STATUS AND ECOLOGY OF THE PRIOLO OR AZORES BULLFINCH, *PYRRHULA MURINA*

BY

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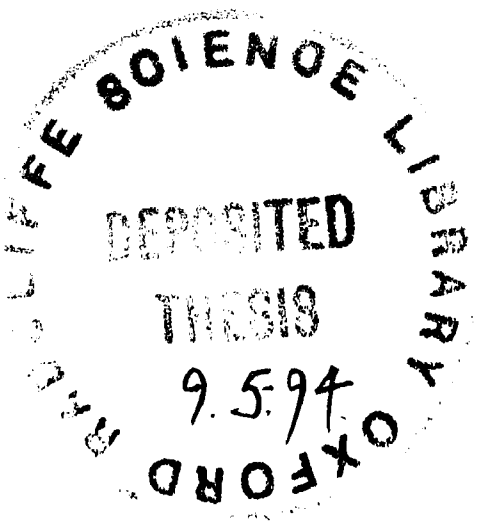

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Status and Ecology of the Priolo or Azores bullfinch, *Pyrrhula murina*.

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ABSTRACT

I studied the seasonal variation in habitat selection, diet, food supply and food selection of the Priolo or Azores bullfinch, *Pyrrhula murina*. This species and its associated habitat, the Azorean native cloud forest, are poorly known and are threatened by afforestation and the invasion of exotic flora. In addition detailed studies of these aspects are lacking for oceanic island birds. Throughout this study a comparison between the ecology of the Priolo and that of mainland Bullfinches is made. The primary aims of this study were (1) to evaluate the importance of three alternative hypotheses in explaining the present distribution and abundance of this bird: habitat structure and composition, food availability and food preference, and (2) propose management strategies.

Point-counts and capture-recapture indicate a population of 60 to 200 pairs. The bird breeds from mid-June to late August. Annual mortality was in the order of 45-50%.

Stations were marked every 200 m along tracks covering all vegetation types in the area. These were walked three times a month to record presence or absence of birds per habitat type. The habitat structure and vegetation composition were recorded at these stations and used to explain the number of times a bird was detected at stations using logistic modelling. Diet was assessed from observations of feeding birds and faecal analysis. Food supply was examined from quadrats placed systematically within foraging habitats and from marked plots of winter food stocks. Food preferences were examined by comparing (a) availability and usage of foods in the field, (b) selected and rejected food items and (c) using food choice trials with captive birds. The importance of seed phenolics in explaining patterns of preferences for species and individual trees in winter was examined.

The distribution of the Priolo was highly associated with native vegetation and its margins all year round. Other habitats were of marginal importance.The precision of habitat selectivity increased in the following direction: summer<autumn<winter.

The diet ranged from invertebrates and herbaceous seeds in summer, to seeds of fleshy fruits in autumn, fern sporangia and tree seeds (of *Clethra arborea*) in winter and, flower buds, fern fronds and moss tips in spring. Introduced species were very important in the diet but in August/September and in April native species were significantly more important. In April, birds were highly dependent on flower buds of *Ilex perado*. At this time, the abundance of seeds and sporangia was at its lowest. An experiment with enclosures showed that the Priolo foraging pressure significantly reduced the number of flower buds.

Food preferences changed throughout the year and seemed a complex function of availability, size, palatability and accessibility of foods. Seeds of fleshy fruits were preferred to those of *C. arborea*. Seeds of *C. arborea* were ignored when flower buds reached a length of 2.8-3.0 mm. In autumn, *C. arborea* was preferred to sporangia of large ferns, but in spring the birds showed the opposite behaviour. Priolos also showed preference for larger items of most winter foods. Phenolic compounds did not explain *C. arborea* tree preference nor why birds switched from seeds to flower buds in spring. Within a small resource spectrum birds should be less discriminating and energy may be the most important factor in food selection.

Overall, the data suggested that a food supply hypothesis was better in explaining patterns of Priolo distribution and abundance than a habitat structure hypothesis but food preference is important for a full understanding of this question. A shortage of preferred foods may occur in late winter. Other available foods may be inadequate. Some implications for the limitation of this population are discussed. The Priolo needs the several mosaics of the native forest to complete its annual cycle. Nowadays, the mature forest mosaic seems to be the least abundant. In terms of conservation it is necessary to control the expansion of exotic plants and, restore and enlarge the area of native forest. It seems especially important to increase the population of flower-bud producing species.

CONTENTS

CHAPTER 1
INTRODUCTION

1.1 About the study of island birds

The study of oceanic island birds has been crucial to the development of evolutionary (e. g. Darwin, 1971; Lack, 1947) and ecological thought (e. g. MacArthur & Wilson, 1967). More specifically, the evaluation of patterns of bird distribution and abundance on islands has strongly influenced most theories of animal distribution (e. g. MacArthur, 1972) and life history (reviewed in Stearns, 1992). Islands usually have relatively low biodiversity but are important sources of speciation. The number of species on islands may be viewed as a function of area, distance from the mainland and a balance between immigration and extinction (MacArthur & Wilson, 1967). Ecological comparisons of insular bird populations with mainland counterparts have revealed that island birds generally occupy broader ecological niches (e.g. MacArthur *et al*, 1972; Diamond, 1975; Cox & Richlefs, 1977; Williamson, 1981; Blondel *et al*, 1988), produce fewer offspring (Lack, 1954) and may have denser populations (Crowell, 1962; Grant, 1965; Blondel *et al*, 1988; Schluter & Repasky, 1990). These differences arise because resource diversity, possible competitors and predators are expected to influence populations differently on islands and main-land masses. Populations of competitors and predators are often lower or even absent on islands.

However, and, despite the long running interest of ornithologists on island birds, very few studies have documented detailed seasonal variations on habitat selection, diet, food selection and annual cycle of oceanic island birds (but see review in Grant & Grant, 1986 for detailed studies on Galapagos finches by Grant and co-workers). In this study, I provide a description and interpretation of these aspects in relation to the Priolo or Azores (or S. Miguel) bullfinch, *Pyrrhula murina*. These data are important to assess patterns of island birds, notably the dynamics of variation in behaviour and in the use of resources. It

may also allow important insights into the processes of niche expansion on insular environments.

The insular isolation that leads to the evolution of endemic taxa also produces vulnerability and high extinction rate. Island birds are very vulnerable to predation by alien predators and find difficult to cope with the deterioration of habitats through the combined onslaught of competition between native flora and aggressive introduced exotic vegetation, browsing by introduced herbivores and increased rate of utilisation of the vegetation by humans (Moors, 1985 and references herein). For instance, Olson & James (1982) showed that at least 40 species of birds disappeared as a result of habitat destruction in Hawaii before Europeans arrived. On high islands the native vegetation at lower altitudes is usually the first to be destroyed. This may prevent birds from normal patterns of movements (Kepler & Scott, 1985; Wilcove *et al*, 1986; Loiselle & Blake, 1991), reduce rates of gene flow between or within populations (Kepler & Scott, 1985; Wilcove *et al*, 1986) and deny them essential resources (Diamond, 1982). What follows is that density may decline even in the remaining pristine habitat fragments, especially if populations depend on part on same resources beyond the borders of the fragments (Kepler & Scott, 1985).

Following colonisation in the XV century the lowland native plant communities of S. Miguel island have almost vanished and the highland native forests have been destroyed and are now fragmented (Sjogren, 1973; Haggar *et al*, 1989; pers. observations). Several exotic plants have been introduced and are now widespread (see section 1.3 below). The total Priolo population is about 100 pairs and is largely restricted to highland native vegetation (Bibby & Charlton, 1991). A detailed autoecological study of this species is thus crucial for its conservation.

1.2 The Priolo or Azores bullfinch: comparison with other bullfinches

The genus *Pyrrhula* is a genus of seven species with an Oriental and Palearctic range, comprises forest-dwelling birds with a predominantly Asiatic distribution (Newton, 1972). According to Voous (1949) its centre of origin and dispersal is situated in southeast Asia.

The Bullfinch, *Pyrrhula pyrrhula*, the only European representative of the genus, occurs throughout temperate and Northern Europe from the Iberian Peninsula, Ireland and Scandinavia to Manchuria, northern China and Japan. Eight subspecies of Eurasian bullfinches, differing in size and plumage coloration, have been described (Goodwin, 1985). In general, the birds become larger and brighter from west to east and from south to north of the range and towards the top of the mountains (Voous, 1949). All northern and western European subspecies are sexually dimorphic: adult males are readily distinguished from adult females by having a reddish breast.

The Priolo should be derived from *Pyrrhula pyrrhula* or some form ancestral to them both, since this is the only European species in the genus. The Priolo (Fig. 1) has five well marked morphological differences from its closest southern European counterparts: (1) it is larger (Table 1); (2) its wing-bar is much greyer; (3) it lacks the white rump; (4) the under tail coverts are brown instead of white and (4) the sexual differences in colour are very slight and insufficient to be able to sex all specimens (see Chapter 5).

Table 1. Wing length: comparison between bullfinches in different European regions.

Region	Male			Female			
	n	Range (mm)	Mean (mm)	n	Range (mm)	Mean (mm)	Reference
N-E Europe- *pyrrhula*	11	89 - 95	91.0	6	87 - 93	89.6	Voous (1949)
Germany- *europoea*	9	88 - 92	90.0	5	85 - 90	87.4	Voous (1949)
S-E Europe- *rossikowi*	11	86 - 92	89.1	2	86 - 87	86.6	Voous (1949)
England- *pileata*	46	79 - 86	83.3	44	78 - 86	82.8	Newton (1966a)
Spain- *iberiae*	20	79 - 84	80.6	20	76 - 81	78.4	Noval (1971)
S. Miguel- *murina*	22	86 - 93	90.0	28	85 - 92	88.7	This study

Fig. 1. The Priolo or Azores (or São Miguel) bullfinch, *Pyrrhula murina*.

Fig. 2. The Azores archipelago in relation to other North Atlantic islands. The island of São Miguel is the only island where the Priolo occurs.

In order to establish the insular characteristics of the Priolo I will assume that bullfinches in S. Miguel were originally derived from the closest mainland ones, those on the Iberian Peninsula. I measured the wing length, bill length, bill depth and tarsus length of 16 specimens of Priolo which are held in Ponta Delgada and in the British Museum (Natural History at Tring). I compared these measures with similar ones for 13 Bullfinches from Northern Portugal and Northern Spain also in the BM (NH). These measurements were entered in a Principal Component Analysis (PCA) to investigate if separation of the two forms was possible using only external morphology.

The first PCA axis explained 91% of the variation and presented high loadings for all measurements (from -0.49 to -0.51). It representes a size axis, which is clearly sufficient to separate the Priolo from Iberian birds (Fig. 3). The second PCA axis explained 4% of the variation and presented a high negative loading for tarsus (-0.70) and a high positive loading for bill depth (0.71). It indicates that the Priolo differs from Iberian birds mainly by having longer tarsus and broader bills. The plot also revealed no clear separation of the sexes in either group, indicating that sexual dimorphism is not important in explaining the observed variation in external morphometrics.

There was clear separation of the two groups on the basis of only a single measurement. Compared with Bullfinches in the Iberian Peninsula, Priolos have long wings, legs and beaks. Beak depth, beak length and tarsus are substantially larger, 22 to 28%, whereas wing length is only 10-11% larger (Table 2). Data from table 2 seems to show that an increase in beak and tarsus size has been more marked than an increase in wing length. Some of the morphological change on S. Miguel can be attributed to allometric consequences of body size change. However, this would not be sufficient by itself to account for the increase in the measured morphological characteristics (see Grant, 1979a).

Genetical differences between bullfinches were also investigated by Dr. Robert Dawson at Nottingham University. A 299 base pair of the cytochrome-b gene (cyt b) of

mitochondrial DNA (mt DNA) was sequenced for four *pileata* (England), one *pyrrhula* (Fair Isle) and five *murina* (São Miguel). The fragment covered the positions 96 to 395. The results showed two fixed transitions (purine/purine and pyrimidine/pyrimidine) substitutions. At position 189 all five *murina* had a T whereas all *pileata* and *pyrrhula* had a C, and at position 243 a similar substitution from a C to a T occurred. These results are preliminary and some of the individuals may be closely related. In addition, mt DNA analysis of *iberiae* birds is needed. However, there appears to be two fixed substitutions separating *murina* from both *pileata* and *pyrrhula* and these differences were consistent among individuals.

Because of its morphological differences, several authors, most recently Goodwin (1985) and Knox (1989), argued that the Priolo should be treated as a full species; but have not provided detailed supporting evidence. Movements of 800 km have been recorded for Iberian birds (Noval, 1971) but, as S. Miguel lies about 1500 km away, regular interchange between the mainland and S. Miguel is most unlikely. Therefore, at present, discussion of the taxonomic status of the Priolo should hinge on the extent of its morphological separation from the mainland Bullfinch, and also on the preliminary results of the mt DNA analysis. These brief analyses supports the fact that the Priolo is morphologically and molecularly distinct from the mainland bullfinches and thus should be regarded as a true species. In fact, the substantial differences between the Priolo and its mainland relatives point out to effective, and presumably long (but see Mayr, 1942 & 1963 about founder effect models), genetic isolation of the former.

Larger size has been documented for many island forms (e.g. the Wren, *Troglodytes troglodytes*, Armstrong, 1955; see reviews in Abbott, 1980 and Williamson, 1981). Other Atlantic passerines, Blue Tit, *Parus caeruleus*, in the Canaries (Grant,1979) and Chaffinch, *Fringilla coelebs*, in the Canaries, Madeira and Azores (Grant, 1979a) have also evolved to large size, except for wings, in comparison to their mainland relatives. Grant presents possible explanations for these evolutionary patterns, which may also apply

to the Priolo. Essentially, larger beaks would be selectively advantageous under conditions of low food diversity and the need to generalize diets. Greater tarsus length would be selected for by the pattern of distribution of food requiring greater bipedal locomotion on thick branches and on the ground, and also to support a heavier body. Lowered predation and competition might also lead to a large size (Williamson, 1981).

Grant (1979a) argued that the relatively shorter wings of Atlantic blue tits and chaffinches may reflect greater sedentariness. The fact that the Priolo wings are larger than those of mainland Bullfinches may reflect either: (a) detailed aspects of its ecology (i. e. high mobility) or (b) a relatively recent colonization of S. Miguel. The second explanation is the least likely because other morphometrics are substantially different from those of mainland bulllfinches (Table 2).

1.3 The study area and historical information

The Azores (Fig. 2) comprise nine main islands lying in mid Atlantic (36-39^{o}N, 25-31^{o}W), subject to a temperate oceanic climate (Medeiros, 1987). The precipitation is about 1000 mm annually at sea level, increasing by 25% for every 100 m increase in altitude (Sjogren, 1984). The Azorean native cloud forests are, together with those of Madeira and the Canaries, considered remnants of the old Tertiary forests that once covered Southern Europe (Tutin, 1953). Altogether 56 plant taxa are endemic, of which 35 are restricted to the cloud forests (Palhinha, 1966; Sjogren, 1984). For plant taxonomy see Palhinha (1966). For a general description of most species see Sjogren (1984).

The Priolo occurs only in the eastern part of the island of São Miguel, in the Oriental group of the archipelago. I have sampled in and around the entire area of native forest to ascertain its range but concentrated most of my other observations on the area around Pico da Vara summit (see Figs. 1 & 2 in Chaper 2). My observations ranged from 100 to about 870 m; native forests were present above 400-500 m (Fig 4).

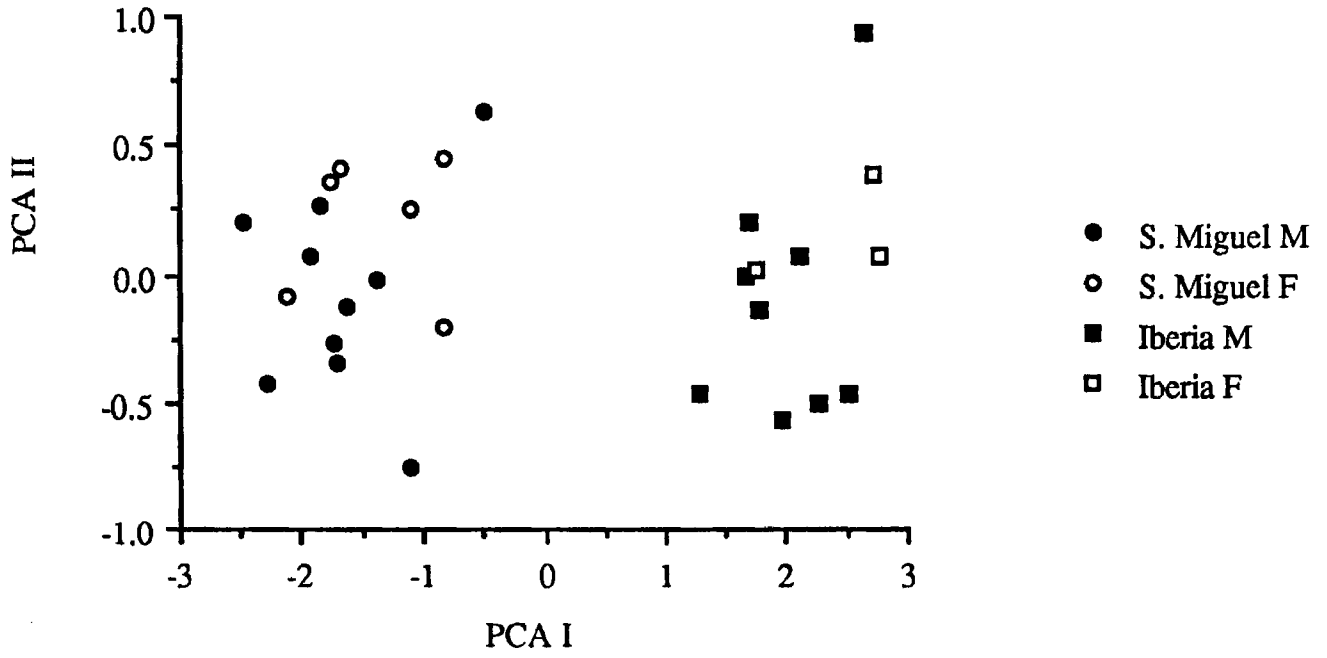


Fig. 3. Bivariate plot locating all the individuals measured in the first and second Principal components. There was a clear separation between the Priolo and Iberian birds just on PCA I.

Table 2. Bullfinch biometrics: comparison between birds (museum specimens) from S. Miguel (SM) and Iberian Peninsula (I).

Males

		n	Range	Mean	SD	% difference	T-test
Wing	SM	10	85.0 - 88.0	86.7	0.98	+9.6	11.25***
	I	10	76.0 - 82.0	79.1	1.92		
Bill l	SM	10	11.5 - 13.0	12.4	0.47	+21.6	10.14***
	I	10	9.5 - 11.0	10.2	0.50		
Bill D	SM	10	9.3 - 11.0	10.2	0.49	+27.8	11.0***
	I	9	7.4 - 8.5	7.9	0.36		
Tarsus	SM	10	18.1 - 22.0	21.1	1.18	+24.1	8.24***
	I	10	15.0 - 18.2	17.0	1.01		

*** P<0.001

Females

		n	Range	Mean	SD	% difference	T-test
Wing	SM	6	83.0 - 87	85.5	1.36	+11.3	12.84***
	I	3	75 - 80	76.8	2.48		
Bill l	SM	6	11.5 - 12.5	12.1	0.38	+22.2	11.00***
	I	3	9.5 - 10	9.9	0.12		
Bill D	SM	6	9.7 - 10.8	10.3	0.38	+25.6	5.65**
	I	3	8.0 - 8.4	8.2	0.21		
Tarsus	SM	6	19.7 - 22.1	20.7	0.79	+23.2	6.85**
	I	3	16.0 - 17.6	16.8	0.80		

*** P<0.001 ** P<0.01

Native vegetation in the east of São Miguel has been cleared for pasture and afforested mainly with *Cryptomeria japonica* (see Fig. 1 in Chapter 2). In addition, the recently introduced aggressive exotic plants, *Pittosporum undulatum*, *Hedychium gardneranum* and *Clethra arborea* are resulting in major changes to the remaining fragments (Sjogren, 1973; LeGrand, 1982; Haggar *et al*, 1989; pers. observations). *P. undulatum* is now largely naturalized and dominates the vegetation around streams below 400 m (Sjogren, 1984).

The Priolo was first described by Godman (1866), who found it confined to mountainous areas. However, in the last century the bird was, at least temporarily, locally abundant in lowland areas, being reported as a pest in orange orchards around Furnas crater lake (see Fig. 2 on Chapter 2) and easily collected for museum specimens (Hartert & Ogilvie-Grant, 1905; Bannerman & Bannerman, 1966). After the last collection of specimens in 1927 the bird was not officially recorded until the late 1970's, when LeGrand (1982) reported a population in the native vegetation around Pico da Vara summit (see Fig. 2 in Chapter 2).

Land use and history of the distribution of endemic vegetation seems to be connected with historical patterns of distribution and abundance of Priolo (Table 3). In Furnas, Priolos appeared to have been common when orange production was high, as it was easily collected for museum specimens (Godman, 1866; Bannerman & Bannerman, 1966) and shot in orange orchards because of its habit of feeding on orange buds (Agricultor Micaelense, 1843, 1848). At the end of the last century a disease destroyed the orange trees (Costa, 1978) and the birds became barely known in Furnas thereafter (Chavigny & Mayaud, 1932). Nowadays, a few orange orchards are still present but they are far from the endemic vegetation and from forest cover, in general; the Priolos seem not to visit them.

In the 1960's, peach orchards existed above Monte Simplicio and Nordeste. Local people remember the bird feeding on peach buds, a fact also mentioned in local newspapers

(Açores, 1970), although Bannerman & Bannerman (1966) did not find any Priolos in two visits there in 1965 and 1966.

The marked decrease in orchards, combined with the increase in forest clearance, pasture land, plantations of *C. japonica* and *P. undulatum* copses probably meant that lowland areas became progressively unsuitable for bullfinches. Upland forests, where the bird may still have been common, remained largely unobserved due to the difficult terrain.

Bibby & Charlton (1991) and Bibby *et al* (1992) found the bird to be mainly restricted to the largest fragment of native vegetation around Pico da Vara summit and estimated the total population size at about one hundred pairs. Females with brood patches were caught from June to August and birds were seen feeding on a wide range of seeds. Apart from these observations and some fragmented historical records (Table 3) no other information exists on the species.

The largest remnant of endemic vegetation, centred on Pico da Vara, seems to have not only a higher density but also diversity of native vegetation. Birds were observed in this area from May until September, but only in September were Priolos observed in the other main fragment of native vegetation above Furnas (Bibby & Charlton, 1991, Bibby *et al*, 1992). An assessment of the impact of exotic plants upon Priolo occurrence is therefore of major conservation importance. In ecological terms, information on population size, distribution in relation to habitat features, diet and food resources are parameters of chief importance.

Fig. 4. The study area in eastern S. Miguel island. The first picture shows the main area of native vegetation around Pico da Vara summit (1105 m, the highest point). This area is surrounded by plantations of *Cryptomeria japonica*, visible in the foreground. Note also the landslips, caused by a storm in September 1986. The second picture shows the view to the north-east. In the foreground, is a patch of native vegetation with *Clethra arborea* (the highest trees). In the background, are plantations of *Cryptomeria japonica* (on the slopes) and copses of *Pittosporun undulatum* (along the main valley).

Table 3. General information about patterns of distribution and abundance of Priolos in a historical context. Statements above the date refer to vegetation changes and below the date to Priolos distribution and abundance. For location of places see Fig. 2 on Chapter 2.

. Orange production reached its peak around 1880-1890 (Costa, 1978). . Endemic vegetation, *Erica azorica*, *Vaccinium cylindraceum* and *Rubus* sp seemed common around Furnas (Bullar & Bullar, 1849).	. Disease destroyed orange orchards early this century (Costa , 1978). . Increase in pasture land (Costa, 1978).
1843-1880	**1881-1930**
. "Harmful birds" feeding on flower buds of orange trees (Agricultor Micaelense, 1843, 1848). . Priolo considered common around Furnas (Godman, 1866).	. Very scarce around Furnas (Hartert & Ogilvie-Grant, 1905; Chavigny & Mayaud, 1932). . Collected in hills around Furnas (Murphy & Chapin, 1929). . Austrian collecter captured 53 birds in 60 days on Spring 1907 (Bannerman & Bannerman, 1966). . Some birds were captured in Furnas by José Correia for the American Museum of Natural History on the 11th and 15th of November 1927 (Bannerman & Bannerman, 1966). . Shot because of its ravages upon orchards (Chaves, 1923). . Seen and captured above Monte Simplicio in 1921 (Botelho, pers. comm.)
. Begining of extensive plantations of *Cryptomeria japonica* around Pico da Vara (Fagundo, pers. comm.). . Increase in pasture land and copses of *Pittosporum undulatum* (Costa, 1978; Fagundo, pers. comm.).	. Further increase in *Cryptomeria japonica* plantations (Fagundo, pers. comm.). . Spread of introduced species, *Hedychium gardneranum*, *Clethra arborea* and *Pittosporum undulatum* (Bannerman & Bannerman, 1966). . Peach and pear orchards above Monte Simplicio and Nordeste.
1931-1960	**1961-1992**
. Not seen by Herr Scheer in 1953/54 on the mountain slopes behind Furnas (Bannerman & Bannerman, 1966). . Seen by foresters and workers during afforestation in the 1950's and 1960's in the hills above Nordeste (Salvador & Others, pers. comm.)	. Seen feeding on peach and pear orchards above Monte Simplicio and Nordeste (Chaves, 1964; Açores, 1970; Mendonça and Others, pers. comm.). . One bird was captured in Furnas (Correio dos Açores, 1971). . Population estimated at 30-40 pairs (LeGrand, 1983). . Population estimated at 100 pairs (Bibby & Charlton, 1991). . Not reported at low altitudes. Largely restricted to native vegetation around Pico da Vara (Bibby & Charlton, 1991) but juveniles seen above Furnas (Bibby *et al*, 1992).

1.4 Aims of this study

This study was designed to evaluate the factors that are likely to explain the present distribution and abundance of the Priolo. Special attention was paid to seasonal variations in habitat selection, diet and food selection because resource-use behaviour tends to be plastic and may vary considerably among seasons and years (Szaro *et al*, 1990). Wiens *et al* (1987) stressed the importance of changes in food availability to assess dynamics of variation in behaviour.

On the mainland, Bullfinches are seed predators (Newton,1967; Snow & Snow, 1988) and have been quite well studied. Seeds from a wide range of plants are taken throughout the year but, in winter and spring, as the supply of seeds diminishes, flower buds form an increasing proportion of the diet. This pattern has been observed in Britain (Newton, 1967) and across continental Europe (Erkamo, 1948; Geroudet, 1964; Maheo, 1965 and Noval, 1971) though all the observations from Continental Europe are qualitative and fragmented. If seeds are available bullfinches take buds in quantity only in spring (Newton, 1964) when they became larger (Greig-Smith *et al*, 1983). Compared with seeds, buds are a poor source of protein, fat and carbohydrates (Summers & Jones, 1976; Summers, 1982; Greig-Smith *et al*, 1983; Matthews, 1983). Early research showed that, if buds are too small, Bullfinches cannot maintain themselves solely on buds. This was specially marked in those years in which seed stocks were depleted in early winter (Newton, 1964, Summers, 1981). Later research showed that the full picture is more complex since physical features, nutrients, behavioural costs of feeding and plant secondary compounds are all likely to influence the birds selection mechanism (Matthews, 1983; Greig-Smith & Wilson, 1985; Greig-Smith & Crocker, 1986; Crocker, 1987). Moroever, energy and nutrient content of seeds may vary between years and individual plants (Matthews, 1983). This later research on the feeding ecology of bullfinches was important in showing that an apparent supply of seeds in mid-winter does not necessarily mean that birds have an adequate food supply. Available seeds may be of low quality.

In view of these studies and brief observations on the Priolo (see above) three possible hypothesis were considered:

1) Habitat structure. This hypothesis views Priolo patterns as a result of vegetation structure and composition.

2) Food availability. This hypothesis argues that Priolo patterns are largely a result of variation in the availability of foods.

3) Food preference. This hypothesis presupposes a role for food availability but suggests that preferred foods play a key role in explaining bird distribution and abundance. If these resources are limiting, Priolo abundance should decline over the period of shortage of preferred foods, though other foods may be widely available. It is implicit in this idea that survival is correlated with the intake of preferred (better quality) foods.

The importance of my study is three-fold. Firstly, general information on the Priolo is of considerable interest in itself because this species and its associated habitat, the Azorean native cloud forests, are poorly known. Secondly, the focus on habitat, feeding resources and selection of foods enables me to explore differences in the feeding ecology of bullfinches that have evolved on a continent and on a small isolated island. Thirdly, I will provide essential information about habitat requirements to assist the future conservation of this bird. Habitat requirements were investigated using variables at two different scales: (1) large-scale variables: vegetation structure and composition, are important in determining the distribution and occurrence of the species and act as proximate factors in habitat selection and (2) micro-scale variables: diet, distribution of feeding resources and food preferences enabling identification of the unique features of the habitat that allow the survival of the species in the area. This is important to assess optimal versus sub-optimal habitat areas.

This thesis has two purposes: (a) investigate the habitat selection, diet, food selection and annual cycle of the Priolo in order to evaluate factors that may explain present distribution and numbers of the Priolo and (b) propose managment strategies.

CHAPTER 2
STATUS, DISTRIBUTION AND HABITAT SELECTION

2.1 INTRODUCTION

A knowledge of the distribution, population size and structure, and habitat selection of endangered species is crucial for their conservation. The study of seasonal variations in habitat selection may reveal which factors are likely to limit population size (Rice *et al*, 1983; Scott *et al*, 1984; Wiens, 1989).

Following the seminal work of MacArthur and co-workers on relationships between avian species and foliage profiles (MacArthur & MacArthur, 1961; MacArthur *et al*, 1962) many ecologists have found that the distribution and abundance of bird species is associated with aspects of habitat structure. Subsequent studies have shown that it is the composition of the vegetation rather than the structure that is often more important in avian choice, especially when investigating individual species rather than communities (Holmes & Robinson, 1981; Rotenberry & Wiens, 1980; Anderson *et al*, 1983; Wiens, 1989). Clearly, different plant species will provide different nesting sites and, more important, will contain different feeding opportunities. Ultimately, only a thorough knowledge of the natural history of the species will determine which habitat components are important to that particular species. To elucidate further the causal link between a species and its habitat, it is necessary to examine habitat responses in habitats that differ in particular ways (Holmes, 1981).

The range of the Priolo is very restricted and seems to have been contracting since last century (Bibby & Charlton, 1991; Bibby *et al*, 1992). In this chapter I determined its status and examined seasonal variations in distribution and habitat selection to support its conservation.

Priolo habitat selection is examined at two scale levels: broad and local. On the broad scale I used general habitat types and examined seasonal variations in Priolo density per habitat type. At the local scale I used vegetation structure and composition variables measured at stations across the study area. The aim was to identify vegetation

characteristics in order to reveal patterns of distribution and abundance. Thus, variables reflecting all the vegetation types present in the range of the Priolo were measured. Also, the composition and size structure of the native forest was examined in detail and a comparison was made between areas where birds were present throughout the year and areas where they occurred only at certain seasons. A broad scale is more appropriate to examine the influence of varying environmental conditions whereas a local scale is more appropriate to examine selective pressures affecting individuals (Anderson *et al*, 1983).

Specific floristic measures, such as seed density, would constitute another level of habitat selection. These will be evaluated in chapter 3. This section deals with variables that are general, and quick and easy to measure. To a certain extent they can reflect the importance of detailed floristic measures and, much more importantly, will offer predictive power and conservation interest. Notably, I needed to know the habitat responses of Priolo to native and exotic forests, habitat structure, and to other habitat features such as landslides and openings (bare ground), altitude and canopy height.

Overall, the results will allow me to evaluate the importance of habitat both structure and composition in explaining Priolo's distribution and abundance. This hypothesis argues for links between the distribution and abundance of Priolos and structural features of the habitat. The importance of a food supply hypothesis in explaining these ecological aspects of the Priolo will be evaluated in the next chapter.

2.2 METHODS

2.2.1 Numbers

2.2.1.1 Distribution

A vegetation map of the entire known range of the Priolo was prepared at 1: 25 000 scale (Fig. 1). Vegetation types were initially interpreted on aerial photographs (from 1981) at a 1: 9 000 to 1: 15 000 scale and then verified on the ground. Steep ground areas were verified using binoculars from well situated points.

Random transects were not possible as the habitat was very inaccessible. Instead, 22 routes were established along walkable tracks covering the entire known range of the Priolo (Fig. 2). To ascertain range and bird density, 8x1 minute point counts were made every 200 m, starting 2 minutes after arrival at the point (1 minute rest and 1 minute imitating [FN] the piping call). All passerine species were recorded. Birds were counted as within on or beyond 30 m of station at first detection. Eight minute counts were not made at regular intervals, but most routes were walked in April/May, August/September and December/January (Table 1). Stations with birds were plotted on a map showing the area of Laurel forest and altitudinal contours.

2.2.1.2 Mobility

All netted Priolos were ringed with a combination of coloured rings so as to be individually recognisable in the field. All captures and sightings were recorded and 1:25 000 maps were made of the occurrence of individual birds. As part of a concentrated effort to identify and detect movements of individual birds, the same colour combination was used on both legs and favourable sites were visited opportunistically up to five times a week.

