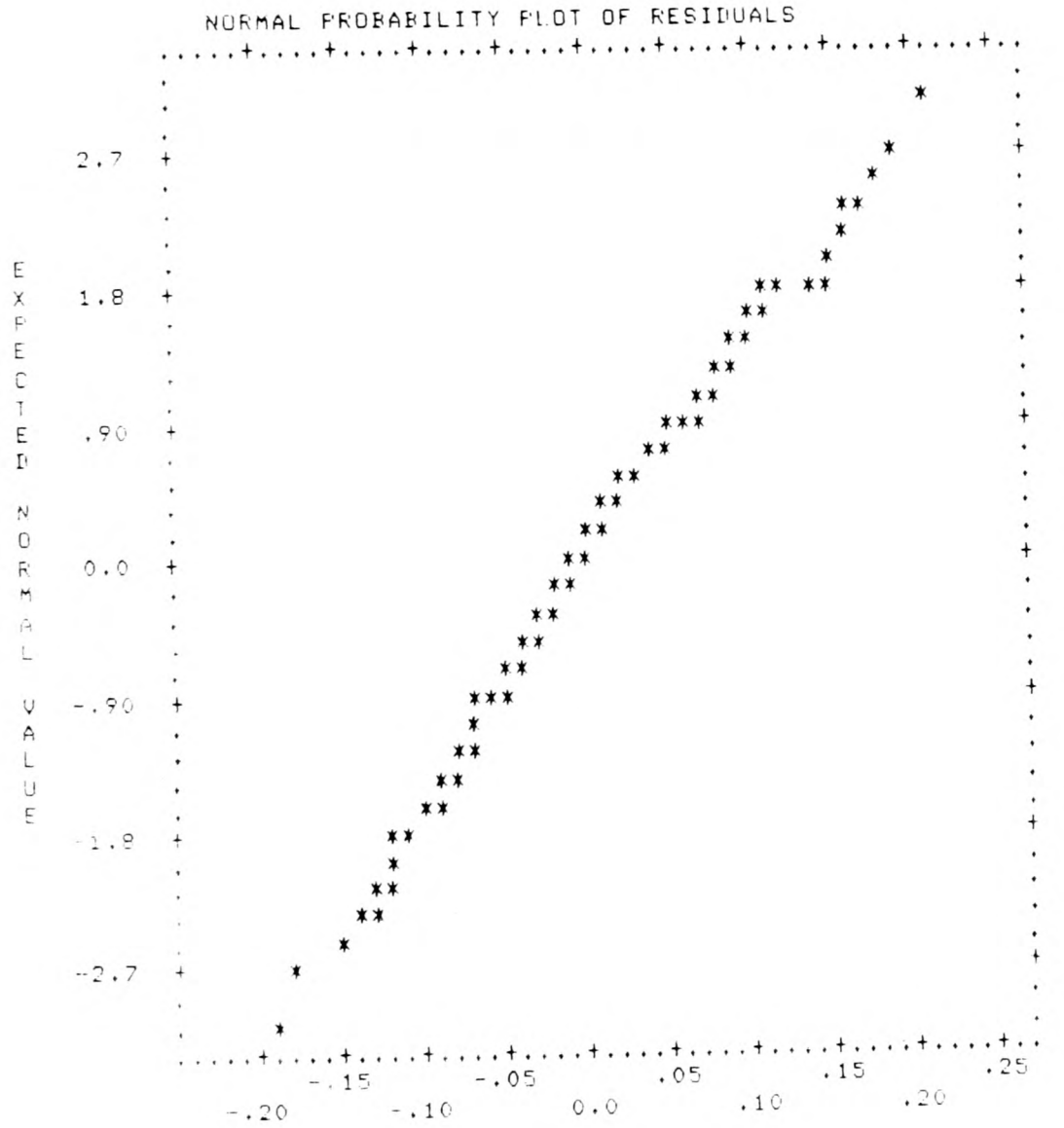
DEPENDENT VARIABLE. . . . . 2 UPS
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

MULTIPLE R 0.2848 STD. ERROR OF EST. 0.0669
MULTIPLE R-SQUARE 0.0811

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	0.1827	21	0.0087	1.942	0.0077
RESIDUAL	2.0687	462	0.0045		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		0.02850					
DATE	6	-0.53667E-04	0.12541E-03	-0.026	-0.428	0.6689	0.53721
TIME	8	0.42177E-04	0.79306E-04	0.027	0.532	0.5951	0.79154
GRALEN	11	-0.82833E-03	0.31677E-02	-0.013	-0.261	0.7938	0.84459
DISTUR	12	-0.00787	0.01314	-0.028	-0.598	0.5499	0.90101
R1	49	0.00161	0.01304	0.009	0.123	0.9018	0.40248
R2	50	0.00892	0.01367	0.047	0.652	0.5145	0.38459
R3	51	-0.00243	0.01684	-0.009	-0.144	0.8855	0.48647
R4	52	-0.01998	0.02411	-0.042	-0.829	0.4076	0.78684
R5	53	0.00819	0.01224	0.050	0.669	0.5036	0.35167
R6	54	-0.01069	0.01578	-0.042	-0.677	0.4985	0.52645
R7	55	0.01714	0.01934	0.055	0.886	0.3759	0.52502
R8	56	0.03035	0.01392	0.159	2.180	0.0297	0.37271
DFAR	59	-0.00833	0.00484	-0.097	-1.721	0.0860	0.63030
MATE	57	-0.00138	0.01069	-0.010	-0.129	0.8971	0.33908
M	58	0.00149	0.00184	0.061	0.810	0.4186	0.35230
COWS	15	-0.01649	0.01211	-0.067	-1.363	0.1737	0.83270
TEMP	44	0.00405	0.00106	0.278	3.810	0.0002	0.37232
PPT	45	-0.35161E-03	0.89951E-03	-0.020	-0.391	0.6961	0.76967
CLOUD	46	0.01515	0.01051	0.085	1.442	0.1499	0.57094
WIND	47	0.22571E-03	0.80346E-03	0.014	0.281	0.7789	0.76198
DCLO	61	0.00153	0.00459	0.016	0.334	0.7383	0.87905



DEPENDENT VARIABLE. . . . . 2 UPS
TOLERANCE 0.0100

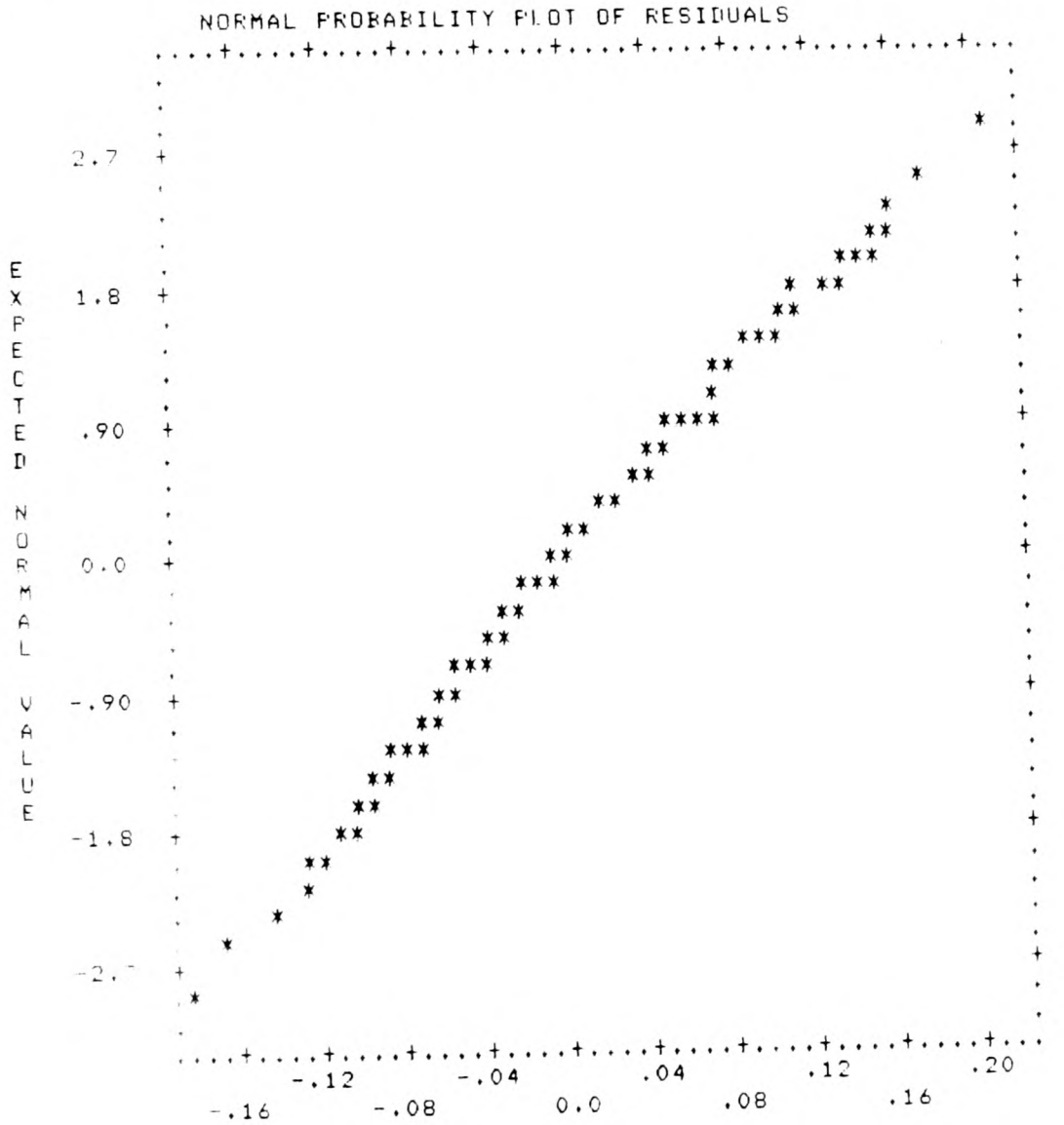
MULTIPLE R 0.3397 STD. ERROR OF EST. 0.0667
MULTIPLE R-SQUARE 0.1154

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	0.1569	17	0.0092	2.072	0.008
RESIDUAL	1.2025	270	0.0045		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		-0.00978					
DATE	6	-0.63429E-04	0.19023E-03	-0.029	-0.333	0.7391	0.43045
TIME	8	0.98918E-04	0.10423E-03	0.065	0.949	0.3435	0.69551
GRALEN	11	0.00265	0.00400	0.040	0.662	0.5087	0.89046
DISTUR	12	-0.01460	0.01456	-0.060	-1.002	0.3171	0.91913
R1	49						VARIABLE NOT USE
R2	50						VARIABLE NOT USE
R3	51						VARIABLE NOT USE
R4	52						VARIABLE NOT USE
R5	53	-0.00173	0.01264	-0.012	-0.137	0.8910	0.41005
R6	54	-0.02104	0.01646	-0.102	-1.278	0.2025	0.50953
R7	55	-0.00571	0.02150	-0.023	-0.265	0.7909	0.43806
R8	56	0.01059	0.01537	0.067	0.689	0.4915	0.34591
DFAR	59	-0.02167	0.00811	-0.176	-2.674	0.0080	0.75817
MATE	57	0.01255	0.01554	0.090	0.807	0.4201	0.26541
M	58	-0.89266E-03	0.26266E-02	-0.037	-0.340	0.7342	0.27345
COWS	15	-0.03150	0.01581	-0.129	-1.993	0.0473	0.78040
TEMP	44	0.00290	0.00141	0.192	2.065	0.0399	0.37755
PPT	45	-0.00129	0.00149	-0.054	-0.871	0.3843	0.84883
CLOUD	46	0.01676	0.01365	0.087	1.228	0.2206	0.65342
WIND	47	0.13908E-02	0.91480E-03	0.103	1.520	0.1296	0.71962
DCLO	61	0.01027	0.00565	0.116	1.817	0.0704	0.80398

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 2 UPS
TOLERANCE 0.0100

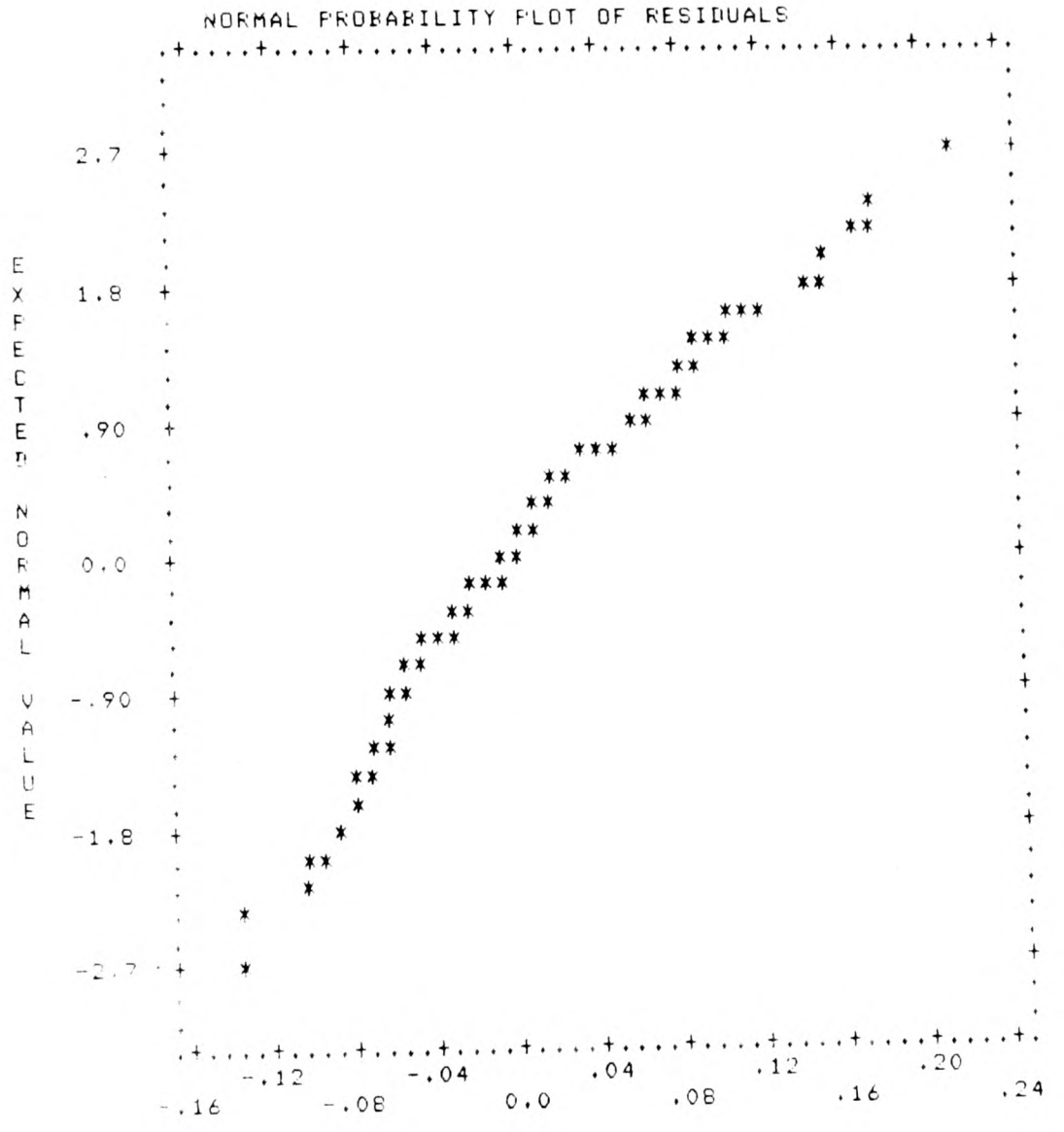
MULTIPLE R 0.3442 STD. ERROR OF EST. 0.0659
MULTIPLE R-SQUARE 0.1185