The analysis of the rates of capture of ringed and unringed birds and distances moved from capture site were used in a first description of the mobility of this population. Afterwards, movement data of individual birds were divided into two seasons for a more detailed analysis: Summer (Jun-Sep) and Winter (Jan-Apr). Sightings of colour-ringed birds in May and Autumn (Oct-Dec) were too few to use in further analysis. The mobility of individual Priolo on Summer and Winter ranges was measured by the distance between consecutive locations. A Mann-Whitney test and a Wilcoxon's test for matched-pairs were

FN Some birds responded to the piping call and approached the station. This may lead to an overestimate of the population density (Bibby *et al*, 1992). However, because bullfinches are non-territorial and typically unobtrusive (Greig-smith & Wilson, 1984) and the vegetation was very dense, the piping call was used to ensure that birds were detected (Johnson et al, 1981).

used to test the null hypothesis that the median distance between consecutive locations of individual birds was equal in both seasons.

Home ranges were calculated using the formula R (radius)=($\sqrt{\sum x_i^2/n}$), where x_i are intercatch distances and n the number of recaptures (Taylor, 1966; Fery, Frochot & Leruth, 1981). This is simply meant to convey an idea of possible home ranges. More preferable methods are available (White & Garrott, 1990) but larger sample sizes would be required.

2.2.1.3 Population size

Two different techniques were used to estimate the population size: (1) the variable circular plot method and (2) the capture-mark-recapture.

(1) The variable circular plot method was developed by Reynolds *et al* (1980) to estimate bird densities in rugged terrain. Given some assumptions (see Buckland, 1987), knowledge of the numbers of birds detected inside and beyond 30 m allows relative density estimates (D) by assuming an exponential relationship between detectability and distance.

$$D=\ln (n/n_1).n/m.\pi.r^2$$

where n=total number of birds detected, n1=number of birds outside the pre-selected radius r and m=number of points.

In order to estimate total population size this density figure (no. birds/ha) was multiplied by the area of the native forest (calculated using a planimeter) where Priolos occurred throughout the year [FN]. Planimeter readings gave a figure between 557 and 585 ha. A figure of 580 ha is used hereafter.

(2) Lincoln index was computed using sightings as net recaptures were too few. Standard errors were calculated according to Bailey (1951). An estimation of the population was calculated, averaging 6 to 11 different estimates in which sample sizes between 3 and 37 birds were used. This minimises the effect of chance variation (Stamm *et al*, 1960). Several assumptions underline the use of the Lincoln index (see Nichols *et al*, 1981).

[FN] Such estimate is very tentative. A better one, allowing stratification of native vegetation by densities and physiognomy was not possible as much of the habitat was very inaccessible.

Movement data showed that caution about two basic assumptions, that animals should mix freely and that no animals should move in and out of the area being sampled during the recapture period, would be necessary (see mobility). Again, this leads to overestimates (Bibby *et al*, 1992)

2.2.2 Habitats.

2.2.2.1 Data collection.

2.2.2.1 General habitats

On nine routes (see Fig. 2) 125 stations were marked systematically every 200 m to allow their relocation. The routes chosen covered all types of habitats and altitudinal gradient in the main distribution area of the Priolo. Each route was walked three times a month (in August, September, January and April routes 4, 5 and 7 were walked only twice); two mornings between 07:30 and 12:00 h and one afternoon between 15:30 and 19:00 h to score the present or absence of Priolos at stations in a three minutes watch. In order to facilitate comparisons between stations, the two morning walks usually started at opposite route ends and no routes were walked during poor weather conditions i.e. high winds, heavy rain and dense fog. Watches started with 15 seconds imitating the bullfinches piping call. Calls and sight records were distinguished, birds were located within on or beyond 50 m of the station and assigned to the habitat type in which they were first detected.

The following habitat types were used: (1) Laurel forest (Laurel) , (2) Laurel edge (L.edge), (3) Short *Cryptomeria* within 200 m of the Laurel forest, which was fairly scattered and with many landslides (Sc< 200m L), (4) Short *Cryptomeria* (< 6 m) beyond 200m of the Laurel forest (Sc> 200m L), (5) Tall *Cryptomeria* (> 6 m)within 200 m of the Laurel forest (Tc< 200m L), (6) Tall *Cryptomeria* beyond 200 m of the Laurel forest (Tc> 200m L), (7) *Pittosporum* within 200 m of the Laurel forest (Pitt< 200m L) and (8) Other habitats and birds in flight (other habitats). Vegetation formations within or beyond 200 m of the Laurel forest were differentiated as habitat types because areas within 200m had

more openings and landslides and were within easy reach of birds from the Laurel forest.

The proportion of each habitat type within 50 m radius of each station was estimated visually. Maps and aerial photographs helped to record habitats within and beyond 200 m of the Laurel forest. This was converted to area so that an index of population density per habitat type (number of sightings per ha) could be determined. Laurel edge was considered to be 10 to 20% of the 50 m radius at each station, where Laurel had adjoined with other vegetation types.

At each station vegetation structure and composition were recorded by visual estimation within a radius of 50 m (Bibby *et al*, 1989). I estimated % coverage of grass (GRAS) and bare ground (GROUND); % volume of foliage between 0 and 0.5 m (FOLA), 1-2 m (FOLB), 2-4 m (FOLC) and > 4 m (FOLD); % volume of foliage of the following vegetation types: Native 0-4 m (NATA) and >4 m (NATB), *C. arborea* 0-4 m (CLEA) and >4 m (CLEB), *P. undulatum* 0-4 m (PITA) and >4 m (PITB) , *C. japonica* 0-4 m (CRYA) and >4 m (CRYB). The canopy height [FN] (CANOPY) of the dominant plant species was recorded and the altitude (ALT) was measured with an altimeter. Native vegetation comprises all species of the Laurel forest plant community (see Palhinha, 1966).

2.2.2.1.2 Structure and composition of the native forest

Three sites both in areas with and without birds were chosen for a detailed examination of vegetation structure and density. Vegetation was sampled by the point-centred quarter technique (Mueller-Dombois & Ellenberg, 1974). In general I followed the techniques used by Haggar (1988) on the study of the structure and composition of cloud forests in Pico island, Azores. Transects were made at each site and points located every 7 m. All transects were 70 m long apart from Malhada which was 63 m long. At each point

[FN] When possible (otherwise the height was estimated visually) this was done in the following way: a tree was aligned using one eye and a stick grasped in the fingers. The stick was moved back and forth until the tip and base of the tree were exactly in line with the upper and lower end of the stick. At this point a mark was scores on the ground, the height of the tree being the distance of this mark to the centre of the tree.

the distance to the nearest tree (woody plant over 6 cm basal girth) in each quarter, and its basal circumference at about 20 cm, were measured. If the bole of the tree had divided below 20 cm then each resultant stem was measured as if the stems had been one.

At each point the distance to the nearest large fern or shrub was also measured in order to assess the understorey vegetation. At each point at all sites I have counted the number of saplings (< 6cm girth) of the endemic species, *Ilex perado* and *Vaccinium cylindraceum*, and the recently introduced exotic species, *Clethra arborea* and *Hedychium gardneranum*, in 2x2 m quadrats.

2.2.2.2 Data analysis

2.2.2.2.1 Overall habitat description

The habitat variables recorded at each station were simplified by Factor analysis. This technique extracts axes of maximum variation that help to summarise habitat patterns (Gauch, 1982). Factors (axes) were interpreted in a varimax rotated matrix. This rotation process attempts to minimise the number of variables that have high loadings in each axis, which enhances the interpretability of the factors without losing information (Norusis, 1991). The position of bird species on the axes were revealed by plotting the mean Factor scores of the stations at which they occurred. This shows the position of Priolo along habitat gradients in relation to other bird species.

2.2.2.2.2 Density per habitat type

Analysis of general habitats fell into two general groups: Native forests (Laurel) and exotic forests (*C. japonica* and *P. undulatum*). Additional divisions were made within both groups as stated above. The percentage of each habitat type within 50 m radius of each station was summed for 125 stations surveyed and converted to area (ha). These calculations showed that, at each visit, 19.6 ha of Laurel and 77.8 ha of exotic forests were surveyed. Additional habitat divisions gave the figures presented in table. At each visit

sightings per ha were calculated as: number of positive records in habitat A/ area of habitat A. The average of three visits provided a monthly index of Priolo density per habitat type. Values are presented as mean ± SE. Statistical differences in Priolo density amongst habitat types were examined within summer, autumn and winter, as defined before, by one way ANOVA followed by the Tukey test.

2.2.2.2.3 Habitat selection

An obvious criticism of studies covering vegetation types along altitudinal gradients is the fact that it is difficult to know to what extent bird habitat responses are due to differences between altitudes, vegetation types or other confounding variables (Avery & Leslie, 1990). This difficulty arises because habitat variables were intercorrelated. A multivariate approach was used because it enables one to assess the importance of certain variables whilst the effect of other variables is kept constant.

Stations used more often are expected to be more important for birds; thus the number of times a bird was recorded within 50 m radius of each station was used as the dependent variable (occurrence). The contribution of composition and structural habitat variables in explaining the variance of occurrence was assessed using logistic regression with the denominator being equal to the number of times a station was surveyed. Three different time periods were considered: summer (May-August), autumn (September-December) and winter (January-April). Logistic regression is an alternative to discriminant analysis when the predictive variables are not normally distributed and the two groups have unequal covariance matrices (Manly *et al*, 1993). Discriminant analysis were also performed using transformed variables so as to bring skewed distributions to normality (Sokal & Rolhf, 1981). Although the results (not reported here) generally agreed with those of the logistic regression the models obtained were less simple.

The logistic models were fitted as stated by Bowden (1990) using the statistical package GLIM (Payne *et al*, 1987). Firstly, the effects of all habitat variables were

examined. Secondly, the effect of omitting each variable in turn was examined by recalculating the model and comparing the deviances between the two models including and excluding the focal variable. The model of best fit was identified when removal of any of the remaining variables would increase significantly ($P<0.05$) the deviance.

2.2.2.2.4 Structure and composition of the native forest

Two measures of abundance, % composition and density (no. of trees per 100 m^2), and two measures of dominance, a dominance index and the mean basal circumference, were produced for each tree species. The dominance index was obtained from the product of the % composition and mean basal circumference. Results for the understorey vegetation and saplings are shown in terms of density only.

Differences in density of plant species between sites was examined with one way analysis of variance. Do plant species have an equal occurrence in the sample points in areas with and without birds? A chi-square was used to test this null hypothesis.

2.3 RESULTS

2.3.1 Numbers

2.3.1.1 Distribution

Details of survey routes are shown in Table 1 which also shows where Priolos were located. Points with Priolo are also shown in Figure 2. The bird was encountered mainly on the East routes largely confined to the native vegetation and its margins around Pico da Vara summit. Only a few records were obtained on the West routes (17 to 22).

Between January and July other areas were also surveyed but no positive records were obtained. There was no significant difference in terms of percentage cover of native vegetation at stations, within native vegetation, of West routes (route 19; mean=69.3% SD=25.63, n=13) and East routes (routes 3, 8, 11, 12; mean=56.3%, SD=23.15, n=25; t=2.65, NS, df=36, data were arcsine transformed). Although route 19 was surveyed six

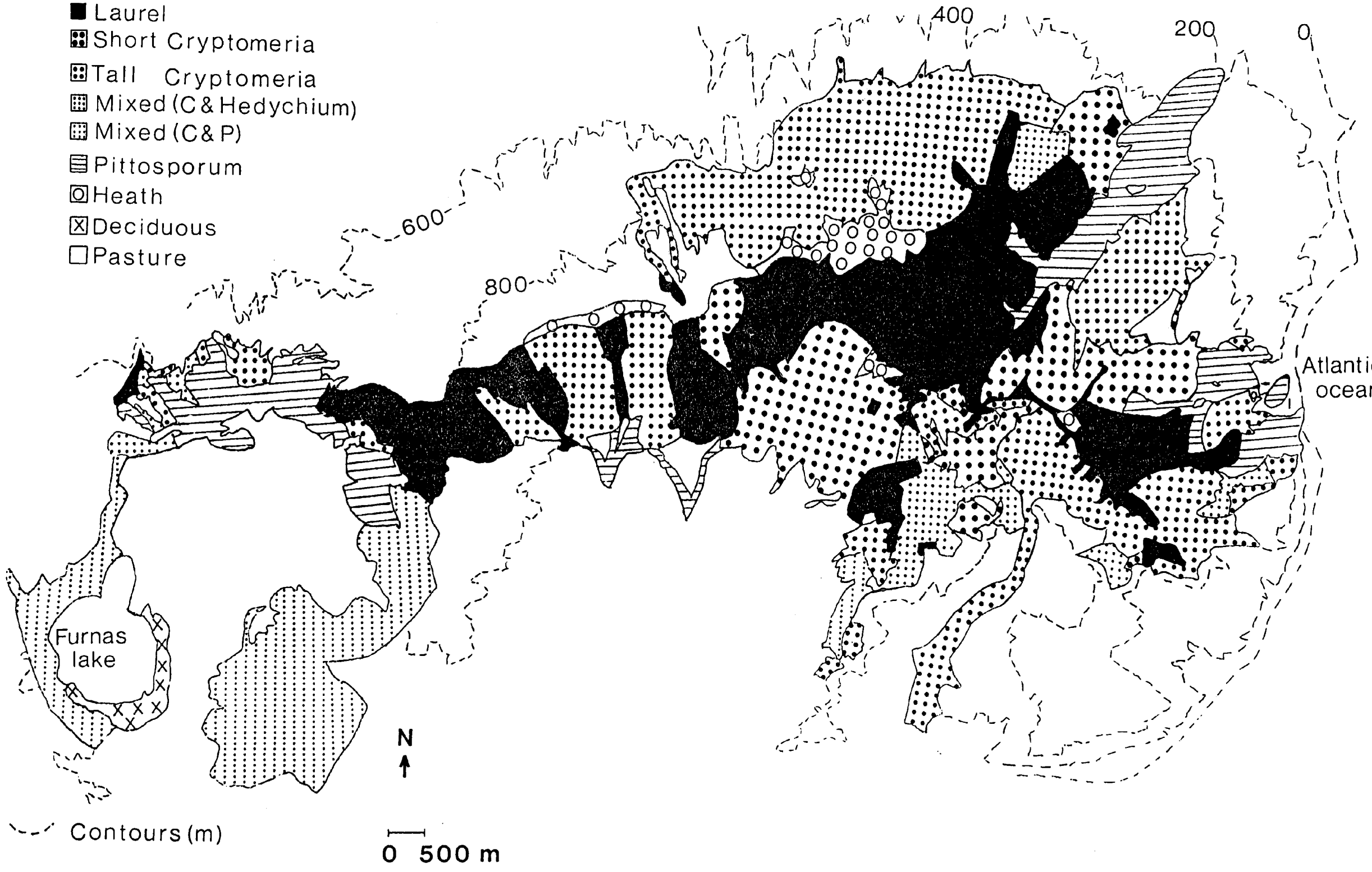
times between January and July no birds were found. In September/October and December the West routes (19, 20, 21, 22) were again surveyed and the following positive records obtained: route 19 (one bird n September), route 20 (one bird in September, two in October and one in December). In route 1, two positive records were also obtained in September but neither in January and May (Table 1).

Table 1. Details of survey routes and records of Priolos during 8 minute point counts. The asterisk indicates routes where presence or absence of birds per habitat type were recorded three times a month. Route numbers correspond to those shown in Figure 2.

Route	No. points	Main habitats	No. birds during surveys						
			A/May 1991	A/May 1992	A/May 1993	A/Sep 1991	Oct 1992	Dec 1992	Jan 1992
1	20	*Pittosporum/Cryptomeria*	0			2			0
2	18	*Cryptomeria*	0			0			
3*	15	Laurel	2	5	5	3		3	
4*	9	*Pittosporum*	0	0	0	0			
5*	9	*Pittosporum*/Pasture	0	0	0	0			
6*	12	*Cryptomeria/Pittosporum*	3	1	2	3		0	
7*	19	*Cryptomeria*	0	0	1	1		0	
8*	23	*Cryptomeria*/Laurel	12	8	6	5			
9*	6	*Cryptomeria*/Pasture	2	0	0	3		0	
10	5	Pasture/Hedges	0			0			
11*	17	Laurel	11	9	7	6			
12*	15	Laurel/*Cryptomeria*	8	2	2				
13	12	*Cryptomeria*/Laurel				6			2
14	10	*Cryptomeria/Clethra*				4			3
15	11	*Cryptomeria*	0			2			
16	8	Laurel				3			2
17	3	Laurel/*Cryptomeria*	0			0			
18	2	Laurel	0			1			
19	13	Laurel	0	0	0	1	0	0	0
20	8	Laurel/*Cryptomeria*	0		0	1	2	1	0
21	3	Deciduous/*Cryptomeria*	0			0			0
22	8	Deciduous	0			0	0		

Fig. 1. (pag. 25). General vegetation types across the entire range of the Priolo. Pasture land with small hedges predominates between sea-level and the general vegetation types indicated on the map.

Fig. 2. (pag. 26). Distribution of the Priolo and location of routes in Eastern S. Miguel. Stations were marked every 200 m on routes 3 to 9 and 12 (n=125) in order to record presence or absence of Priolos in different habitat types and estimate bird density.


Laurel
Short Cryptomeria
Tall Cryptomeria
Mixed (C & Hedychium)
Mixed (C & P)
Pittosporum
Heath
Deciduous
Pasture
400
200
0
600
800
Atlantic ocean
Furnas lake
N
Contours (m)
0 500 m

26

N

0 500 m

400

200

0

600

800

1000

NORDESTE

MALHADA

PICO DA VARA

TRONQUEIRA

SALTO DO CAVALO

PICO DO BURACO

MONTE SIMPLICIO

BARTOLOMEU

FURNAS

Furnas lake

Atlantic ocean

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22

□ Largest area of laurel forest

2– Routes

• Points with birds

---- Contours (m)

The birds recorded on routes 1 and 20 in September and October were juveniles; for other records the age could not be determined as birds were heard but not seen. The Priolo is the only species that feeds on fern fronds and sporangia in spring, leaving conspicuous marks (see Chapter 3). No marks of feeding birds were found from March to June which corroborates the view that, during this time period, birds were no longer present in these areas.

2.3.1.2 Mobility

No evidence was found for territoriality, as most sightings of breeding birds overlapped extensively.

Netting was carried out in several places from May until September. Three sites were used quite regularly (A=route 2, st11; B=route1 st7 and C=route 1 st6;). Site A was a large *Polygonum capitatum* patch in Ribeira do Guilherme valley, 550 and 450 m away from sites B and C, respectively. Sites B and C (road sites) comprised two patches of *P. capitatum*, one patch of *Leontodon filii* and a gap between *C. japonica* and Laurel forest mixed with Pines. The two sites were 200 m apart.

Figure 3 shows the cumulative number of Priolos caught in each netting session in relation to cumulative netting effort. In 1991 the capture rate of new birds at all sites approached zero, but only in site C was the cumulative curve better described by logarithmic regression (r^2=0.87) than by linear regression (r^2=0.78). In the other sites the cumulative curve was better described by linear regression (r^2(A and B)=0.93) than by logarithmic regression (r^2=0.75 and 0.85). Clearly, the netting effort should have been greater. In 1992, the effort was increased by restricting netting to sites A and C only. The cumulative curves were closely fitted by a logarithmic relationship (r^2 = 0.95 at site A; 0.93 at site C). In the winter of 1992, the cumulative curve for site B was also better described by logarithmic regression than by a linear relationship (r^2=0.84 and 0.69 respectively). These cumulative curves conform to the patterns expected of a resident population. In all

sets of data, except for site A in 1991, the effort accumulated was sufficient to show that the capture rate of new birds approached zero. The total capture rate also decreased throughout. This implies that birds, after a while, became infrequent visitors to the sites because sightings of colour-ringed birds showed that they had not left the area.

Table 2 shows that "road birds" (birds ringed in sites B and C) were sighted significantly more often in the road than in the valley. "Valley birds" (birds ringed in site A) were sighted more often in the valley in 1991 and on the road in 1992. Neither difference was significant (Table 2). It is likely that this was mainly a reflection of the lower visibility conditions in the valley. In 1992 three valley birds accounted for 22 of the 23 sightings on the road. If these are omitted from the analysis the remaining five birds were sighted significantly more in the valley (Table 2). The cumulative curve for site A in 1991 shows a sudden influx of new birds in July. There was a tendency for these birds to be seen more often elsewhere than in the valley whereas birds caught prior to this period were sighted more often around the valley than elsewhere (Table 3). This suggests that the "influx birds" were birds making excursions from nearby areas. This analysis suggest that these sites were used mainly by a small number of resident birds and less by birds making excursions from nearby areas.

More direct evidence about the patterns of Priolo displacement over summer is presented in Figure 4 showing the cumulative distance moved between successive sightings of individuals with a larger sighting sample size from end May/June until September. Most individuals showed some large scale movements of the order of 500 m or more (Table 4) and, in general, a consistent pattern of a large number of small movements over short periods. This indicates that birds commonly spend short periods within a relatively small area. These results suggest that birds have multiple centres of activity within their wide summer home ranges.

The median of the mean distance moved between consecutive locations by individual Priolos in summer was significantly greater than that moved by birds in the

winter (Mann-Whitney test=9, $P<0.01$, $n_1=14$ and $n_2=10$; Table 4). It was possible to calculate the mean distance between successive sightings for six individuals both in summer and in the following winter. When a Wilcoxon's test for matched pairs was applied to these data it gave further support for the difference between summer and winter ranges of Priolo ($t=0$, $P<0.05$, $N=6$).

Although based on a small number of records (Table 4) these results should reflect a real difference rather than a sampling error because the coverage of the study area was similar in both seasons. It remains possible, however, that birds in the winter were moving extensively along inaccessible areas of native forest and coming back to the area where they were sighted. This seems unlikely because several individuals were located in the same area almost every day for periods up to ten days.

The longest movements were recorded in May (Table 4). Three birds, commonly seen (throughout the Summer and from February to April) around 700 m were located feeding on herbaceous seeds at about 300 m. One bird ringed by C. J. Bibby in July 1990 at 730 m was also observed at 300 m in late May of 1992.

Nevertheless, of the 26 birds that were seen at least during eight months, 24 (92%) were seen again near their netted site. From three Priolos ringed by C. J. Bibby in July 1990, two were again recaught in the same place in June 1991 and the third one was recaught in the same place in July 1992. Finally, the four birds that were caught in June/July 1991 and seen regularly in 1992 and 1993 (Green-green, Red-red, White-red and Green-red; Table 4) were, despite some long movements, seen around their netted site throughout the summer and winter every year. These results suggest a picture of wide home ranges but fidelity to a habitual base. Such wide ranging reflected the fruiting of food plants (Chapter 3).

Table 2. Proportion of sightings of road and valley birds (see text for explanation) by the road and the valley. In 1992 values for all valley birds (n=8) and birds seen commonly in the valley (n=5, in brackets) are shown.

1991	No. of birds	Total no. of sightings	% sightings in the valley	$\chi 2$ (df=1 with Yates correction)
Valley birds	11	18	72	2.72 NS
Road birds	11	57	4	47.43 ***
1992				
Valley birds	8 (5)	35 (13)	34 (92)	2.80 NS (7.70**)
Road birds	14	26	0	24.00 ***

***=P<0.001, **=P<0.01, NS=Not significant

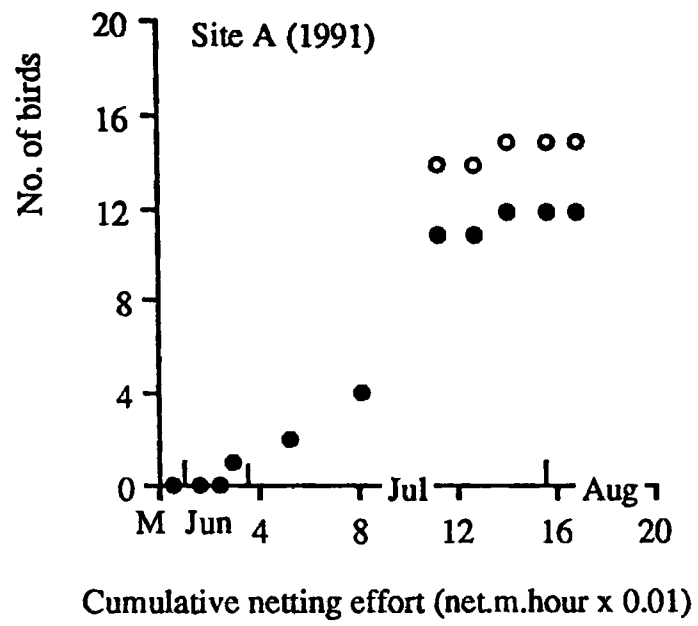
Table 3. Influx birds (see text for explanation) sighted in the valley and elsewhere in 1991.

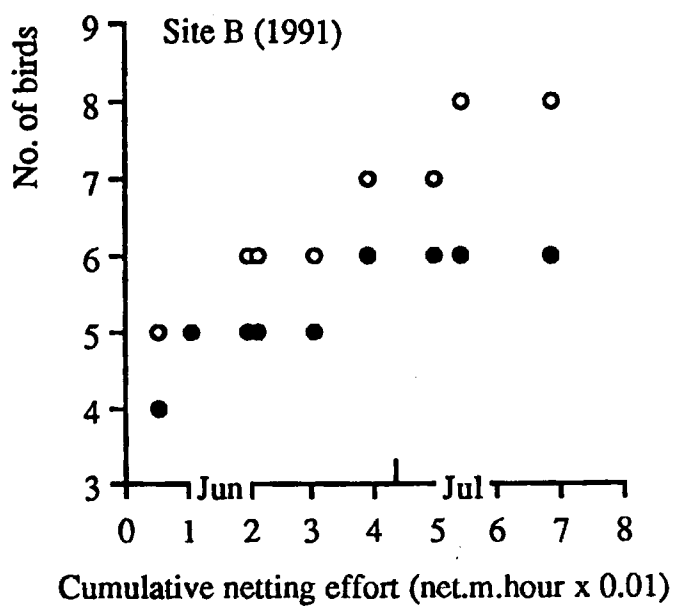
	No. of birds	Birds sighted in the valley	Birds sighted elsewhere
Resident birds	4	4	1
Influx birds	7	2	4

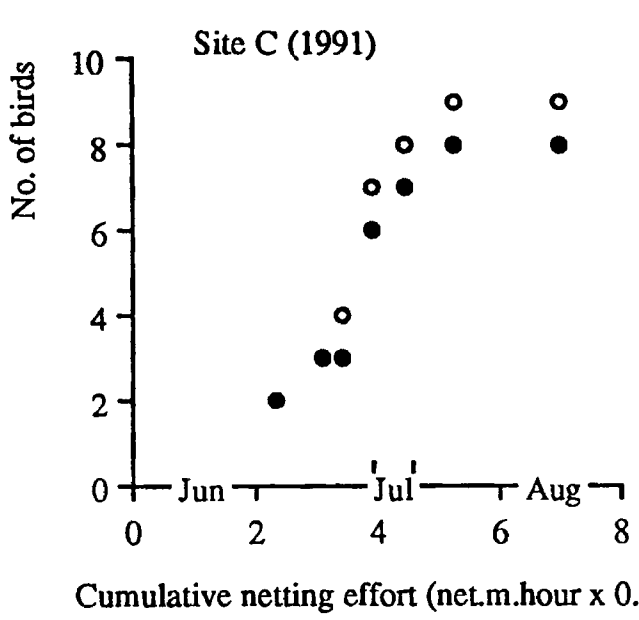
2.3.1.3 Population size and structure

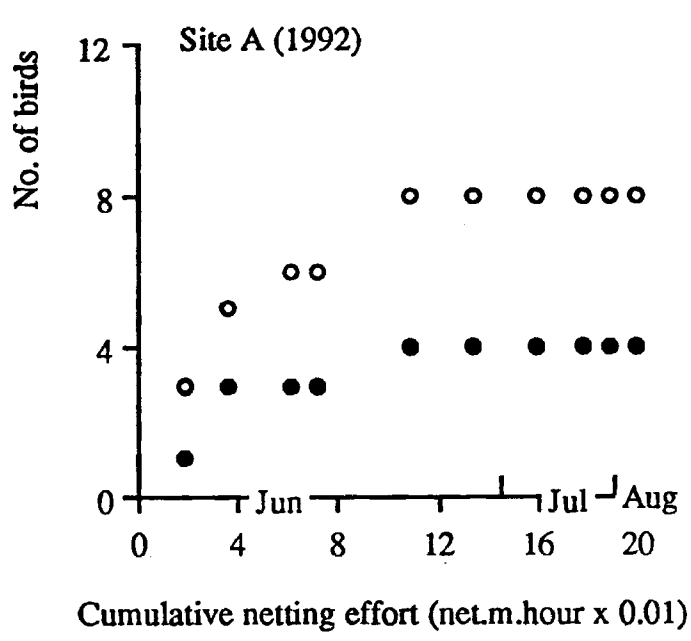
Tables 5 and 6 show population estimates using the variable circular plot method (Table 5) and Lincoln index (Table 6). The total number of birds detected in 99 point counts was not significantly different between 1991, 1992 and 1993 (χ^2=3.73, df=2; Table 5). A significant decrease in population estimates (N) was obtained using the second method: in summer along routes 8, 9 and 6, 8, 9, 11 between 1991 and 1992 (χ^2=6.18, P<0.05 and χ^2=26.47, P<0.001) and in winter between 1992 and 1993 (χ^2=7.52, P<0.01, all df=1 with Yates correction; Table 6).

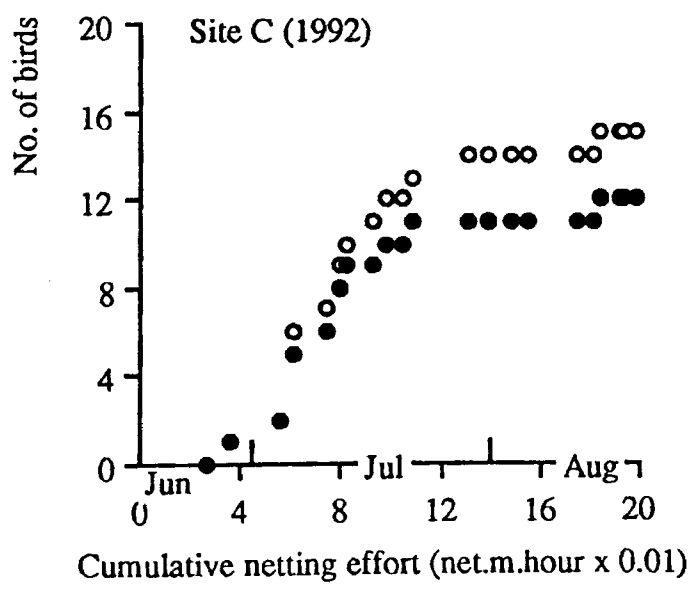
The estimates obtained using Capture-recapture may be influenced by the sample size of birds recaptured i.e. if the number of birds recaptured is negatively correlated with determined population size (N), the population estimates are biased because only a small proportion of the birds ringed is being sampled. This may occur because of movements and/or changes in home ranges. In the summer of 1991, population estimates were not influenced by the sample size of birds recaptured (routes 8, 9: rs=0.19, n=6 and routes 6, 8, 9, 11: rs=0.04, n=11). In 1992 there was a positive correlation for routes 8, 9 (rs=0.24) and a negative correlation for routes 6, 8, 9, 11 (rs=-0.23, n=10). This suggests that the











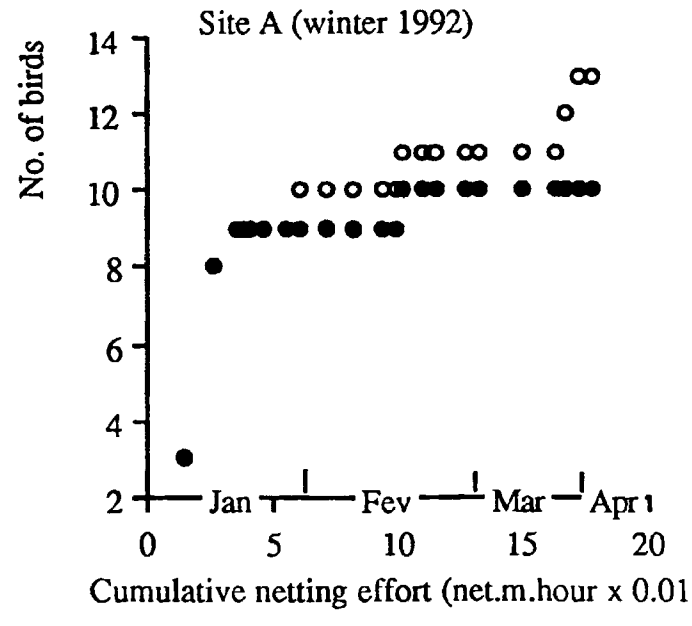


Fig. 3. Numbers of Priolos captured at three sites in relation to cumulative netting effort. Unfilled symbols indicate the cumulative totals of all Priolo captures, and filled symbols indicate previously uncaught birds, for each netting session.

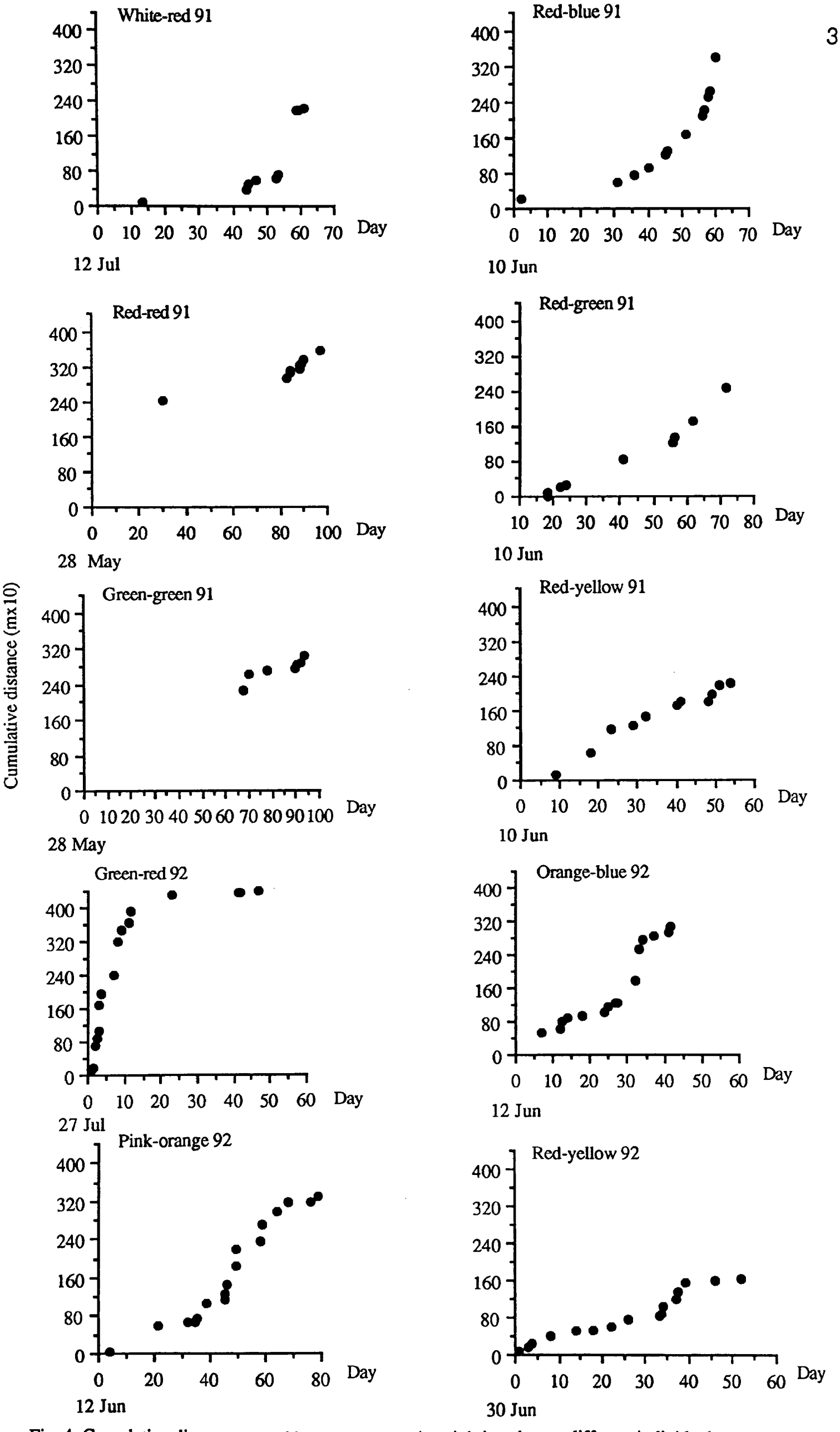


Fig. 4. Cumulative distance moved between successive sightings by ten different individuals over summer. The date on day zero indicates capture date.

Table 4. Comparison between summer and winter mobility of colour-ringed birds. Summer home ranges were calculated using sightings from early June to mid September. For winter home ranges, sightings from early January to late April were used.

Bird	Sex	Mean distance between successive sightings (m)	No. records	Time span (days)	Longest movements (m)	Home range (ha)
Summer						
White-red	f	88	12	60	Sep-1450	4.69
Red-blue	f	200	15	62	Jul-350; Aug-750, 425	31.72
Red-yellow 91	f	165	13	53	Jun-500, 530	4.07
Red-yellow 92	f	79	17	49	Aug-188	9.40
Green-green 91	m	75	7	24	May-2275; Aug-375	12.59
Green-green 92	m	150	11	84	Jun-425	38.86
Green-red	f	213	18	50	Jul-603, 550, 425; Aug-800	18.09
Pink-orange	m	163	18	82	Jun-425, 525; Jul-300; Aug-375	18.09
Orange-blue	f	106	20	96	Jun-550; Sep-500, 775; Nov-425	26.59
Blue-white	m	168	9	72	Jul-475	16.80
Red-red	f	100	9	64	May-2450; Jun-500	14.34
Red-green	m	138	10	59	Jun-575; Jul-375, 350; Aug-775	43.27
Red-white	f	90	8	67	Aug-300	9.18
White-green	m	128	4	32	Aug-150	5.38
Average		133.1	12	61		18.33
Winter						
Pink-red	?	65	12	90	Mar-163	2.72
Pink-blue	?	70	8	62	Mar-175	3.01
Pink-orange 92	m	61	16	85	Apr-178	2.25
Pink-orange 93	m	88	12	15	Mar-164	2.99
Green-green	m	89	7	32	Mar-363	9.74
White-green	m	29	7	36	Apr-53	0.38
Red-yellow	f	95	6	48	Mar-178	3.98
Red-red	f	103	6	32	Apr-153	6.48
Orange-blue	f	69	5	54	Mar-115	2.79
Blue-blue	f	83	6	19	Apr-200	4.49
Average		75.2	9	47		3.88

decrease in bird numbers along routes 8, 9 between 1991 and 1992 was real and little influenced by sample size. Winter estimates were moderately influenced by sample size both in 1992 (rs= -0.34, n=7) and 1993 (rs=-0.41, n=8) but neither correlations were significant.

Population estimates over summer are certainly overestimates. Movement data showed that birds were highly mobile and were entering and leaving the area being sampled. In winter Priolos remained faithful to small areas for up to four months and large scale movements were not recorded. Although based on a smaller number of birds, these estimates provide a more reliable figure. The small samples and area covered (Table 6b) suggest, however, that these may be underestimates. The discrepancy between summer and winter estimates is visible in table 6. Using a similar number of ringed birds, summer estimates invariably gave about 20 more individuals than winter estimates.

2.3.2 Habitats

2.3.2.1 Habitat description

The ordination of the vegetation structure and composition data by Factor analysis extracted three interpretable axes. The first factor (28.6% of the total variance) has a high negative loading for ALT, a low negative loading for CRYA and high positive loadings for PITA and PITB (Table 7). This is mainly an exotic forest axis. It represents a transition from short *C. japonica* plantations at high altitudes to tall stands of *P. undulatum* at low altitudes.

The second factor (22.7% of the total variance) has a high negative loading for GRAS and high positive loadings for FOLD, CRYB and CANOPY (Table 7). In ecological terms this axis represents a transition from pasture (negative scores) to tall *C. japonica* plantations (positive scores) at mid-altitudes.

Table 5. Population estimates: variable circular plot method. Point counts were made in May/June, prior to the start of the breeding season. In order to estimate total population size (total N), bird density was multiplied by the area of native forest (calculated using a planimeter) where Priolos occurred throughout the year.

Year	No. birds in 99 point counts	Density (birds/ha)	Total N (birds/ha x 580 ha)
1991	36	0.58	336
1992	25	0.46	267
1993	22	0.48	278

Table 6. Population estimates (N): Lincoln index. (a)summer, (b) winter. The visible area covered by the routes fits approximately 4.8 and 2.8 times into the main area of native vegetation where Priolos occurred throughout the year, enabling an estimation of total population size (total N).

(a)

	Routes 8,9			Routes 6, 8, 9, 11		
	No. birds ringed	N	SE	No. birds ringed	N	SE
1991	8	45	23.7	14	89	46.9
	11	58	26.0	16	107	56.7
	16	61	15.2	19	76	46.5
	19	76	27.7	26	182	97.2
	20	140	74.8	29	164	86.1
	22	55	17.3	30	120	60.0
				31	103	35.3
				33	128	38.9
				34	122	29.8
				35	420	402.1
				37	153	50.4
Average (Total N)	16	73 (x4.8=350)	30.8	28	151 (x2.8=423)	86.4
1992	7	36	14.6	10	26	9.1
	13	59	21.1	11	99	93.3
	16	40	15.5	17	85	43.9
	18	50	12.8	20	60	28.3
	21	40	8.0	25	75	35.4
	22	44	15.6	27	88	25.8
	23	44	63.6	29	87	41.0
				31	76	16.3
				32	64	22.6
				33	66	10.7
Average (Total N)	13	45 (x4.8=216)	21.6	24	73 (x2.8=204)	32.6

(b)

	Routes 8, 9.		
1991	No. birds ringed	N	SE
	10	34	12.8
	11	40	15.0
	12	36	14.7
	13	33	17.8
	15	38	20.5
	19	38	9.0
	20	26	2.7
	21	30	4.7
Average (total N)	15	34 (x4.8=163)	12.1
1992	3	5	1.8
	5	12	4.1
	6	12	4.2
	7	18	6.4
	11	66	60.3
	12	24	17.0
	14	39	15.4
Average (total N)	8	25 (x4.8=120)	15.6

Finally, the third factor (15.3% of the total variance) presents high positive loadings for CLEA, CLEB and NATB and a low positive loading for NATA (Table 7). This axis represents an increase in native vegetation and *C. arborea* towards high altitudes. It also shows a transition from pure stands of small (usually <3 m) native vegetation to tall (usually >3 m) stands of native vegetation being invaded by *C. arborea* .

Figure 5 shows the mean position of all bird species on the three factors. The Priolo was the only bird species that fell well above the average on the third axis. No other species showed such a high association with native vegetation.

2.3.2.2 Density per habitat type

Table 8 shows the area of each habitat type measured within 50 m radius of each station (n=125 stations). Figure 6 considers Priolo density in two habitat groups, native and exotic forests. Overall, the Priolo monthly density was dramatically higher in native forests in summer (F=78.93), autumn (F=49.13) and winter (F=123.59; all P<0.001,

df=7, 88). The difference was specially marked in winter when the Priolo was virtually absent in the exotic forests.

Figure 7 considers Priolo density in 8 different habitat types. These showed striking monthly variations among habitat types, which generally paralleled the patterns obtained with the GLIM analysis. Three features arise from figures: (1) Laurel forest was the only habitat consistently used throughout the year; in winter and early spring Laurel forest accounted for up to 90% of the Priolo records. (2) The edge of the Laurel forest and areas in its vicinity were heavily used in summer and autumn. (3) Stands of tall *C. japonica* and *P. undulatum*, usually more than 200 m away from Laurel areas were of marginal importance.

Table 7. Variable scores along the three factors.

Variable name	Habitat variable	Factor 1	Factor 2	Factor 3
NATA	% foliage volume of Native vegetation below 4 m	-0.16	-0.49	0.57
NATB	% foliage volume of Native vegetation above 4m	0.10	-0.19	0.76
CLEA	% foliage volume of *Clethra arborea* below 4 m	-0.28	-0.03	0.80
CLEB	% foliage volume of *Clethra arborea* above 4 m	-0.06	0.055	0.87
CRYA	% foliage volume of *Cryptomeria japonica* below 4 m	-0.58	0.44	-0.17
CRYB	% foliage volume of *Cryptomeria japonica* above 4 m	-0.51	0.79	-0.15
PITA	% foliage volume of *Pittosporum undulatum* below 4 m	0.88	0.53	0.05
PITB	% foliage volume of *Pittosporum undulatum* above 4 m	0.95	0.02	-0.15
GRAS	% cover of herbaceous vegetation	0.03	-0.68	-0.23
GROUND	% cover of bare ground	0.11	-0.21	0.15
FOLA	% foliage volume 0 - 0.5 m	0.53	-0.16	0.13
FOLB	% foliage volume 1 - 2 m	-0.02	-0.29	0.28
FOLC	% foliage volume 2 - 4 m	-0.12	0.17	0.28
FOLD	% foliage volume >4 m	-0.02	0.93	-0.15
CANOPY	Canopy height of dominant plant species (m)	0.31	0.75	-0.03
ALT	Altitude (m)	-0.76	0.00	0.27

Table 8. Area of each habitat measured within 50 m radius of the 125 marked stations.

Habitat code	Habitat type	Area (ha)
Laurel	Laurel (native) forest	19.6
L. edge	Laurel edge	3.2
Sc< 200m L	Short (<6m) *Cryptomeria japonica* within 200 m of the Laurel forest	15
Sc> 200m L	Short *Cryptomeria japonica* beyond 200 m of the Laurel forest	5.5
Tc< 200m L	Tall (>6m) *Cryptomeria japonica* within 200 m of the Laurel forest	6.5
Tc> 200m L	Tall *Cryptomeria japonica* beyond 200 m of the Laurel edge	21.6
Pitt.< 200m L	*Pittosporum undulatum* within 200 m of the Laurel forest	17.9
Other habitats	Other habitats.	8.1

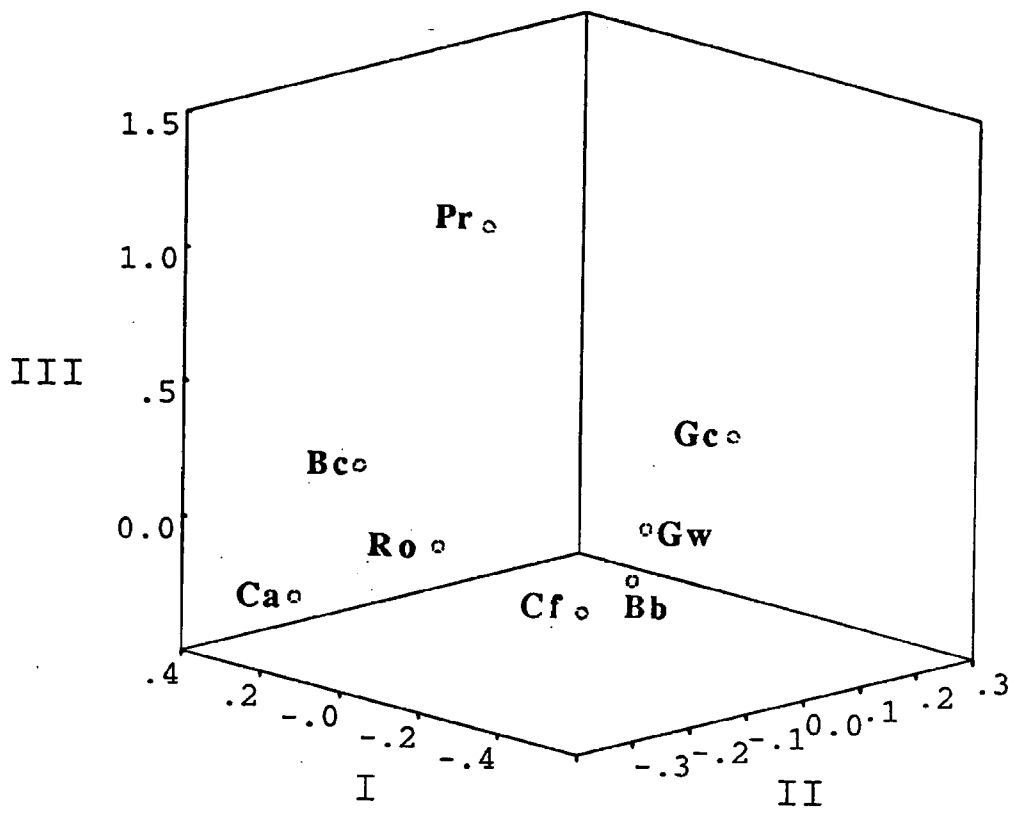


Fig. 5. Position of S. Miguel Passerines along the first three Principal Components of vegetation data (see text for explanation). Birds are:
Pr=Priolo, *Pyrrhula murina.*
Ca=Canary, *Serinus canarius canarius.*
Ro=Robin, *Erithacus rubecula.*
Bb=Blackbird, *Turdus merula azorica.*
Gw=Grey Wagtail, *Motacilla cinerea patriciae.*
Gc=Goldcrest, *Regulus regulus sanctae-mariae.*
Cf=Chaffinch, *Fringilla coelebs moreletti.*
Bc=Blackcap, *Sylvia atricapila atlantis.*

The remaining habitats (other habitats) at lower altitudes, mixed copses of *P. undulatum* and *Acacia melanoxylon* (also exotic), very small areas of deciduous trees and orchards, pasture with hedges and fields of *H. gardneranum*; and, at higher altitudes, pasture with hedges and heath, were practically not used. During the study only 4 birds were seen in hedges, situated very close to short stands of *C. japonica* with openings.

Priolo densities were highly significantly different between habitats in summer (F=43.60), autumn (F=20.54) and winter (F=31.58; all one way ANOVA P<0.001, df=7,88). Tukey tests were performed in order to explain these results. The summer ANOVA was accounted for by a higher mean density in L.edge when compared with Laurel (q=15.8) and with all exotic forest habitats (16.2 < q < 19.9). The ANOVA for autumn was explained by a difference in mean density between L. edge - Laurel (q=7.4), L. edge - exotic forest habitats (8.5 < q < 13.7) and Laurel - exotic forest habitats (4.9 < q < 6.2) except Short Cryptomeria. Priolo density in short *C. japonica* beyond 200 m of Laurel was also higher than the one in tall *C. japonica* beyond 200 m of Laurel (q=5.1). This suggests that as *C. japonica* plantations get older they became more unsuitable for Priolos.

In the winter ANOVA the mean Priolo density in Laurel was higher than the density in L. edge (q=10.6) and all other habitat types (14.8 < q < 16.3). A significant difference between L.edge and all tall *C. japonica* within 200 m of Laurel (q=4.4) accounted also for the winter ANOVA.

There were peaks in the density of Priolo in the exotic forest habitat types: (1) *P. undulatum* in May/June and November/December (2) tall *C. japonica* within 200 m of the Laurel forest and tall *C. japonica* beyond 200 m of the Laurel forest in July/August and (3) short *C. japonica* beyond 200 m of the Laurel forest in September/October (Fig. 7). Juvenile dispersal may have accounted for the autumn peak in *P. undulatum* and short stands of *C. japonica.*

The concentration of Priolos in areas of tall *C. japonica* within 200 m of Laurel in July/August 1991 can be examined through sightings of Priolos during transect counts (Fig. 7). Direct observations of coloured ringed birds showed that the July/August peak in 1991 was due to no more than 6-8 birds. These positive records were obtained because birds moved quite extensively along the road, which traverses areas of tall *C. japonica*, as they fed on herbaceous plants. Comparison with the slight changes in Priolo occurrence

within *P. undulatum* (Fig. 7) seems to point to the fact that this habitat was also used by a very small number of individuals. On the other hand, sightings of colour-ringed birds along the edge of a similar sized-area of laurel forest in route 8 showed that this was used by at least 20 to 30 individuals. In summary, there is direct evidence that less important habitats are used by a very small number of individuals whereas the majority of the birds are concentrated within the native forest and its edges.

2.3.2.3 Habitat selection

The habitat parameters that accounted for habitat selection showed some seasonal variation. A given parameter can be important either because birds preferred or avoided areas with relatively high abundance of that parameter. These two different processes can be distinguished by the sign of the coefficient in the logistic regression. Native vegetation and *C. arborea* were highly preferred ($P<0.001$) during all seasons, which implies that they are very important criteria for habitat occupancy. Small stands and individual *C.arborea* trees were scattered within the endemic forest, which makes it difficult to assess its sole influence upon Priolo. Areas with bare ground were preferred in summer and autumn. Tall stands of *P. undulatum* and areas with tall canopy were avoided. (Table 9). All exotic species presented taller canopy (usually >6 m) than native species (usually <5 m). A surprising finding was the fact that tall *C. japonica* and short *P. undulatum* were highlighted as preferred ($P<0.05$ or $P<0.01$) in summer and autumn and, summer and winter, respectively.

Examining the important variables in the logistic models (Table 9) suggests that, to a large extent, the same criteria can be used to characterise the Priolo's habitat selection during all seasons: (1) four habitat parameters (NATA, NATB, CLEB, CANOPY) were consistently of higher importance ($P<0.001$ or 0.01), (2) changes in the degree of significance of these parameters were uncommon and (3) significant habitat parameters

were either consistently preferred or avoided. More seasonal variability was found among the less important variables in the models (Table 9).

Generally, when the effects of vegetation composition were held constant, altitude and habitat structural variables were of little importance in explaining habitat occupancy. Foliage density measures were significant in only 33.3% of the steps compared with 83.3% for native vegetation, 50% for *C. arborea* and *C. japonica* and 66.6% for *P. undulatum*. Nonetheless, a major seasonal difference in preference for foliage profiles was detected. Tall vegetation (>2 m) was avoided in summer whereas short vegetation (<2 m) was avoided in autumn and winter.

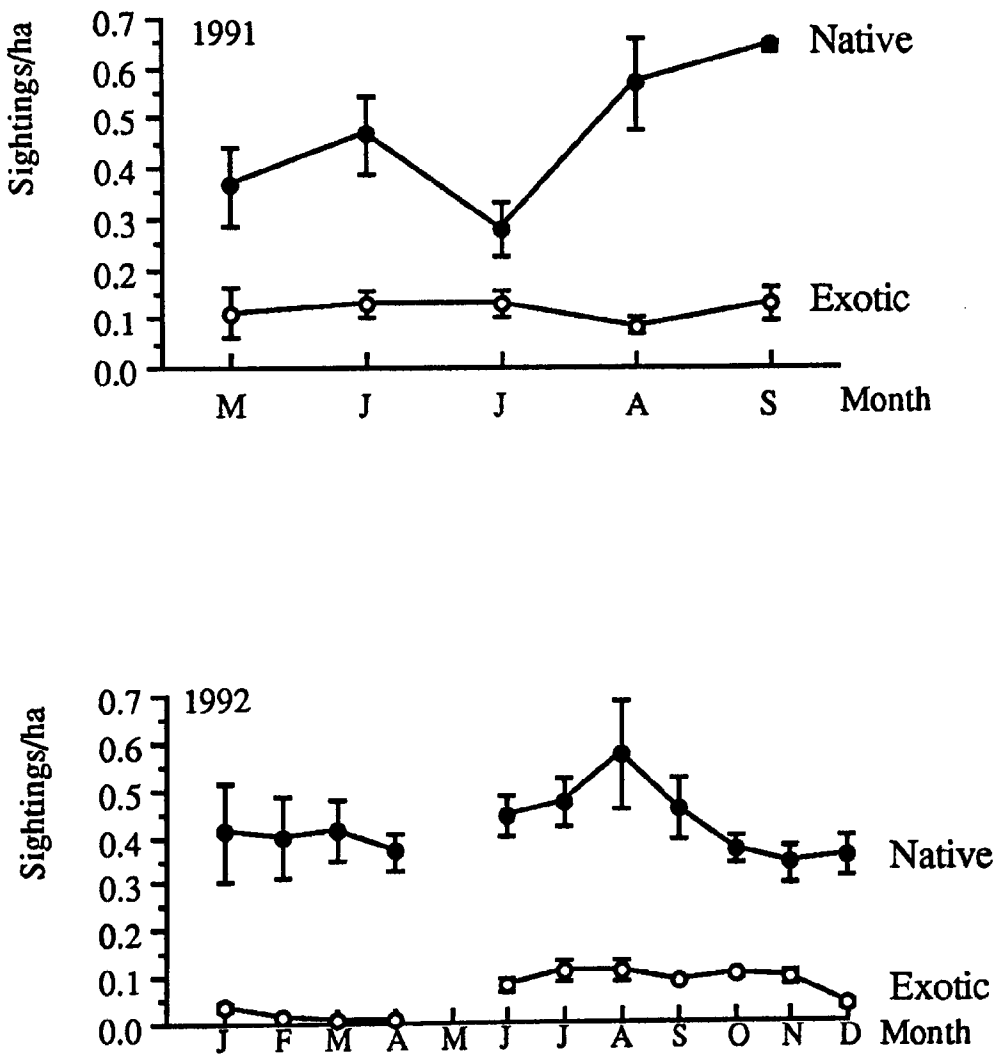


Fig. 6. Priolo density as sightings/ha in native and exotic vegetation present at sampling stations. Values are mean ± S. E of three visits per month (see methods).

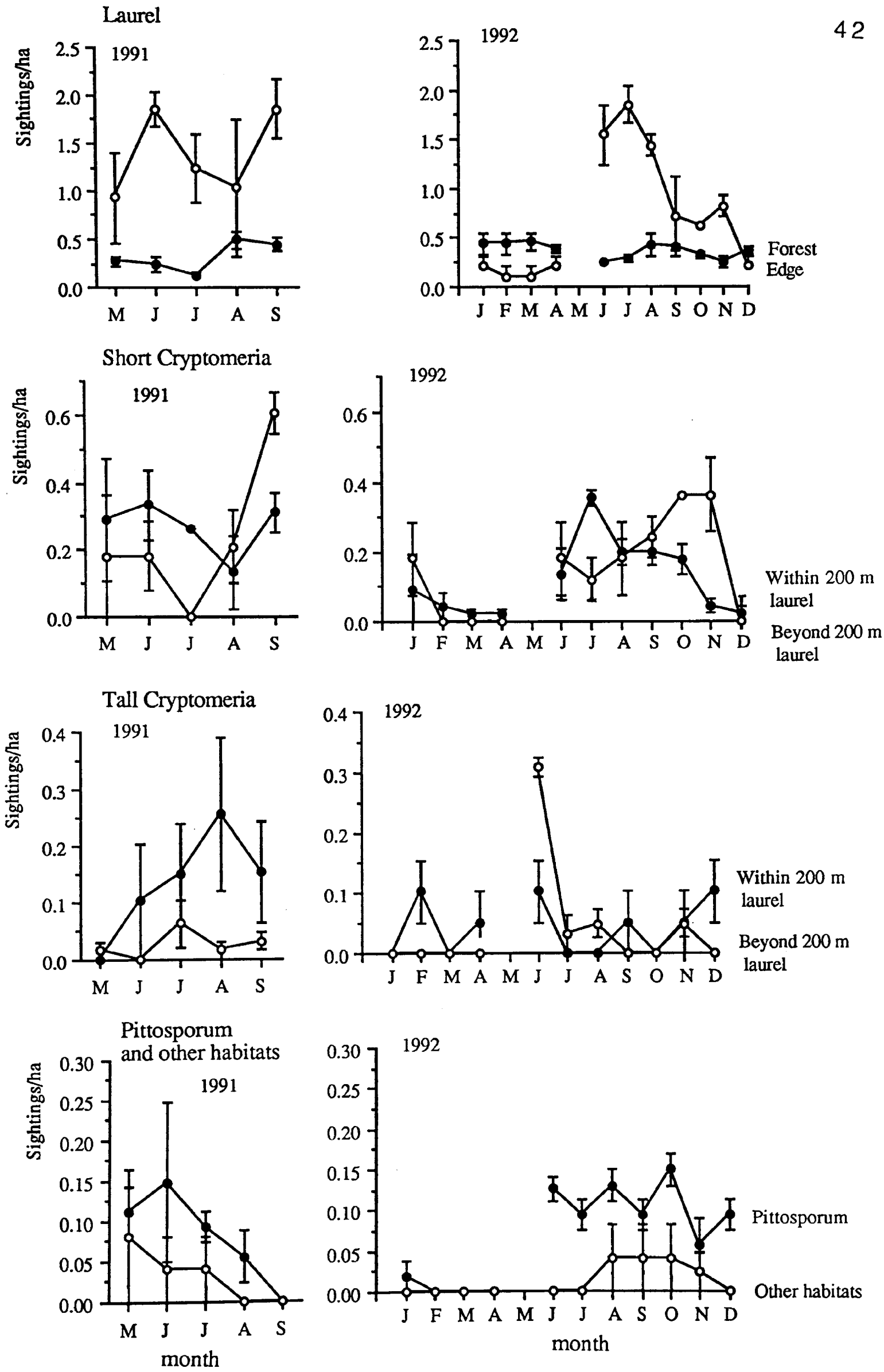


Fig. 7. Priolo density as sightings/ha in different habitat types present at sampling stations (Table 8). Values are mean ± S. E. of three visits per month (see methods). Note the different scale for different habitats.

The difference in deviance between models provides a chi-square test of goodness of fit with degrees of freedom equal to the difference in the number of parameters estimated for the two models being compared (Bowden, 1990; Manly *et al*, 1993). The winter model gave a much better fit than the summer ($\chi 2=121.1$, $P<0.001$, df=5) and autumn models ($\chi 2=97.8$, $P<0.001$, df=6). The difference in deviance between the autumn and summer models was less but still highly significant ($\chi 2=23.2$, $P<0.001$, df=6). This indicates that precision of habitat selectivity increases in the following direction: summer<autumn<winter.

2.3.2.4 Forest structure and composition

Twelve species of trees were present in the study areas although *Prunus lusitanica* ssp *azorica*, *Myrica faia* and *Frangula azorica* were not present in the sample plots. The mean tree density in areas with birds varied between 84 and 91 trees/100m^2 whereas in areas without birds it varied between 57 and 141 trees/100 m^2.

Table 9. Logistic models: Comparison between seasons. Variable codes as in table 7.

Variable	Summer	Autumn	Winter
NATA	0.74***	NS	1.74***
NATB	0.98***	1.09***	1.62***
CLEA	NS	NS	NS
CLEB	0.80***	2.23***	1.04**
CRYA	NS	NS	NS
CRYB	0.60**	0.85**	NS
PITA	0.68*	NS	0.79*
PITB	-1.69***	NS	-2.13**
GRAS	NS	NS	NS
GROUND	0.68**	0.65*	NS
FOLA	NS	-0.81*	NS
FOLB	-0.69**	NS	-1.41**
FOLC	-0.59**	NS	NS
FOLD	NS	NS	NS
CANOPY	-0.13***	-0.29***	-0.31***
ALT	-0.002*	NS	NS
Final deviance	235.19	211.95	114.12

***=P<0.001, **=P<0.01, *=P<0.05, NS=Not significant.

The inter species density (Table 10) varied significantly between sites (one way ANOVA after square root transformation, F=8.97, P<0.01, df=8, 54). In all sites *Laurus azorica* and *Erica azorica* were the species with greater importance both in abundance and dominance (Tables 10 & 11). The mean basal circumference of *Laurus azorica* was significantly different between areas with and without birds (mean=0.30 cm, SD=0.19 and mean=0.17 cm, SD=0.08; t=4.27, P<0.001, df=81) but the difference for *Erica azorica* was not significant (mean=0.27 cm, SD=0.13 and mean=0.26 cm, SD=0.14; t=0.20, NS, df=62). In terms of adult native tree populations, the major difference between areas with and without birds is the low occurrence of *Ilex perado* in the latter; it was two to six times less common in both abundance and dominance. When expressed in terms of the dominance index, the importance of *Ilex perado* was heightened (Table 11). Its relative occurrence in the sample points was significantly higher in areas with birds (14.7%, n=116) than in areas without birds (2.5%, n=120; χ^2=9.72 P<0.01, df=1 with Yates correction). Moreover, the mean basal circumference was also significantly higher (mean=0.26, SD=0.14 and mean=0.16, SD=0.08; t=2.33, P<0.03, df=26). For *Vaccinium cylindraceum* the difference both in density and dominance between areas with and without birds were small. Both the relative occurrence (8.6%, n=116 and 14.6%, n=120; χ2=0.58 NS, df=1 with Yates correction) and the mean basal circumference (mean=0.11 cm, SD=0.02 and mean=0.14 cm, SD=0.07; t=1.52, df=25) were not significantly different between areas. Although it presented approximately similar densities to those of *Ilex perado* (Table 10), the small basal diameters of the individuals decreased the importance of *Vaccinium cylindraceum* in terms of dominance (Table 11).

Of the exotic trees *Clethra arborea* occurred significantly more often in areas with birds (19.8%, n=116) than in areas without birds (5.8%, n=120; χ^2=9.18, P<0.01, df=1 with Yates correction). The difference between the mean basal circumference in both areas approached significance (mean=0.26 cm, SD=0.17 and mean=0.14 cm, SD=0.07; t=1.9, P<0.07, df=28). Higher abundance in areas with birds was probably a reflection of the

more open canopy of the forest at those sites. *Clethra arborea* was absent from Pico do Buraco (Table 10) simply because the ground was densely carpeted with *Hedychium gardneranum*.

Under the canopy, the dominant species varied also between sites (one way ANOVA after square root transformation $F=7.39$, $P<0.01$, $df=4,25$; Table 12). The proportion of both *Woodwardia radicans* and *Culcita macrocarpa* was higher in areas with birds (39.7% and 21.6%, n=116) than in areas without birds (5.8% and 20.0%, n=120), but only the former was significant ($\chi 2=36.8$, $P<0.001$ and $\chi 2=0.018$, NS, $df=1$ with Yates correction). In the areas without birds, *Woodwardia radicans* was found only at Salto do Cavalo W (Table 12). *Osmunda regalis* was recorded only in Malhada, although it was also present in Tronqueira and Bartolomeu. This sampling method is not adequate to record the occurrence of less abundant ferns such as *Osmunda regalis*. This fern was present in 20% of the 2 m^2 quadrats in areas with birds, whereas in areas without birds it was only present in 3.3% of the quadrats. This was not significant using a G-test, but perhaps this was only a reflection of the small sample size. Nonetheless, it appeared that *Osmunda regalis* tended also to be more common in the largest fragment of endemic vegetation than in other areas.