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	0.1043	16	0.0065	1.504	0.1025
RESIDUAL	0.7763	179	0.0043		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		0.12508					
DATE	6	-0.12753E-03	0.18655E-03	-0.067	-0.684	0.4951	0.51405
TIME	8	0.32046E-05	0.14986E-03	0.002	0.021	0.9830	0.54492
GRALEN	11	-0.00473	0.00528	-0.074	-0.897	0.3712	0.72723
DISTUR	12	0.01695	0.03079	0.040	0.550	0.5827	0.93919
R1	49	0.00397	0.01401	0.029	0.283	0.7773	0.47028
R2	50						VARIABLE NOT USE
R3	51	-0.01180	0.01819	-0.067	-0.649	0.5171	0.45609
R4	52	-0.02837	0.02450	-0.093	-1.158	0.2485	0.76112
R5	53						VARIABLE NOT USE
R6	54						VARIABLE NOT USE
R7	55						VARIABLE NOT USE
R8	56						VARIABLE NOT USE
DFAR	59	-0.00316	0.00661	-0.047	-0.477	0.6337	0.50328
MATE	57	-0.01296	0.01572	-0.094	-0.825	0.4107	0.38089
M	58	0.00543	0.00291	0.214	1.867	0.0635	0.37364
COWS	15	-0.88635E-03	0.20249E-01	-0.004	-0.044	0.9651	0.76360
TEMP	44	0.00274	0.00198	0.198	1.379	0.1696	0.23795
PPT	45	-0.57858E-03	0.13207E-02	-0.043	-0.438	0.6618	0.52062
CLOUD	46	0.00782	0.01762	0.048	0.444	0.6576	0.41808
WIND	47	-0.00130	0.00200	-0.056	-0.651	0.5158	0.66104
DCLD	61	-0.01383	0.00884	-0.132	-1.564	0.1197	0.69337

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 2 OPS
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

MULTIPLE R 0.3091 STD. ERROR OF EST. 0.0665
MULTIPLE R-SQUARE 0.0955

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	0.2108	25	0.0084	1.905	0.0057
RESIDUAL	1.9959	451	0.0044		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		0.04844					
DATE	6	0.86945E-05	0.13105E-03	0.004	0.066	0.9471	0.50707
TIME	8	0.26116E-04	0.81790E-04	0.017	0.319	0.7496	0.73370
GRALEN	11	-0.00130	0.00319	-0.020	-0.408	0.6834	0.87259
DISTUR	12	-0.00811	0.01316	-0.029	-0.617	0.5377	0.90963
R1	49	-0.00100	0.01321	-0.005	-0.076	0.9395	0.39962
R2	50	-0.00207	0.01463	-0.011	-0.141	0.8876	0.35042
R3	51	-0.01082	0.01750	-0.041	-0.618	0.5366	0.44950
R4	52	-0.02696	0.02436	-0.057	-1.107	0.2691	0.76156
R5	53	0.00198	0.01270	0.012	0.156	0.8762	0.32407
R6	54	-0.01611	0.01628	-0.063	-0.989	0.3231	0.48898
R7	55	0.01080	0.01958	0.035	0.551	0.5816	0.50623
R8	56	0.02449	0.01464	0.127	1.674	0.0949	0.34589
MAFAR	59	0.00905	0.01008	0.053	0.898	0.3694	0.57955
FEMFAR	60	-0.01762	0.00906	-0.119	-1.944	0.0525	0.53559
MIDFAR	61	-0.01533	0.01185	-0.063	-1.293	0.1966	0.83907
MATE	57	-0.62303E-04	0.11142E-01	-0.000	-0.006	0.9955	0.31295
M	58	0.00150	0.00189	0.062	0.793	0.4284	0.33194
COWS	15	-0.01664	0.01214	-0.068	-1.371	0.1711	0.81913
TEMP	44	0.00375	0.00108	0.259	3.479	0.0005	0.36312
PPT	45	-0.58686E-03	0.92527E-03	-0.033	-0.634	0.5262	0.71921
CLOUD	46	0.01406	0.01070	0.079	1.314	0.1894	0.55595
WIND	47	0.16869E-03	0.82332E-03	0.011	0.205	0.8377	0.74067
MACLO	63	0.01153	0.01472	0.041	0.783	0.4339	0.72610
FEMCLO	64	0.00292	0.00866	0.019	0.337	0.7362	0.64642
MIDCLO	65	-0.00531	0.00688	-0.037	-0.772	0.4405	0.87074

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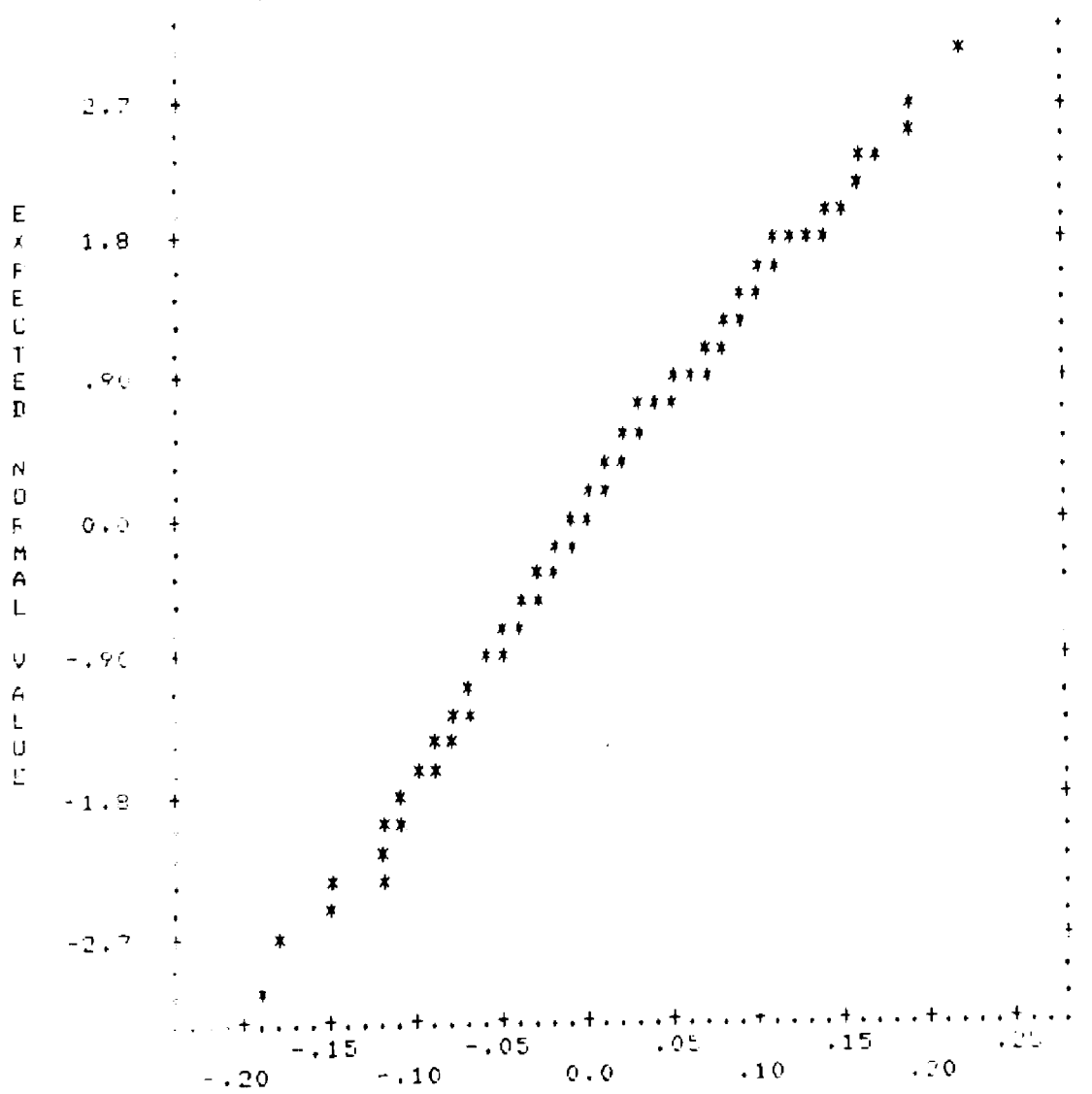
ALL

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 2 UPS
TOLERANCE 0.0100

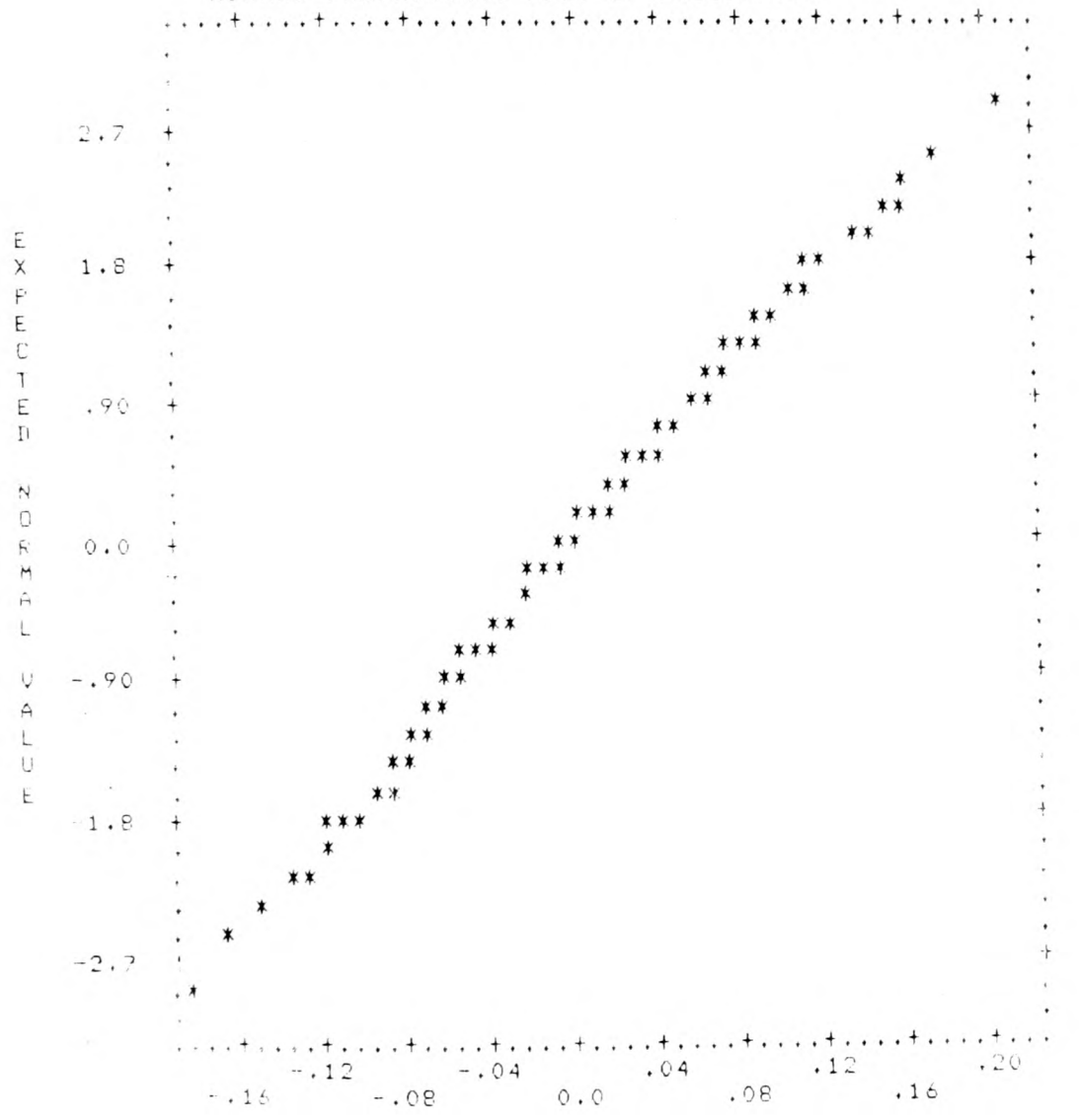
MULTIPLE R 0.3829 STD. ERROR OF EST. 0.0661
MULTIPLE R-SQUARE 0.1466

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	0.1976	21	0.0094	2.152	0.0030
RESIDUAL	1.1500	263	0.0044		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		0.05280					
DATE	6	0.74240E-04	0.19714E-03	0.034	0.377	0.7065	0.40376
TIME	8	0.39850E-04	0.10668E-03	0.026	0.374	0.7090	0.65242
GRALEN	11	0.00140	0.00400	0.021	0.350	0.7268	0.88329
DISTUR	12	-0.01445	0.01459	-0.059	-0.991	0.3228	0.90042
R1	49						VARIABLE NOT U
R2	50						VARIABLE NOT U
R3	51						VARIABLE NOT U
R4	52						VARIABLE NOT U
R5	53	-0.01197	0.01343	-0.085	-0.892	0.3734	0.35898
R6	54	-0.03009	0.01740	-0.147	-1.729	0.0850	0.44035
R7	55	-0.01575	0.02166	-0.064	-0.727	0.4677	0.42405
R8	56	-0.00163	0.01624	-0.010	-0.100	0.9204	0.31386
MAFAR	59	0.01400	0.02011	0.050	0.696	0.4869	0.64099
FEMFAR	60	-0.02650	0.01615	-0.119	-1.641	0.1021	0.61502
KIDFAR	61	-0.03760	0.01528	-0.155	-2.460	0.0145	0.81899
MATE	57	0.01322	0.01637	0.094	0.808	0.4201	0.23870
M	58	-0.42634E-03	0.26393E-02	-0.018	-0.162	0.8718	0.26859
COWS	15	-0.03215	0.01612	-0.132	-1.995	0.0471	0.73790
TEMP	44	0.00220	0.00144	0.145	1.536	0.1258	0.36473
PPT	45	-0.00142	0.00148	-0.060	-0.963	0.3366	0.84004
CLOUD	46	0.01867	0.01422	0.097	1.313	0.1903	0.59569
WIND	47	0.13189E-02	0.97077E-03	0.097	1.359	0.1754	0.63972
MACLO	63	0.02623	0.02023	0.095	1.297	0.1959	0.60274
FEMCLO	64	0.01340	0.01265	0.087	1.059	0.2905	0.47788
KIDCLO	65	-0.00200	0.00819	-0.015	-0.244	0.8071	0.85039

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 2 UPS
TOLERANCE 0.0100

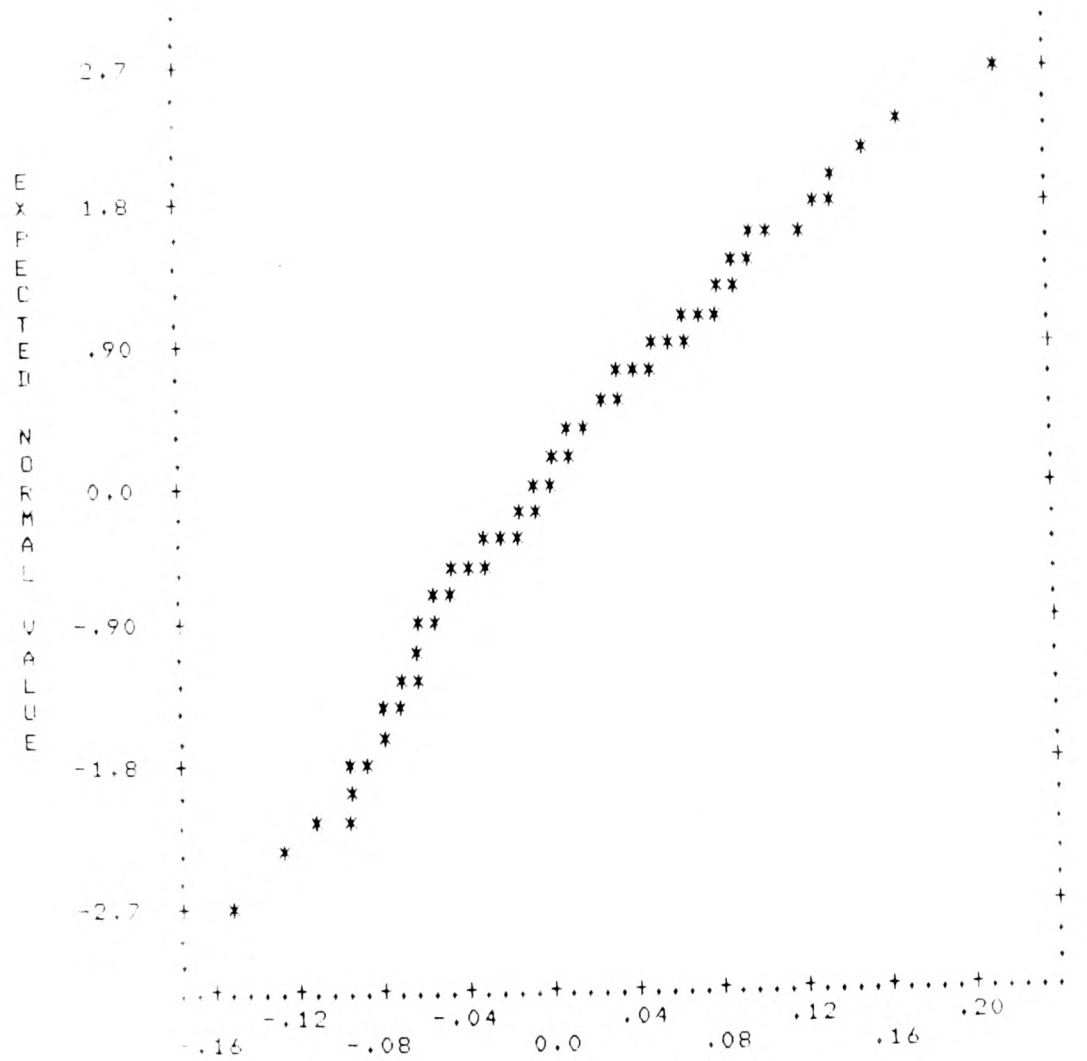
MULTIPLE R 0.3821 STD. ERROR OF EST. 0.0650
MULTIPLE R-SQUARE 0.1460