In terms of saplings, the population of both *Clethra arborea* and *Hedychium gardneranum* were, by far, much greater than the population of *Ilex perado* and *Vaccinium cylindraceum*, both in areas with and without birds (one way ANOVA after square root transformation $F=5.17$, $P<0.01$, $df=3, 20$; Table 13). For single species comparisons, the number of saplings in areas with birds was, with the exception of Pico do Canario for *Hedychium gardneranum*, generally higher than in areas without birds. Pico do Canario presented an extremely high density of *Hedychium gardneranum*, and the population of *Ilex perado* of both adult trees and saplings was absent.

Table 10. Tree density (number per 100 m^2) and % composition (in brackets): comparison between areas where birds were recorded throughout the year (=birds) and areas were birds were seen only in autumn (=no birds).

	Total tree density	*Laurus azorica*	*Erica azorica*	*Ilex perado*	*Viburnum tinus*	*Vaccinium cylindraceum*	*Juniperus brevifolia*	*Clethra arborea*	*Pittosporum undulatum*	*Picconia azorica*
Birds										
Tronqueira	91	30 (32)	16 (18)	9 (10)	9 (10)	9 (10)		18 (20)		
Bartolomeu	84	25 (30)		19 (23)	8 (10)	11 (12)		21 (25)		
Malhada	88	17 (19)	34 (38)	10 (11)	5 (6)	2 (3)	5 (6)	12 (14)	2 (3)	
No birds										
Pico Buraco	57	16 (28)	28 (50)			13 (22)				
S. Cavalo E	86	37 (42)	28 (33)	4 (3)		11 (12)		4 (8)		2 (3)
S. Cavalo W	141	60 (42)	35 (25)	4 (3)	4 (10)	11 (8)		18 (12)		

Table 11. Dominance index (see text for explanation) and mean basal circumference (in cm; in brackets): comparison between areas with and without birds (as defined in Table 10).

	Laurus azorica	*Erica azorica*	*Ilex perado*	*Viburnum tinus*	*Vaccinium cylindraceum*	*Juniperus brevifolia*	*Clethra arborea*	*Pittosporum undulatum*	*Picconia azorica*
Birds									
Tronqueira	1 (31.4)	0.64 (37.4)	0.29 (29.2)	0.06 (9)	0.11 (11.7)		0.32 (16.4)		
Bartolomeu	1 (31.7)		0.7 (29.6)	0.18 (17)	0.14 (10.8)		0.89 (34.1)		
Malhada	0.43 (18)	1 (20.9)	0.26 (18.7)	0.05 (8.0)	0.03 (8.0)	0.27 (40.0)	0.49 (28.8)	0.20 (60.0)	
No birds									
Pico Buraco	0.35 (18.1)	1 (28.6)			0.22 (13.8)				
S Cavalo E	0.82 (17.3)	1 (27.7)	0.12 (21.5)	0.16 (11.2)	0.16 (11.2)		0.07 (12.0)		0.02 (7.0)
S. Cavalo W	1 (14.9)	0.78 (19.9)	0.04 (10.0)	0.26 (22.3)	0.26 (22.3)		0.29 (14.9)		

Table 12. Understorey density (number of plants per 100 $m^{2)}$: comparison between areas with and without birds (as defined in Table 10).

	Total density	*Myrsine africana*	*Woodwardia radicans*	*Culcita macrocarpa*	Others +	*Osmunda regalis*
Birds						
Tronqueira	176	44	106	22	4	
Bartolomeu	216	38	92	33	54	
Malhada	253	112	35	98		7
No birds						
Pico buraco	69	64		5		
Salto Cavalo E	205	133		67	5	
Salto Cavalo W	253	152	44	4	6	

+ Mainly *Polystichum* sp but also some *Athyrium* sp.

Table 13. Sapling density of two native and two exotic species (number of saplings per 100 $m^{2)}$: comparison between areas with and without birds (as defined in table 10). Saplings were all plants less than 6 cm basal girth. In the case of *H. gardneranum* this means that all individual plants were counted.

	Ilex perado	*Vaccinium cylindraceum*	*C.lethra arborea*	*Hedychium gardneranum*
Birds				
Tronqueira	10	20	385	150
Bartolomeu	75	40	495	200
Malhada	83	117	544	717
No birds				
Pico Buraco		15		2090
Salto Cavalo E	30	140	100	60
Salto Cavalo W	10	30	230	780

2.4 DISCUSSION

2.4.1 Distribution and population estimates

In terms of distribution and population estimates my findings are similar to those of Bibby and Charlton (1991) though I walked a wider network of tracks and thus relied on larger sample sizes. The results are clear in showing a striking association with the largest fragment of native vegetation. The fact that in autumn only juveniles were seen (some birds that were heard but not seen could have been adults) in the hills above Furnas suggests the possibility of juvenile dispersal. Generally speaking, it was possible to define an area of higher density towards the east of the bird's range (which might coincide with the breeding area) and an area of lower density towards the west (which may be occupied mainly during juvenile dispersal). This area to the west of the range must have been occupied throughout

the year when the bird was reported feeding on buds of orange trees around Furnas in the last century (Chapter 1). The native forest in this area seems now sub-optimal for the Priolo: it seemed younger and less mature and had significantly lower densities of large ferns and flower-bud producing species than the native forest to the east of the range.

It must be noted that the areas that were accessible (covered by the routes) were mainly on the edge of the native forest. Consequently, the density values obtained may not be representative of the whole range (see Bibby *et al*, 1992 for a full discussion of this problem). Population size appeared fairly stable using the variable circular plot method. Results from capture-recapture over summer indicate a steady decline; however these estimates should be viewed with great caution because the summer population was highly mobile. Winter estimates were much less affected by this bias and showed a slight decline from 1992 to 1993. Nevertheless, the full range of the Priolo was clearly established with this study; and both the relative ease with which birds were located (Bibby & Charlton, 1991) and ringed, reaching asymptotic values (Fig. 3), give confidence in these estimates.

2.4.2 Ranging behaviour

My capture-recapture study shows that the Priolo is a largely sedentary bird which commutes to small areas. However, on a local scale, the Priolo ranges widely, has multiple centres of activity and takes infrequent excursions. This largely agrees with data obtained for Bullfinches in Britain, both from capture-recapture (Summers, 1979; Greig-Smith & Wilson, 1984) and radio-tracking studies (Greig-Smith, 1985; Crocker, 1987). For the Priolo, the longest movements recorded were around 3 km whereas Bullfinches in Western Europe rarely move more than 5 km (Aubry, 1970, Noval, 1971, Summers, 1979).

Newton (1964) noted a great deal of local movements of British Bullfinches over summer as new plants came into seed. Radio-tracking by Crocker (1987) showed that home ranges of British Bullfinches are of the order of 5 to 6 ha. Some birds commuted between several separated activity centres, but these were never more than 500 m apart.

For Priolos, distances between successive sightings as far apart as 700 or 800 m were quite common over summer. Clearly, Priolos appear much more mobile over summer than bullfinches in Britain. This may be explained by the high proportion of tall vegetation (especially exotic vegetation) that is unsuitable for foraging within the home range. Clearly, such high mobility reflected the heterogeneous temporal and spatial distribution of foods (Chapter 3).

The mist netting and sighting data that I acquired show that, in winter, the Priolo remains faithful to small areas for several months, with distances between successive sightings being less than 200m. Winter home ranges, based on a small number of records and calculated with a less accurate method, gave very similar results to those obtained by radio-tracking by Crocker (1987) for British Bullfinches (Priolo: mean sightings = 9, mean range = 3.88 ha; England: mean sightings = 113, range = 4.32 ha). Greig-Smith (1985) used radio-tracking to plot home ranges and found that most birds remained largely within 1-2 ha for periods of a few weeks. Home ranges changed frequently, but most shifts were within one km. In a two-year study, also using radio-tracking, Crocker (1987) found that Bullfinches spent most of their winter time within home ranges less than 5 ha and, although some birds had several activity centres, these were never more than 500 m distant.

2.4.3 Habitat selection

The degree and intensity of habitat selection varied seasonally. Overall, the summer and autumn models gave a poorer fit than the winter model and, in summer, five more variables were selected as habitat selection discriminators than in winter. This suggests either less specialisation or more complex habitat selection in summer and autumn than in winter. The inclusion of *C. japonica* and *P. undulatum* in the summer and autumn models gave further support to this idea. Therefore, the Priolo seems to face more severe ecological interactions in winter than in summer, which is consistent with theories developed by Fretwell (1972).

Logistic modelling showed that vegetation composition is likely to be more important than habitat structure in accounting for habitat selection. This was also found in other studies (Rotenberry & Wiens, 1980; Bibby *et al*, 1985; Bibby *et al*, 1989) and is contrary to the initial conjectures of MacArthur & MacArthur (1961). Unlike vegetation composition variables, when foliage density measures were important discriminators, their inclusion in the model represented an avoidance. Nevertheless, cover should be important because birds were never recorded in open fields.

The Priolo density was significantly higher in native vegetation than in exotic vegetation at all seasons. At first sight, this may be viewed as a support for the habitat structure hypothesis. However, if native vegetation and food abundance are correlated, it will be difficult to distinguish between a habitat structure and a food supply hypothesis. Bird density varied seasonally amongst habitats, although foliage density measures did not vary in unison. Variation in vegetation composition was obvious as most herbaceous plants and deciduous shrubs and ferns were absent in winter. The importance of vegetation composition may not be fundamental, but rather a correlate of food abundance. The results suggest that birds might be moving independently according to variations in food abundance between different habitat types.

A preference for native vegetation may simply reflect the superiority of this habitat in terms of food resources. Bare ground and short vegetation were associated with bird presence in summer, probably owing to the fact that they reflected numerous openings and landslides with herbaceous vegetation that provide food for this bird (Chapter 3, Bibby & Charlton, 1991; Bibby *et al*, 1992). However, the importance of a historical component cannot be ruled out (O'Connor & Fuller, 1985). Priolos might show high fidelity to native vegetation because of a longer period of adaptation to this type of vegetation; the evaluation of alternative habitats may be costly (Rosenzweig, 1981). I have no data to discuss the importance of this factor.

Seasonal variations in habitat selection, demonstrated in this study, mean that if a clear view of the mechanisms is to be obtained, a seasonal evaluation of discriminators is necessary (Anderson *et al*, 1983; Rice *et al*, 1983; Wiens, 1989). Many studies have examined selection over one season, either breeding or wintering. Ideally reasonable sample sizes should be obtained over short periods (according to species) in order to track changes in relationships. I also found that a wider range of habitats is used in summer than in winter. Alatalo (1981) and Bilcke (1982) reported the opposite for woodland birds in Holland and Finland. Reduced habitat heterogeneity and, therefore, foraging opportunities mean that island birds may have to use a relatively wider range of habitats during the breeding season. Therefore, in terms of resource utilisation, reproduction might be potentially more costly for island birds. This may be a major difference between insular and continental species and requires further detailed study.

Finally, this exploratory habitat analysis raises several questions: (1) Is habitat selection better correlated with food resources (food supply hypothesis) than with habitat structure? (2) Is the higher precision of habitat selection in winter a result of lower food availability? (3) Can the apparent flexibility gained in summer and autumn be explained by food resources being more widespread and/or abundant? I will consider these questions in the next chapters.

For practical purposes I have shown that the Priolo is highly associated with natural vegetation all year round. Although other habitats may be moderately used in summer and autumn, they were virtually not used in winter. It is thus imperative for the Priolos future that the natural forests be preserved.

2.4.4 Population structure of native forests

The size structure of the forest was quite different between areas with birds and those without. As a whole the forest at Salto do Cavalo seems to be younger and less mature. It presented a higher tree density of most species, resulting in a more closed forest.

As a result, the populations of both saplings and understorey large ferns were much smaller. The areas within the largest fragment of native vegetation, where trees are older and as a consequence the forest is more open, are more suited for the establishment of recruits. Although this is important for the regeneration of the population of endemic species, the number of recruits of these species were 10 to 75 times less than the number of recruits of exotic species. Thus, a future forest dominated by exotic species, *C. arborea* and/or *H. gardneranum*, may be anticipated in some areas such as Pico do Canario. Studies on the ecological requirements of exotic species are necessary in order to understand the invasion of the native forests.

The comparison of the mid-altitude forests structure in S. Miguel with that of Pico (Haggar, 1988) suggests that Pico-forests are closer to a pristine stage. S. Miguel is about the same size as Pico but holds a human population 5 to 6 times greater. Not just human pressure seems to have been greater, but also the influence of exotic plant species have contributed to a marked change in the structure and composition of the mid-altitude cloud forests in S. Miguel.

The less mature forest at Salto do Cavalo may be explained by historical factors. Goats were present in both sampled areas until 10 - 20 years ago, but as Salto do Cavalo was more accessible, it was more popular amongst goat shepards (Fagundo, pers. comm.). Goats seem to feed selectively on *I. perado* and *V. cylindraceum* (pers. observations). Extraction of top soil for pineapple greenhouses appeared also to have been common in some areas (Fagundo, pers. comm.). As a consequence, the forest at Salto do Cavalo may have been more disturbed than the forest at Tronqueira and Bartolomeu, and only recently has it shown some recovering. Do these differences in composition and size structure of the native forest at the two sites explain why Priolos are not present all year round at the forest above Furnas? In order to evaluate this question it is necessary to quantify the diet of this bird (Chapter 3).

CHAPTER 3
DIET AND FOOD RESOURCES

3.1 INTRODUCTION

A knowledge of an animal's diet gives a guide to its food requirements and provides the baseline to examine its food-environment interactions. Considerable theoretical and experimental research has been devoted to the optimal choice of foods (MacArthur & Pianka, 1966, Pulliam, 1974, Pyke *et al*, 1977, Krebs, 1978, Stephens & Krebs, 1986) because of the large range of potential applications of foraging theory (Stephens & Krebs, 1986). Ultimately the theory should predict exactly an animal's diet under varying circumstances. Current models are too inadequate to characterise the diets of species under conditions of changing resource variety and spatial distribution (Smith *et al*, 1978, Grant & Grant, 1980) although scope for model development in this direction does exist (Stephens & Krebs, 1986).

The food requirements of most bird species are poorly known. Much information on diet shifts through time and changes in feeding behaviour when environmental conditions vary is still needed. In ecological terms this is important to explain species patterns.

Since the minimum necessary times for foraging and the energy expenditure are inverse functions of food availability, foraging efficiency, when defined as energy intake per unit of energy expenditure, will decrease as food availability decreases (Robbins, 1983). Demonstration that bird numbers track resource abundance may be the first indication that food is a limiting resource (Wiens, 1986). Lack (1966) first suggested that most bird populations should be limited by food supply outside the breeding season. Discussion of population control has often been examined in terms of determining which single factor limits population size (Lima,1986). Several mortality agents e.g. predation and weather conditions and social behaviour may also be important in the limiting process (Newton, 1980). Simulation models developed by Lima (1986) and McNamara & Houston (1987) in which feeding efficiency was analysed as a trade-off between starvation and

predation pointed to the fact that the combined effects of weather, food availability and predation can be important in limiting populations. For island granivores, however, food shortage is likely to be the most important factor (Schluter & Repasky, 1991) since weather is relatively stable throughout the year (irregularly and unpredictable weather might also play a role but this fact will not be considered) and predators are often absent on islands. This chapter will, therefore, consider the importance of food as a limiting factor of the Priolo population.

Newton (1964) showed that food shortage seems to control the Bullfinch population in Marley wood, Oxford: in some years birds suffered heavy mortality when seed stocks were depleted. Sedentary species facing a period of food scarcity respond both physiologically and behaviourally (Foster, 1977; McNamara & Houston, 1987; Stuebbe & Ketterson, 1982). Behavioural modifications, such as the ones being considered in this study, are usually manifest through changes in feeding ecology. Thus, species may exhibit local movements, increase the time spent foraging and explore other habitats and/or food items. Such responses have been documented for Bullfinches in Britain (Crocker, 1987; Matthews, 1983; Newton, 1964). Mainly, when winter seeds were no longer available, the birds turned to alternative foods: flower buds of wild and fruit trees. Historical records suggest that bud-feeding may also be an important element in the feeding ecology of the Priolo in winter (Chapter 1).

In this chapter I will characterise, in quantitative terms, seasonal variation in diet, food resources and feeding in relation to changes in the availability of foods. This information is crucial to understand the food requirements of the Priolo and is used to address the following questions:

(1) Are Priolo patterns of distribution and abundance explained by food supply? Such a hypothesis predicts that : (a) bullfinch abundance is correlated with food availability, (b) declines during the period of food shortage and (c) alternative foods, not normally taken, should be exploited over this period.

(2) Which foods may be limiting the present's population distribution and abundance?

3.2 METHODS

3.2.1 Feeding observations

These were obtained during morning and afternoon searches for feeding birds. The study area was covered three to five times each month by different routes (see Chapter 2) and the food, feeding sites, group size (when possible) and foraging height (ground, herb, shrub, tree) of all the birds encountered were noted. Routes where birds where encountered more often were visited two to three times every ten days.

Recording the time that each bird spent feeding on each food item would have been desirable but was not practicable when so many flew off from feeding patches as I approached. Thus, the rule "one bird, one food= one record" (Newton, 1964a) was adopted. Sightings of colour-ringed birds (Chapter 2) suggested that records were obtained from many independent individuals. These records were then combined each month to give the % composition of each food in the diet.

3.2.2 Faecal analysis

Faeces were obtained from samples produced by netted birds, and during feeding observations. If netted birds did not defecate during handling, they were kept in individual cloth bags for up to 5 minutes. Priolo faeces are larger and easily distinguished from faeces of canaries and chaffinches. Fragments in the faeces were identified to species by comparison with previously prepared reference collections. Faeces data are shown in two ways: (1) the proportion of faeces containing each type of food item and (2) the proportion of fragments of each food in relation to the total number of fragments present in the overall sample. All items were first scaled as follows; 1-only one item, 2-two or three items, 3-four or five items, 4-six to ten items and 5-more than ten items. This scale was used in order to standardise observations as most items had between five to ten fragments and

some items, such as fern sporangia and seeds of *Leicesteria formosa*, were present in large numbers (20 to 350 fragments) since a single sporangia or fruit will yield many fragments. Analysis were performed separately for faeces collected from netted birds and from feeding birds. As no significant differences were found the data were grouped.

3.2.3 Distribution and abundance of foods

Plant species in the study area were examined every month and their phenologies noted. In order to relate changes in feeding with changes in abundance of various food plants, I counted the number of seed heads or fruits of individual food plants in 40 x 5 m transects at the stations of routes 6, 8 and 11 (Fig. 2 of Chapter 2). Such changes were examined using Spearman correlation coefficients between abundance and consumption of foods along those routes.

The abundance of seeds taken by Priolo in the various habitat types present in the study area was estimated from 0.25 m^2 plots (n=160 to 260) placed systematically along transects within the area in between route 8 and 11. Seed heads of different species of plants wholly within and also those heads overhanging the quadrat were counted. Very abundant seed heads were estimated by sub-sampling (for tall woody plants I estimated the number of seed heads above the quadrat). The numbers of seeds were then estimated by multiplying these values by the average number of seeds per seed head of 10 seed heads of each plant species. Data obtained in this way (number of seeds per quadrat) was highly skewed. Nevertheless it gives an estimate of seed abundances.

The number of times a food plant species was present in 0.25 m^2, scaled to a percentage, was computed to give an index of patch abundance. This was termed percentage of occurrence. Differences in the occurrence of plant foods between habitat types were examined using chi-square.

3.2.4 Winter food stocks

In order to identify the time of minimum food abundance and provide a measure of the decline of food stocks throughout the winter 40 plots of food plants were sampled (Newton, 1964).

The procedure for each plant species was as follows. *Rubus* sp and *L. formosa*: each plot was formed by marking part of the plant with a numbered plastic strip, which involved the count of, at least, three clusters of fruits per plant. *Vaccinium cylindraceum*: points were located every two meters along transects and the nearest plant with fruits was marked. *Clethra arborea*: two branches (above and below 2 m) were selected from every third tree encountered along transects. *Hedychium gardneranum*: one plant was marked every metre along routes 6 and 11 (Chapter 2). In 1991 the number of fruits previously held by each plant was back-calculated from the structure of the fruit capsules. *Culcita macrocarpa* and *Woodwardia radicans*: every first frond with sporangia, encountered along two transects in route 8 (including Laurel and *C. arborea* stands), was marked .

3.2.5 Does food availability explain Priolo distribution and abundance?

In order to test this hypotheses I have correlated food availability (from quadrats) with bullfinch density (from point counts) and examined changes in feeding behaviour.

To a great extent, *Ilex perado* flower buds are the only food supply available to Priolo from late March to the end of April (see results). Does feeding Priolo significantly reduce this food supply? In the hope of throwing some light on this question I have compared the number of flower buds in exposed and netted branches of *I. perado*. Seven branches, each one in a separate tree and area were netted prior to the start of the bud-feeding period. The number of buds in these and adjacent exposed branches were counted in early March and again in mid-May. A Wilcoxon paired-sample test (one tailed) was

performed to test the hypothesis that the median proportion of buds still present in May in netted branches is higher than that in exposed ones.

3.3 RESULTS

3.3.1 Feeding behaviour

In general, birds obtained their food items directly from the plants and not from the ground. They were seen apparently feeding on the ground 28 times, but on only four occasions were there seeds on the ground for the birds to have picked up; other times they apparently picked up small stones. Most seeds are husked, and only the kernel is swallowed but some very small seeds, such as those of *Epilobium* and *Hypericum humifusum*, are swallowed whole (see Newton, 1967), especially when unripe (i.e. when the seed coat is presumably still digestible). The bill of the Priolo is too short and broad to extract seeds from cones of *Cryptomeria japonica* . Fallen seeds can apparently be taken from the ground, if have fallen in clear openings. Most of the ground seeds were leaf-covered, which must be important to account for the lack of ground-feeding. The bill of the bullfinch is also weak (Newton, 1967) and suitable to bite only into soft seed-heads, fleshy fruits and buds. This readily explains why hard fleshy fruits (of *Juniperus brevifolia*, *Ilex perado* and *Myrsine africana*) and flower buds (*Laurus azorica* and *Pittosporum undulatum*) are not taken by Priolos. When feeding on fleshy fruits the pulp is discarded and the seed is husked. Leaf buds were of marginal importance when compared with flower buds.

Foraging techniques were noted according to finch foraging positions, as defined by Newton (1967a). These varied according to the food plants foraged. Low weed seeds, e.g. *Polygonum capitatum*, were taken while standing on the ground or perching on nearby twigs. All other foods were obtained mainly while clinging to bent stems or perching; hovering was very little used: five feeding records on *L. formosa*, one on *Rubus* sp and two on *Sonchus* sp. Birds also cling to vertical stems of *Scrophularia auriculata* and

Rumex sp, and leaned forwards in *L. formosa*, *Osmunda regalis* and *S. auriculata* but, on several occasions, they could not reach or pick up their foods.

In May, weed seeds, mainly *P.capitatum*, were localised and flocks of up to eight Priolos and communal flocks of Priolos, Canaries and Chaffinches exploited this food supply. In summer most birds were seen feeding singly or in pairs. Feeding patches were approached from cover and food plants around the edge of landslides were exploited before those in the middle.

3.3.2 Seasonal variations in diet

3.3.2.1 Feeding observations

Seeds, leaves, buds and flowers of 39 plant species (Appendix 1) were eaten by Priolos. The majority of the food came, however, from only 12 plant species (Tables 2 & 3). Six main types of food were taken: (1) herbaceous plant seeds in late spring and summer, (2) invertebrates in early summer, (3) seeds from fleshy fruits in late summer and autumn, (4) tree seeds in winter, (5) fern sporangia [FN1] in winter and (6) fern fronds [FN2], moss tips [FN3], leaves and flower buds in spring (Fig. 1).

The majority of the invertebrates taken were *Hemiptera* nymphs hatching in and then emerging from rolled up leaf edges of *Laurus azorica*.. When feeding on *L.azorica* leaves

FN1 In two species, *Woodwardia radicans* and *Culcita macrocarpa*, the birds took the sorus, rejecting the indusium. Indusia formed a conspicuous litter beneath the ferns. The other species taken, *Osmunda regalis*, the sporangia and clustered in fertile pinnules (sometimes the whole fertile pinnule) growing from the middle of the leaf or at the apex. These sporangia are not arranged in sori and do not possess an annulus. For consistency I will use only the term sporangia (except when actual sori were measured).

FN2 The birds took the leaves of *Pteridium aquilinum* and *Osmunda regalis*, from pinnae inrolled when young to fronds of about one month old; although younger fronds seemed preferred. Priolos perched on the stem and took most of the leaves within reach leaving conspicuous bill marks in the part of the leaf attached to the stem. Stems of young *P. aquilinum* were also broken and chewed.

FN3 Priolos took tips of *Polytrichum* sp (especially *Polytrichum commune*). Its leaves are stiff, elongate and tapering gradually to acute points. Only the point with marginal leaves was taken, leaving a conspicuous stem without its point. These marks were present along extensive colonies of this moss.

birds always dropped bits of leaf which suggests that they were taking mostly the insect larva. In fact, counts of leaves with and without marks of Priolos in three heavily used *L.azorica* trees showed a highly significant preference for leaves with rolled up leaf edges (Table 1).

The summer diet was similar in 1991 and 1992 (Table 2). The only marginal difference was a shift in importance of *Prunella vulgaris* and *H. humifusum* from July in 1991 to August in 1992. In contrast, the picture obtained for March to May presented moderate quantitative variations (Table 2). In 1993, the proportion of *C. arborea* in the March-diet was only half of that in 1992 whereas the proportion of *C. macrocarpa* increased sevenfold. From March to April of 1993, tips of moss (*Polytrichum* sp)were 14 times and fronds of *Pteridium aquilinum* were up to five times more important than in 1992 (Table 2).

When the diet was analysed in terms of native and recently introduced species it was found that native species comprise a significant proportion ($P<0.05$) of the monthly records only in two time periods: August/September and April (Fig. 2).

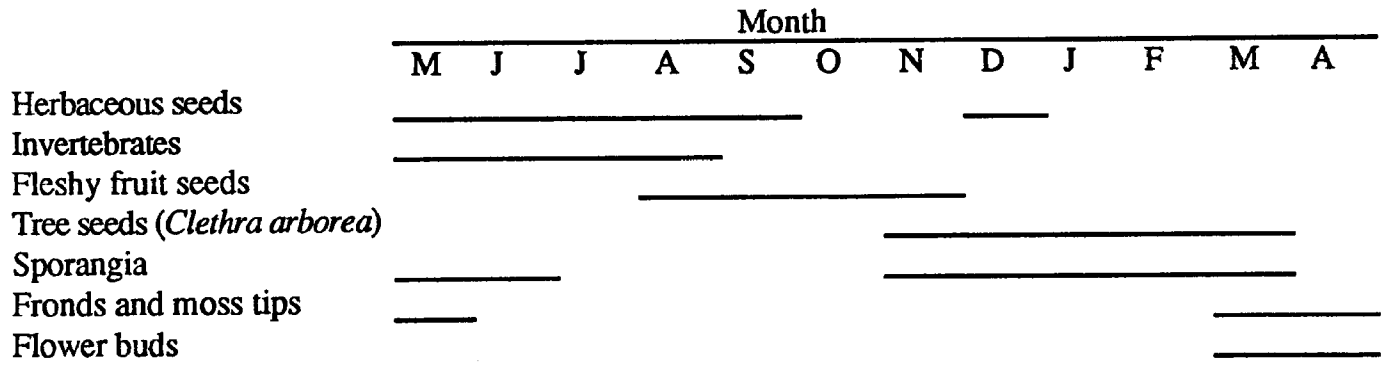


Fig. 1. Seasonal patterns of consumption of the main classes of food.

Table 1. Comparison between marks of feeding Priolos in leaves, of *Laurus azorica*, with rolled up leaf edges (with invertebrates) and without rolled up leaf edges. The figures represent all leaves of a branch heavily used by the birds in each tree. The birds bite mainly in the middle of the leaf leaving an obvious bill mark. A tiny part of rolled up leaf edge is visible on each side of the bill mark.

	No. of leaves with rolled up edges	% of leaves with marks of Priolos	No. of leaves without rolled up edges	% of leaves with marks of Priolo	$\chi 2$ (df=1 with Yates correction)
Tree 1	87	86.2	66	10.6	83.2***
Tree 2	95	84.2	81	7.4	101.1***
Tree 3	100	90.0	70	11.4	103.1***

*** $P<0.001$

3.3.2.2 Faecal analysis

The picture obtained from faecal analysis presents good qualitative agreement with that obtained from observations of feeding behaviour (Tables 2 & 3) although most of the vegetable non-granivorous material cannot be identified. Fresh faeces from fern fronds were dark green and those from buds were light green; both were fine-textured as distinct from the pale brown coarse faeces typical of birds feeding predominantly on fern sporangia and seeds [FN]. Quantitative agreement was less marked. Monthly rank correlations between tables 2 and 3 are all > 0.52 but only July-September ($P<0.02$), November ($P<0.01$), December and February ($P<0.05$) were significant.

Faecal analysis showed also that small amounts of vegetable material and grit are taken regularly. Like the picture given by feeding observations this method showed also that sporangia of *C. macrocarpa* and vegetative material were far more important in the March and April diets of 1993 than in 1992 (Table 3).

3.3.3 Patterns in food production

Figure 3 shows the time period when seeds, sporangia and buds of important food plants were available. In summer all but two herbaceous plants had the bulk of their seed production during a period ranging from 1,5 to 3,5 months. A very few individuals were also flowering in autumn. Only *P. capitatum* and *H. humifusum* showed two distinct fruiting periods. Fleshy fruits were available for about four months. *C. arborea* and ferns had more extended periods of food availability: nine and six months respectively.

Small changes in phenological patterns were observed during the three year study. The initiation and termination of fruiting in most herbaceous and shrub species shifted about 10 to 15 days from 1991 to 1992. Figure 4 shows that from 1991 to 1993 the production of seeds by *P. capitatum* was delayed about 20 to 30 days within and between

[FN] Seed coats appeared highly fragmented. The walls of sporangia appeared broken (some highly fragmented) in the faeces. Tiny bits of fern frond leaves could also be identified. Acute tips of moss appeared orange/yellow.

Table 2. Seasonal variation (% composition in diet) in food consumption (one bird, one food=one record).

Month	M		J		J		A		S		O	N	D	J	F	M		A	
Year	91	93	91	92	91	92	91	92	91	92	92	92	92	92	92	92	93	92	93
No. records	86	57	141	111	202	196	124	158	101	108	55	98	57	83	73	92	81	70	58
Seeds																			
*Polygonum capitatum**	44	25	57	66	39	49	3	6		1	1	8	33						
Luzula purpureo splendens	4		2	2	2	2	2	2											
Sonchus sp		2	5	2	2			<1											
Hypericum humifusum			2		9	3	7	7	3										
Prunella vulgaris					24	17	8	18	<1										
Potentilla erecta					6	6	5	2	1	1									
Leontodon filii					1		10	38	36	34									
Vaccinium cylindraceum					2	1	41	10	6	14	7								
Leicesteria formosa *					1		12	7	14	22	60	34	7						
Rubus sp +							5	3	27	20	18	10							
Clethra arborea *							2		8	3	10	14	37	47	63	57	31	22	3
Other species [a]	3	2	5	1	4	8	2	4	1	2		2	2	10	5	2	6	3	1
F.Buds (fb), Leaves (l), Sporangia(s)																			
Ilex perado (fb) FN	9	21												4	3	29	9	66	60
Pteridium aquilinum (l)*	6	26	2													1	1	5	25
Osmunda regalis (l)	8	7	2	4															
Osmunda regalis (s)Fn	13	2	11	12		2					2	26	12	13	9	2	2		
Woodwardia radicans (s)												4	9	23	13	5	35	3	7
Culcita macrocarpa (s)															2	1	14		2
Polytrichum sp (l)																			
Other species (l & ovules) [b]	6	10	7	1	6	3	2	2	4	3	2	2		3	5	3	2	1	2
Invertebrates	7	5	7	12	4	9	1	1											

a especially *Epilobium obscurum*, *Sagina* sp, *Scrophularia auriculata*, *Rumex* sp, *Cyperaceae*, *Cryptomeria japonica*, *Hedychium gardneranum*, *Calluna vulgaris*, *Erica azorica* and three species of grass.

b especially*Vaccinium cylindraceum*, *Leicesteria formosa*, *Scrophularia auriculata* (ovules), *Pinus* sp, *Cryptomeria japonica*, *Juniperus brevifolia*, *Hygrangea macrophyla*, two species of tree trunk moss and two species of grass.

* recently introduced species.

\+ two species were present: *Rubus ulmifolius* s s. and *Rubus hochstetterorum* (endemic).

FN *Ilex perado* is dioecious, i.e. sexes are present in separate trees. Mostly male flowers appeared to have been taken but no distinction was made during feeding observations.

Fn Fertile pinnules growing from the middle of the leaf were densely covered by sporangia. At first these were green and then became brown. Only green sporangia were taken. Spores are released in the brown phase.

Table 3. Diet quantification from faecal analysis. (A) % of faeces that contained each food item. (B) % composition in relation to the number of fragments present in feaces (see methods). For the period June - September two to four faecal samples from 1991 were included in the analysis.