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(2 TAIL)
REGRESSION	0.1234	20	0.0062	1.462	0.1025
RESIDUAL	0.7218	171	0.0042		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		0.13939					
DATE	6	-0.37625E-03	0.22689E-03	-0.196	-1.658	0.0991	0.35831
TIME	8	0.13032E-04	0.15443E-03	0.008	0.084	0.9328	0.51285
GRALEN	11	-0.00413	0.00535	-0.065	-0.773	0.4406	0.69585
DISTUR	12	0.02066	0.03060	0.050	0.675	0.5005	0.92554
R1	49						VARIABLE NOT USE
R2	50	0.70720E-03	0.14777E-01	0.005	0.048	0.9619	0.43729
R3	51	-0.01520	0.01939	-0.088	-0.784	0.4342	0.39241
R4	52	-0.02132	0.02559	-0.071	-0.833	0.4058	0.68012
R5	53						VARIABLE NOT USE
R6	54						VARIABLE NOT USE
R7	55						VARIABLE NOT USE
R8	56						VARIABLE NOT USE
MAFAR	59	-0.65253E-03	0.12102E-01	-0.005	-0.054	0.9571	0.52047
FEMFAR	60	-0.00886	0.01189	-0.080	-0.745	0.4575	0.43107
KIDFAR	61	0.03663	0.02261	0.153	1.620	0.1070	0.56295
MATE	57	-0.00789	0.01692	-0.058	-0.466	0.6416	0.32412
M	58	0.00441	0.00309	0.177	1.428	0.1551	0.32374
COWS	15	0.01128	0.02094	0.046	0.539	0.5908	0.69644
TEMP	44	0.00344	0.00207	0.255	1.659	0.0990	0.21214
PPT	45	0.39228E-03	0.14217E-02	0.029	0.276	0.7829	0.43730
CLOUD	46	0.00450	0.01798	0.028	0.250	0.8028	0.40926
WIND	47	-0.28419E-03	0.21676E-02	-0.012	-0.131	0.8958	0.60272
MACLO	63	-0.03204	0.02412	-0.112	-1.328	0.1858	0.69990
FEMCLO	64	-0.00410	0.01478	-0.026	-0.278	0.7817	0.56801
KIDCLO	65	-0.00973	0.01389	-0.058	-0.700	0.4848	0.71732

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 3 DOWNS
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

MULTIPLE R 0.4197 STD. ERROR OF EST. 0.3259
MULTIPLE R-SQUARE 0.1762

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	10.4906	21	0.4996	4.704	0.0000
RESIDUAL	49.0596	462	0.1062		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		-0.58875					
DATE	6	0.14903E-02	0.61073E-03	0.141	2.440	0.0150	0.53721
TIME	8	0.13210E-02	0.38620E-03	0.167	3.420	0.0007	0.75158
GRALEN	11	-0.02912	0.01543	-0.087	-1.888	0.0597	0.84458
DISTUR	12	-0.07279	0.06400	-0.050	-1.137	0.2560	0.92171
R1	49	-0.03596	0.06349	-0.038	-0.566	0.5715	0.40258
R2	50	-0.17556	0.06657	-0.179	-2.637	0.0086	0.38650
R3	51	-0.06520	0.08199	-0.048	-0.795	0.4269	0.48647
R4	52	-0.23297	0.11739	-0.094	-1.985	0.0478	0.78684
R5	53	0.01140	0.05960	0.014	0.191	0.8484	0.35167
R6	54	-0.06191	0.07683	-0.047	-0.806	0.4208	0.52645
R7	55	-0.05932	0.09417	-0.037	-0.630	0.5290	0.52502
R8	56	0.05555	0.06779	0.057	0.819	0.4130	0.37271
DFAR	59	-0.01239	0.02357	-0.028	-0.526	0.5994	0.63230
MATE	57	-0.00551	0.05204	-0.008	-0.106	0.9158	0.33908
M	58	-0.02399	0.00896	-0.190	-2.676	0.0077	0.35230
COWS	15	-0.10408	0.05895	-0.082	-1.766	0.0781	0.83270
TEMP	44	0.00215	0.00518	0.029	0.415	0.6786	0.37232
PPT	45	-0.00466	0.00438	-0.051	-1.063	0.2883	0.76967
CLOUD	46	-0.09465	0.05116	-0.103	-1.850	0.0649	0.57094
WIND	47	0.00403	0.00391	0.050	1.030	0.3035	0.76198
DCLO	61	-0.07144	0.02235	-0.147	-3.196	0.0015	0.83905

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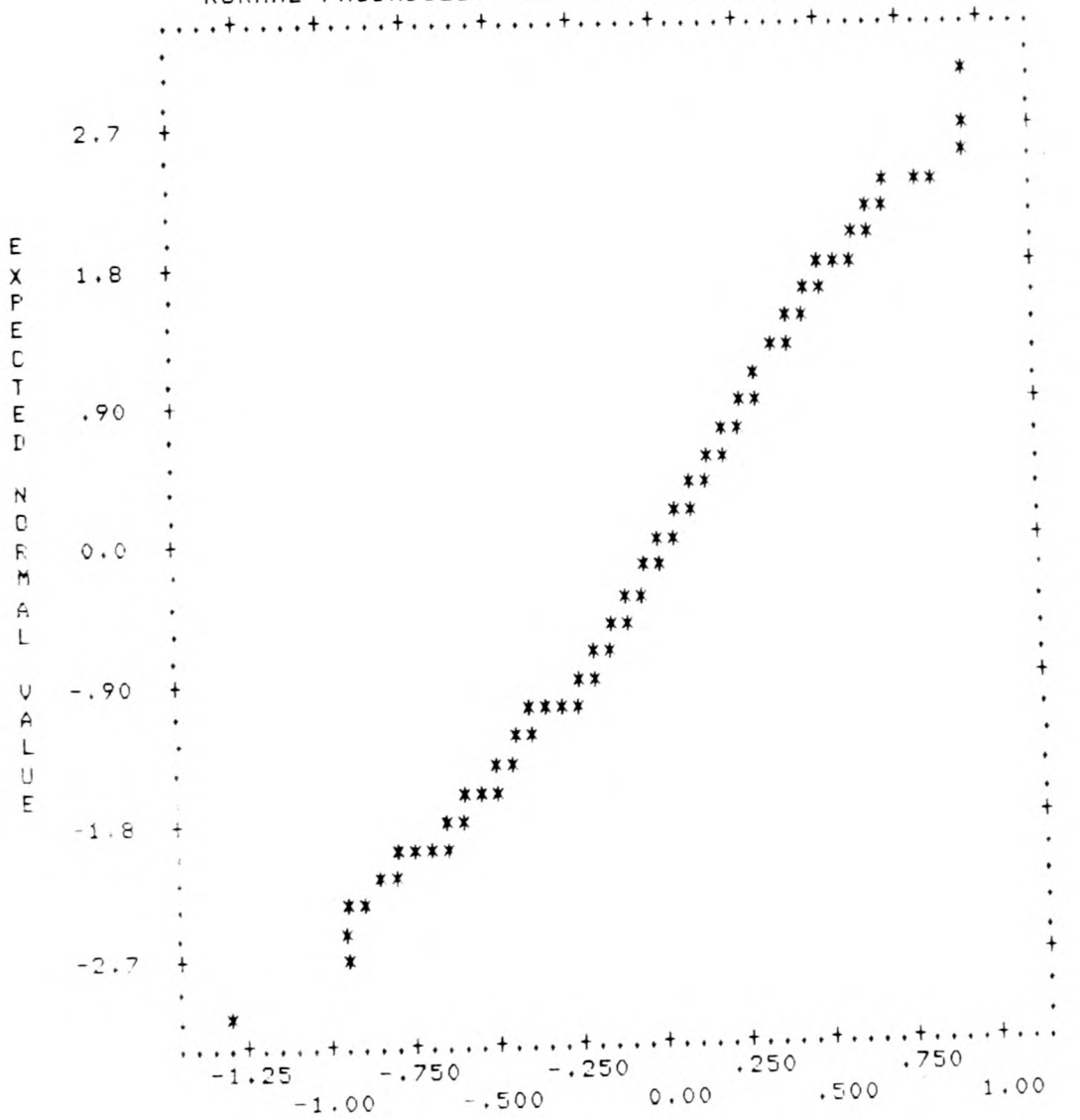
ALL



DEPENDENT VARIABLE. . . . . 3 DOWNS
TOLERANCE 0.0100

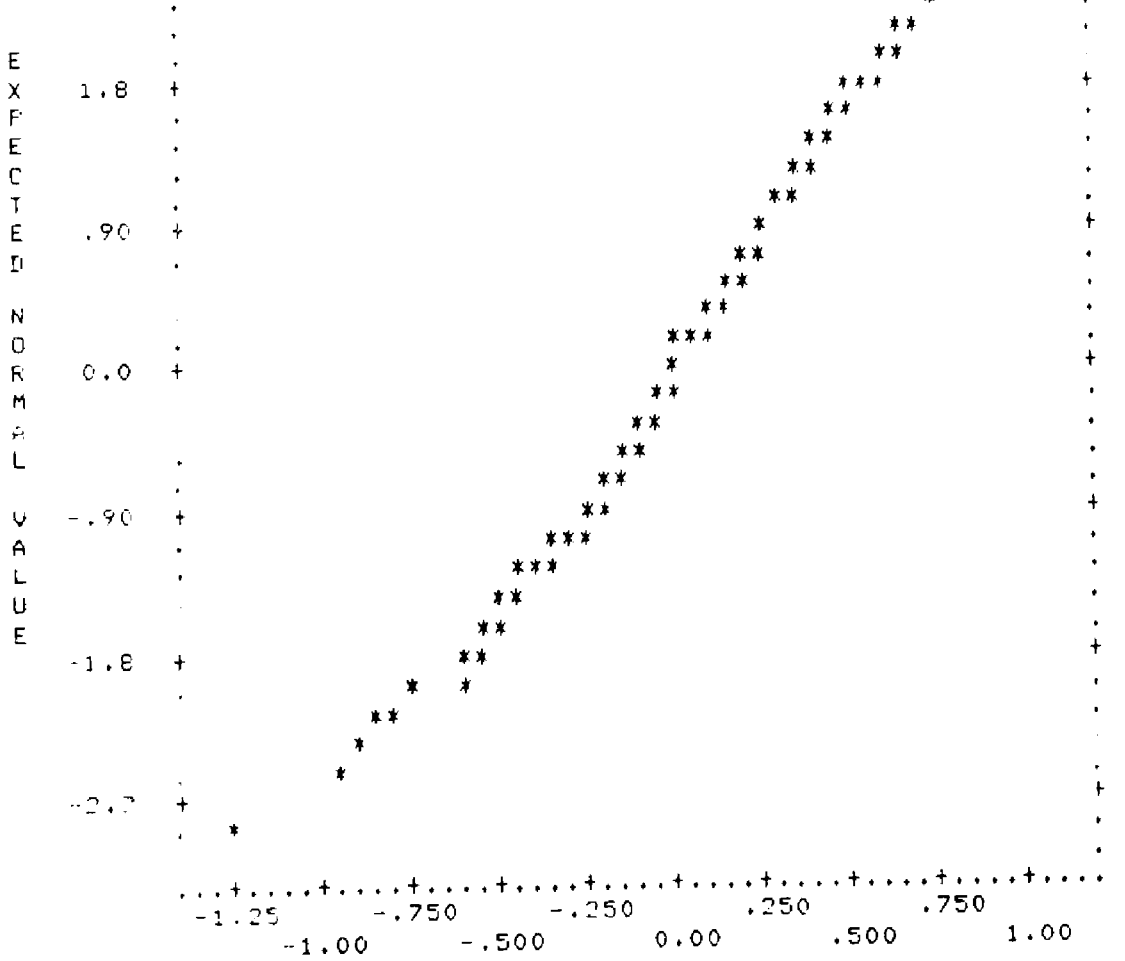
MULTIPLE R 0.4099 STD. ERROR OF EST. 0.3221
MULTIPLE R-SQUARE 0.1680

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	5.6561	17	0.3327	3.208	0.0000
RESIDUAL	28.0038	270	0.1037		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		-0.28801					
DATE	6	0.14131E-03	0.91802E-03	0.013	0.154	0.8778	0.47045
TIME	8	0.12712E-02	0.50301E-03	0.168	2.527	0.0121	0.69551
GRALEN	11	-0.04130	0.01929	-0.126	-2.141	0.0332	0.89046
DISTUR	12	-0.06591	0.07028	-0.054	-0.938	0.3487	0.91970
R1	49						VARIABLE NOT USED
R2	50						VARIABLE NOT USED
R3	51						VARIABLE NOT USED
R4	52						VARIABLE NOT USED
R5	53	0.00561	0.06100	0.008	0.092	0.9268	0.41005
R6	54	-0.05869	0.07945	-0.057	-0.739	0.4607	0.50953
R7	55	-0.07648	0.10374	-0.062	-0.737	0.4616	0.43806
R8	56	0.06351	0.07418	0.081	0.856	0.3927	0.34591
DFAR	59	-0.01531	0.03912	-0.025	-0.392	0.6957	0.75817
MATE	57	-0.00246	0.07500	-0.004	-0.033	0.9739	0.26541
M	58	-0.02558	0.01268	-0.214	-2.018	0.0446	0.27345
COWS	15	-0.11742	0.07630	-0.097	-1.539	0.1250	0.78040
TEMP	44	0.00430	0.00678	0.057	0.634	0.5269	0.37755
PPT	45	-0.00327	0.00717	-0.027	-0.456	0.6489	0.84883
CLOUD	46	-0.11559	0.06587	-0.121	-1.755	0.0804	0.65342
WIND	47	0.00569	0.00441	0.084	1.290	0.1982	0.71962
DCLO	61	-0.06255	0.02728	-0.142	-2.293	0.0226	0.80399

NORMAL PROBABILITY PLOT OF RESIDUALS



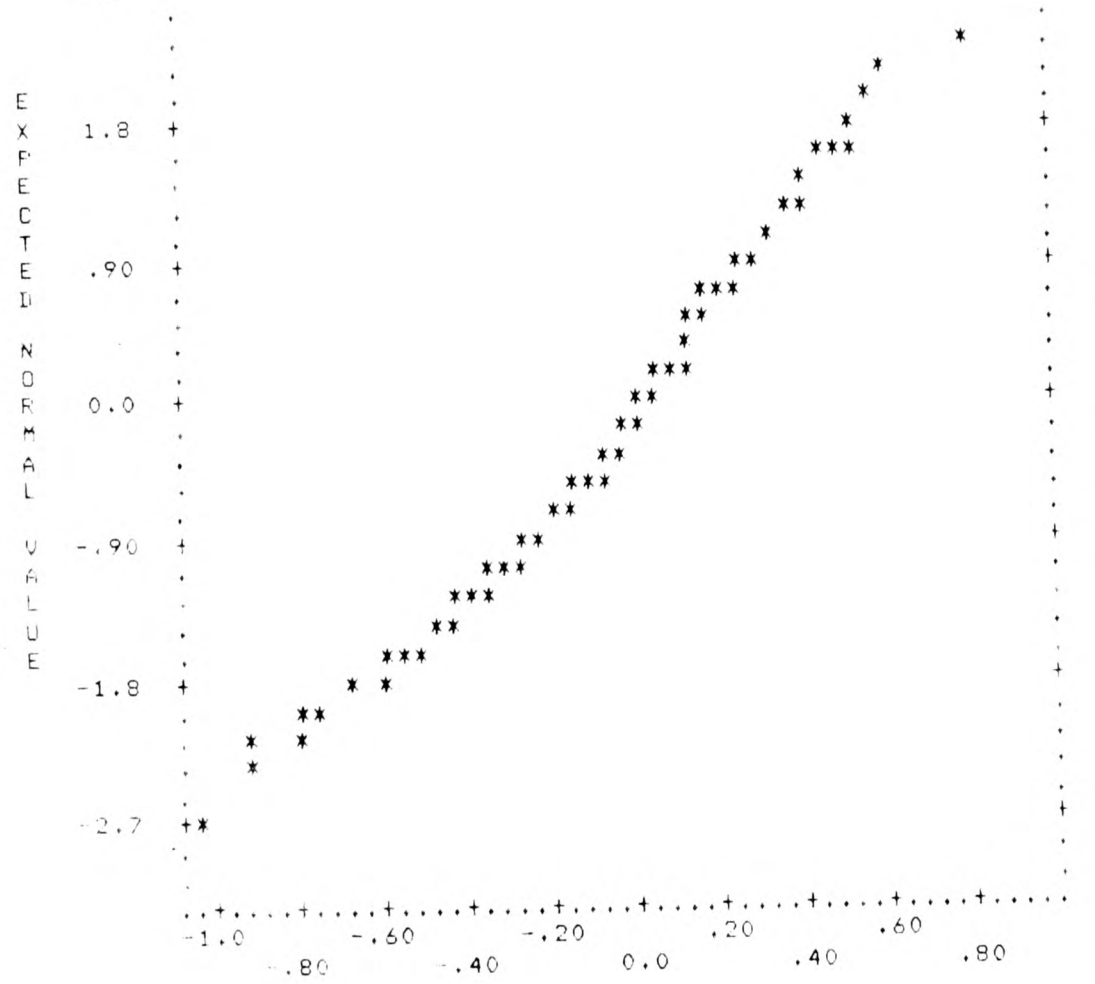
DEPENDENT VARIABLE. . . . . 3 DOWNS
TOLERANCE 0.0100

MULTIPLE R 0.4605 STD. ERROR OF EST. 0.3310
MULTIPLE R-SQUARE 0.2120

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	5.2758	16	0.3297	3.010	0.0002
RESIDUAL	19.6068	179	0.1095		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		-2.21567					
DATE	6	0.32267E-02	0.93750E-03	0.319	3.442	0.0007	0.51405
TIME	8	0.21879E-02	0.75311E-03	0.261	2.905	0.0041	0.54697
GRALEN	11	0.00916	0.02654	0.027	0.345	0.7305	0.02723
DISTUR	12	-0.16487	0.15471	-0.073	-1.066	0.2880	0.23919
R1	49	0.20928	0.12607	0.288	1.660	0.0986	0.14477
R2	50	0.09004	0.12315	0.122	0.731	0.4656	0.15363
R3	51	0.19897	0.14543	0.214	1.368	0.1730	0.18013
R4	52						VARIABLE NOT USED
R5	53						VARIABLE NOT USED
R6	54						VARIABLE NOT USED
R7	55						VARIABLE NOT USED
R8	56						VARIABLE NOT USED
DFAR	59	-0.03630	0.03324	-0.102	-1.092	0.2763	0.50328
MATE	57	0.03865	0.07901	0.053	0.489	0.6253	0.38089
M	58	-0.03232	0.01461	-0.240	-2.212	0.0282	0.37364
COWS	15	-0.16920	0.10176	-0.126	-1.663	0.0981	0.76360
TEMP	44	0.00674	0.00997	0.092	0.676	0.4997	0.23795
PPT	45	-0.00742	0.00664	-0.103	-1.118	0.2651	0.52062
CLOUD	46	-0.00807	0.08857	-0.009	-0.091	0.9275	0.41808
WIND	47	-0.00545	0.01003	-0.044	-0.543	0.5877	0.46106
[illegible]	61	-0.08922	0.04444	-0.160	-2.008	0.0462	0.49337



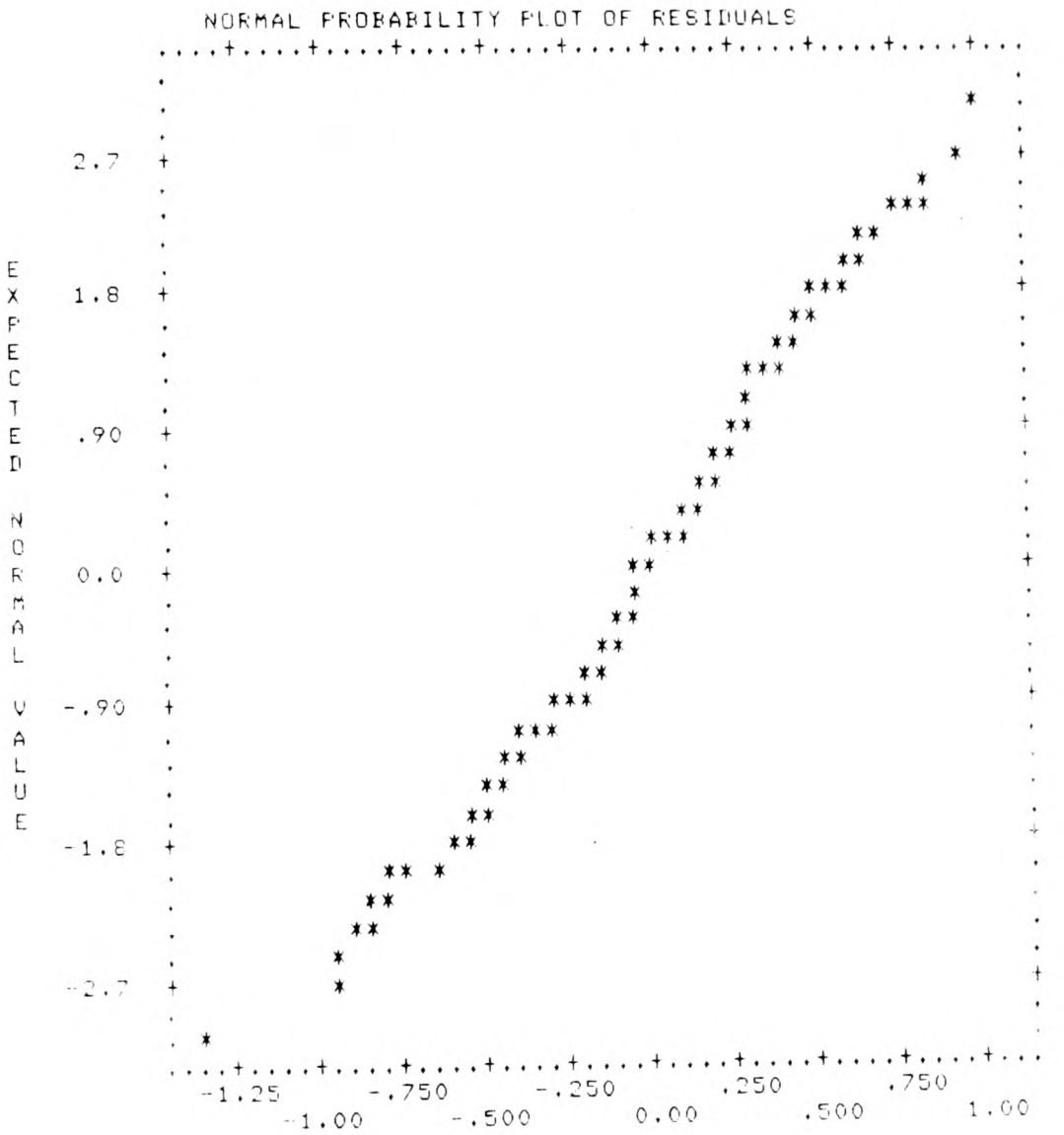
DEPENDENT VARIABLE. . . . . 3 DOWNS
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

MULTIPLE R 0.4286 STD. ERROR OF EST. 0.3278
MULTIPLE R-SQUARE 0.1837

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	10.9017	25	0.4361	4.059	0.0000
RESIDUAL	48.4527	451	0.1074		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		-0.65892					
DATE	6	0.14509E-02	0.64568E-03	0.134	2.247	0.0251	0.50707
TIME	8	0.14090E-02	0.40298E-03	0.177	3.497	0.0005	0.70370
GRALEN	11	-0.02796	0.01569	-0.083	-1.782	0.0755	0.83259
DISTUR	12	-0.08210	0.06482	-0.057	-1.267	0.2059	0.90963
R1	49	-0.03712	0.06507	-0.039	-0.570	0.5687	0.38892
R2	50	-0.19978	0.07207	-0.199	-2.772	0.0058	0.35042
R3	51	-0.10603	0.08623	-0.078	-1.230	0.2195	0.44550
R4	52	-0.24350	0.12004	-0.099	-2.029	0.0431	0.76158
R5	53	-0.00954	0.06257	-0.011	-0.152	0.8789	0.32427
R6	54	-0.08734	0.08023	-0.066	-1.089	0.2769	0.48898
R7	55	-0.07374	0.09649	-0.046	-0.764	0.4452	0.50623
R8	56	0.04499	0.07211	0.045	0.624	0.5330	0.34589
MAFAR	59	0.07006	0.04965	0.079	1.411	0.1589	0.57955
FEMFAR	60	-0.08580	0.04466	-0.112	-1.921	0.0553	0.53559
KIDFAR	61	-0.00631	0.05841	-0.005	-0.108	0.9141	0.83807
MATE	57	-0.00948	0.05490	-0.013	-0.173	0.8630	0.31295
M	58	-0.02292	0.00933	-0.181	-2.457	0.0144	0.33194
COWS	15	-0.09744	0.05982	-0.077	-1.629	0.1041	0.81913
TEMP	44	0.00230	0.00532	0.031	0.433	0.6655	0.36312
PPT	45	-0.00531	0.00456	-0.058	-1.165	0.2445	0.71921
CLOUD	46	-0.09256	0.05272	-0.100	-1.756	0.0798	0.55595
WIND	47	0.00263	0.00406	0.032	0.649	0.5164	0.74067
MACLO	63	-0.08979	0.07255	-0.062	-1.238	0.2165	0.72610
FEMCLO	64	-0.09066	0.04269	-0.112	-2.124	0.0342	0.64643
KIDCLO	65	-0.05446	0.03391	-0.073	-1.606	0.1089	0.87076



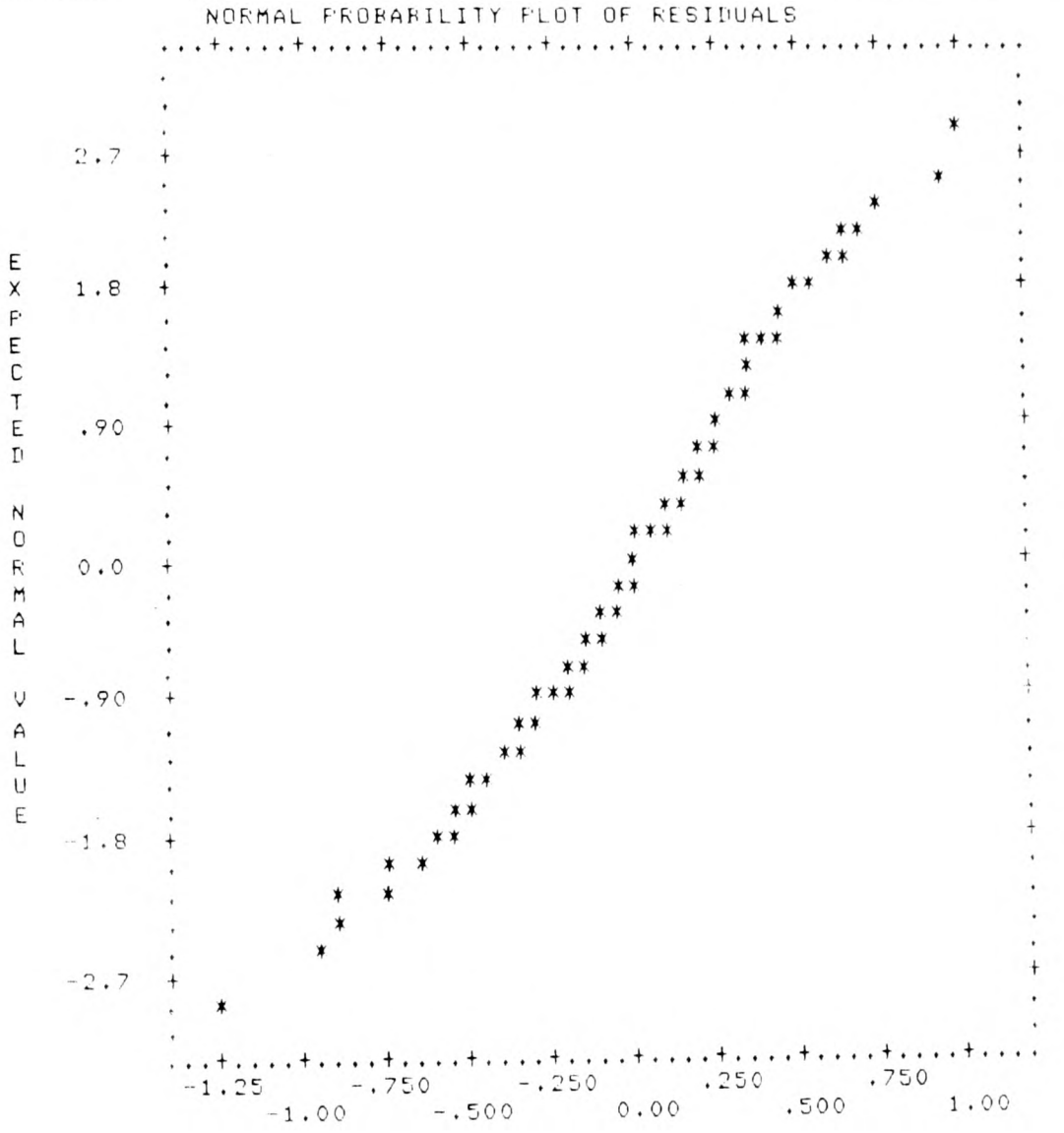
DEPENDENT VARIABLE. . . . . 3 DOWNS
TOLERANCE 0.0100

MULTIPLE R 0.4307 STD. ERROR OF EST. 0.3225
MULTIPLE R-SQUARE 0.1855

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	6.2311	21	0.2967	2.852	0.0001
RESIDUAL	27.3599	263	0.1040		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		-0.37751					
DATE	6	0.26275E-03	0.96154E-03	0.024	0.273	0.7849	0.40376
TIME	8	0.13903E-02	0.52034E-03	0.184	2.672	0.0080	0.65241
GRALEN	11	-0.04038	0.01949	-0.123	-2.072	0.0393	0.88320
DISTUR	12	-0.08151	0.07117	-0.067	-1.145	0.2531	0.90042
R1	49						VARIABLE NOT US
R2	50						VARIABLE NOT US
R3	51						VARIABLE NOT US
R4	52						VARIABLE NOT US
R5	53	-0.03242	0.06550	-0.046	-0.495	0.6210	0.35898
R6	54	-0.10552	0.08489	-0.103	-1.243	0.2150	0.44835
R7	55	-0.10694	0.10565	-0.087	-1.012	0.3124	0.42405
R8	56	0.03433	0.07923	0.043	0.433	0.6651	0.31386
MAFAR	59	0.16233	0.09810	0.115	1.655	0.0992	0.64099
FEMFAR	60	-0.15890	0.07879	-0.143	-2.017	0.0447	0.61502
KIDFAR	61	0.02913	0.07454	0.024	0.391	0.6963	0.81899
MATE	57	-0.02089	0.07982	-0.030	-0.262	0.7938	0.23870
M	58	-0.02319	0.01287	-0.193	-1.801	0.0728	0.26859
COWS	15	-0.12624	0.07862	-0.104	-1.606	0.1095	0.73798
TEMP	44	0.00360	0.00700	0.047	0.514	0.6076	0.36473
PPT	45	-0.00324	0.00722	-0.027	-0.449	0.6537	0.84004
CLOUD	46	-0.09908	0.06935	-0.103	-1.429	0.1542	0.59559
WIND	47	0.00251	0.00474	0.037	0.530	0.5968	0.63972
MACLO	63	-0.05028	0.09865	-0.037	-0.510	0.6107	0.60274
FEMCLO	64	-0.10591	0.06169	-0.138	-1.717	0.0872	0.47789
KIDCLO	65	-0.06528	0.03993	-0.099	-1.635	0.1033	0.85039