(A)

Month	M	J	J	A	S	O	N	D	J	F	M		A		M
Year	91	92	92	92	92	92	92	92	92	92	92	93	92	93	93
No. feaces	4	23	27	16	13	9	14	12	13	7	14	37	31	89	42
Seeds															
P. capitatum	100	78	89	56	7	11	29								17
L. p. splendens		4	11	6											
Sonchus sp		4													
H. humifusum			7	19											
P. vulgaris			15	19											
P. erecta			19	19	8										
L. filii			4	81	54	22	7								
V. cylindraceum				31	54	67	7					5		4	
L. formosa				56	69	100	93	50							
Rubus sp				6	39	67	29	8							
C. arborea						11	21	33	92	86	79	22	19	4	
Other species			4	19			7	8							7
Unidentified		13	19	32	31	22	7	8			7	5		3	7
Sporangia															
O. regalis	50	65	48												
W. radicans					8		93	83	39	14		8			
C. macrocarpa							21	42	100	57	79	97	42	36	
Veg. remains	25	48	41	6	8			25	46	57	57	65+	93	98	98
Invertebrates		9	4	6	8										
Grit		17	11	44	54	33	36	42	54	29	64	38	16	42	10

+ of these 51% were from *Polytrichum*.

(B)

Month	M	J	J	A	S	O	N	D	J	F	M		A		M
Year	91	92	92	92	92	92	92	92	92	92	92	93	92	93	93
No. fragments		197	243	180	137	103	190	166	157	59	129	363	207	695	232
Seeds															
P. capitatum		41	42	19	1	1	10								7
L. p. splendens		1	3	1											
Sonchus sp		2													
H. humifusum			2	4											
P. vulgaris			5	4											
P. erecta			3	2	1										
L. filii			2	30	18	2	1								
V. cylindraceum				6	19	22	2					1		1	
L. formosa				15	29	44	33	12							
Rubus sp				3	10	22	7	1							
C. arborea						2	3	5	19	30	23	9	8	2	
Other species			<1	2			2	1							2
Unidentified		4	5	7	6	3	1	2			7	1		<1	1
Sporangia															
O. regalis	30	38	27												
W. radicans					4		33	30	17	9		4			
C. macrocarpa							6	9	41	34	42	49	26	20	
Veg. remains	11	13	10	1	4			4	14	22	23	29+	64	63	87
Invertebrates		<1	<1	<1	<1										
Grit		1	1	6	8	4	2	6	9	5	10	7	2	14	3

+ 0f which 23% were from *Polytrichum*

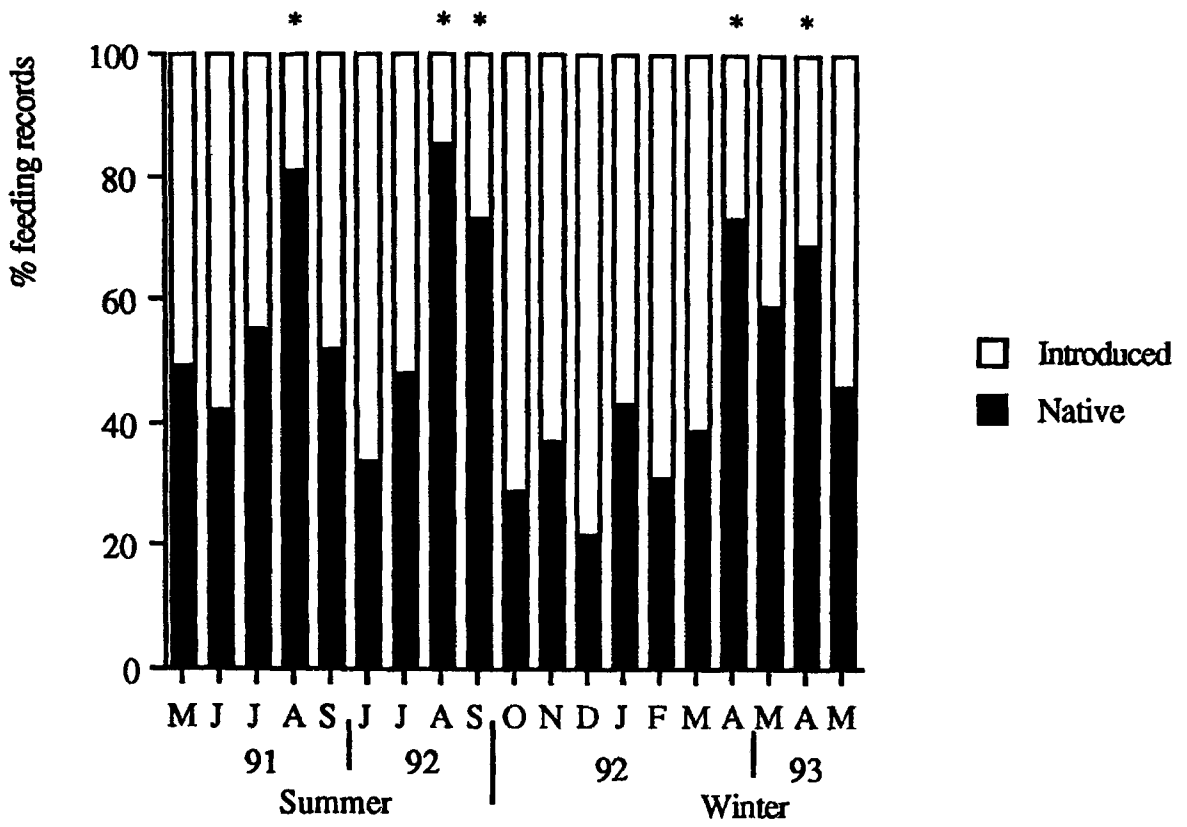


Fig. 2. Percentage of feeding records in introduced and native flora. The asterisk shows the months in which the percentage of records in native flora was significantly higher than those in introduced flora ($P<0.05$, chi-square, df=1 with Yates correction).

high and low altitudes. At high altitudes (600 to 750 m), where birds are present throughout the year and breed, *P. capitatum* produced seeds about one month later (Fig. 4).The sequence of species fruiting remained the same. Fruiting periods overlapped as the number of fruits of one species decreased and the number of another increased.

3.3.4 Seasonal variations in food abundance per habitat type

Table 4 documents seasonal variation in the abundance of food resources per habitat type. It shows that food species varied among habitat types both within and among sampling periods. No foods were detected in either *C. japonica* plantations or *P. undulatum* copses although some plantations of *C. japonica* had an understorey of *C. arborea.*

When compared with Laurel forest, open habitats had the majority of feeding resources in summer; more than 3 times as many seed-bearing plant species were found there than in Laurel forest ($G=5.7$, df=1, $P<0.05$). From the nine plant species that

provided at least 5% of the diet in summer only *V. cylindraceum* and *O. regalis* were present more often in Laurel, though the proportion of quadrats with *O. regalis* did not differ significantly between habitats.

In August 1992, the differences in the occurrence of *P. capitatum*, *Leontodon filii* and *L. formosa* between habitats were not significant, presumably because many fruits had already been predated in some habitats. However, for *L. formosa* and *Rubus* sp, quadrats in August/September 1991 show that the edge of the forest held significantly larger crops of these fleshy fruits than other habitats (Table 4). Such a pattern may be difficult to reveal once fruits start to be predated, especially if birds feed selectively amongst habitats.

The winter and spring picture is rather different. As all fleshy fruits were practically over by December the large majority of the feeding resources became increasingly concentrated in areas of laurel forest. In March, and especially in April, the important feeding resources were restricted almost entirely to the endemic forest (Table 4).The overall monthly mean number of plant species that comprise more than 3% of the diet fell from 2.84 in the summer to 1.25 in the winter as almost all preferred herbaceous seeds declined to extinction. It is apparent from table 4 that total food abundance declined over winter and reached a minimum in late March/early April.

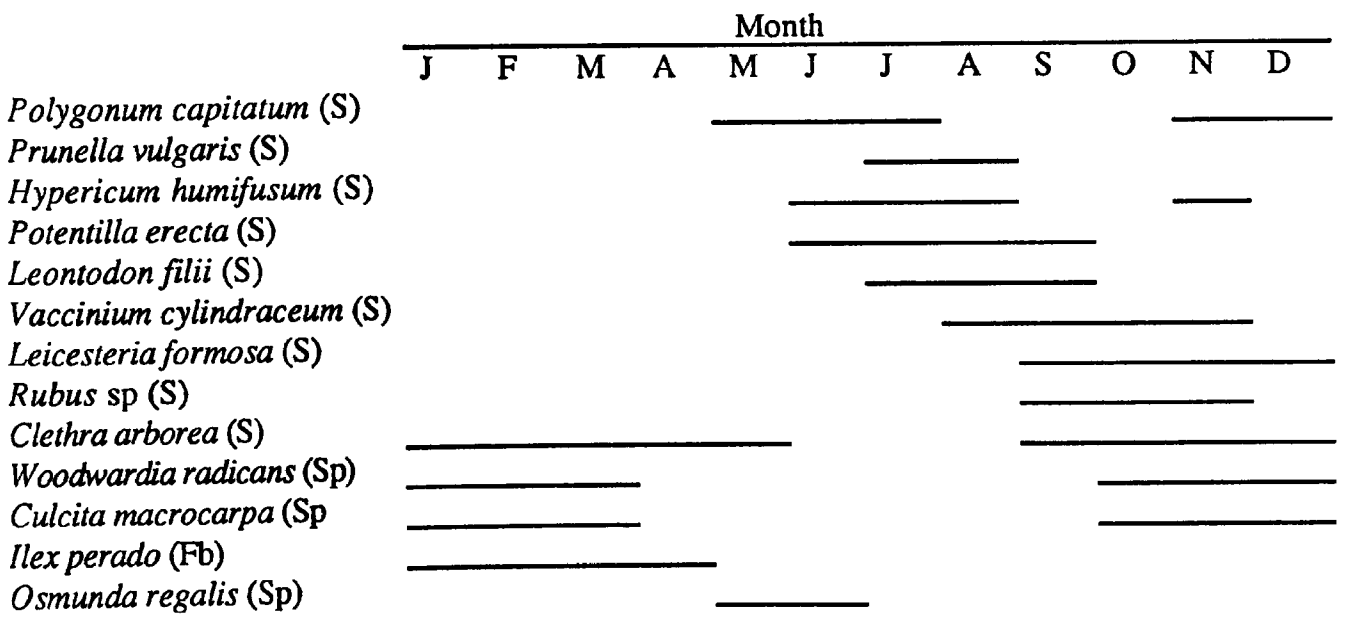


Fig. 3 Annual patterns of seed (S), sporangia (Sp) and flower bud (Fb) availability. Only plants that comprised more than 5% in the diet are shown.

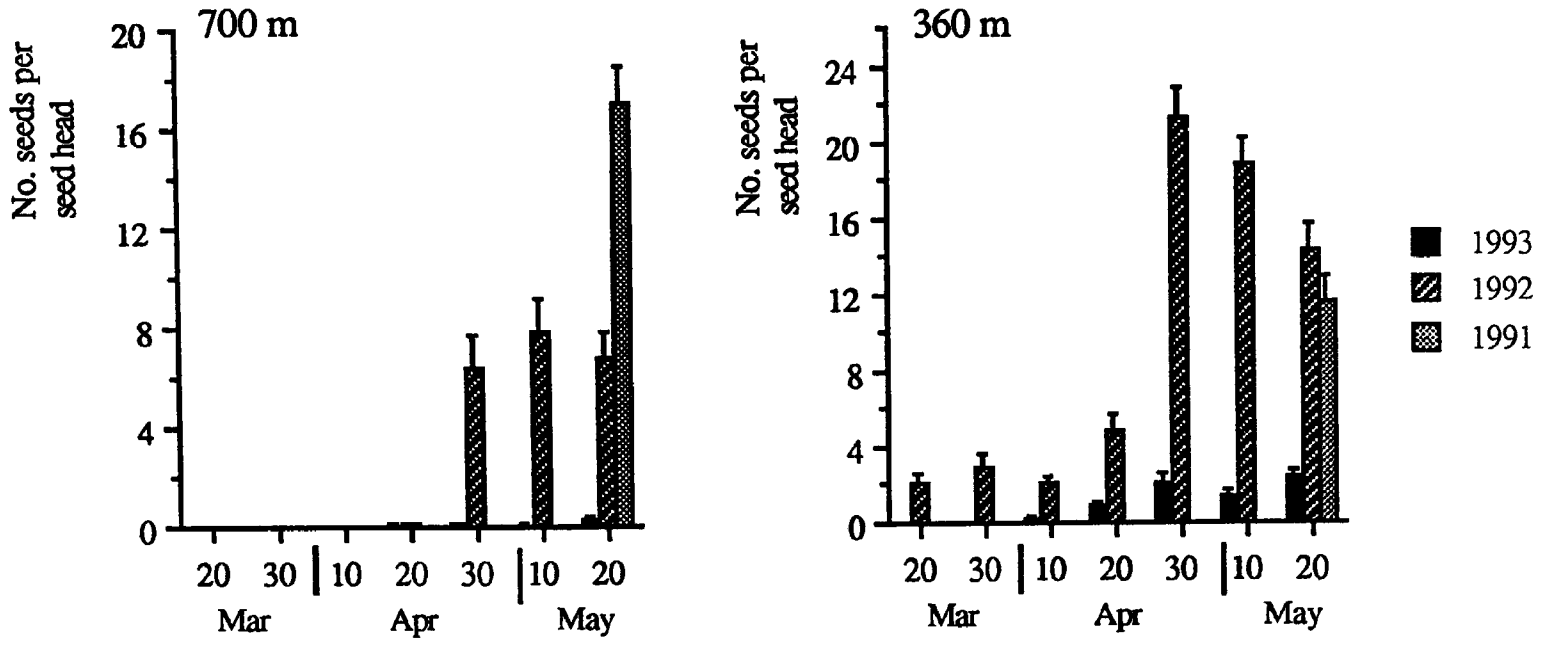


Fig. 3. Pattern of seed production by *Polygonum capitatum* at two different altitudes. Values are mean number of seeds per seed head ± S. E. (n=25).

3.3. 5 Foraging in relation to changes in the availability of foods

Availability of foods influenced diet as birds fed opportunistically on new plants as they came into seed. Most resources were taken from the time they first became available. In fact, seeds of most species, either from herbaceous plants or fleshy fruits, were consumed even before they were ripe. Only in *Potentilla erecta* was I able to note a lag phase of approximately 10-15 days between the seeds becoming available and the time the birds started feeding on it.

In summer, the number of available plant species with seeds, in each 15 days period, that Priolos were likely to utilise, and the number of species consumed were significantly positively correlated both in 1991 and 1992. (Fig. 5). Clearly, birds tracked the major resources to a great extent. This kind of association was also significant for summer and early autumn when important feeding resources were considered individually. Priolo fed mostly on *P. capitatum* (1991: rs=0.92, n=6; 1992: rs=0.89, n=7, both $P<0.03$), *P. erecta* (1992: rs=0.97, $P<0.05$, n=5), *V. cylindraceum* (1992: rs=0.89, $P<0.04$, n=6) and *Rubus* sp (1992: rs=0.93, $P<0.04$, n=6) during the months when they

were most abundant (Fig. 6). Some other associations were apparent but the data were insufficient to test, namely *P. vulgaris* and *L. filii* which were present in the habitat for two to three months only. Seeds of *H. humifusum* were consumed in July and August but not in November when *H. humifusum* had a second fruiting period. Uncommon foods e.g. seeds of *Cyperaceae* ssp were consumed sporadically.

The relationship between food consumption and abundance was not significant for *L. formosa* (1992: rs=0.6, P<0.18, n=6; Fig. 6) because, in late autumn, when the abundance of fruits decreased, it was still highly consumed. Fruits of *L. formosa* remained on the plants for longer because: (1) It fruited later than the two other fleshy fruits and (2) its fruits are presumably more difficult to get as birds had to hover to get them. Hovering was quite common in late autumn when birds took the last remaining fruits on the plants.

Table 4. Frequencies of occurrence of plant species, that contributed > 5% in the diet, in different habitat types and (in brackets) the number of seeds /0.25 m^2 (for *Osmunda regalis* this is number of fertile secondary pinnules, for *Woodwardia radicans* and *Culcita macrocarpa* number of sori, and for *Ilex perado* number of flower buds) . Frequency of occurrence is the proportion of times a food plant species occurred in 0.25 m^2 quadrats. Chi-square tests were carried out on these measures. Sample size in 1991 varied between 160 and 260 quadrats. In 1992 it was 200.

(A) Summer

	Laurel	Lanslide	Stream bank	Road	Roadside wall	Forest edge	P< (χ2)
1991							
Jul							
Polygonum capitatum			37 (240)	6 (35)	10 (79)		0.001
Prunella vulgaris		1 (3)	5 (20)	9 (88)	9 (37)		0.001
Hypericum humifusum		1 (41)	1 (7)	22 (187)	<1 (<1)		0.001
Potentilla erecta	2 (<1)	11 (28)	10 (13)	3 (2)	41 (59)		0.001
Aug/Sep							
Pprunella vulgaris		<1 (1)	1 (3)	9 (19)	1 (1)		0.001
Hypericum humifusum		<1 (6)		24 (505)	<1 (1)		0.001
Leontodon filli		13 (233)	9 (199)	<1 (4)	7 (79)		0.001
Leicesteria formosa		4 (247)	5 (210)		3 (123)	36 (1371)	0.001
Vaccinium cylindraceum	5 (45)						
Rubus sp	3 (10)	6 (29)	1 (4)		10 (79)	11 (81)	0.001
1992							
Jun							
Osmunda regalis	3 (90)	3 (150)	2 (32)		1 (65)		NS
Polygonum capitatum			20 (88)	5 (9)	12 (96)	42 (361)	0.001
Aug							
Polygonum capitatum			7 (6)	5 (10)	7 (8)		NS
Hypericum humifusum		1 (7)		8 (112)			0.01
Prunella vulgaris		1 (2)	2 (7)	33 (103)	4 (3)		0.001
Leontodon filli		14 (104)	10 (50)		9 (88)		NS
Vaccinium cylindraceum	4 (6)						
Leicesteria formosa		1 (1)	2 (10)		1 (4)		NS

(B) Winter

	Laurel	Landslide	Stream bank	Road	Roadside wall	Forest edge	P< (χ2)
1992							
Oct							
Vaccinium cylindraceum	4 (2)				<1 (<1)		
Leicesteria formosa		6 (38)	6 (63)		8 (84)	12 (153)	NS
Rubus sp		3 (2)			7 (6)	6 (7)	NS
Clethra arborea	14 (99)						
Dec							
Leicesteria formosa		<1 (<1)					
Clethra arborea	9 (61)						
Culcita macrocarpa	10 (558)	1 (<1)					0.001
Woodwardia radicans	5 (337)	6 (1180)	2 (625)		2 (133)		NS
Polygonum capitatum			12 (15)		6 (4)	+	NS
Jan/Fev							
Clethra arborea	12 (62)						
Woodwardia radicans	4 (24)	5 (56)	3 (12)		5 (22)		NS
Culcita macrocarpa	10 (88)	2 (11)			2 (29)		0.001
Mar/Apr							
Clethra arborea	13 (57)						
Ilex perado	16 (47)						

+ Not sampled. NS=Not significant.

Fig. 5. Relationship between the number of seed plant species consumed by Priolo in summer and the number available that the Priolo was likely to utilize in 15 days period.

The changes showed by marked plants in winter should parallel the changes occurring in the food-stocks of the study area. The SEs (Table 5) on most of the samples were small suggesting that the method was adequate for all plant species except, perhaps, *C. macrocarpa*. In fact, sporangia of *C. macrocarpa*, were still found in the faeces in April when they were no longer available on the marked plants.

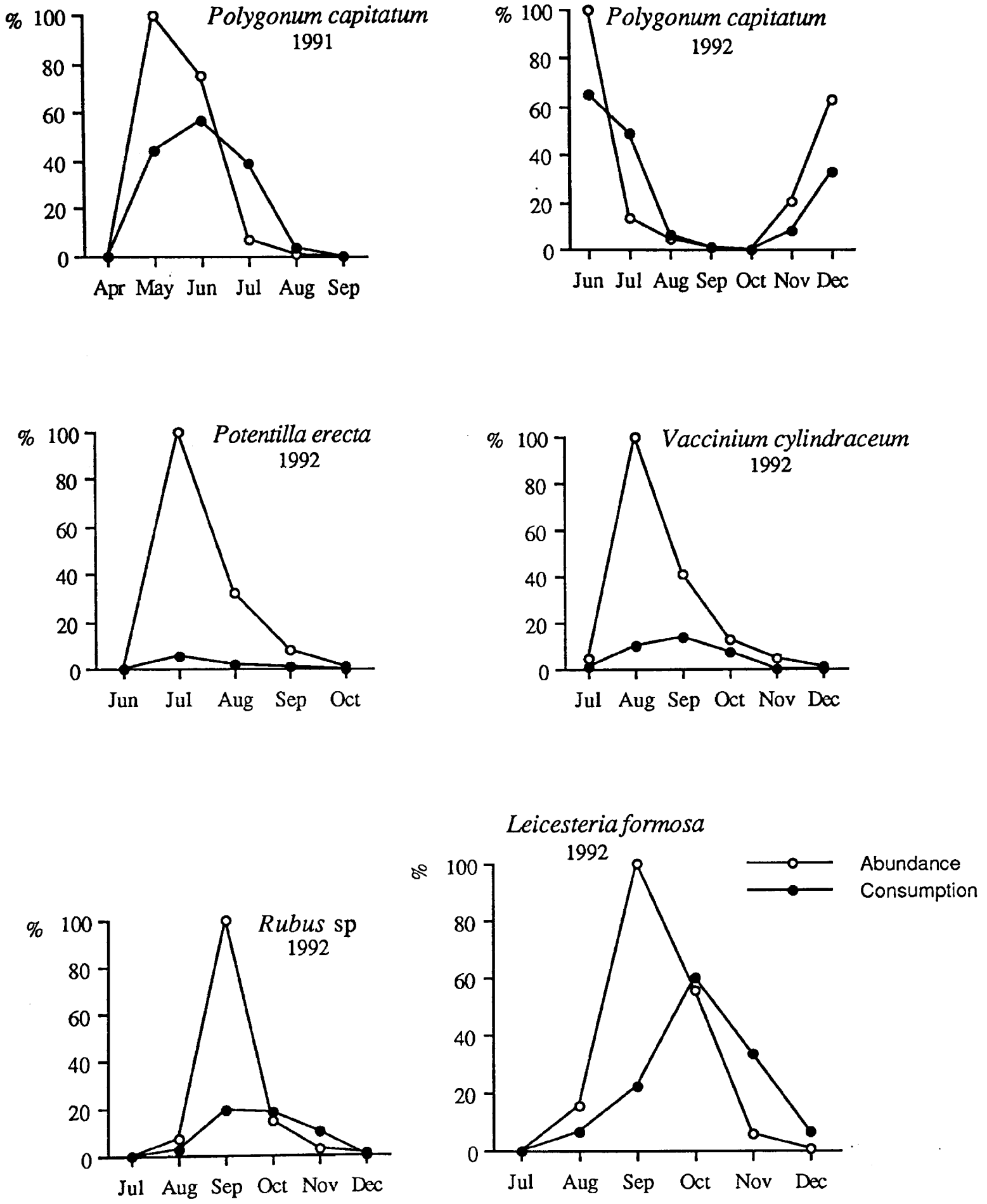


Fig. 6. Relation between abundance and the degree of consumption of important summer and autumn foods. Consumption is indicated by the percentage of the food plant in the feeding records. For abundance the highest monthly record was given 100% and the other ones were scaled accordingly (Grant & Grant, 1980).

For plots of fleshy fruits, *V. cylindraceum*, *Rubus* sp and *L. formosa* , marked at the end of September 1991 no seeds were left by January 1992. During the same time period the seed stock of *C. arborea* had fallen by 30% (Table 5). Marked plots of fleshy fruits at August/September of 1992 showed a high depletion rate of all three fleshy fruits species in the first month: 0.74, 0.80 and 0.65 (Table 5). Chaffinches and especially blackcaps fed extensively on fleshy fruits and can be regarded as Priolo competitors for these foods. Three lines of evidence suggest that fleshy fruits were highly preferred: (1) Fruits were taken rapidly and even when unripe; (2) Very few fruits were observed to rot on the forest understorey; (3) Birds were observed feeding on fruits when they were very scarce in late autumn.

Seeds of *H. gardneranum* were rarely taken even when they were abundant from November to January. On two occasions birds were observed taking one seed and then flying away to feed on sporangia of *W. radicans*. It soon became apparent that birds were selecting larger *C. arborea* fruits (see seed selection). Thus, if the smallest fruits (less than 2.5-3.0 mm) are discounted, about 35% of the seed stock was still available for Priolos in April 1992 and 23% in April 1993 (Table 5), though after the 9th of April these seeds were not recorded in the diet of Priolos. Were Priolos largely responsible for the decline in *C. arborea* seeds? Many seed clusters fell during heavy rain and winds. Chaffinches and canaries also fed on seeds of *C. arborea*, but mainly in January and February. Before January they took mainly seeds of *C. japonica* and, in March, started feeding on seeds of herbaceous plants.

Marked plots of ferns indicated a rapid decline of sporangia from January onwards to almost complete extinction in April (Table 5). The birds foraged on 45% and 87.5%, respectively, of the *C. macrocarpa* and *W. radicans* fertile pinnules marked (n=40). This difference was highly significant ($\chi 2=14.31$, df=1 with Yates correction). Since *W. radicans* does not mature earlier than *C. macrocarpa*, this suggests that only when the former was less available did Priolos fed on the latter. Fern sporangia are an ephemeral

food supply; once open the spores are released and, as a consequence, their nutritious value is lost. A much lower proportion of *P. aquilinum* was taken than would be expected from its abundance. Along stations one to two of route 11, in a 0.5 m strip, only 21 out of 478 (4.4%) fronds showed signs of having been fed on by Priolos, whereas along stations six to seven of route 8, 82 out of 404 fronds (20.3%) were pecked. This discrepancy was probably only a reflection of the number of birds involved. Many fronds of *O. regalis* were also not taken (see fern selection; Chapter 6). Thus, overall, fern consumption seemed to depend on the availability of much preferred foods. This was specially so for fern fronds.

Table 5. Decrease in food stocks along the winter. Values are % of mean items present each month and SE (in brackets) from 40 marked plots. Small fruits of *C. arborea* refer to fruits with less than 2.5 - 3.0 mm in diameter.

	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Vaccinium cylindraceum 1992	100	25 (4.4)	8 (2.1)	2 (0.8)	0.3 (0.2)				
Rubus sp 1992		100	20 (5.2)	5 (1.6)	0.8 (0.4)				
Leicesteria formosa 1992	100	35 (5.3)	7 (2.4)	3 (1.9)					
Clethra arborea 1991/1992	100				70 (5.1)	59 (5.7)	46 (6.1)	41 (6.1)
- All fruits									
Without small fruits						51 (5.2)	38 (5.6)	32 (5.7)	
Clethra arborea 1992/1993		100	97 (0.5)	92 (1.3)			31 (5.4)	29 (5.2)	
- All fruits									
Without small fruits							25 (5.1)	23 (5.0)	
Hedychium gardneranum		100			47 (6.4)	11 (3.3)	0.8 (0.6)	0	
Woodwardia radicans 1992/1993		100	76 (12.3)	74 (13.1)			13 (8.2)	0	
Culcita macrocarpa 1992					100	67 (8.9)	29 (9.2)	0.2 (0.2)	
Culcita macrocarpa 1992/1993			100	99 (0.5)			35 (9.0)	5 (3.8)	

3.3.6 Does food supply explain the Priolo distribution and abundance?

There was a significant positive correlation between the monthly number of bullfinches in transect counts (n=6) and: (1) the number of plant species that comprised more than 5% in the diet (r_s=0.93, P<0.05) and (2) the mean number of seeds and buds in 0.25 m^2 quadrats (r_s=0.94, P<0.01; Fig. 7). Ideally, I would need biomass density to compute these correlations. When sori were included the correlation was not significant (r_s=0.46, P<0.25) but these are expected to have low biomass. The correlation with the frequency of occurrence of plant species in quadrats was nearly significant (r_s=0.82, P<0.06). These measures of food abundance should reflect seasonal variations in food availability, suggesting that variation in food supply explains major variations in Priolo abundance. My regular quadrat sampling and marking of individual plants established the time of minimum seed and sporangia availability to be March/April. Priolo abundance was lower at this time and mortality of first-year birds appeared to have been greater (Chapter 5). Such parallels suggests that food may be limiting in late winter.

Furthermore, the median proportion of flower buds still present in May in netted branches was significantly higher than that on exposed branches (Wilcoxon paired-sample test, T=1, P<0.02, n=7; Fig 8). Losses were not only caused Priolo predation. Parasites were probably present and could easily enter the net. Despite this, the number of buds on netted branches remained up to four times higher than numbers on exposed branches .

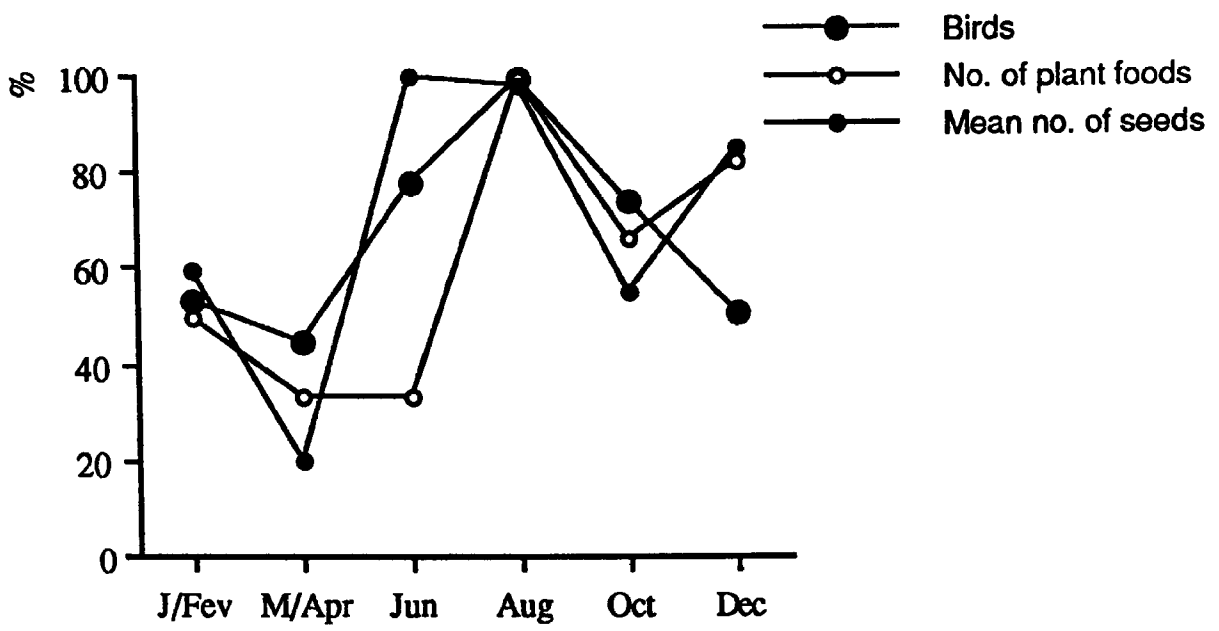


Fig. 7. Relation between the number of Priolos recorded in transect counts and two measures of food abundance in the area: the number of plant species that comprised more than 5% in the diet and, the mean number of seeds and buds in 0.25 m^2 quadrats. All Figures are represented as follows: the highest monthly record was given 100% and the other ones were scaled accordingly (Grant & Grant, 1980). It should be noted that the increase in the proportion of birds from M/April to June, when they were not breeding (Chapter 5), suggests that some birds were feeding elsewhere in April, so marked routes did not reflect the whole picture. Birds could also be less conspicuous in March/April when they were feeding on flower buds in dense forest.

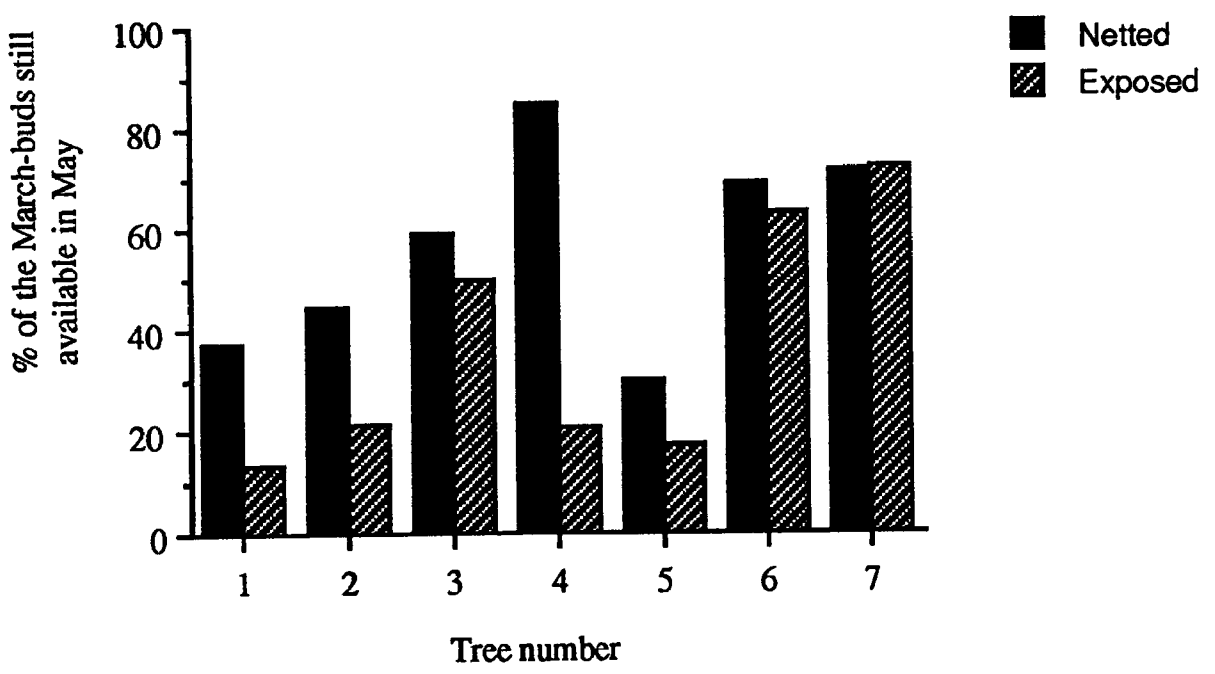


Fig. 8. Comparison between the percentage of March flower buds still available in May in netted and exposed branches.