DEPENDENT VARIABLE. . . . . 3 DOWNS
TOLERANCE 0.0100

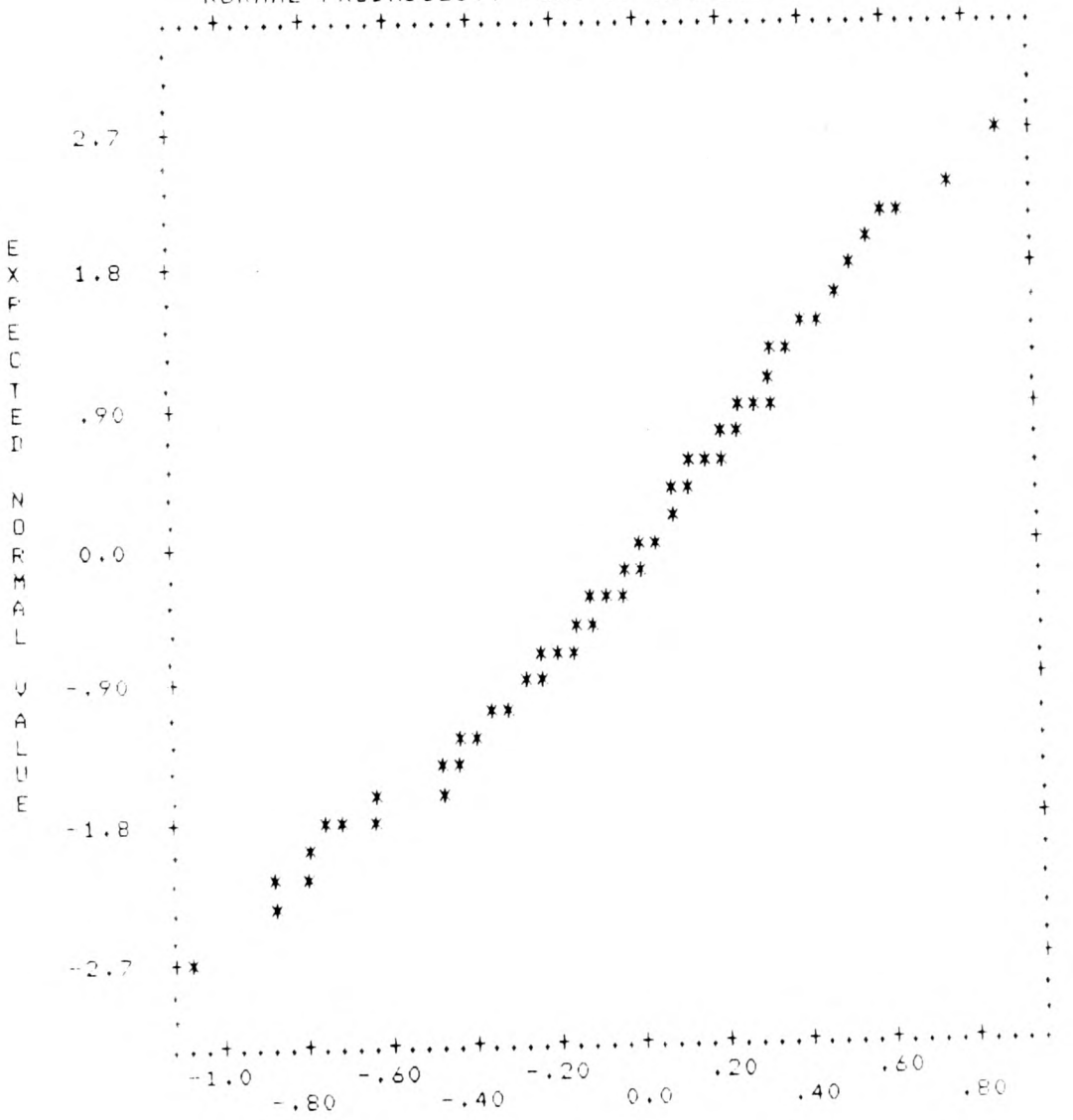
MULTIPLE R 0.4772 STD. ERROR OF EST. 0.3347
MULTIPLE R-SQUARE 0.2278

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	5.6504	20	0.2825	2.522	0.0007
RESIDUAL	19.1589	171	0.1120		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		-2.39993					
DATE	6	0.00421	0.00117	0.405	3.605	0.0004	0.35827
TIME	8	0.22777E-02	0.79564E-03	0.269	2.863	0.0047	0.51285
GRALEN	11	0.00854	0.02754	0.025	0.310	0.7568	0.65581
DISTUR	12	-0.19423	0.15767	-0.086	-1.232	0.2197	0.92553
R1	49	0.24136	0.13183	0.330	1.831	0.0689	0.33521
R2	50	0.09380	0.12561	0.125	0.747	0.4562	0.16065
R3	51	0.19394	0.15200	0.208	1.276	0.2037	0.16944
R4	52						VARIABLE NOT US
R5	53						VARIABLE NOT US
R6	54						VARIABLE NOT US
R7	55						VARIABLE NOT US
R8	56						VARIABLE NOT US
MAFAR	59	0.02233	0.06235	0.033	0.358	0.7207	0.52047
FEMFAR	60	-0.07368	0.06127	-0.123	-1.203	0.2308	0.43107
KIDFAR	61	-0.21371	0.11649	-0.164	-1.835	0.0683	0.56295
MATE	57	0.01659	0.08718	0.022	0.190	0.8493	0.32412
M	58	-0.02637	0.01592	-0.196	-1.656	0.0995	0.32374
COWS	15	-0.19091	0.10786	-0.143	-1.770	0.0785	0.69644
TEMP	44	0.00271	0.01068	0.037	0.254	0.8001	0.21214
PPT	45	-0.01053	0.00732	-0.146	-1.437	0.1525	0.43730
CLOUD	46	-0.01642	0.09264	-0.019	-0.177	0.8596	0.40926
WIND	47	-0.01071	0.01117	-0.083	-0.959	0.3389	0.60272
MACLO	63	-0.08682	0.12425	-0.056	-0.699	0.4856	0.69990
FEMCLO	64	-0.14045	0.07617	-0.164	-1.844	0.0669	0.56801
KIDCLO	65	-0.06312	0.07159	-0.070	-0.882	0.3792	0.71732

NORMAL PROBABILITY PLOT OF RESIDUALS



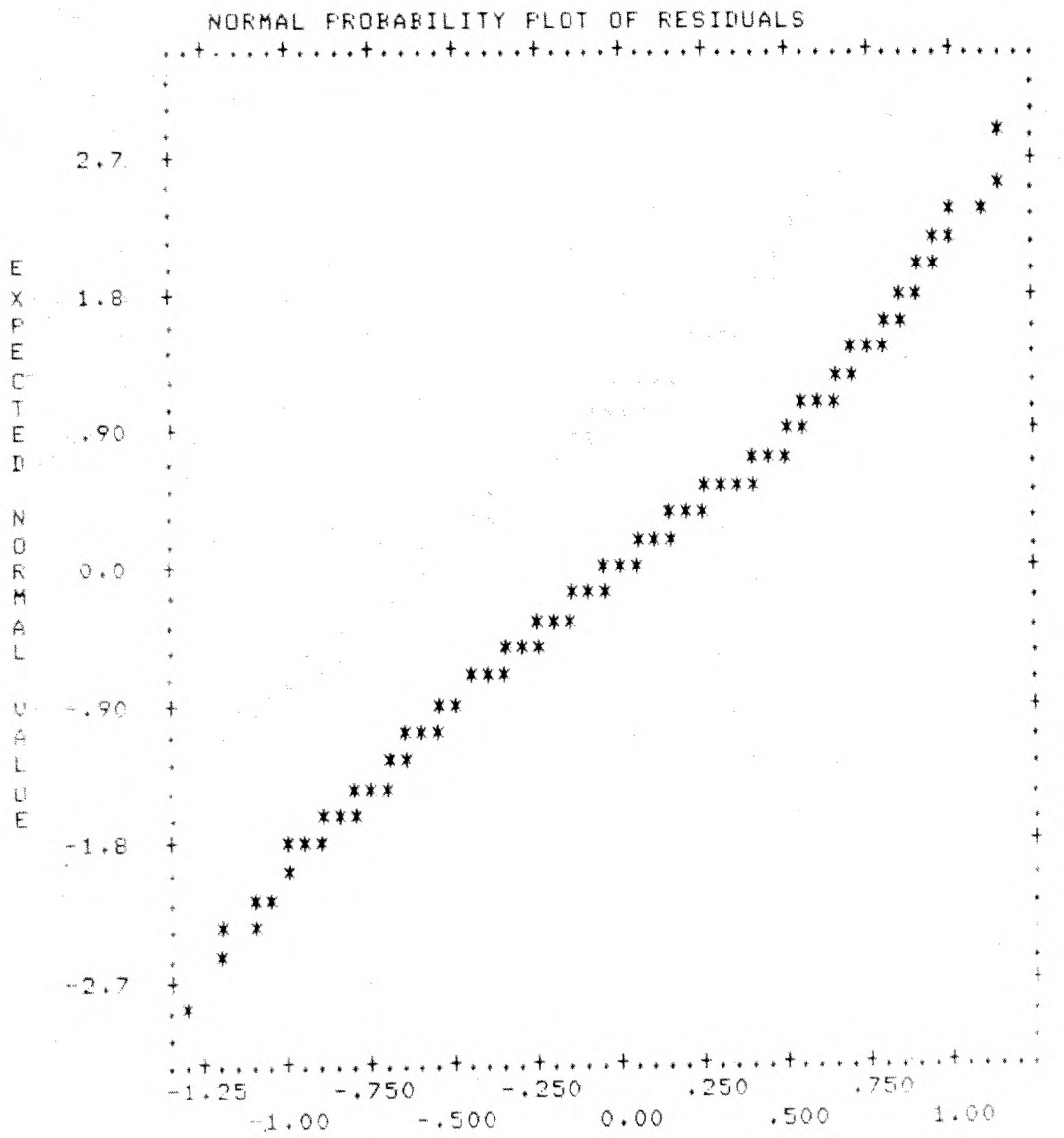
DEPENDENT VARIABLE. . . . . 42 LENGTH
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

MULTIPLE R 0.3415 STD. ERROR OF EST. 0.5361
MULTIPLE R-SQUARE 0.1167

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	11.2347	21	0.5350	1.861	0.013
RESIDUAL	85.0750	296	0.2874		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		1.54814					
DATE	6	0.00102	0.00124	0.062	0.822	0.4115	0.53169
TIME	8	0.35033E-03	0.80219E-03	0.028	0.437	0.6626	0.45234
GRALEN	11	-0.01085	0.03388	-0.019	-0.320	0.7491	0.87815
DISTUR	12	-0.37730	0.13084	-0.166	-2.884	0.0042	0.89571
R1	49	-0.21217	0.13004	-0.143	-1.632	0.1038	0.39074
R2	50	-0.47183	0.13082	-0.338	-3.607	0.0004	0.34064
R3	51	-0.23214	0.16706	-0.111	-1.390	0.1657	0.46414
R4	52	-0.61411	0.22182	-0.175	-2.769	0.0060	0.74903
R5	53	-0.21777	0.12420	-0.162	-1.753	0.0806	0.34854
R6	54	-0.33195	0.15861	-0.156	-2.093	0.0372	0.53549
R7	55	-0.27363	0.21411	-0.091	-1.278	0.2023	0.59037
R8	56	-0.13323	0.14321	-0.083	-0.930	0.3530	0.37687
DFAR	59	-0.00369	0.04689	-0.005	-0.079	0.9374	0.62328
MATE	57	0.04145	0.10387	0.037	0.399	0.6902	0.34050
M	58	-0.02000	0.01910	-0.095	-1.047	0.2959	0.36295
COWS	15	-0.01673	0.11565	-0.009	-0.145	0.8850	0.84164
TEMP	44	0.00442	0.01059	0.037	0.418	0.6764	0.37706
PPT	45	0.00115	0.00836	0.009	0.137	0.8910	0.74599
CLOUD	46	0.06792	0.10622	0.048	0.639	0.5231	0.53260
WIND	47	0.00399	0.00835	0.030	0.478	0.6330	0.75272
DCLO	61	-0.08533	0.04429	-0.116	-1.927	0.0550	0.87800



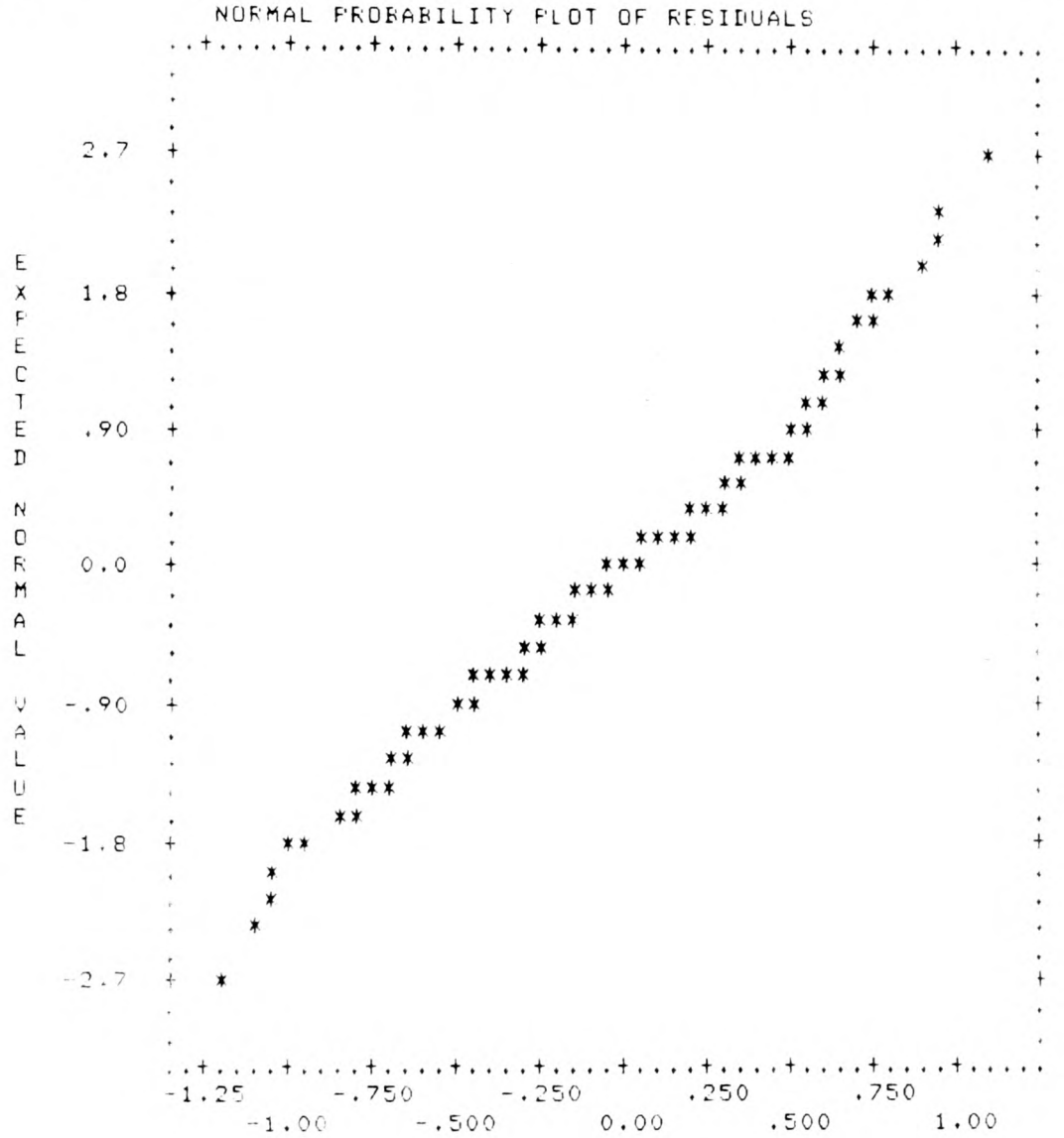
DEPENDENT VARIABLE. . . . . 42 LENGTH
TOLERANCE 0.0100

MULTIPLE R 0.3607 STD. ERROR OF EST. 0.5271
MULTIPLE R-SQUARE 0.1301

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	6.4425	17	0.3790	1.364	0.161
RESIDUAL	43.0663	155	0.2778		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		1.29353					
DATE	6	-0.00309	0.00212	-0.171	-1.460	0.1463	0.41147
TIME	8	0.99313E-03	0.10800E-02	0.083	0.920	0.3592	0.49784
GRALEN	11	0.02660	0.04642	0.045	0.573	0.5674	0.89510
DISTUR	12	-0.32985	0.14270	-0.184	-2.311	0.0221	0.89003
R1	49						VARIABLE NOT USED.
R2	50						VARIABLE NOT USED.
R3	51						VARIABLE NOT USED.
R4	52						VARIABLE NOT USED.
R5	53	-0.19997	0.12915	-0.183	-1.548	0.1236	0.40358
R6	54	-0.30641	0.16315	-0.194	-1.878	0.0623	0.52340
R7	55	-0.28429	0.23390	-0.130	-1.215	0.2260	0.49306
R8	56	-0.05947	0.15742	-0.048	-0.378	0.7061	0.34700
DFAR	59	-0.03819	0.08804	-0.040	-0.434	0.6650	0.67277
MATE	57	0.15985	0.15656	0.149	1.021	0.3088	0.26465
M	58	-0.03717	0.02821	-0.186	-1.318	0.1896	0.28282
COWS	15	-0.11266	0.15540	-0.061	-0.725	0.4696	0.79239
TEMP	44	0.01924	0.01489	0.162	1.293	0.1981	0.35597
PPT	45	0.01806	0.01287	0.116	1.404	0.1624	0.81488
CLOUD	46	-0.00761	0.14478	-0.005	-0.053	0.9582	0.59422
WIND	47	0.00780	0.00948	0.073	0.823	0.4120	0.71399
DCLO	61	-0.11730	0.05799	-0.176	-2.023	0.0448	0.74386



DEPENDENT VARIABLE. . . . . 42 LENGTH
TOLERANCE 0.0100

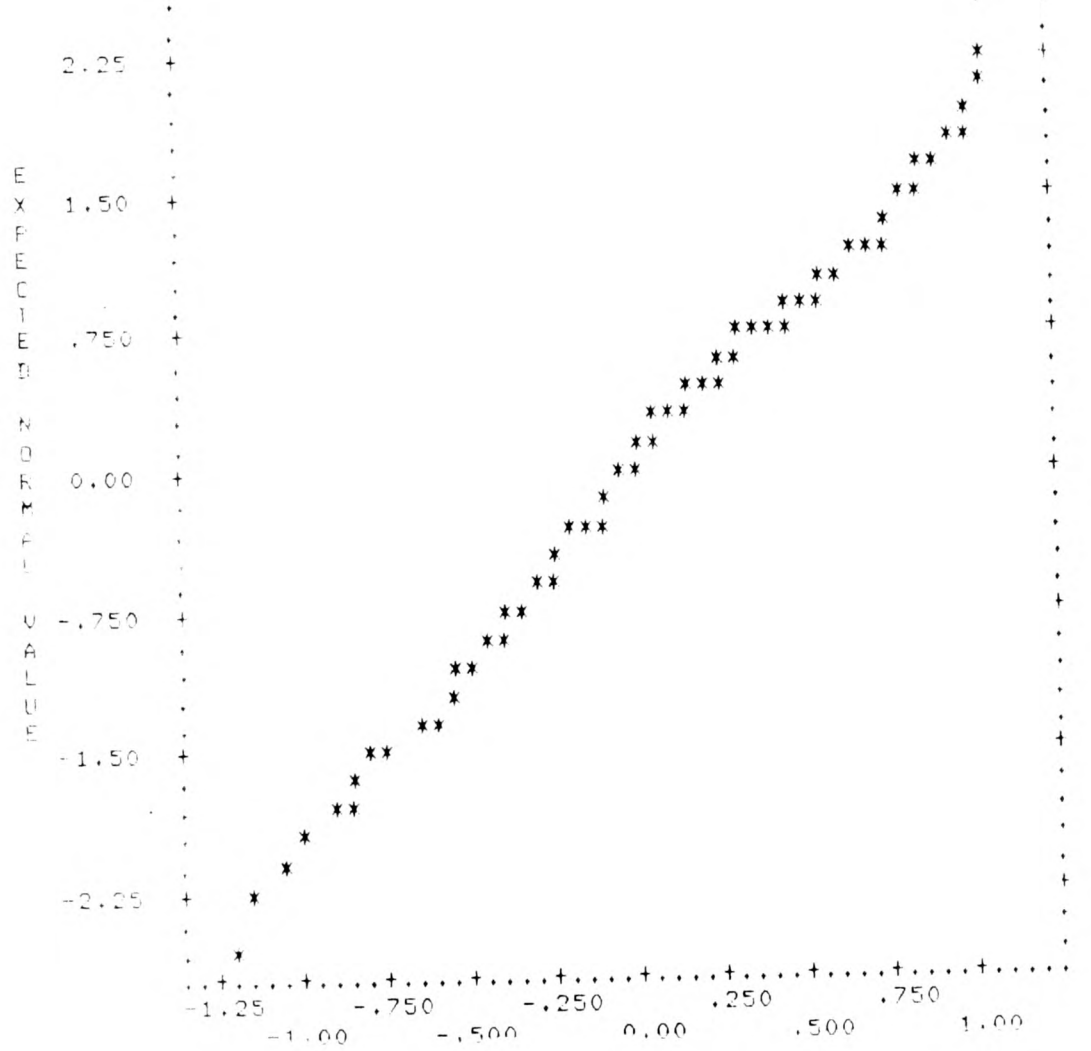
MULTIPLE R 0.4420 STD. ERROR OF EST. 0.5341
MULTIPLE R-SQUARE 0.1953

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	8.8642	16	0.5540	1.942	0.0220
RESIDUAL	36.5139	128	0.2853		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		0.20486					
DATE	6	0.00328	0.00170	0.213	1.928	0.0561	0.5141
TIME	8	0.00106	0.00148	0.079	0.719	0.4736	0.5024
GRALEN	11	-0.06304	0.05060	-0.111	-1.246	0.2151	0.7926
DISTUR	12	-0.74014	0.33229	-0.188	-2.227	0.0277	0.8791
R1	49	-0.01834	0.18966	-0.016	-0.097	0.9231	0.2327
R2	50	-0.36401	0.17144	-0.321	-2.123	0.0357	0.2746
R3	51						VARIABLE NOT USED
R4	52	-0.43755	0.26841	-0.179	-1.630	0.1055	0.5238
R5	53						VARIABLE NOT USED
R6	54						VARIABLE NOT USED
R7	55						VARIABLE NOT USED
R8	56						VARIABLE NOT USED
DFAR	59	-0.01952	0.06161	-0.035	-0.317	0.7519	0.5253
MATE	57	-0.02074	0.15047	-0.018	-0.138	0.8906	0.3565
M	58	-0.01739	0.02844	-0.079	-0.612	0.5419	0.3792
COWS	15	-0.12367	0.18522	-0.061	-0.668	0.5055	0.7554
TEMP	44	0.01277	0.01883	0.107	0.678	0.4988	0.2548
PPT	45	-0.01615	0.01298	-0.141	-1.244	0.2157	0.4902
CLOUD	46	0.34525	0.16896	0.255	2.043	0.0431	0.4026
WIND	47	-0.02374	0.01986	-0.118	-1.195	0.2342	0.6500
DCLO_	61	-0.00280	0.08149	-0.003	-0.034	0.9727	0.6522

NORMAL PROBABILITY PLOT OF RESIDUALS



DEPENDENT VARIABLE. . . . . 42 LENGTH
TOLERANCE 0.0100
ALL DATA CONSIDERED AS A SINGLE GROUP

MULTIPLE R 0.3642 STD. ERROR OF EST. 0.5341
MULTIPLE R-SQUARE 0.1326

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	12.4295	25	0.4972	1.743	0.0173
RESIDUAL	81.3022	285	0.2853		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		1.06898					
DATE	6	0.13646E-03	0.13187E-02	0.008	0.103	0.9177	0.49636
TIME	8	0.83897E-03	0.83208E-03	0.066	1.008	0.3142	0.70341
GRALEN	11	-0.00552	0.03439	-0.010	-0.160	0.8727	0.95550
DISTUR	12	-0.37164	0.13105	-0.166	-2.836	0.0049	0.88756
R1	49	-0.17743	0.13110	-0.121	-1.353	0.1770	0.38328
R2	50	-0.42140	0.13755	-0.297	-3.064	0.0024	0.32398
R3	51	-0.18466	0.17255	-0.090	-1.070	0.2854	0.43260
R4	52	-0.55073	0.22445	-0.159	-2.454	0.0147	0.72651
R5	53	-0.17796	0.12839	-0.134	-1.386	0.1668	0.32577
R6	54	-0.28625	0.16272	-0.136	-1.759	0.0796	0.50586
R7	55	-0.21788	0.21567	-0.073	-1.010	0.3132	0.57800
R8	56	-0.07620	0.15094	-0.046	-0.505	0.6141	0.35923
MAFAR	59	-0.06367	0.09937	-0.046	-0.641	0.5222	0.58898
FEMFAR	60	-0.03800	0.08713	-0.034	-0.436	0.6631	0.50077
KIDFAR	61	0.17918	0.12787	0.087	1.401	0.1622	0.78769
MATE	57	0.05497	0.11030	0.050	0.498	0.6186	0.30640
M	58	-0.02531	0.01991	-0.121	-1.271	0.2047	0.33467
COWS	15	-0.01118	0.11621	-0.006	-0.096	0.9234	0.82911
TEMP	44	0.00890	0.01076	0.075	0.827	0.4089	0.37189
PPT	45	0.00278	0.00872	0.021	0.318	0.7506	0.68029
CLOUD	46	0.06788	0.10978	0.048	0.618	0.5368	0.51145
WIND	47	0.00128	0.00870	0.010	0.147	0.8829	0.72851
MACLO	63	-0.12082	0.14322	-0.056	-0.844	0.3996	0.68033
FEMCLO	64	-0.12114	0.08710	-0.097	-1.391	0.1653	0.62066
KIDCLO	65	-0.03723	0.06844	-0.033	-0.544	0.5868	0.83670

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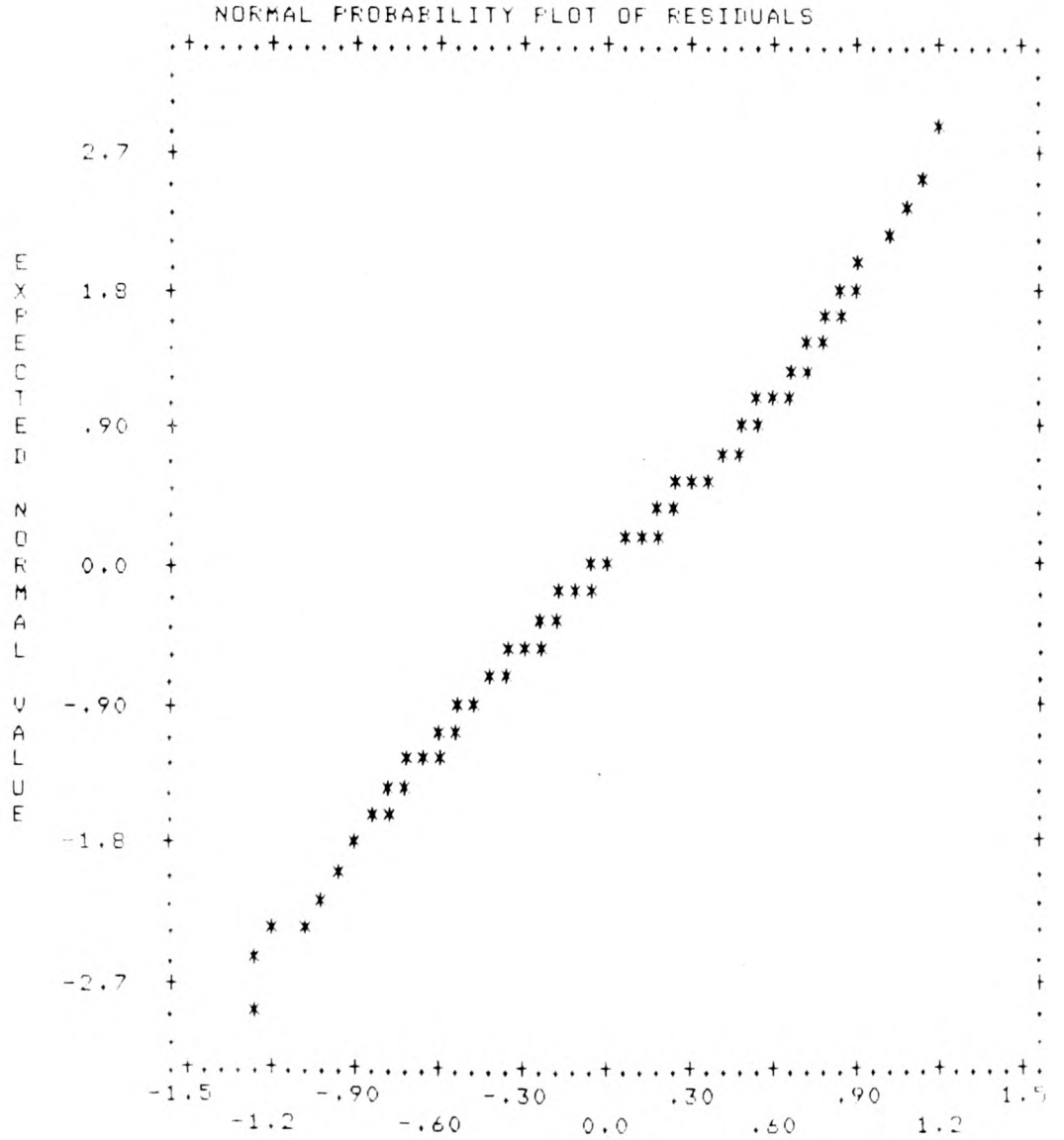
ALL