3.4 DISCUSSION

3.4.1 Diet: which method to assess it?

All methods of assessing diets have their problems. Bullfinches feed above the ground most of the time and the plants exploited can be easily quantified (Newton, 1967). Single point observations may overlook conspicuous foods, and, second, miss rare foraging behaviours. I covered a large area regularly and obtained records from many individuals (as suggested by sightings of colour-ringed birds), thus minimising bias. This method is preferable to sequential observations in the sense that it approximates a sample of independent foraging observations, although I obtained some observations on the same individuals on different occasions. Morrison (1984) and Wagner (1981) employed both methods on insectivorous passerines and obtained virtually the same results. Each of my monthly sample periods included more than 40 observations, thus exceeding the minimum sample size recommended by Brennan & Morrison (1990) to reach stability of means and variances.

Since different seeds have coats of different hardness and are digested at different rates (Newton, 1967) faecal analysis may overestimate the importance of hard seeds (perhaps especially *P. capitatum* and *L. formosa*) and underestimate soft seeds (especially *C. arborea*). It may also emphasise items like fern sporangia because a single one contains many spores. Faecal analysis has been used successfully in several studies (e.g. Waugh & Hails, 1983; Ralph *et al*, 1985). Neither direct observations nor faecal analysis may elucidate the true proportion of animal foods in the diet of Priolo. The importance of *Hemiptera* emerging from *L. azorica* leaves was clearly established because of their conspicousness.

The comparison of feeding observations with faecal analysis showed that seeds of herbaceous plants are likely to be less important than measured by direct observations whereas seeds of fleshy fruits and sporangia should be more important because of their occurrence, respectively, in open areas and dense forest. Foods occurring in dense forest

are still recorded regularly in the faeces about two to three weeks after I had stopped seeing the birds feeding on them. Thus, both methods are necessary to get an overall low-bias diet picture.

3.4.2 Diet: comparison with other bullfinches

Fern fronds and sporangia and moss tips are the main differences between Priolo's diet and that of other bullfinches. To my knowledge, fern feeding has never been reported for other bullfinches though across its Asian range there is very little information on foods (Newton, 1967). Also, small size items, such as seeds of *Hypericum* (0.5 mm), were more important in the diet of the Priolo than in that of British Bullfinches (Newton, 1967). The simplest explanation for this difference is that, being an island, S. Miguel has a reduced plant community and, therefore, less resource diversity. This also helps to explain why the Priolo explores alternative food supplies such as ferns and moss.

Previously, only Newton (1967) had assessed quantitatively the diet of bullfinches throughout the whole year. Other diet assessments were carried out only for the autumn and/or winter seasons (Summers, 1981; Crocker, 1987; Snow & Snow, 1988). Other observations were made across Europe but they are qualitative or semi-quantitative (Erkamo, 1948; Eber, 1956; Sokolowski, 1958; Wright & Summers, 1960; Maheo, 1965; Dement'ev & Gladkov, 1970; Noval, 1971).

With the exception of fern and moss feeding, the registered seasonal pattern of food consumption by Priolo is very similar to the one observed throughout Europe: seeds of herbaceous plants and invertebrates in late spring and summer, seeds from fleshy fruits in autumn, tree seeds in winter and flower buds in spring. Variations in this pattern seem to depend largely on differences in available plant species between habitats and seasonal availability of food types. For instance, Newton (1967) found weed seeds to be more important in open habitats than in woodland areas; the opposite happens with invertebrates. In autumn bullfinches feed on fleshy fruits as long as they are available; In Russia

(Dement'ev & Gladkov, 1970) and in the Azores (this study) seeds of *Vaccinium* are important. In England, Newton (1964) and Snow & Snow (1988) found *Rubus* to be of most importance but, again, this varied between locations (Crocker, 1987).

Flower buds of various deciduous and conifer trees are taken in Northern and Eastern Europe, in England mainly *Crataegus monogyna* and in Spain (Noval, 1971) and Japan (Numatwa, 1989) *Prunus* sp. There is an endemic *Prunus* in the Azores, *Prunus lusitanica* ssp *azorica*, but is now extremely scarce. All over Europe, Bullfinches eat the flower buds of a wide range of cultivated fruit trees: apples, pears, cherries, plums and gooseberries as long as the orchards are close to forest cover (Wright & Summers, 1960; Newton, 1964; Matthews, 1983). Flower buds of pear, orange and peach trees were also taken by Priolo when orchards were common in Eastern S. Miguel (see Chapter 1).

Such a strong similarity in diets suggests that all bullfinches possess similar physiology and feeding behaviour and that their distribution and abundance may be explained by similar environmental factors. Although bullfinches seem to feed opportunistically they are less versatile in terms of foraging positions and take less food from the ground compared with other finches (Newton, 1972). They are more specialised and have complex diet requirements depending on many plant types. In terms of conservation, a mosaic of vegetation types is necessary to supply all these foods. In the Azores, the montane forest is the only ecosystem that presents such a structure (This study, Haggar, 1988).

3.4.3 Food supply

My results of seasonal variations in diet are similar to those found in other studies of oceanic island birds. For instance, Galapagos finches showed significant differences in diet and foraging behaviour between the wet season and the dry season (Smith *et al*, 1978). Also, the Priolo responded similarly to the environmental changes in food, mainly by moving to new plant species and foraging locations, but still using the same foraging

techniques, rather than adjusting its foraging behaviour to, for example, feed more on the ground.

My data spanned only two or three years and interpretation of annual patterns is, therefore, tentative. Substantial changes were noted in the proportion of total foraging on seeds and flower buds and other foods, from foraging primarily on seeds and flower buds in March 1992 to moss tips and fern fronds in March 1993. Similarly, Galapagos finches fed primarily on soft seeds in March 1976 but changed to *Opuntia* buds, flowers and nectar in March 1977 and to insects in March 1978 (Boag & Grant, 1984). Monthly and yearly variations in diet are a major characteristic of most avian-habitat relationships (e. g. Newton, 1967; Wiens et al, 1987; Hejl & Verver, 1990; Szaro et al, 1990; This study) and must be taken into account in order to obtain ecologically significant patterns.

Two useful diet predictions of the foraging theory are: (1) animals should generalise diets as food becomes scarce and (2) less profitable foods should be included in the diet as food availability declines (Stephens & Krebs, 1986). The Priolo did not select foods in the proportions in which they occurred in the environment although most resources were exploited. Also, small seeds such as those of *Hypericum* (0.5 mm) were a quite important feeding resource in June and July when they were most abundant. This contrasts with Newton's (1967) observations of Marley wood Bullfinches in which the proportion of the various seed species in the diet were not related directly to their availability. Many common plants were not exploited and seeds smaller than 1 mm (such as those of *Hypericum*) were of little importance in the diet. Some fern species, especially *P. aquilinum*, were common in Wytham but were never recorded in the diet of Bullfinches (Newton, pers. comm.).

Therefore, using a comparative approach between habitats it appears that bullfinches generalise their diet in the habitat with less feeding resources which is consistent with prediction (1). Prediction (2) seems also to be supported as fern fronds and mosses were included in the diet when seed and flower bud abundance declined. Reduced feeding resources in the island habitat helps to explain why the Priolo tracked foods to a

great extent. Assuming that predation is minimal these results raise the possibility that the Priolo population fluctuates seasonally and annually in accordance with seed abundance. Apparently this has been so for the Galapagos finches (Grant & Grant, 1980; 1980a; Grant, 1986; Schluter, 1982). With most available food resources being apparently fully exploited in the summer of 1991 and 1992, the Priolo density seems to represent an approximate ceiling in those years.

Does this imply that the Priolo distribution and abundance are explained by food supply? In this study I obtained circumstantial evidence for this hypothesis : (1) changes in relative densities of foods in habitat types were matched by shifts in the occurrence of Priolo; (2) the seasonal abundance of the Priolo increased and declined seasonally, in accordance with the availability of its foods; (3) Although fern fronds and moss tips were abundant throughout the year they were only taken when preferred foods (seeds and sporangia) were least abundant. Thus, is this population limited by food availability ? Most of the debate of this kind arises from the question: what kind of evidence is necessary to show that this factor is the causal one in limiting populations? Convincing data would be obtained with food supply experiments (Newton, 1980). I have shown that the food supply was at its lowest in the end of the winter. Mortality of first year birds appeared greater in this period (Chapter 5). Overall mortality was lower in 1991/92 than in 1992/93 (Chapter 5), in which larger flower buds and herbaceous seeds (Chapter 4) became available later. These parallels raise the possibility that some foods may be limiting in late winter. Newton (1964) came to the conclusion that seed shortage seems to control the Bullfinch population in Marley wood, Oxford: heavier mortality was detected during years of seed shortage. In the winter of 1961/62 and 63/64 the ash and bramble crop ran out by January and from then onwards flower buds were the main food whereas in 1962/63 seeds of bramble, dock and ash were still plentiful in April and birds had not taken flower buds in quantity until March.

I am aware that other factors such as parasites may also play a role in limiting populations. There is no reason to believe that they should be important for the Priolo. No ectoparasites were detected in the specimens examined. In addition, faecal samples from 22 different individuals were examined for parasites by Prof. Ali Anwar but none was detected.

What foods may be limiting the present abundance of the Priolo? From the complexity of the seasonal changes in proportions of different seeds and fruits and the use of vegetable material by Priolo it seems that this question is not answered simply on the basis of food availability. In March, feeding wild birds showed signs of being very hungry, even in the evening; they had their wings drooped, feathers puffed out and were very approachable. These observations suggest that, in March, both *C. arborea* and *C. macrocarpa* may not be adequate foods (nonetheless, the introduction of *C. arborea* may have improved winter survival). Historical records corroborate this view. In the 60's birds were seen feeding on peach and pear flower buds in March at lower altitudes along streams (Açores, 1970; Mendonça and others, pers. comm.). Then the population of *C. arborea*, which was introduced around 1960, was much smaller and the population of large ferns as well as other native species must have been greater. An immediate reason for such long distance movements is that the food supply at higher altitudes was not adequate.

Newton (1964) presented circumstantial evidence that the onset of flower bud-feeding by Bullfinches in Marley wood, Oxford, depends on the availability of winter seed stocks, especially ash, which in Marley acted as a buffer. He demonstrated that, in January, British Bullfinches cannot maintain their weights solely on flower buds. Summers (1981) obtained a negative correlation between the % of Bullfinch guts containing ash seeds and the amount of damage done to Conference trees, a highly preferred pear cultivar, for the years 1969/75. This gave further support for the link between flower bud feeding and scarcity of ash seeds. However, this relation is not simple and seems to hold only for early winter. (1) In fact, Summers' correlation was significant only for January. (2) This

study and Newtons' (1964) observations show that, although there may be no shortage of seeds Bullfinches much prefer flower buds in Spring. (3) Substantial damage to cultivars has been recorded even when winter seed stocks are abundant (Flegg & Matthews, 1979, 1980), although this happened during a warm winter, i. e. buds swelled earlier.

Thus, winter food selection (Chapter 4) is of considerable importance because it may be that the existing foods are insufficient to meet the minimal Priolo requirements. Nevertheless, *I. perado* exposed branches had significantly lower numbers of flower buds at the end of the bud-feeding period. Whether this affects the Priolo is unclear: (a) Some trees with relatively lower numbers of flower buds might still provide a large reward for searching Priolos and (b) I do not know if the seven experimental plots are representative of the whole area. A better designed experiment was not possible; most of the area of native forest is inaccessible. Nonetheless, this experiment suggests that a further decrease in the density of *I. perado* may be critical to the survival of this bird. The lower density of *I. perado* in the native forest above Furnas (Chapter 2) should be important to explain the absence of Priolos in this area over winter.

CHAPTER 4
FOOD SELECTION

4.1 INTRODUCTION

The last chapter evaluated the importance of food availability in explaining the abundance and distribution of the Priolo. This factor was important but it is not the only one; there is another dimension to diet, food preference, which is directly related to quality. Optimal foraging, anti-herbivore hypothesis and defence theories all assume that certain plant foods are of higher quality for herbivores than others. Therefore, individuals that are forced to feed on low quality foods must may a price in reduced survival.

Firstly, it should be born in mind that foods taken depend on the morphology (e.g. beak length, jaw strength and so on) and feeding behaviour of the bird species (Newton, 1972; Grant & Grant, 1986). Secondly, several studies have shown that processes underlying food selection are complex since many factors may operate at once. For instance, Crome (1975) showed that plant form and fruit size, colour, ripeness and nutrient content were all associated to some degree with apparent fruit preferences by pigeons. Particular foods may be selected because of their physical characteristics (Willson, 1971; Willson & Harmeson; 1973; Newton, 1972; Snow & Snow, 1988), energy content (Krebs, 1978; Sutherland, 1982), nutrients (Moss, 1972), secondary compounds (Buchsbaum *et al*, 1984; Jakubas *et al*, 1989) or a mixture of these variables (Greig-Smith & Wilson, 1985, Diaz, 1990).

Several factors have been claimed to account for Bullfinch seed and bud selection. Small seeds of ash seem to be preferred because they are easy to handle (Matthews, 1983). Similarly, feeding experiments with sunflower seeds showed that heavy seeds can be very costly to bullfinches in terms of handling time (Greig-Smith & Crocker, 1986). These studies suggested that physical characteristics of the seeds, namely size and weight, may be used as cues in seed selection by bullfinches. On the other hand, Greig-Smith & Wilson (1985) showed that winter seed selection among ash trees is enhanced by a high fat content

in the seed and reduced by a high content of phenolic compounds. Protein apparently had no influence on the bird's tree seed selection.

In years when ash seeds were not available British Bullfinches fed on flower buds from January. Newton (1964) and Summers (1982) observed that birds feed first on the large buds of wild trees. Additionally, it is well known that birds feed selectively on buds of certain cultivars (Wright & Summers, 1960; Newton, 1964; Summers, 1982), which are energy-rich (Summers, 1982), have higher concentrations of certain nutrients (Summers & Jones, 1976; Greig-Smith *et al*, 1983) and may be less distasteful (Greig-Smith, 1985a). All these variables were correlated with bud size but this fact is not discussed by the authors. Matthews (1983) examined the influence of size, calorific value, protein and digestibility and found size to be the most marked and consistent factor to separate a preferred from a non-preferred cultivar.

These studies presented data on what can be considered "high" and "low" quality food for Bullfinches. Under field conditions it is difficult to define "high quality" and "low quality" resources because the quality of food plants may change continually through the seasons (Cooper-Driver *et al*, 1977; Ottosson & Andersen, 1983; Buchsbaum & Valiela, 1987). The assessment of shifts in food preference through time is therefore important, but has not been examined in detail.

I decided to take a general overview of food preference using the framework from British Bullfinches and evaluating shifts in food preference. I have concentrated on the period ranging from October until April, which is when survival is most likely to be influenced by the existence of "good quality" foods (Chapter 3). March and April are especially important because there is evidence for food scarcity. Firstly, I examined and determined food preferences with field observations and food choice trials with captive birds. When compared with the winter diet of British Bullfinches, that of the Priolo is simple. The main foods from January to April are seeds of *Clethra arborea*, fern sporangia and, in Spring, only one species providing flower buds (*Ilex perado*) is taken. These foods

are remarkably light and should be easy to handle. Nevertheless, behavioural costs of feeding were examined from continuous observation of bullfinches feeding on these foods. Dealing only with light-weight and easy to handle foods I predicted that size would be an important variable in explaining food selection. Within the same plant species larger food items are expected to have higher energy content and thus benefit birds more (Stephens & Krebs, 1986). Size selection was examined comparing accepted and rejected food items in the field and in captivity.

Nutrients were not examined. Seeds of fleshy fruits are likely to contain more fat than the light weight seeds of *C. arborea* and fern sporangia but they lasted only until late November (Chapter 3). Fatty foods are important for the over-winter survival of Bullfinches (Newton, 1969; Greig-Smith, 1985). Preliminary phenolic assays of *C. arborea* seeds have shown that these do not have enough fat to interfere with the phenolic assays (Watkins, pers. comm.; see section 4.2.5 in this chapter). This means that *C. arborea* seeds have very low concentrations of fat. Likewise, fern sporangia are not expected to be fat-rich but this needs to be investigated. Therefore, the most promising chemical compound affecting the birds selection were phenolic compounds. These are regarded as key components in theories of plant defence and their importance in feeding ecology has recently been given much attention (see reviews on Rosenthal & Janzen, 1979; Bernays *et al*, 1989; Rosenthal & Berenbaum, 1991). The importance of phenols for Priolo was expected on the basis of studies that have demonstrated inverse correlations between phenolic levels and food consumption by several herbivores (Rosenthal and Janzen, 1979; Buchsbaum *et al*, 1984; Bernays *et al*, 1989; Jakubas *et al*, 1989; Snyder, 1992) including Bullfinches (Wilson, 1984; Wilson & Blunden, 1984; Greig-Smith and Wilson, 1985). Therefore I investigated how the foraging pattern of the Priolo is related to the variation in phenolic content of the two seed species available in winter: *C. arborea*, taken throughout the winter, and *Hedychium gardneranum*, which is rarely taken.

An overall question is asked: is the abundance of "good quality" food the ultimate factor in limiting the Priolo population?

4.2 METHODS

4.2.1 Seed, Flower-bud and fern species selection

The dimensions (length, width and depth) of used and unused seeds (n=20) and sori (n=50) were taken with a 0.1 mm resolution calliper and compared with t and z tests.

The average size of flower buds was assessed every 10 days, by measuring the length (to the nearest 0.1 mm, using a caliper) from the bud's tip to the base of the largest bud-scale, on each of 25 buds (two from each tree).

In late May/early June, the number of fern fronds of different species with and without marks resulting from feeding Priolos were counted within a 0.5 m strip along route 11. Frond preference was determined using chi-square.

I computed herbaceous seed preference indices using Jacobs' (1974) index, Log Q. This is an improved ratio of the proportion of a given seed type in the diet to that in the environment and, unlike previous indices, is independent of the relative abundance of the foods (Jacobs, 1974). The index is: Q=r (1-p)/p (1-r), in which r=proportion of a given food type in the birds ration and p=the proportion of the same food in the environment.

To compute seed diet proportions (r) I used the feeding records obtained within the area where food abundance (from quadrats, chapter 3) was quantified. The proportion of each food in the environment (p) was calculated using the no.seeds/0.25 m^2 quadrat. The dimensions (length, width and depth) of 10 seeds (because dimensions were very consistent) of each species were taken using a 0.1 mm resolution calliper and the average calculated. From the spectrum of seed sizes consumed, larger ones are expected to be more profitable. Seed depth is the intermediate of three orthogonal dimensions: length, depth and width, and was used in correlations with seed preference.

4.2.2 Behavioural costs of feeding

When feeding birds were close enough to observe through binoculars all events were dictated into a tape-recorder. Later on all events were timed to the nearest 0.5 s with a stopwatch. I attempted to record the numbers of food items consumed during timed intervals. For fern sori and flower buds it was only possible to time the number of pecks per unit time, as birds seemed to take several items at once. For *C. arborea,* it was possible to time behaviour for individual fruits. The comparison of intake rates between foods is presented in terms of pecking rates i.e the time from when Priolos began extracting a food item to when they attempted to pluck the next one. This does not tell me how much energy are the birds obtaining. It was used simply to convey an idea of possible behavioural costs of feeding.

Fruiting structures like those of *C. arborea* (Fig. 2) suggest that fruit accessibility from a perch may be an important cost for feeding Priolo. To assess this, the distance to the origin of the stem of remaining and taken fruits, after intensive feeding periods, was measured in 15 stems.

4.2.3 Feeding experiments

4.2.3.1 Food choice

Aviary choice tests were used to check patterns of food preference detected in the field. Birds were netted around mid-day and housed in flight cages. On the day of capture they were fed with wild plants (*Leicesteria formosa* and *Rubus* sp in October and *Polygonum capitatum* in December) taken by birds in the wild. All birds consumed the foods given. Trials started the morning following capture after overnight food deprivation.

Trials began after first peck and lasted for 30 minutes. The next trial was initiated after 30 minutes of food deprivation. Morning trials lasted until 11 am, then birds were allowed to feed freely for one hour before proceeding to the next trial after one hour of food

deprivation. At the end of the day birds were allowed to feed freely for at least one hour before dark.

All trials were choice tests between two plant species taken in the wild at the time of the experiment. Both foods were presented in large quantities and positioned to the birds as they appear in nature. During a trial the number of pecks on each food type and the order in which they were delivered was recorded. After trials, the plants were checked to record the number of items taken. Some choice trials were replicated once with left and right position reversed. Preference was determined by chi-square (df=1 with Yates correction) using the number of pecks to each food type.

Six individuals were tested. In October, individuals A and B were used in choices between fleshy fruits and *C. arborea*. In December individuals C and D were offered choices between *C. arborea/Hedychium gardneranum*, *C. arborea/P. capitatum*, *C. arborea*/tree seeds and *C. arborea/* ferns, *Woodwardia radicans* and *Culcita macrocarpa* (Table 1). In December, I also carried out trials with cones of *Cryptomeria japonica* and individual seeds of *C. japonica* and *Pittosporum undulatum*. Seeds were offered both on the ground and on a piece of wood. In March and April, individuals E and F were allowed to choose between (a) small (< 2.8 - 3.0 mm length) or large flower buds (> 3.0 mm) of *I. perado*/seeds of *C. arborea* and *C. macrocarpa/C. arborea*, and (b) between flower bud species, *I. perado/Viburnum tinus* ssp *subcordatum* and *I. perado/Laurus azorica* (Table 1). These trials were especially important to demonstrate (a) if a switch in preference from seeds to flower buds and ferns is supported and (b) if indeed other flower-bud species are ignored (Chapter 3). Birds were released by mid-day on the day following the last trial, after being given plenty of seeds.

In early April one bullfinch was housed in an outside aviary (20x5 m) and fed firstly, solely on seeds of *C. arborea* and secondly, on sunflower seeds, supplemented several times a week by fresh buds and other wild foods. After 25 days, each of 10 feeding

trials of *I. perado/C. arborea*, *I. perado/Pteridium aquilinum* and *C. arborea/P.aquilinum* were carried out.

4.2.3.2 Maintaining weights on *C. arborea*

In order to have a clearer view of the value of *C. arborea* seeds to the Laurel forest granivorous birds I attempted to keep, individually, two chaffinches, two canaries and one Priolo solely on *C. arborea* seeds in March/April. The chaffinches and canaries were caught in November, housed in outside aviaries, and fed on a commercial seed mixture until the experiment. The Priolo was caught in early April, housed in a 20x5 m outside aviary and kept on a mixture of sunflower seeds and wild foods for 20 days prior to the experiment. During the experiment all birds were weighed to the nearest 0.1 g every day at dusk. The Priolo was released on the 35th day.

4.2.4 Size selection of winter food items

After intensive feeding periods on sori, flower buds and seeds, the sizes of selected and rejected (1) sori (2) flower bud scales and (3) fruits that remained in the cluster and nearby untouched clusters, were measured with a view to identifying size selection patterns. All these foods occur in dense clusters, so there should be much scope for birds to select the most profitable items.

A similar procedure was used with two captive birds in Spring. Seeds of *C. arborea*, flower buds of *I. perado*, and sori of *W. radicans* were measured and given to the birds during 30 minute food choice trials (see above). After the trial, rejected items were removed and measured.

4.2.5 Phenolic content of winter seeds

4.2.5.1 Sample preparation

In winter, the most abundant seeds for Priolos are those of *H. gardneranum* and *C. arborea*. The first is rarely taken and the second presents a marked seasonal variation in consumption after ripening in September. Its intake is low until January, then rises sharply from January to mid March and stops in early April (chapter 3). Moreover, although Priolo feeds on many *C. arborea* trees, some seem to be preferred more than others. Thus I asked the questions: (1) Does *H. gardneranum* have higher concentrations in phenolics than *C.*

Table 1. Experimental choices offered to captive Priolos and reasons for expected results.

Experimental choice	Expected result (preference for)	Reason
Autumn/winter		
C. arborea/fleshy fruits		*Rubus*, *L. formosa* and *V. cylindraceum* seem much preferred in the wild.
C. arborea/Rubus sp	*Rubus* sp	
C. arborea/L. formosa	*L. formosa*	
C. arborea/V. cylindraceum	*V. cylindraceum*	
C. arborea/H. gardneranum	*C. arborea*	*H. gardneranum* is virtually ignored in the wild.
C. arborea/herbaceous seeds		Although *P. capitatum* is an important food in summer it may not be preferred in winter.
C. arborea/P. capitatum	unclear	
C. arborea/ other exotic tree seeds		
C. arborea/P. undulatum	*C. arborea*	*P. undulatum* is ignored in the wild.
C. arborea/C. japonica	*C. arborea*	*C. japonica* is ignored (not taken from cones).
C. arborea /ferns		
C. arborea/W. radicans	unclear	Though*W. radicans* has relatively large sporangia the nutritive value of these may be smaller.
C. arborea/C. macrocarpa	*C. arborea*	Sporangia of *C. macrocarpa* are relatively small.
Ferns		
W. radicans/C. macrocarpa	*W. radicans*	It has larger sporangia.
Winter/Spring		
C. arborea/flower buds		
C. arborea/I. perado (small buds)	*C. arborea*	Buds are small (early developmental stage).
C. arborea/I. perado (large buds)	*I. perado*	Buds are larger.
C. arborea/ferns		
C. arborea/C. macrocarpa	*C. macrocarpa*	*C. arborea* seeds may be too dry.
Buds		
I. perado/V. tinus	*I. perado*	*V. tinus* is ignored in the wild.
I. perado/L. azorica	*I. perado*	*L. azorica* is ignored in the wild.

arborea? (2) How do phenolics in *C. arborea* vary seasonally? (3) Is phenolic content inversely correlated with Priolo preferences for individual *C. arborea* trees?

Thirty *C. arborea* trees were marked in October and during two periods, 30 October - 20 December and 10 March - 30 April, samples of fruits were taken every 10 days from the branches to provide material for phenolic assays. In order to answer the above questions samples were prepared and compared as follows: (1) Phenolic content was compared in individual *H. gardneranum* and *C. arborea* plants in March. (2) Six seasonal samples of *C. arborea* were obtained for each period mixing three to five fruits from each tree. Also, samples from five different trees were obtained in November and again in March. (3) Samples for all individual trees were obtained in March. In order to measure the birds' preference for individual trees, nets (of 50 cm diameter) were attached to the trees near ground level to collect fruits that fell or were dropped by birds while feeding. The % of fallen fruits that were split by Priolos gives a conservative index of Priolo foraging pressure (Greig-Smith & Wilson, 1985).

4.2.5.2 Chemical analysis

Samples were frozen after being collected. Fruits were defrosted in a heated room and seed samples were stored in plastic containers. All analyses were done in the Central Science Laboratory of MAFF in June under the supervision of Dr. R. Watkins.

Upon arrival in the laboratory all samples were milled and stored in plastic containers in a desiccator at 4°C until required (Julkunen-Tiitto, 1985). It was necessary to de-fat the *H. gardneranum* seed powder (but not *C. arborea*), as high concentrations of lipids interfere with the phenolic assay (Krygier et al, 1982). Milled samples (1.0 g) were extracted with 3 volumes (10 ml) of hexane to remove the lipid soluble fraction. The solvent was then discarded, and the residue dried and analysed for phenolics.

Samples were extracted using an adaptation of the method described by Wilson (1984). Dry seed powder (50 mg) was extracted in 50% (aqueous) methanol (5 ml)

containing 0.5M-HCL, for 16 hours at 4°C. Acid was present in the extraction medium to ensure a high level of solubility of phenolic material. An aliquot (2 ml) of the clear supernatant was removed for assay. This extraction procedure was followed in triplicate for each sample.

The concentration of free phenolics was determined using an adaptation of the method described by Julkunen-Tiitto (1985). This assay is more sensitive than that described by Folin & Denis (1915) and does not react so readily with interfering reducing substances. Crude extract (100 µl) was diluted with water to 2 ml. Folin-Ciocalteu phenol reagent (0.5 ml) was added and the solution was mixed vigorously. Exactly 1 1/2 minutes later, 1 ml of sodium carbonate solution (30% w/v) was pipetted and the mixture was mixed well. After 20 minutes the absorbance of the solution was read at 735 nm against a water blank. Each assay was performed in triplicate.

The concentrations of phenolics in all samples were determined from calibration curves of standards of tannic and gallic acid. Both standards used showed an almost linear relationship between absorbance and standard concentration (tannic acid, r^2=0.998; gallic acid, r^2=0.999). Gallic acid produced the most intense reaction and is recommended to determine the concentration of free phenolics (Hagerman & Butler, 1989). Tannic acid was also used so a comparison with previous studies could be made.

4.3 RESULTS

4.3.1 Behavioural costs of feeding

Figure 1 shows the average pecking rate for the most important winter foods. It shows that sori, flower buds and moss tips are consumed much faster than seeds. The differences amongst sori and vegetative food items were not significant (ANOVA: F=1.30, NS, df=3, 258). Among seeds the differences were significant (ANOVA: F=9.26, P<0.001, df=2, 268) because *C. arborea* are consumed more rapidly than *Rubus* sp or *Vaccinium cylindraceum.*

For most of the *C. arborea* fruits (n=211 pecks) the Priolo requires a searching period of less than one second. However, for 9.8% of the fruits this was on average 9.2 s. Once plucked, only 4.9% of the fruits were dropped (probably accidentally). The Priolo takes about 5.5 s before plucking the next fruit.

Figure 2 shows that, in general, *C. arborea* fruit size decreases along stems although only 20% of the variance in fruit size was explained by distance to stem origin. When individual stems are taken into consideration the relationship remains largely the same. From 13 stems examined, 11 showed a negative relationship but this was significant in only four (Table 2). The other two, the smallest, showed a positive but non significant relationship (Table 2). After periods of intense feeding, fruits on the tips of stems were more likely to be present than fruits on the lower parts of the same stem. From 15 stems examined, in all but one stem the average distance of remaining fruits to stem origin was bigger than the distances of taken fruits (Table 3). This suggests that accessibility influenced fruit choice. In all but four stems the last three marginal fruits were left on the clusters. On two occasions, in February, the birds broke two stems whilst trying to reach marginal fruits.

Since marginal fruits are usually smaller, it is difficult to separate the effects of size and accessibility using field observations. Experiments (see Moermond & Denslow, 1983) are needed to tackle this question. However, the observations suggest that accessibility is a potential cost for Priolo feeding in *C. arborea* trees. Such a cost might well be balanced against fruit size.

Table 2. Spearman rank correlation between *Clethra arborea* fruit size and distance to stem origin (see Fig. 2). Examples of 13 clusters, each one from a different tree, are shown.

Cluster	No. fruits (one side of the cluster)	rs (between fruit size and distance to stem origin)	P<
1	13	-0.37	NS
2	10	-0.53	NS
3	9	-0.16	NS
4	10	-0.53	NS
5	9	-0.13	NS
6	9	-0.83	0.05
7	12	-0.73	0.01
8	11	-0.74	0.01
9	14	-0.75	0.01
10	8	-0.27	NS
11	10	-0.43	NS
12	8	+0.30	NS
13	6	+0.10	NS

NS=not significant

Table 3. Distance of taken and remaining *Clethra arborea* fruits to stem origin, measured after periods of intensive feeding by Priolos.