DEPENDENT VARIABLE. . . . . 42 LENGTH
TOLERANCE 0.0100

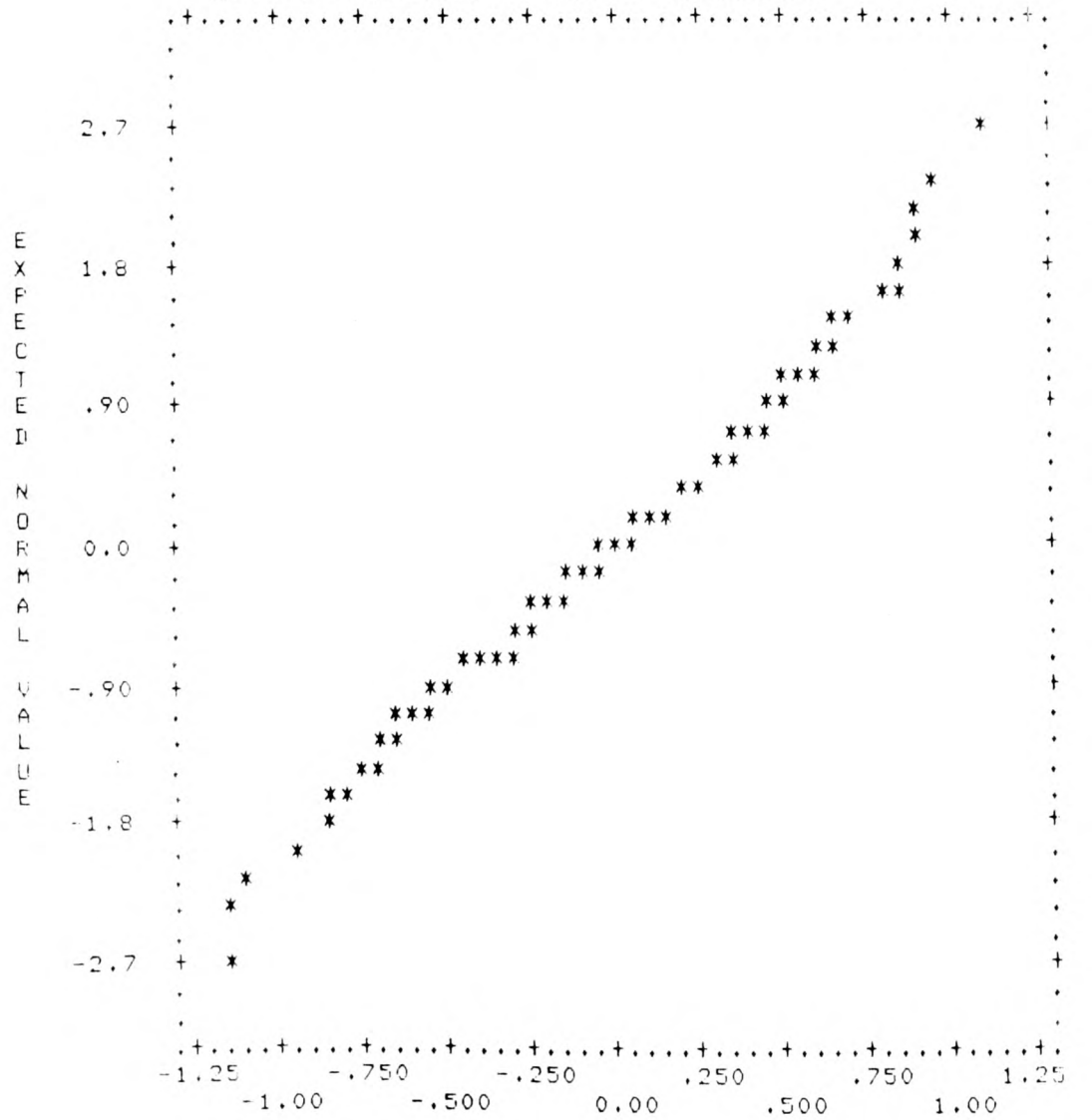
MULTIPLE R 0.3979 STD. ERROR OF EST. 0.5264
MULTIPLE R-SQUARE 0.1583

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	7.7119	21	0.3672	1.325	0.1676
RESIDUAL	41.0052	148	0.2771		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		0.60979					
DATE	6	-0.00426	0.00226	-0.231	-1.890	0.0607	0.37905
TIME	8	0.00158	0.00111	0.133	1.425	0.1562	0.65466
GRALEN	11	0.04103	0.04700	0.070	0.873	0.3841	0.88293
DISTUR	12	-0.32767	0.14343	-0.184	-2.284	0.0238	0.98023
R1	49						VARIABLE NOT USE
R2	50						VARIABLE NOT USE
R3	51						VARIABLE NOT USE
R4	52						VARIABLE NOT USE
R5	53	-0.16664	0.13748	-0.153	-1.212	0.2274	0.35929
R6	54	-0.28083	0.17309	-0.179	-1.622	0.1068	0.46498
R7	55	-0.24762	0.23706	-0.114	-1.045	0.2979	0.47920
R8	56	-0.01264	0.16917	-0.010	-0.075	0.9406	0.31650
MAFAR	59	-0.20294	0.20182	-0.101	-1.006	0.3163	0.56658
FEMFAR	60	0.00886	0.16785	0.005	0.053	0.9580	0.56847
KIDFAR	61	-0.10551	0.22619	-0.042	-0.466	0.6416	0.71036
MATE	57	0.10524	0.16972	0.098	0.620	0.5362	0.22949
M	58	-0.03671	0.02860	-0.184	-1.284	0.2012	0.27822
COWS	15	-0.05453	0.15973	-0.030	-0.341	0.7333	0.74922
TEMP	44	0.02825	0.01567	0.235	1.803	0.0735	0.33443
PPT	45	0.01717	0.01296	0.112	1.325	0.1872	0.80186
CLOUD	46	0.05618	0.15263	0.038	0.368	0.7133	0.53938
WIND	47	0.00725	0.01055	0.067	0.688	0.4927	0.59560
MACLO	63	0.02789	0.22486	0.013	0.124	0.9015	0.53260
FEMCLO	64	-0.28829	0.14036	-0.241	-2.054	0.0412	0.41377
KIDCLO	65	0.85907E-03	0.82749E-01	0.001	0.010	0.9917	0.80724

NORMAL PROBABILITY PLOT OF RESIDUALS



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DEPENDENT VARIABLE. . . . . 42 LENGTH
TOLERANCE 0.0100

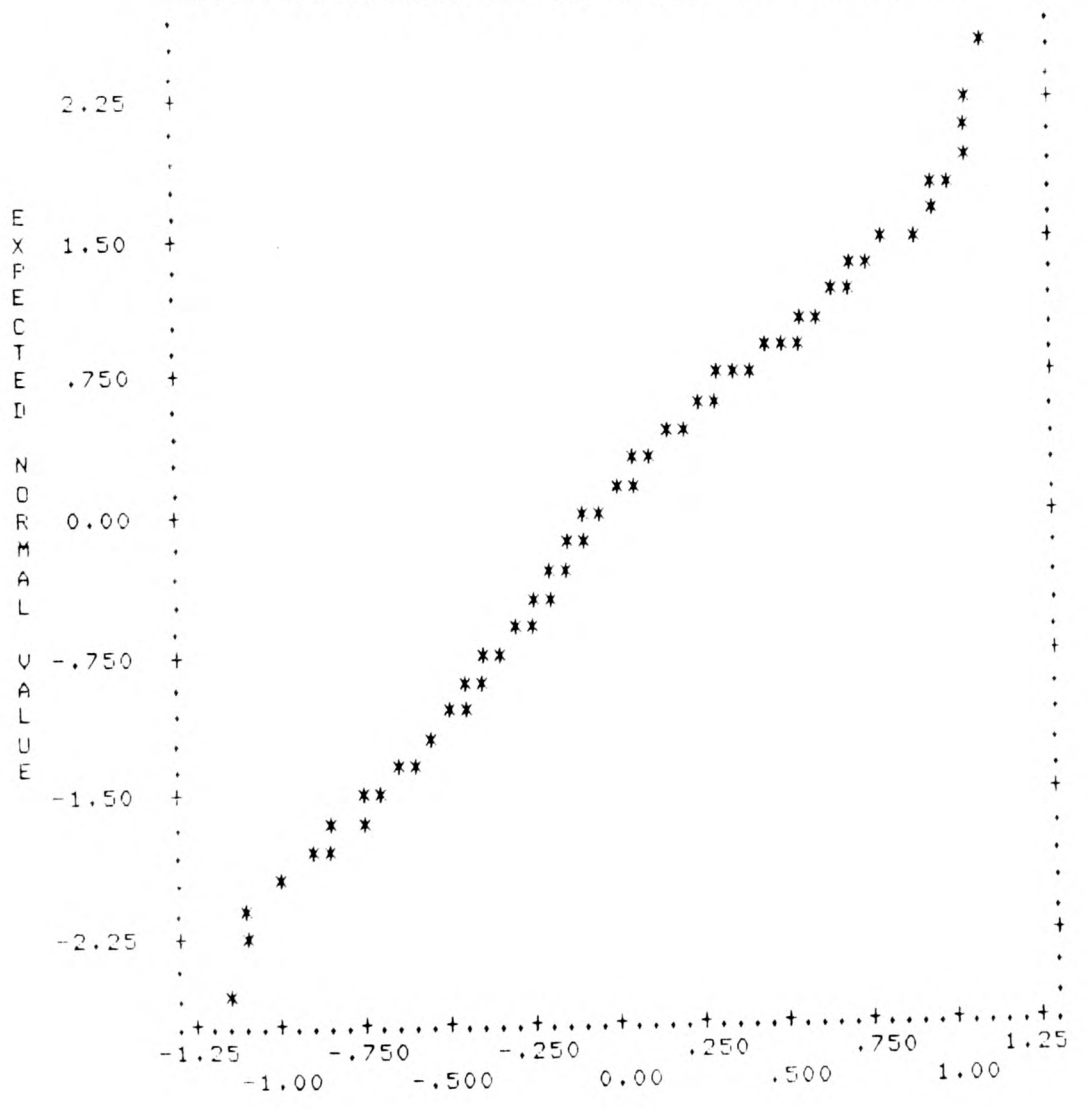
MULTIPLE R 0.4632 STD. ERROR OF EST. 0.5347
MULTIPLE R-SQUARE 0.2145

ANALYSIS OF VARIANCE

	SUM OF SQUARES	DF	MEAN SQUARE	F RATIO	P(TAIL)
REGRESSION	9.3700	20	0.4685	1.639	0.054
RESIDUAL	34.3027	120	0.2859		

VARIABLE		COEFFICIENT	STD. ERROR	STD. REG COEFF	T	P(2 TAIL)	TOLERANCE
INTERCEPT		-0.12557					
DATE	6	0.00248	0.00219	0.159	1.131	0.2603	0.33014
TIME	8	0.00117	0.00155	0.087	0.757	0.4505	0.49178
GRALEN	11	-0.07988	0.05248	-0.143	-1.522	0.1306	0.74510
DISTUR	12	-0.71493	0.33537	-0.185	-2.132	0.0351	0.86559
R1	49	0.37954	0.23542	0.329	1.612	0.1095	0.15714
R2	50	0.04780	0.22564	0.042	0.212	0.8326	0.16534
R3	51	0.42744	0.27686	0.289	1.544	0.1252	0.18726
R4	52						VARIABLE NOT USE
R5	53						VARIABLE NOT USE
R6	54						VARIABLE NOT USE
R7	55						VARIABLE NOT USE
R8	56						VARIABLE NOT USE
MAFAR	59	-0.04231	0.12362	-0.038	-0.342	0.7328	0.52518
FEMFAR	60	0.01242	0.11871	0.014	0.105	0.9169	0.37377
KIDFAR	61	0.11031	0.19795	0.063	0.557	0.5784	0.51428
MATE	57	0.05368	0.16954	0.048	0.317	0.7521	0.28735
M	58	-0.02831	0.03202	-0.130	-0.884	0.3784	0.30133
COWS	15	-0.09177	0.19552	-0.046	-0.469	0.6396	0.68111
TEMP	44	0.01273	0.02056	0.108	0.619	0.5370	0.21420
PPT	45	-0.00904	0.01431	-0.080	-0.631	0.5291	0.40432
CLOUD	46	0.31977	0.17861	0.234	1.790	0.0759	0.38416
WIND	47	-0.02433	0.02262	-0.114	-1.076	0.2842	0.58780
MACLO	63	-0.19129	0.21189	-0.092	-0.903	0.3685	0.62780
FEMCLO	64	0.08432	0.13882	0.066	0.607	0.5447	0.55836
KIDCLO	65	-0.03296	0.14207	-0.024	-0.232	0.8169	0.63112

NORMAL PROBABILITY PLOT OF RESIDUALS



APPENDIX II

The method for estimating relatedness

The set of pairs of rabbits is taken, and within each pair one is designated as the donor, one as the recipient. Their genotypes at a number of loci are known, and the problem is to estimate the mean across pairs of the within pairs relatedness, of the donor rabbit to the recipient rabbit, within the population of pairs from which it is assumed the observed pairs are a random sample. The following notation is used:

Let i index the pairs, i=1,2...I, where I is the number of pairs

Let l index the loci, l=1,2...L, where L is the number of loci

Let m index the alleles of the donor rabbit at a given locus, m=1 for a homozygote at that locus, and m=1,2 for a heterozygote.

Let μ_{ilm} be the population frequency of the mth allele at the lth locus of the donor rabbit in the ith pair.

Let x_{ilm} be the frequency of that allele in the donor, equalling one half for a heterozygote and one for a homozygote.

$$v_{il} = 0.5\mu_{ill}(1 - \mu_{ill})(1 - \rho) + 0.5\rho(1 - \rho)(1 - \mu_{ill})^2$$

$$n_{il} = (x_{ill} - \mu_{ill})v_{il}^{-1}(y_{ill} - \mu_{ill})$$

$$d_{il} = (x_{ill} - \mu_{ill})v_{il}^{-1}(x_{ill} - \mu_{ill})$$

2) Donor i is a heterozygote at locus l, and there are two alleles at locus l in the population:

$$v_{il} = 0.5\mu_{ill}(1 - \mu_{ill})(1 - \rho)^2 + 0.25\rho(1 - \rho)$$

$$n_{il} = (x_{ill} - \mu_{ill})v_{ill}^{-1}(y_{ill} - \mu_{ill})$$

$$d_{il} = (x_{ill} - \mu_{ill})v_{il}^{-1}(x_{ill} - \mu_{ill})$$

3) Donor i is a heterozygote at locus l, and there are more than two alleles at locus l in the population:

$$v_{ill} = 0.5\mu_{ill}(1 - \mu_{ill})(1 - \rho)^2 + 0.25\rho(1 - \rho)$$

$$v_{il2} = 0.5\mu_{il2}(1 - \mu_{il2})(1 - \rho)^2 + 0.25\rho(1 - \rho)$$

$$c_{il} = - 0.5(\mu_{ill}\mu_{il2})(1 - \rho)^2 - 0.25\rho(1 - \rho)(\mu_{ill} + \mu_{il2})$$

$$w_{ill} = v_{il2}/(v_{ill}v_{il2} - c_{il}^2)$$

$$w_{il2} = v_{ill}/(v_{ill}v_{il2} - c_{il}^2)$$

$$u_{il} = -c_{il}/(v_{il1}v_{il2} - c_{il}^2)$$

$$\begin{aligned} n_{il} = {} & (x_{il1} - \mu_{il1})w_{il1}(y_{il1} - \mu_{il1}) \\ & + (x_{il2} - \mu_{il2})w_{il2}(y_{il2} - \mu_{il2}) \\ & + (x_{il1} - \mu_{il1})u_{il}(y_{il2} - \mu_{il2}) \\ & + (x_{il2} - \mu_{il2})u_{il}(y_{il1} - \mu_{il1}) \end{aligned}$$

$$\begin{aligned} d_{il} = {} & (x_{il1} - \mu_{il1})w_{il1}(x_{il1} - \mu_{il1}) \\ & + (x_{il2} - \mu_{il2})w_{il2}(x_{il2} - \mu_{il2}) \\ & + (x_{il1} - \mu_{il1})u_{il}(x_{il2} - \mu_{il2}) \\ & + (x_{il2} - \mu_{il2})u_{il}(x_{il1} - \mu_{il1}) \end{aligned}$$

Then these are used to compute two summary statistics for each pair of rabbits, as follows, the summations being over $\underline{l}$:

$$N_i = \Sigma n_{il}$$

$$D_i = \Sigma d_{il}$$

For a single pair of rabbits, b (the estimate of β) and t^2 (the estimate of the sampling error of b) are obtained as:

$$b = N_i/D_i$$

$$t^2 = 1/D_i$$

For a set of rabbits, N_i and D_i are combined to produce four summary statistics, the summations being over $\underline{i}$:

$$N = \Sigma N_i$$

$$D = \Sigma D_i$$

$$S = \Sigma D_i^2$$

$$Q = \Sigma N_i^2 / D_i$$

Finally, these numbers are used to find b and s^2, the estimates of β and σ^2, and t^2, the estimate of the sampling variance of b, as follows:

$$b = ND^{-1}$$

$$s'^2 = [Q - bN - (I-1)]/[D - D^{-1}S]$$

$$s^2 = \max\{0, s'^2\}$$

$$t'^2 = D^{-1}(1 + [Q - bN - (I-1)]/[D^2S^{-1} - 1])$$

$$t^2 = D^{-1}(1 + [\max(0, Q - bN - (I - 1)]/[D^2S^{-1} - 1])$$

There is one set of these estimates for each value of ρ, the 'guessed' value of β. The next step is to form confidence intervals for each value of ρ. The estimates s'^2 and t'^2 are unbiassed when $\rho = \beta$, although it is preferable to use the s^2 and t^2 which have a smaller mean square error. Each value of β can be tested for rejection by using estimates for a range of values of ρ. A value is rejected if ρ lies outside the two standard error range.

APPENDIX III

Genotypes of rabbits

These are the genotypes of all of those rabbits successfully scored at at least one locus. Listed are the rabbit identities, their ages: Adult (A) or Juvenile (J), their capture-location, and the codes of the alleles present at each locus (Chapter 9), '9 9' signifies no score obtained at that locus. Females are underlined.

Walney
Areas North(N), South(S), East(E), West(W), Found dead (D).

Age	Area	No.	Car-2	Pgd	Ada	Est-1	Mpi	A	B	Trf
A	N W	2	2 2	2 2	2 2	1 2	9 9	3 3	1 2	f
A	N	3	1 2	2 2	1 2	1 1	9 9	2 3	1 2	f
A	N	4	1 2	2 2	1 2	1 1	1 2	1 3	2 2	9
A	S	5	1 1	2 2	1 2	1 1	2 2	3 3	2 2	f
A	N	6	2 2	2 2	1 2	1 1	1 2	1 3	2 2	f
A	N	7	2 2	2 2	2 2	1 1	1 2	2 2	1 2	f
A	N	8	1 2	2 2	2 2	1 1	9 9	2 3	1 2	f
A	N	9	1 2	9 9	9 9	1 1	9 9	1 3	2 2	9
A	E	10	1 2	9 9	9 9	1 2	9 9	2 2	1 2	s
A	E	11	1 2	9 9	9 9	1 1	9 9	3 3	2 2	9
A	E	12	1 2	1 1	2 2	2 2	1 2	3 3	2 2	f
A	W	13	1 2	1 2	1 2	1 1	2 2	1 2	2 2	f
A	W	14	2 2	9 9	2 2	1 1	9 9	3 3	2 2	9
A	W	15	1 2	1 2	1 2	1 2	9 9	3 3	1 2	9
A	S	17	2 2	9 9	9 9	1 1	9 9	3 3	1 2	s
A	S	21	1 1	9 9	9 9	1 1	9 9	1 3	2 2	f
A	S E	22	1 2	1 2	2 2	1 1	1 2	3 3	1 2	f
A	E	23	1 2	9 9	9 9	1 2	9 9	3 3	2 2	s
A	D	24	2 2	2 2	1 2	1 1	2 2	2 3	1 2	f
A	E	25	2 2	2 2	1 1	1 1	2 2	3 3	2 2	s
A	W	26	9 9	9 9	9 9	9 9	9 9	1 3	2 2	9
J	W	27	1 2	9 9	9 9	1 1	9 9	9 9	9 9	9
A	W	28	1 2	1 2	9 9	1 1	1 2	3 3	2 2	f
A	E	29	1 2	1 2	1 2	1 1	2 2	1 3	2 2	f
J	S	30	2 2	2 2	2 2	1 1	9 9	9 9	9 9	s
J	W	31	1 2	2 2	2 2	9 9	9 9	9 9	9 9	9
J	W	32	1 2	1 2	1 2	1 1	1 2	9 9	9 9	f
J	W	33	1 1	2 2	2 2	1 1	2 2	9 9	2 2	f
J	N	34	2 2	2 2	2 2	1 2	1 1	9 9	2 2	f
J	N	35	1 1	1 2	2 2	1 1	1 2	9 9	9 9	f
J	N	36	1 1	1 2	1 2	1 2	2 2	9 9	2 2	f

Age	Area	No.	Car-2	Pgd	Ada	Est-1	Mpi	A	B	Trf
J	W	37	2 2	2 2	1 2	1 1	9 9	9 9	9 9	s
J	N	38	1 2	1 2	2 2	1 2	2 2	9 9	9 9	f
J	S	39	1 2	2 2	1 1	1 1	2 2	3 3	2 2	f
J	W	40	1 2	2 2	1 2	1 1	2 2	3 3	2 2	f
J	W	41	1 2	2 2	2 2	1 2	2 2	9 9	1 2	f
J	W	42	2 2	1 2	2 2	9 9	9 9	9 9	9 9	9
J	E	43	1 2	2 2	2 2	1 1	2 2	3 3	9 9	f
J	W	44	1 2	2 2	2 2	1 1	9 9	9 9	2 2	9
J	E	45	1 1	2 2	1 2	1 1	2 2	9 9	9 9	9
J	N	46	1 1	2 2	1 2	2 2	1 2	3 3	2 2	f
A	N	47	1 2	2 2	1 2	1 1	2 2	1 2	1 2	f
J	S	48	1 2	2 2	1 2	1 1	2 2	3 3	2 2	f
J	W	49	1 1	1 2	2 2	1 2	2 2	9 9	9 9	f
J	W	50	2 2	2 2	2 2	1 2	2 2	1 3	1 1	f
J	N	51	1 2	2 2	2 2	1 1	2 2	9 9	9 9	9
J	E	52	1 2	2 2	1 2	1 1	1 2	2 3	1 2	f
J	E	53	2 2	1 2	1 2	1 1	2 2	1 3	1 2	f
J	S	54	1 1	2 2	2 2	1 2	2 2	3 3	2 2	f
J	N	55	2 2	2 2	2 2	1 1	2 2	3 3	2 2	f
A	N	56	1 2	1 2	2 2	2 2	2 2	1 3	2 2	f
A	W	57	1 2	2 2	2 2	1 1	2 2	3 3	2 2	f
J	W	58	2 2	1 2	1 2	1 1	2 2	9 9	2 2	f
J	E	59	1 2	2 2	2 2	1 1	1 2	2 3	2 2	f
A	W	60	1 2	2 2	1 2	1 1	1 2	1 3	1 2	f
J	N	61	1 2	2 2	1 1	1 2	1 1	3 3	2 2	f
J	N	62	1 2	2 2	2 2	1 1	1 2	3 3	2 2	f
A	W	63	2 2	2 2	1 2	1 1	1 2	1 2	2 2	f
J	N	64	1 2	1 1	2 2	1 2	2 2	3 3	2 2	f
J	E	65	1 1	2 2	2 2	1 1	2 2	9 9	9 9	s
J	N	66	1 1	2 2	1 2	1 1	2 2	3 3	2 2	f
J	S	67	1 1	2 2	2 2	1 1	1 2	3 3	2 2	f
J	N	68	1 2	2 2	1 2	1 2	2 2	1 3	2 2	f
J	S	69	1 2	1 2	1 2	1 1	2 2	1 3	2 2	f
J	N	70	2 2	2 2	2 2	1 2	1 2	2 3	2 2	f
A	E	71	1 2	1 2	1 1	1 1	2 2	1 3	2 2	f
J	E	72	1 2	1 2	2 2	1 2	2 2	3 3	2 2	f
J	E	73	1 1	1 2	1 2	1 1	2 2	1 3	1 2	f
J	S	74	1 2	2 2	1 2	1 1	2 2	3 3	2 2	f
J	S	75	1 2	2 2	1 1	1 2	2 2	3 3	1 2	f
J	N	76	1 2	1 2	2 2	1 2	1 2	2 3	2 2	f
J	S	77	1 1	9 9	1 1	9 9	2 2	1 3	2 2	f
J	N	78	1 2	1 1	2 2	1 1	2 2	2 3	2 2	f
J	N	79	1 1	1 2	2 2	1 1	2 2	9 9	2 2	f
J	N	101	1 1	1 2	2 2	1 1	9 9	2 2	2 2	f
J	N	102	1 2	1 2	1 2	2 2	1 2	3 3	2 2	f
J	N	103	1 2	2 2	1 1	1 1	9 9	9 9	2 2	f
J	E	104	2 2	2 2	1 2	1 1	2 2	2 3	2 2	f
J	S	105	1 1	2 2	2 2	1 1	2 2	1 3	1 2	f
A	N	106	2 2	2 2	1 2	2 2	1 2	3 3	2 2	f
J	N	107	1 1	1 2	2 2	1 1	2 2	3 3	2 2	f
J	N	108	1 2	2 2	1 2	1 1	1 2	2 3	1 2	f
J	S	109	1 2	2 2	2 2	1 1	2 2	1 3	2 2	f
J	W	110	1 2	2 2	2 2	1 2	1 2	3 3	1 2	f
J	S	111	1 2	2 2	2 2	1 1	2 2	3 3	2 2	f
J	N	112	1 1	1 2	1 2	2 2	1 2	1 3	2 2	f
J	S	113	1 2	1 2	2 2	1 1	2 2	3 3	1 2	f

Age	Area	No.	Car-2	Pgd	Ada	Est-1	Mpi	A	B	Trf
J	N	114	2 2	2 2	2 2	2 2	1 2	3 3	2 2	f
J	N	115	1 1	1 2	1 2	1 1	2 2	1 3	2 2	f
J	N	116	2 2	1 2	1 2	1 1	1 2	2 2	2 2	f
J	N	117	1 2	2 2	1 2	1 1	1 2	2 3	2 2	f
J	N	118	1 2	1 2	2 2	1 1	1 2	1 3	2 2	f
J	S	119	1 2	2 2	1 2	1 1	2 2	3 3	1 1	f
J	S	120	1 2	2 2	2 2	1 1	2 2	3 3	2 2	f
J	N	121	2 2	1 2	2 2	1 2	2 2	3 3	2 2	f
J	S	122	1 2	1 2	1 2	1 1	2 2	2 3	2 2	f
J	S	123	1 1	2 2	2 2	1 1	9 9	3 3	1 2	f
J	N	124	1 2	1 2	1 2	1 1	1 1	2 2	2 2	f
J	N	125	1 2	2 2	2 2	1 1	2 2	3 3	1 2	f
J	N	126	1 2	2 2	1 2	1 1	2 2	9 9	2 2	f
J	N	130	1 2	2 2	2 2	9 9	1 2	9 9	9 9	9
J	W	131	1 1	2 2	2 2	1 1	1 1	9 9	9 9	9

Oxford

Areas: Areas are labelled as in Fig 3.3. U=Upper fields, off the map. Pgd was invariant

Age	Area	No.	Car-2	Ada	Est-1	Mpi	A	B	Trf
A	E	1	2 2	1 1	1 1	2 2	1 2	1 3	f
A	E	4	1 2	1 3	1 1	2 2	9 9	9 9	s
A	B	9	1 1	1 1	2 2	1 1	1 2	2 2	f
A	B	10	1 2	1 3	1 1	1 1	1 1	2 2	f
A	E	11	1 1	1 3	2 2	1 1	1 1	1 1	9
A	B	12	1 2	1 3	1 1	1 2	1 1	2 2	f
A	B	13	1 1	1 3	1 1	1 2	1 1	2 3	9
A	C	14	1 1	1 1	1 1	1 2	1 2	1 1	f
A	C	15	1 2	1 2	1 1	2 2	2 3	1 3	f
A	D	16	1 1	1 3	1 1	2 2	1 3	1 3	f
A	U	17	1 1	1 3	1 2	1 2	1 1	1 1	9
A	U	18	1 1	1 3	1 2	9 9	1 2	1 2	9
A	U	19	1 1	1 3	1 1	2 2	1 2	1 2	9
A	E	20	1 2	2 3	1 1	2 2	1 3	2 3	f
A	E	21	1 2	3 3	1 1	2 2	1 1	2 2	9
A	E	22	1 2	1 2	1 1	9 9	1 3	3 3	s
A	B	23	1 2	2 3	1 1	1 2	1 2	1 2	9
A	B	24	1 2	1 3	1 2	1 2	1 2	2 2	f
A	F	25	1 1	1 3	1 2	9 9	1 2	2 2	9
A	F	26	1 1	1 2	1 1	1 2	1 2	2 3	s
A	U	27	1 1	1 1	2 2	2 2	1 1	1 3	s
A	F	28	1 1	1 2	2 2	1 1	9 9	9 9	s
A	F	29	2 2	1 3	1 1	2 2	1 2	2 2	f
A	F	30	1 1	2 3	1 2	1 2	1 1	3 3	f
A	C	31	1 1	1 1	1 1	1 2	1 3	1 3	s
A	B	32	1 1	1 1	1 2	9 9	1 2	3 3	9
A	B	33	2 2	1 3	1 1	1 2	9 9	9 9	f
J	C	38	1 1	1 2	1 1	1 2	1 3	1 1	s
J	B	40	1 1	3 3	2 2	1 2	1 1	1 2	9
J	B	41	1 2	1 3	1 2	1 2	1 1	1 2	9
J	B	42	1 2	1 1	1 2	2 2	1 3	2 3	9
J	B	43	1 2	1 1	1 1	1 2	1 1	2 3	f
A	E	47	1 1	3 3	1 2	9 9	9 9	9 9	9
A	E	48	1 1	3 3	1 1	1 2	9 9	9 9	9
J	B	49	1 2	1 3	1 1	9 9	9 9	9 9	9
A	C	50	1 2	1 1	1 1	2 2	9 9	1 2	9
A	C	51	1 2	1 3	1 1	1 2	9 9	9 9	f
A	B	52	1 2	1 3	1 1	1 2	9 9	9 9	f
A	E	53	2 2	2 3	1 1	1 2	9 9	9 9	f
A	E	54	1 2	1 2	1 1	9 9	9 9	9 9	9
J	E	55	1 2	2 3	1 1	1 2	9 9	9 9	s
J	E	56	1 2	3 3	1 1	2 2	9 9	9 9	f
J	E	57	1 2	3 3	1 1	1 2	9 9	9 9	f
A	F	58	1 2	2 3	1 1	1 2	9 9	9 9	9
A	F	59	1 2	1 1	2 2	2 2	9 9	9 9	9
A	F	60	1 2	2 3	2 2	9 9	9 9	9 9	f
J	B	61	1 1	1 3	1 2	1 2	9 9	9 9	f
A	B	300	1 2	1 3	2 2	1 2	1 1	1 3	f
A	B	301	1 1	1 3	1 2	1 2	1 2	1 3	f
A	U	302	1 1	3 3	1 1	1 1	1 1	1 2	f
A	U	303	1 1	1 3	2 2	9 9	1 3	1 2	f

Age	Area	No.	Car-2	Ada	Est-1	Mpi	A	B	Trf
A	U	304	1 1	2 3	1 2	9 9	1 3	1 2	f
A	U	305	1 1	2 3	1 2	1 1	3 3	2 3	f
A	U	306	1 2	1 2	1 2	9 9	1 3	1 3	f
A	U	307	1 1	1 1	2 2	9 9	1 1	1 2	f
A	U	308	1 1	1 3	1 2	1 1	1 2	1 3	f
A	U	309	1 2	1 3	1 1	9 9	1 2	2 3	f

Berkshire

Pgd invariant. Mpi, A, and B not tested. Sexes and locations of rabbits unknown.

No.	Car-2	Ada	Est-1	Trf
1	1 1	2 2	1 2	f
2	1 2	1 2	1 1	f
3	1 1	1 3	1 1	f
5	1 1	2 2	1 1	f
6	1 1	1 2	1 2	s
8	1 1	1 2	1 1	s
9	1 1	2 2	1 1	s
10	1 1	2 2	1 1	s
11	1 1	2 3	1 1	f
13	1 2	2 2	1 1	s
14	1 2	1 3	1 1	s
16	1 2	1 2	1 2	s
17	1 1	1 2	1 1	9
19	2 2	2 2	1 2	f
20	1 2	2 2	1 2	f
21	1 2	2 2	1 2	s
22	1 1	2 2	1 2	f
23	1 1	1 3	1 1	s
24	1 2	2 3	1 2	f
25	1 1	2 2	1 2	s
26	1 2	2 2	1 2	f
27	1 1	1 2	2 2	s
28	1 2	1 2	1 1	f
30	1 1	2 2	1 2	f
32	1 1	2 2	1 1	f
33	1 1	2 3	1 1	s
34	1 2	3 3	1 1	s
35	1 1	3 3	1 2	s
36	1 2	2 3	1 2	s