		Distance of taken fruits to stem origin			Distance of remaining fruits to stem origin	
Cluster	n	range (cm)	mean (cm)	n	range (cm)	mean (cm)
1	17	1.4 - 10.4	6.5	8	3.3 - 12.6	8.6
2	12	3.6 - 11.3	7.5	5	3.9 - 11.8	9.7
3	14	3.0 - 12.2	7.9	5	2.9 - 14.2	9.4
4	19	2.8 - 13.0	8.0	6	2.6 - 13.8	10.6
5	20	1.8 - 12.5	6.5	6	2.8 - 11.6	7.3
6	15	1.7 - 11.7	7.1	5	4.2 - 11.7	9.3
7	12	3.4 - 8.5	5.9	9	9.1 - 11.3	10.3
8	10	4.1 - 11.9	7.3	6	9.4 - 11.6	11.0
9	8	4.9 - 10.4	8.9	6	5.5 - 11.9	8.8
10	6	5.1 - 11.3	7.6	10	9.4 - 13.2	11.7
11	7	3.8 - 8.6	6.2	4	3.4 - 8.5	7.6
12	8	3.6 - 8.9	5.8	5	5.1 - 10.4	8.8
13	16	4.7 - 10.9	7.8	5	3.8 - 12.1	8.5
14	6	7.5 - 10.5	7.1	11	5.4 - 14.7	11.0
15	14	5.8 - 8.3	7.1	14	7.3 - 11.7	9.4

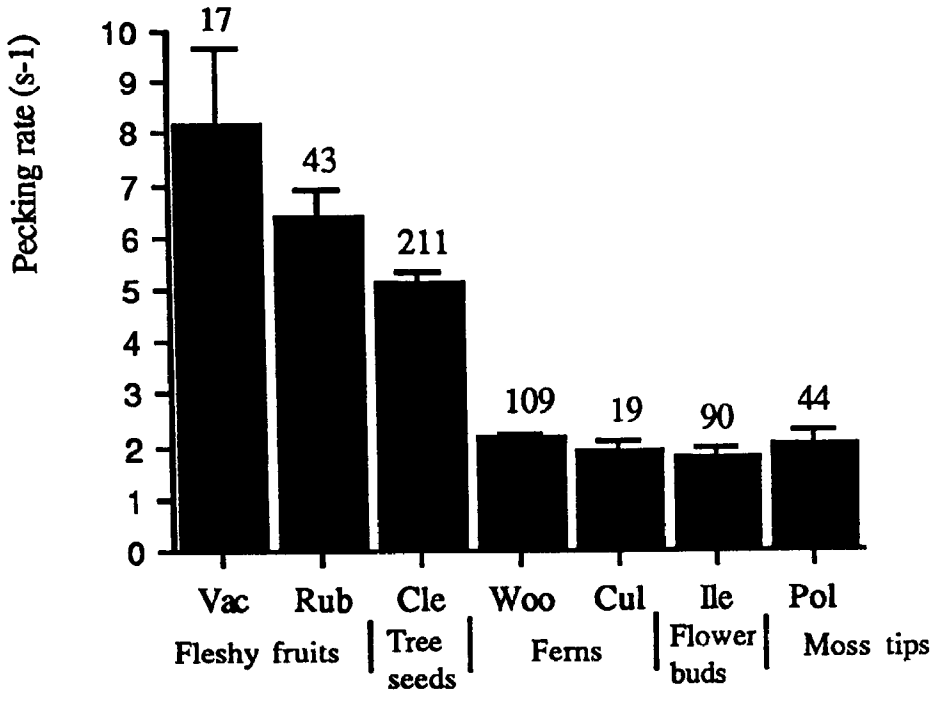
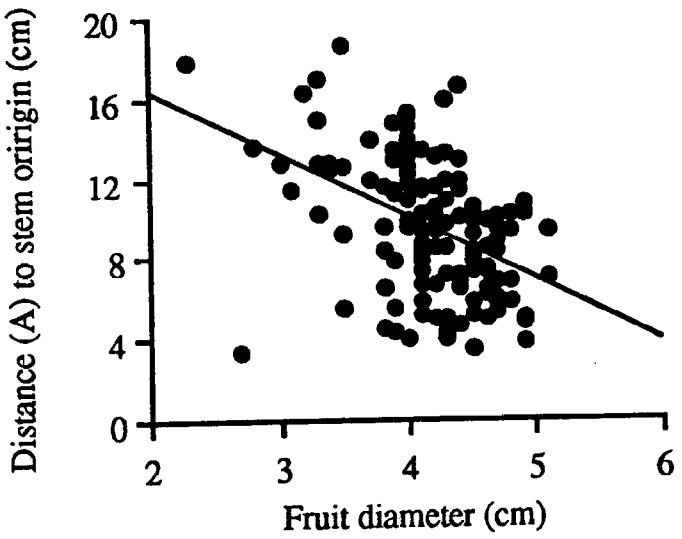


Fig. 1. Mean pecking rate ± S. E. for *Vaccinium cylindraceum* (Vac), *Rubus* sp (Rub), *Clethra arborea* (Cle), *Woodwardia radicans* (Woo), *Culcita macrocarpa* (Cul), *Ilex perado* (Ile) and *Polytrichum* sp (Pol). Pecking rates represent the time from when Priolos began extracting an item to when they attempted to pluck the next one. Numbers above bars indicate sample size.



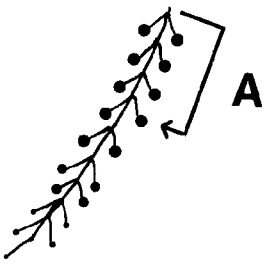


Fig. 2. *Clethra arborea* fruit diameter as a function of distance to stem origin. $Y=-3.09_X+22.45$, $r^2=0.2$, n=128. Each cluster of *C. arborea* has usually between 7 to 14 fruits on each side. On the right is a sketch of a cluster showing a decrease in fruit size in relation to the origin of the stem. An example of this distance (A) is shown for one fruit.

4.3.2 Feeding experiments

Table 4 compares selection of food items in a wild and a captive situation. Preference determined by choice trials was consistent between individuals. Apart from two trials all birds made statistically significant and consistent choices between alternatives.

As expected, in autumn, all fleshy fruits were strongly preferred to tree seeds (*C. arborea*). Herbaceous seeds (*P. capitatum*) were also preferred (Table 4). Apart from one peck of bird C at tree seeds, fleshy fruits always comprised 100% of the food consumed. At the start of each trial, birds A and B flew straight to fleshy fruits; bird C looked at each food and then picked up fruits of *L. formosa*. When tree seeds were tested against *H. gardneranum*, only the former was taken (Table 4). Even when *H. gardneranum* was presented to the birds without an alternative choice the birds did not feed on it.

When I offered the birds *C. japonica* cones they were not able to get seeds out of them, although bird A tried once and bird B twice. On the other hand, when individual seeds were presented on a piece of wood and on the ground, they promptly consumed all the seeds that were on the piece of wood in a rapid succession. Afterwards they started looking for seeds on the ground, which they could pick up quite easily. Seeds of *P. undulatum* were never consumed. In all five attempts, the seeds of *P. undulatum* that were picked up were mandibulated in the beak and rejected after two to five seconds. Therefore, a null hypothesis that the birds were equally likely to eat or reject seeds of *P. undulatum* was rejected ($P<0.05$, binomial test).

Both birds C and D showed a similar behaviour pattern in the choice trials of *C. arborea* vs *W. radicans* done on two consecutive days. The birds showed a complete switch in preference from *W. radicans* to *C. arborea* . During the first trial the birds concentrated only on *W. radicans*. During the second trial they concentrated on *C. arborea* but left 2 and 6 times respectively, to feed on *W. radicans*. Pooled data revealed a preference for *W. radicans* (Table 4). The *C. arborea*/*C. macrocarpa* trial revealed a highly significant preference for *C. arborea* (Table 4).

Finally, in the trial involving both fern species, bird C showed a significant preference for *W. radicans* and bird D was unselective (Table 4). Bird C made fewer movements between both alternatives than bird D (1; 5). On the whole, bird D was less selective than bird C in choosing between fern species.

Feeding trials in Spring confirmed a switch in preference from tree seeds to flower buds (*I. perado*) once these got larger (>2.8 mm), which agrees with expectation. However, bird F (Table 4) did not significantly prefer tree seeds when they were presented with small flower buds (Table 4). Flower bud species that were not eaten by Priolos in the wild were also not taken by captives. Apart from trials shown on Table 4, fresh flower buds of *P. undulatum*, *L. azorica* and *V. tinus* were offered to bird F on three consecutive days. Each species was left in the aviary for a day but none was taken. As expected, a switch in preference from seeds to sporangia was also obtained. Further feeding trials with bird F after 20 days of acclimatisation confirmed a strong preference for flower buds when compared with the two other main foods available in Spring: tree seeds and fronds (Fig. 3). Furthermore, bird F did not show a clear preference between tree seeds and fronds. Thus, though not preferred and presumably less profitable than other foods in early winter, tree seeds seem to get progressively unsuitable as they mature.

Finally, both chaffinches and canaries were unable to maintain their weight on *C. arborea* seeds. Both chaffinches died after three days having lost 3.4 g (13-15%). The canaries lost 0.7-1.2 g (5- 8%) after two days and regained weight when reintroduced to a commercial seed mixture. Most of the *C. arborea* seeds were ignored and left untouched.

When the individual Priolo F was housed in the outside aviary I tried to keep it solely on *C. arborea* supplemented with fern sporangia. The bird showed symptoms of starvation even after one day and almost died after three days. I had to hand-feed it with bits of sunflower seeds and it regained weight. After 20 days the bird was introduced to a diet solely of *C. arborea* seeds and lost 0.9 g (3%) in 24 hours. This weight was regained when feeding on sunflower seeds.

Ideally more Priolos should have been used in experiments and these should have lasted longer. Nevertheless, these results point out that wild Priolos, as well as wild chaffinches and canaries, in April, may not survive on *C. arborea* seeds alone. The fact that these are taken may enable the birds to lose weight less rapidly.

4.3.3 Selection of food items

4.3.3.1 Herbaceous seeds

Jacobs' (1974) index of seed preference, log Q, showed that herbaceous seeds were not taken in proportion to their abundance in the environment (Table 5). Spearman rank correlation coefficients between seed depth and preference were positive for both July and Aug/September. In July 91 and August 92 it was significant at the 0.05 level and in Aug/September 91 it was close to being significant ($P<0.07$; Table 5). Thus, Priolos exhibit a positive selection towards larger seeds. These should be more profitable in terms of energy obtained per unit handling time, which is consistent with the predictions of foraging theory.

4.3.3.2 C. arborea seeds

C. arborea fruits are available on approximately linear stems (Fig. 2) in dense clusters. The fruits are globular and each one has three small seeds. In February, fruits weighed between 10 and 33 mg and the three seeds between 1 and 9 mg. Measurements of a sample of 99 and 28 fruits, respectively, revealed that fruit size was significantly correlated with seed size ($r=0.86$, $P<0.001$) and fruit weight with seed weight ($r=0.86$, $P<0.001$). It can be seen from figure 2 that the relative variability of *C. arborea* fruits is small (example of 3 different trees; tree1: mean=4.2, SD=0.55, n=54; tree 2: mean=4.3, SD=0.48, n=133; tree 3: mean=4.1, SD=0.48, n=73); most fruits are between 3.2 and 4.4 mm in diameter.

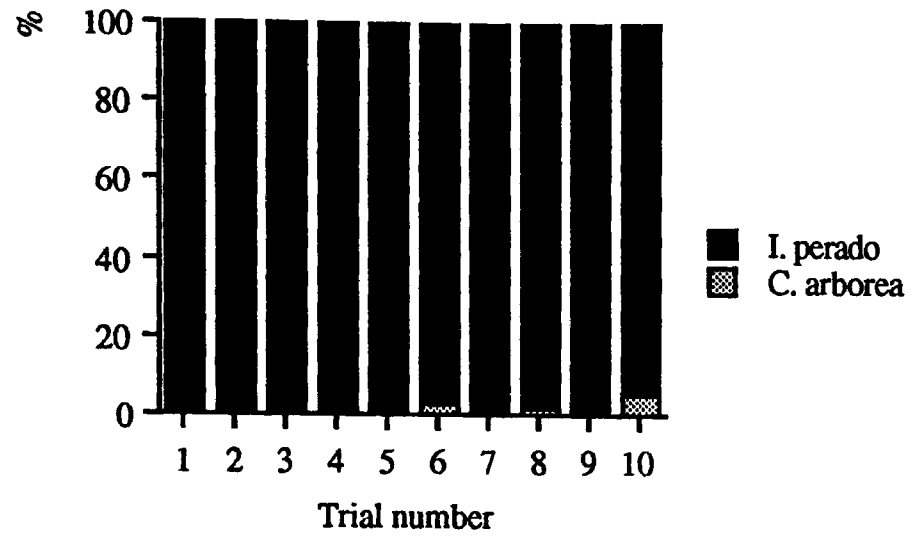
Table 4. Comparison between plant species selection between wild and captive birds. Selection by wild Priolo is expressed both as the number of feeding records on each plant (Autumn/winter: fleshy fruits, 15 September - 15 October; other foods, 15 December - 15 December. Spring: March) and as the ratio of the number of feeding observations for each plant relative to *C. arborea*. Selection by captive Priolo is expressed as the ratio of the number of pecks on each plant to the number of pecks in *C. arborea*, excepted otherwise indicated.

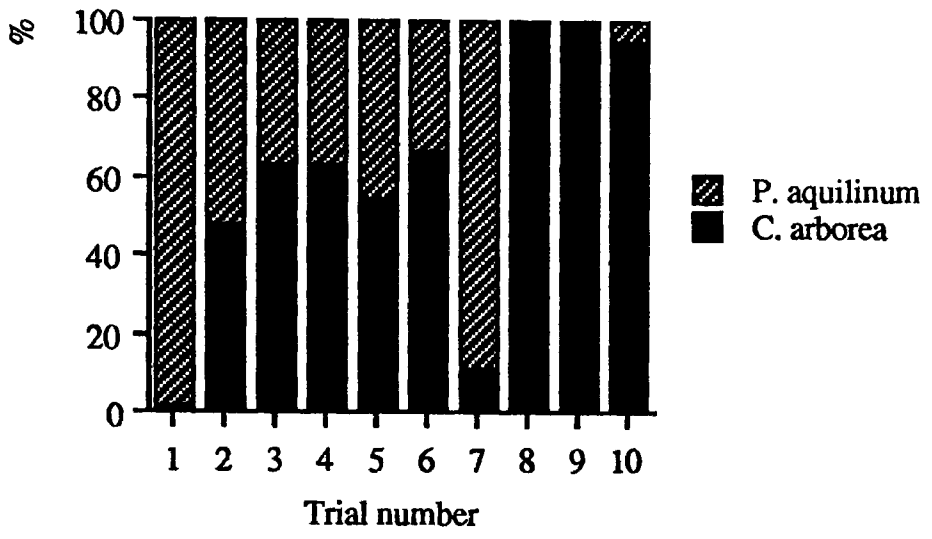
When two or three trials were carried out SE is presented in brackets. All trials were highly significant ($P<0.001$) using a chi-square (df=1 with Yates correction) except those indicated with NS (not significant).

	No. feeding records	Field selection ratio	Captivity selection ratio Bird			
Bird			A	B	C	D
Autumn/winter						
C. arborea vs						
1- Fleshy fruits						
L. formosa	29	5.8	7+	16+	14.0	
V. cylindraceum	10	2	158+	77+		
Rubus sp	16	3.2	28+	11+		
C. arborea	5	1	1	1	1	
2- Other foods						
P. capitatum	25	1.04			40.5 (33.5)	46.8 (29.1)
W. radicans	24	1			23.6 (23.4)x	39.4 (36.6)x
C. macrocarpa	6	0.25			0.3	0.5
H. gardneranum	1	0			0	0
C. japonica	1	0			0	0
P. undulatum	0	0			0	0
C. arborea	24	1			1	1
W. radicans (ratio with *C. macrocarpa*)					18.7	0.68 NS
Winter/Spring						
Bird			E	F		
I. perado (small buds)			0.19	1.08 NS		
I. perado (large buds)	28	3.5	309.0 (133.0)	58.1 (19.2)		
C. macrocarpa	22	2.75	15.2	6.4		
C. arborea	8	1	1	1		
Ratio with *I. perado*						
V. tinus	0	0	0	0		
L. azorica	0	0	0	0		

+ Represents absolute number of pecks because the number of pecks in *C. arborea*=0

x Two trials were done. Overall, there was a preference for *W. radicans* but both birds showed a significant preference for *W. radicans* in the first trial and a significant preference for *C. arborea* in the second trial.





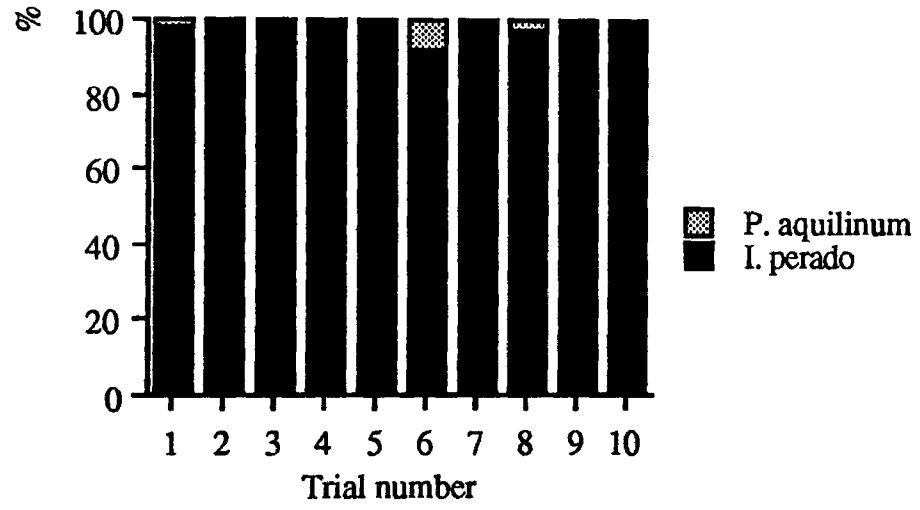


Fig. 3. Feeding trial preferences for bird F. Figures represent the % of pecks in each food during 30 minute trials carried out after 20 days of acclimatisation in an outside aviary. Sample size varied between 0 to 8 for *Clethra arborea* and 94 to 294 for *Ilex perado* in the trial *C. arborea/I. perado*; 2 to 97 for *Clethra arborea* and 23 to 58 for *Pteridium aquilinum* in the trial *C. arborea/P. aquilinum*; and 0 to 2 for *Pteridium aquilinum* and 41 to 216 for *Ilex perado* in the trial *I. perado/ P. aquilinum*.

Table 5. Comparison of Priolos summer seed preferences (Jacobs Log Q) with seed depth using Spearman rank correlations.

	Preference index (log Q)			Seed depth (mm)
	Jul 91	Aug 91	Aug 92	
Cyperaceae	1.4			1.12
Polygonum capitatum	1.05	0.79	1.03	1.06
Prunella vulgaris	0.67	0.11	0.34	1.08
Leontodon filii	0.35	0.5	0.91	0.65
Potentilla erecta	0.23	-0.23	-0.22	1.08
Luzula purpureo splendens	0.1		-0.07	0.75
Sonchus sp	0.22			1.27
Hypericum humifusum	-0.34	-0.96	-0.35	0.48
Grasses	-0.56		-1.89	0.49
Epilobium obscurum	-0.74	0	0	0.52
Sagina sp	-1.29			0.49
Scrophularia auriculata	-1.83	0	-2.71	0.5
Vaccinium cylindraceum		0.76	0.94	1.24
Leicesteria formosa		-0.45	0.72	0.99
Rubus sp		0.78		1.92
Correlation (rs)	0.66*	0.59+	0.65*	

* P<0.05 + P<0.07

Comparison of sizes of fruits that remained in clusters after several periods of intense feeding with sizes of fruits in untouched nearby clusters, in four different trees, revealed that remaining fruits were significantly smaller in trees one, two and three. In tree four this difference was not significant. In captivity Priolo showed also a strong preference for larger fruits (Fig. 4). Similarly with sori of *W. radicans* the preference ranking of sizes was influenced by the relative variability of fruit sizes in each tree. For instance, sizes that were, on average, rejected in tree one were taken in tree three.

4.3.3.3 Flower Buds

The birds took only developing flower buds of *I. perado* . Other flower buds widely present but never taken were those of: (1) *P. undulatum*, in January and February, (2) *L. azorica*, from February to April and (3) *V. tinus* from January to April. Flower bud length of *L. azorica* (mean=8.17, SD=0.46, n=25) and *P. undulatum* (mean=9.58, SD=1.99, n=25) is much larger than that of *I. perado* (Fig. 5) and, especially those of *L. azorica*, were harder. Flower buds of *V. tinus* are of similar size to those of *I. perado* and present also similar development (Fig. 5). They are, however, in large inflorescences, and should be more difficult to pluck (Newton, 1967a). Other endemic species, *Prunus lusitanica* ssp *azorica* and *Frangula azorica*, although providing flower buds, were too scarce to be of any significant importance for Priolos.

Flower buds of *I. perado* were only taken in quantity at the end of March and early April (Chapter 3), when there was a sudden increase in their size. Measurements showed that, in general, these buds became profitable only after they have reached a length of about 2.8 - 3.0 mm. In 1992 they reached these sizes in late March but, in 1993, presumably because of weather conditions, only in early April (Fig. 5).

Flower bud length was a highly significant predictor of bud feeding ($F=48.89$, $P<0.001$, $df=1, 8$; Fig. 6). Flower buds were harvested at high rates (mean= 30 bites per minute; Fig. 1). The birds took several bites in quick succession and then spent some time handling them, after which the scales of large buds were dropped and, with these, entire small flower buds. This behaviour was mostly common in March when the trees had large quantities of small flower buds. The length (in mm) of taken and rejected flower bud scales was highly significantly different both in the wild and in captivity (Fig. 4).

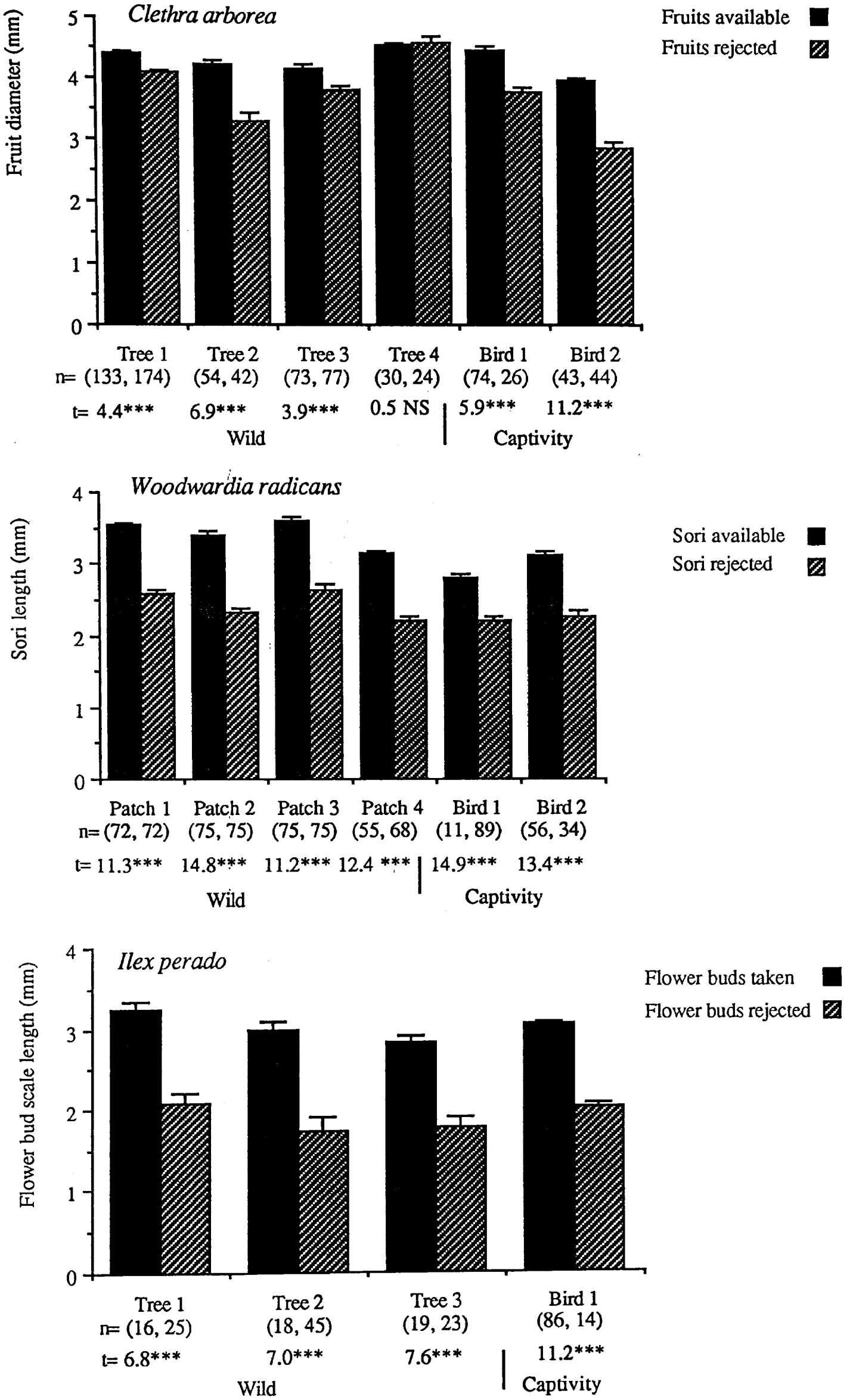


Fig. 4. Comparison between sizes of selected and rejected food items in the wild and with two captive birds (see text for explanation). Values are mean ± S.E. ***=P<0.001, NS=Not significant.

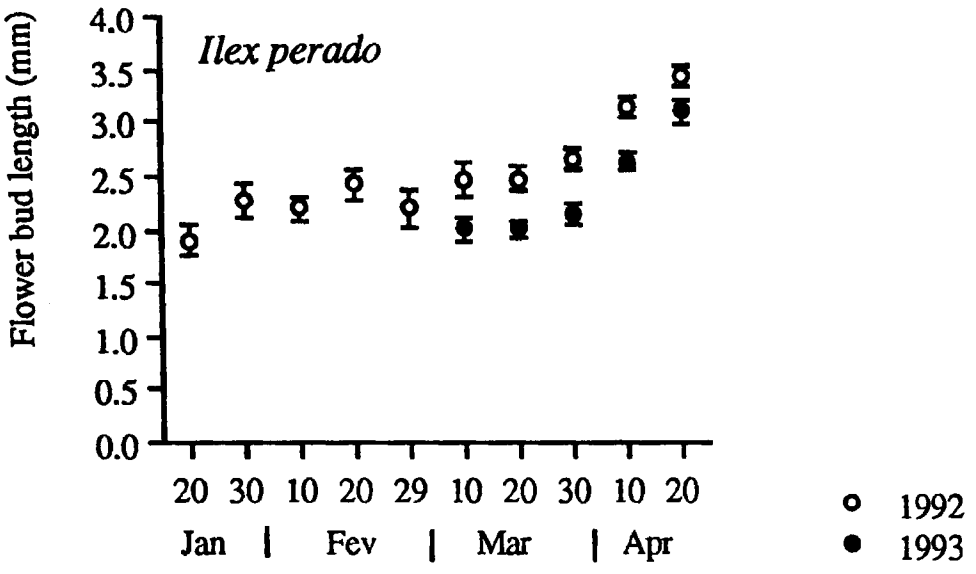


Fig. 5. Seasonal changes in the length of flower buds of *Ilex perado* and *Viburnum tinus* (mean ± S. E. of 25 buds). Two buds were sampled from each tree.

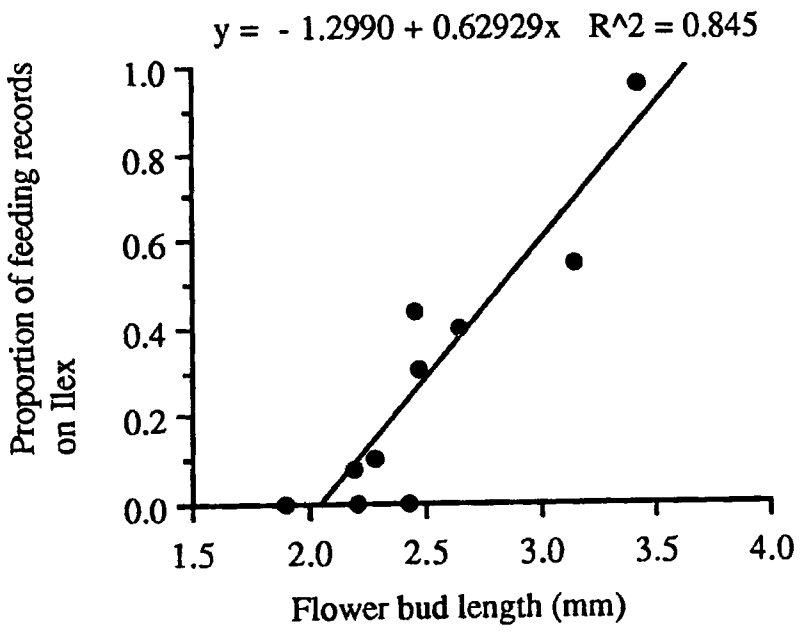


Fig. 6. Simple regression between *Ilex perado* flower bud intake and flower bud length. Each point represents the proportion of feeding records on *Ilex perado* and the average flower bud length for a 10 days period from the 20 th of January to the 20 th of April.

4.3.3.4 Ferns

4.3.3.4.1 Interspecific fern selection.

4.3.3.4.1.1 Sori

In winter three main fern species provided sori, W. *radicans*, *C. macrocarpa* and *Polystichum sp*, [FN] but only the first two, bearing significantly larger sori were taken (shown below are sizes of sori in mm and Z-tests between *C. macrocarpa* and *Polystichum* sp and, *W. radicans* and *Polystichum* sp; n=50)

Polystichum sp: mean=1.0, range=0.7-1.4

C. macrocarpa: mean=2.99, range=2.7-3.4, Z=43.08, P<0.001.

W. radicans: mean=3.708, range=2.9-4.2, Z=49.76, P<0.001.

The pattern of sporangia feeding was influenced most by sori size. The peak on *W. radicans* feeding in November/December shifted to *C. macrocarpa* in January as the abundance of *W. radicans* decreased (Chapter 3). Sporangia feeding declined from February to March and April as spores were shed from sporangia. Nonetheless, in January, both sporangia types were available. Counts of the number of large fronds of both species with and without marks of Priolo in a 0.5 m strip along route 11 revealed a highly significantly higher predation on *W. radicans* than on *C. macrocarpa* (57.7 and 7.4% respectively, $\chi 2=69.45$ df=1 with Yates' correction P<0.001, n=130 and 122). Again sori of *W. radicans* are significantly larger than those of *C. macrocarpa* (Z=12.80 P<0.001).

[FN] *W. radicans* presents oblong sori in two rows along either side of the midrib of the pinnules. Sori of *C. macrocarpa* are reniform and those of *Polystichum* are circular. All have an indusium. Sori are present in large quantities and spread underneath the whole fertile frond. They are very easy to obtain by a bird perched on the stem or leaf. Sporangia walls of different species may pose different constraints on the digestibility of spores but, at present, no data is available to evaluate this.

4.3.3.4.1.2 Fronds

Birds fed only on young fern fronds. *P. aquilinum* became available earlier and so was taken in April and early May. However, in mid-May, when *Osmunda regalis* became available birds fed selectively on it, although other young fern fronds, including P. *aquilinum*, were much more abundant (Table 6). On several occasions birds took bits of large, well developed leaves of both *P. aquilinum* and *O. regalis*. These were mandibulated but, usually, were then dropped. This behaviour was never observed when the bird fed on sporangia, which suggests a deliberate rejection of less suitable parts of the fern.

Consumption of *O. regalis* frond, but not *O. regalis* sporangia, was associated with cover. The distance to the nearest vegetation of selected (mean=0.19 m, SD=0.21, n=31) and rejected fronds (mean=1.32 m, SD=1.24, n=32) was highly significantly different ($t=4.97$, $P<0.001$, $df=61$). The distance to nearest vegetation of selected sporangia (mean=1.26, SD=1.23, n=36) was significantly greater than that of selected fronds ($t=4.5$, $P<0.001$, $df=65$). If ferns far from cover are more likely to produce sporangia than ferns closest to cover this result is biased. However, the correlation between distance to nearest vegetation and % of sporangia consumed (assessed visually and arcsine transformed) was not significant ($r=-0.21$, $P<0.10$, $n=60$). Furthermore, there were enormous amounts of fronds both within and far from cover that were never eaten. Travelling further to feed on sporangia suggests that these are much preferred over fronds.

4.3.3.4.2 Intraspecific fern selection

4.3.3.4.2.1 W. radicans

Sori of *W. radicans* are available in a continuous range of sizes; size of sori decreases linearly along pinnae and pinnules (Fig. 7). The sizes on the tips of pinnae and pinnules are significantly smaller than the sori closer to the petiole. Measurements of sori size showed that Priolos exhibited strong size selectivity in each one of these botanical structures (Fig. 7). Overall, birds did not seem to take sori below 2.5 mm length. At the

pinnate and primary pinnule levels the sori on the tips remained untouched. At the secondary pinnule level the sori on the tips either remained untouched or large bits of the pinnule contained smaller sori were dropped (indusia were usually rejected and formed a conspicuous litter beneath the ferns). In the wild the length of sori still present in the part of the pinnule where the birds foraged was highly significantly bigger than the length of rejected sori ($P<0.001$; Fig. 4). Captive birds also showed marked size selection (Fig. 4).

It is important to quantify the extent of overlap between selected and rejected sori. Because of the linear decrease in sori towards the edge the birds might have a simple rule of thumb such as: "reject the edge of the frond". With this rule the bird would achieve the expected result (reject small sori) with, possibly, the least time foraging. If large overlap between the two classes does exist, one might expect this to occur although experiments would be needed to prove this. In fact, there was quite extensive overlap between sizes selected and rejected in the overlap range 2.5-3.3 mm. Within this range the preference ranking of sizes was influenced by the relative variability of sizes in each patch encountered. In three different patches the length of fronds and the size of sori, of fronds selected and rejected, were both significantly different (Table 7). Birds selected bigger fronds which, as expected, had bigger sori. In patch one the sizes (in mm) of sori of selected ferns were bigger than in patch two (range 3.2-4.4, mean=3.85 vs range 2.5-3.4, mean=2.9) and extensive overlap occurred between (a) sizes of sori of fronds rejected in patch one and (b) sizes of sori of fronds selected in patch two (range 2.2-3.1, mean=2.76 vs range 2.5-3.4, mean=2.96; Table 7). Overall a) and b) were significantly different ($t=2.31$, $P<0.02$, $df=62$), although the significance was lower when compared with sizes of sori selected and rejected only within a single patch ($P<0.001$).

I also investigated the individual and combined importance of size of sori (in mm), length of the frond (in m) and cover (as distance in metres to nearest tree or shrub) to predict predation on sporangia of *W. radicans* (measured as the % of the total number of fertile primary pinnules predated). A stepwise multiple regression selected only the variable

size of sori (Table 8) which explained 59% of the total variance in *W. radicans* predation. In a non-stepwise procedure all variables were significant although size of sori was more important (P<0.0004) than the other two variables (P<0.01 and P<0.04). Together the three variables accounted for 73.7% of the total variance in *W. radicans* sporangia predation; only 15% more than sori size by itself, which, therefore, largely explains predation on this fern species.

Table 6. Fern selection. Comparison between ferns of different species (all with fresh green leaves in May/June) with and without bill marks of Priolo. All ferns within a 0.5 m strip along route 11 were examined.

	1991 (May)		1992 (Jun)	
	No. of ferns	% of ferns with marks of Priolos	No. of ferns	% of ferns with marks of Priolos
Woodwardia radicans	716	1.8	754	0.1
Pteridium aquilinum	267	5.2	243	4.9
Osmunda regalis	86	52.3	130	55.4
Others*	262	1.1	622	0.3
χ^2	368.0 (P<0.001)		765.6 (P<0.001)	

* especially *Culcita macrocarpa*, *Polystichum* sp and *Blechnum spicant.*

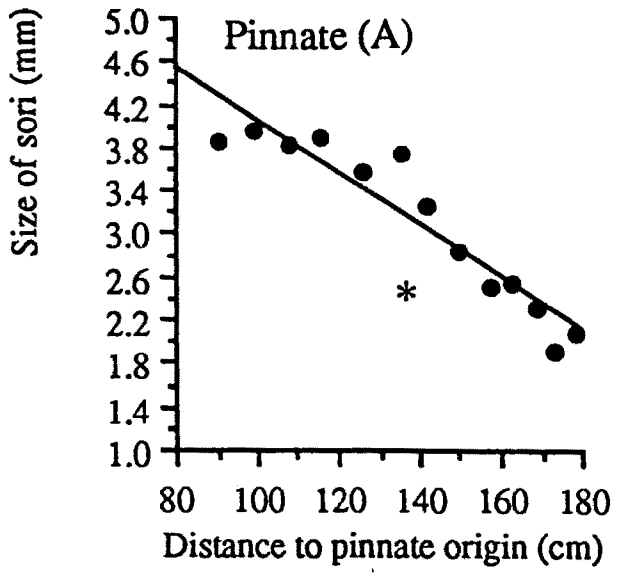
Table 7. *Woodwardia radicans* sporangia selection: comparison between frond length and sori size of fronds selected and rejected in three different patches.

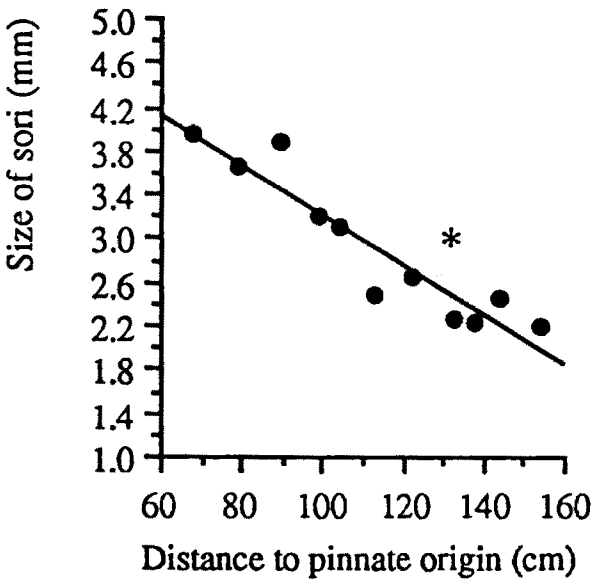
	Frond length				Sori size			
	n	Range (m)	Mean (m)	T- test	n	Range (mm)	Mean (mm)	T- test
Patch								
1 Selected	10	1.6 - 2.5	2.2		30	3.2 - 4.4	3.86	
Rejected	9	1.0 - 1.7	1.4		34	2.2 - 4.4	2.76	
				5.96***				15.4***
2 Selected	9	1.4 - 1.6	1.5		30	2.5 - 3.4	2.92	
Rejected	8	0.6 - 1.3	1.0		30	2.1 - 3.1	2.5	
				6.98***				6.36***
2 Selected	7	1.3 - 1.7	1.4		30	2.7 - 3.5	3.11	
Rejected	6	0.9 - 1.3	1.1		30	2.3 - 3.1	2.67	
				4.19**				8.31***

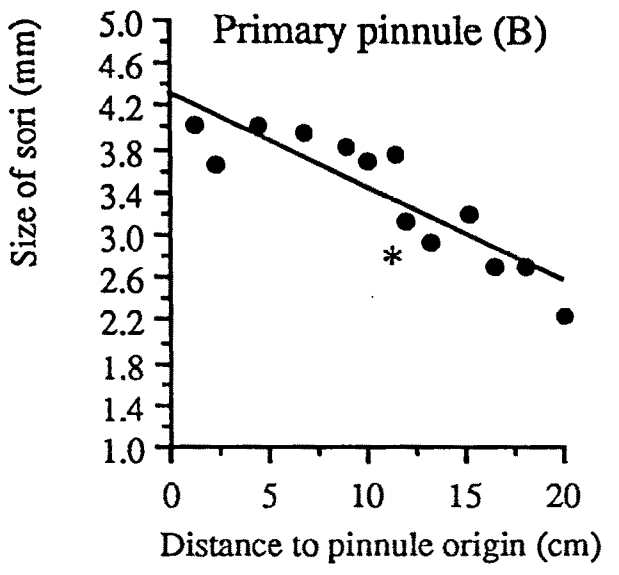
** P<0.01, *** P<0.001

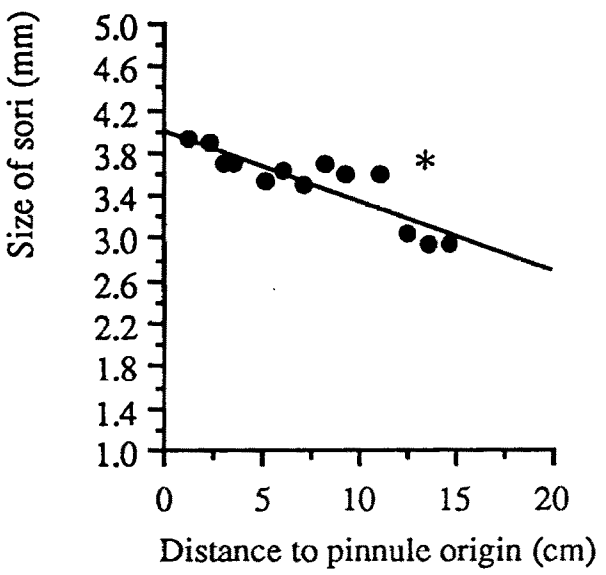
Table 8. *Woodwardia radicans* fertile frond selection: multiple linear contribution of three independent variables to the total variance in the % of total number of fertile primary pinnules taken (arcsine transformed) by Priolos. Values for a non stepwise and stepwise regression are shown. N=20.

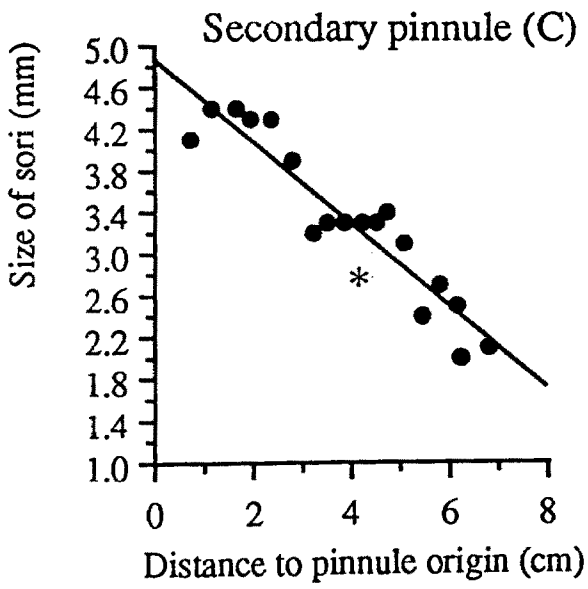
Significance of regression	Variables	Significance of coefficient	Regression model
F=14.98, P<0.0001	Sori size (x1)	0.0004	$Y=-38.68+17.81_{x1}$
	Cover (x2)	0.01	$-9.44_{x2}+19.57_{x3}$
	Frond length (x3)	0.04	
Stepwise			
F=25.9, P<0.0001	Sori size (x1)	0.0001	$Y=-19.37+19.81_{x1}$

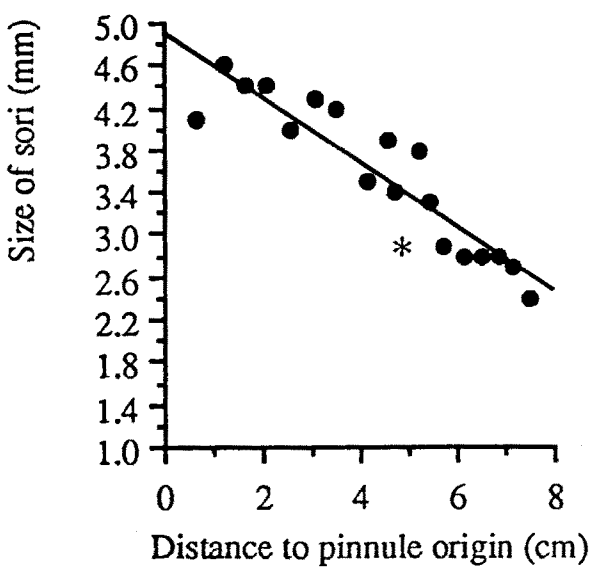












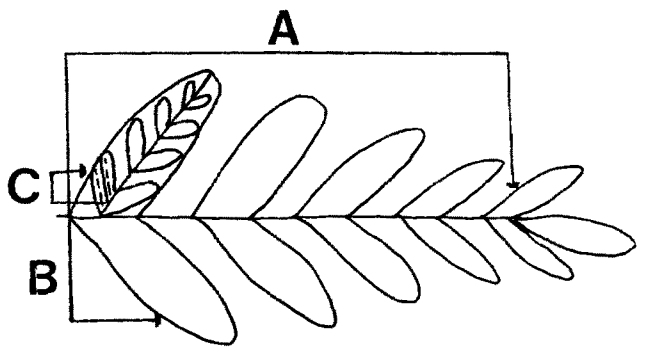


Fig. 7. Relationship between size of sori and distance to the petiole in *Woorwardia radicans*. Examples for each of two fern structures are shown. Sizes below * were not taken by Priolos. For the pinnate and secondary pinnule each dot represents the average of the first three sorus in each structure. Examples of a distance (A, B and C) from a sorus to the origin of each structure is shown.

4.3.3.4.2.2 P. aquilinum

The toxicity of *P. aquilinum* to living organisms has been known for many years, mainly because toxic carcinogens (specially cyanogenic glycosides) have been found in this species (Rosenberger & Heeschen, 1960; Evans & Mason, 1965; Cooper-Driver, 1976). There are wide variations among different individuals in terms of toxic compounds (Cooper-Driver, 1976) but, two generalities were made: (1) toxins are of higher concentration in young fronds whereas tannins are of higher concentration in the old fronds (Cooper-Driver, 1976; Rhoades & Cates, 1976) and (2) there is a marked decrease in cyanogenic compounds between the tips and lower parts of the same frond (Cooper-Driver, 1976).

Since Priolos only take young fronds, if carcinogens are effective deterrents, one should expect the birds to feed selectively on the lower parts of the fronds. My data support this hypothesis. In three different places along route 8, stations 6 to 7, the proportion of frond tips that were predated was significantly less than the proportion of frond tips that were not predated (all $P<0.001$, chi-square with df=1 and Yates' correction).

1: 7.27% of tips taken, $\chi^2=38.47$, n=55.

2: 9.83% of tips taken, $\chi^2=37.77$, n=61.

3: 3.33 of tips taken, $\chi^2=50.42$, n=60.

It is possible that birds were feeding mainly on acyanogenic plants (Cooper-Driver & Swain, 1976) but the birds' behaviour suggested deliberate rejection of unsuitable parts of the fern: most tips remained untouched (in older fronds they could also be less accessible but this is unlikely in young fronds) or were dropped deliberately. Conspicuous frond tips could be identified underneath the fronds. Once I saw a bird picking up a very young frond (almost in crozier stage) and dropping it immediately.

4.3.4 Phenolic content of winter seeds

Contrary to my expectations the phenolic content in whole seeds of *H. gardneranum* was not significantly different from the phenolic content of whole seeds of *C. arborea* (t=0.48, df=17, Table 9) but the difference in phenolic content between kernels of *H. gardneranum* and seeds of *C. arborea* was highly significant (t=6.6, P<0.001, df=17; Table 9). When the husks of *H. gardneranum* were removed (wild Priolos were seen doing this twice) and analysed about 90% of the phenolic compounds were isolated in the husks (Table 9). This may help to explain why *H. gardneranum* is rarely taken. The seed is quite large and soft and it might be difficult to de-husk. One bullfinch in November dehusked part of a seed in 68 s. In all other observations the seeds were mandibulated for about 10 seconds (mean=9.63, SD=2.68, n=4) and rejected. Pulp was presumably taken. Table 9 shows also that variation in phenolic levels is relatively small.

Analysis of samples of *C. arborea* at intervals throughout the winter revealed a consistent increase in the phenolic content from October until late December and a sharp decrease by March (Fig. 8). Thus, after fruits had ripened in September/October, the concentration of total phenolics rises until late December and decreases in March/April. At five individual trees, analyses were performed in November and again in March, showing that total phenolics in individual trees invariably decrease by 50 to 75% from one period to the other (Table 7). These results help to explain why seeds of *C. arborea* are not taken in quantity before mid-December though preferable seeds (of fleshy fruits) are already very scarce in November (Chapter 3).

C. arborea feeding records obtained from September to November were all in places less than 500 m high. A group of 2 and 5 birds feeding in *C. arborea* in November at about 480 and 400 m of altitude, respectively were seen selecting brown (more mature) fruits. Then, the large majority of trees above 600 m had only green (immature) fruits. Thus, although every tree follows the seasonal pattern described earlier, trees at higher and

lower altitudes should present asynchronous curves i.e. at lower altitudes seeds will mature first and, therefore, their phenolic content will decrease earlier.

Despite the sharp decrease in phenolics in March wild birds were not seen taking *C. arborea* seeds after early April. An index of preference for individual trees showed a very poor negative correlation (r= -0.04; n=29; Fig. 9) with phenolic content in March. This correlation was slightly improved when trees 11, 12 and 25 were omitted from the analysis (r=-0.16; n=26). A captive bullfinch even ate *C. arborea* seeds provided in mid-May. About 600 seeds from two different trees were provided during each of 6 feeding experiments in which seeds were left in the aviary for two days. Only 10 to 15% of such "over-mature" seeds were taken on the first day and almost none in the second day. Overall, these results suggest that birds may make some discrimination between trees on the basis of their phenolic content, but this does not explain tree preference nor why wild birds stop feeding on *C. arborea* seeds in early April.

Table 6. Concentration of phenolic compounds of seeds in March 1993. Values are mg/g dry weight based on gallic and tannic acid equivalents.

	Gallic acid		Tannic acid	
	Mean (SD)	Range	Mean (SD)	Range
Hedychium gardneranum (n=4)				
Whole seed	10.0 (0.92)	8.9 - 10.9	13.8 (1.17)	12.2 -1 5.0
Kernel	5.7 (0.68)	4.9 - 6.4	7.4 (0.99)	6.2 - 8.5
Husk	90.0 (8.01)	79.7 - 99	127.4 (11.8 7)	112.4 -1 40.8
Clethra arborea (n=29)	10.4 (3.28)	4.6 - 17.7	14.3 (4.83)	5.8 - 25.2

Table 7. Concentration of phenolic compounds of seeds of five *C. arborea* trees in November and March. Values are mg/g dry weight based on gallic acid equivalents.

	November	March
Tree 1	24.56	12.66
Tree 2	20.56	5.88
Tree 3	18.26	10.55
Tree 4	24.53	14.43
Tree 5	15.66	5.02

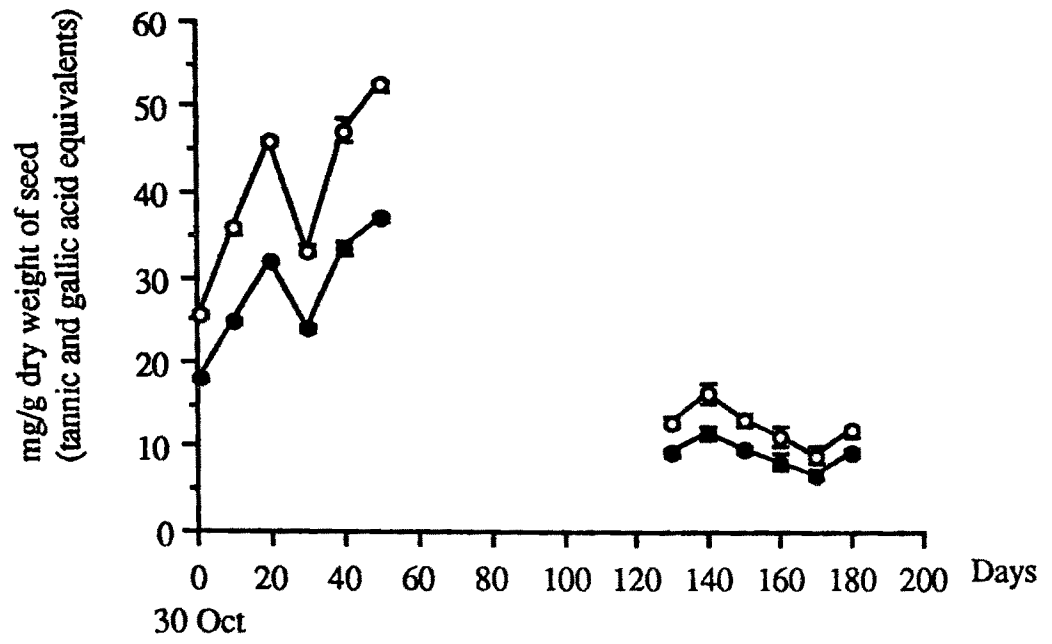


Fig. 8. Variation in phenolic content of *Clethra arborea* seeds: comparison between autumn and spring levels. Each sample consisted of three to five seeds from 30 trees. Filled symbols represent gallic acid and unfilled symbols tannic acid. Values are mean ± S.E.

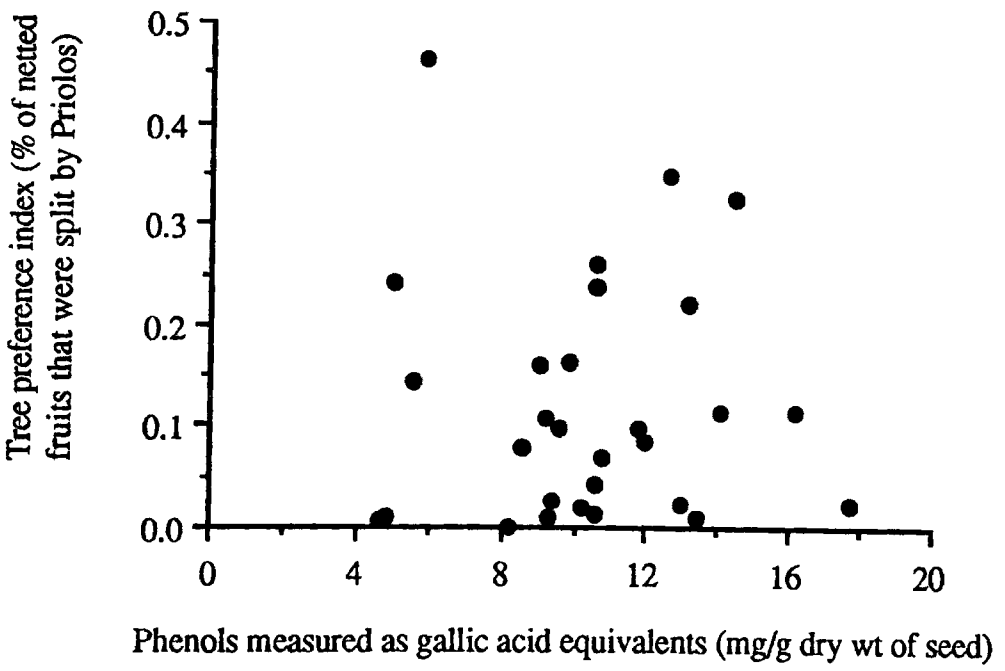


Fig. 9. Relationship between an index of *Clethra arborea* tree preference and the phenolic content of seeds of each tree sampled on the 10th of March. The correlation was not significant (r=-0.04, n=29).

4.4 DISCUSSION

4.4.1 Feeding experiments

The feeding experiments did not involve a rapid change of diet, which seems to affect the behaviour of bullfinches (Newton, 1964; Matthews, 1983). Also, Priolos, like other birds e. g. the Spruce grouse (Pendergast & Boag, 1971) might need modifications of the gastro-intestinal tract in order to utilise a different diet. On the other hand, it might be argued that the birds were not used to the aviary. I suggest that they should not be, in order to compare choices actually available at the time. By avoiding these biases this feeding experiments provide a way of evaluating preferences of wild foods (see also Moermond & Denslow, 1983).

The Priolo was selective when choosing between food types. Within each season their choices were relatively consistent. This implies the presence of rational decision making (McCleery, 1978; Moermond & Denslow, 1983). Similar trials had opposite results at different times of the year suggesting that food preference changes continually. A switch from *C. arborea* to fern sporangia occurred when seeds were old (6 months) and dry. In the case of buds, a small increase in size lead to a marked switch from seeds to buds. Thus, Priolo food selection is a dynamic procedure, varying temporally according to changes in physical and chemical characteristics of foods, which are expected to affect the birds' net reward.

Birds may readily follow these changes due to differences in food appearance such as colour, size, etc. For instance, an increase in bud length is associated with a marked increase in nutrients (Greig-Smith *et al*, 1983). In order to provide a realistic picture of diet and food selection, diet shifts need to be considered. In general, seasonal variations in the diet of herbivores may be the result of complex selection mechanisms among temporally available assemblages of foods (Moermond & Denslow, 1983). Finally, such temporal changes may, like patterns of food variability, impose constraints on food selection mechanisms (Greig-Smith & Crocker, 1986; Crocker, 1987).

4.4.2 Behavioural costs of feeding

To the Priolo, costs such as fruit loss and time manipulating fruits seem to be unimportant. Searching time may be more costly in the end of the winter when larger fruits are scarcer or less accessible. The degree of accessibility will depend on the length of the stem and the overall structure of tree branches. These will vary between branches and between trees. Thus, it is very difficult to generate precise quantitative definitions of accessibility and its effect on the Priolo foraging behaviour.

In winter ash seeds are very important for British Bullfinches. These are much larger than *C. arborea* and behavioural costs of feeding may be great. Bullfinches dropped (very large seeds or those with high levels of phenolics), deliberately or accidentally, 51% of the fruits they plucked (Greig-Smith & Wilson. 1985). As winter progresses and seed stocks are depleted this may be a serious cost to feeding Bullfinches and thus it may pay to handle seeds for longer periods (Greig-Smith, 1984).

4.4.3 Seed selection

In terms of seed selection the pattern for the Priolo was large size both for summer herbaceous seeds and winter tree seeds of *C. arborea*. Newton, although not making quantitative comparisons of the degree of usage versus availability of herbaceous seeds, noted a similar behaviour in the Marley wood bullfinches in Oxford. Large seeds should yield proportionally more energy per unit handling time and thus the birds should benefit more by concentrating on large seeds. This agrees with the expectations from foraging theory (Krebs, 1978) and has been widely reported for other seed-eating birds (Willson, 1971; Schluter, 1982a; Diaz, 1990; Grant, 1986).

In terms of preference for seed types, Priolos behave like British Bullfinches as seeds of fleshy fruits are preferred to tree seeds. The evidence in Britain is indirect. Feeding observations (Newton, 1967) and analyses of gut contents (Newton, 1967; Summers, 1981) showed that *Rubus* seeds are quite important in their diet even in late

winter when they are less available. I obtained direct and indirect evidence for this. The first came from food choice trials with captive birds. The second is apparent from the comparison of feeding records with abundance of stocks of fleshy fruits (Chapter 3): these seeds were heavily taken when stocks were low; similar results were obtained by Newton (1964). Brambles, for example, are rich in fat (32.5 mg/g dry weight, Greig-Smith and Wilson, unpublished data; in Crocker, 1987) and Bullfinches can survive and maintain weight on a diet solely of bramble seeds in mid January (Matthews, 1983). They are also relatively easy to handle (Fig. 1) and presumably do not contain important concentrations of phenolic compounds.

In relation to the selection of *C. arborea* seeds, Priolos selected larger and easily accessible fruits. In 1992 and 1993 the birds were seen feeding in 67 and 32 trees, respectively; and more had marks of feeding birds. This contrasts with Newton's (1964a) findings for Marley wood Bullfinches, which fed only from 5 out of 105 seeding ash trees. However, Matthews (1983) stated that "very few of the ash trees were totally ignored by Bullfinches. Some were preferred to others, but when the stocks of preferred seeds deteriorated, the less preferred seeds were also taken".

The phenolic content of *C. arborea* seeds may have influenced Priolos' preferences as birds did not take seeds in quantity until December, when levels of phenolics were higher. High levels of phenolics can lead to low palatability, depressed growth rates, an increase in faecal nitrogen i. e. by reducing the availability of proteins in the diet and the activity of digestive enzymes (Mole & Waterman, 1987a); but it is still an open question as to what animals are really avoiding when they reject astringent food (Butler *et al*, 1985; Bernays *et al*, 1989; Mole & Waterman, 1987). Over the period since Feeny (1969) drew attention to the importance of phenolics as feeding deterrents it has been well established that herbivores do avoid these compounds (Milton, 1979; Buchsbaum *et al*, 1984; Lindroth & Batzli, 1984; Tahvanainen *et al*, 1985; Bernays *et al*, 1989; Jakubas *et al*, 1989; Snyder, 1992).

Levels of phenolics in *C. arborea* increased until seeds were mature and then decreased. What are the advantages of this pattern to *C. arborea*? As seeds mature they became more suitable for herbivores. Thus, it may pay the plant to build up levels of phenolic secondary compounds in order to minimise predation. Once seeds become dry they, may be, come quite unsuitable for herbivores so there will be no need to maintain high phenolic levels. This explanation assumes that it is costly to maintain high levels of phenolics. Alternatively, it could be more costly to remove them, which may be necessary for the seeds to germinate well. This seems a good strategy for wind-dispersed seeds. For seeds like those of *H. gardneranum*, where dispersion by frugivores is important, it should be more advantageous to possess high levels of phenolics in the husk. It should be noted that these plants are exotic in the Azores, *C. arborea* is endemic from Madeira island and *H. gardneranum* from the Himalayas, and no information is available on the predators or dispersers that may have influenced these patterns of chemical defence.

Phenolic levels in December (mean=52.3 mg/g; Fig. 8) are much higher than those found to affect ash seed consumption by Bullfinches in Britain (mean=22.7 mg/g; Greig-Smith & Wilson, 1985) but they did not completely inhibit Priolos from taking seeds. Birds may only show a clear aversion to very high phenolic levels. Alternatively, the birds may tolerate high levels of some phenolics in a small proportion of the total diet if these phenolics are absent in the rest of the diet (Rosenthal & Berenbaum, 1991). This hypothesis presupposes the existence of a varied diet but, it is not supported because *C. arborea* seeds comprise a great proportion of the diet in winter. In early March, phenolic levels in *C. arborea* seeds were smaller than those of ash seeds (Greig-Smith & Wilson, 1985). It might be that once phenolic levels decrease they get below a level of influencing the birds' preferences. However, if fat (or, in general, energy) levels are low, phenolics may be unimportant in seed choice. A relation of this kind exists in Primates. To them, protein seems to be the limiting factor (Milton, 1979; Oates *et al*, 1980) and phenolics only become important in food selection when protein levels are high (Bernays *et al*, 1989). *C.*

arborea seed samples had no lipids to interfere with the phenolic assays, which means that their concentrations of fat are very low. The fact that Priolos readily discriminate between seeds on the basis of their size suggests that energy may be a limiting factor. The importance of size in accounting for seed preference is likely to depend on the chemical compounds of the seeds. Providing that handling time is not costly and that seed chemical compounds show little variation, then bullfinches would benefit more by concentrating on large seeds.

The winter picture is quite different for British Bullfinches. They feed on ash seeds, which come in a range of sizes, both within and between trees, and this is likely to affect their ease of handling. There is an enormous difference in terms of behavioural costs of feeding between ash and *C. arborea* seeds. In comparison with seeds of ash (weight up to 80 mg), seeds of *C. arborea* are much smaller (weight up to 10 mg) and relatively easier to handle. Captive Bullfinches feeding on ash take up to 55 s to husk seeds and up to 220 s to break up the kernel (Matthews, 1983). Virtually no ash seeds were processed in less than 70 s. Priolos processed seeds of *C. arborea* in 2.5 to 20 s (average 5.3 s). Matthews found that captive Bullfinches prefer bunches of small seeds (average weight 31 mg). Of the seeds taken from the bunches, 16% of small seeds were successfully husked whereas only 7% of the large seeds (average weight 45.1 mg) were. In an experiment where 16 birds were provided only with large seeds all but one bird lost weight and after 3 days 5 birds had died having lost 2.7-6.4 g (12-27% body weight) even though 66 % of the ash seeds remained unhusked. Captive Bullfinches lost weight also when feeding on medium size seeds. Only when fed on small seeds did birds maintain and gained weight (Matthews, 1983).

Although not presenting quantitative data, Matthews argued for a non significant relationship between preferred trees and ash seed size. Greig-Smith and Wilson (1985) compared handling times of birds observed feeding in ash trees with the average key weight for each tree, but as they pointed out these were favoured trees and comparison over

the full range of available trees (and therefore fruit sizes) was not possible. I suspect that a reliable measure of average ash tree seed size would be difficult to obtain. Greig-Smith & Crocker (1986) stated that preliminary field studies of ash seed consumption revealed size selectivity both within and among individual ash trees. Their experiments with sunflower seeds showed that heavy fruits can be very costly to Bullfinches in terms of handling time. Thus, although the fat and phenolic content of seeds were important in explaining tree preference (Greig-Smith & Wilson, 1985) the importance of size has probably not been fully evaluated. Presumably, phenolics became important in tree seed selection because fat levels in ash seeds are high.

The end of *C. arborea* feeding seems to be determined by the appearance of new food supplies (e. g. buds) and a reduction in the desirability of the seeds themselves. My data suggest that such reduction in attractiveness is not brought out by the phenolic content of the seeds but by the fact that seeds get very dry and, presumably, also difficult to digest. Birds should be fed solely on *C. arborea* and their faeces analysed for % of digested material in order to evaluate this hypothesis. Nonetheless, in April one captive Priolo as well as chaffinches and canaries could not survive on *C. arborea* seeds alone. Likewise, British captive Bullfinches do not survive on a diet of ash seeds in April (Wright & Summers, 1960). Even in August, when ash seeds are still green, they are less digestible than canary seeds (83% compared with 94%). By May they are only 65% digestible, which is close to the digestibility of the outer leaves of pear buds, and birds usually discard these leaves (Matthews, 1983).

In order to have a better picture of the value of these seeds for Priolos, analysis of nutrients would be necessary. Nevertheless, feeding experiments showed that all foods with the exception of perhaps *C. macrocarpa* in early winter are preferred to seeds of *C. arborea*. Thus, *C. arborea* may lie on the borderline between an adequate and an inadequate food for this bird. The results suggest that preferable *C. arborea* seeds are available only

for January and February as a result of a combination of availability of other seeds and the palatability of these seeds.

4.4.4 Flower bud selection

I. perado provides the only important source of flower buds for Priolos. In Britain and Continental Europe a wider range of species is taken (Crocker, 1987; Newton, 1964). Five variables: bud size, time of swell, growth stage, the arrangement of buds within the plants and availability of other foods can readily be invoked to explain the selection of *I. perado* by Priolo.

Flower buds of *I. perado* are much shorter than flower buds of *L. azorica* and *P. undulatum* which, despite their enormous availability, were never seen to be taken. About 40 trees were inspected but none showed any evidence of use. Flower buds of *P. undulatum* were available in January and February when other foods, fern sporangia and *C. arborea* seeds, were still plentiful. This may account for the fact that these buds were not taken although studies with British Bullfinches (see below) suggest that flavour may be implicated. *V. tinus* ssp *azorica* was the only species providing similar flower buds to *I. perado* but they may be difficult to pluck because of their arrangement in large central inflorescences. The birds have to lean forward, cling to vertical stems or hover. These positions are not common in feeding Bullfinches (Newton, 1967a; This study). That buds easier to pluck should be preferred agrees well with optimal foraging theory which predicts that animals, specially during periods of food shortage, should maximise energy intake per unit handling time. Other flower buds known to be taken by bullfinches in Europe and Japan are those of Prunus trees (Numazawa, 1989; Newton, 1967; Noval, 1971). There is an endemic *Prunus* in S. Miguel, *Prunus lusitanica* ssp *azorica*, but this is now extremely scarce. When flower buds of this species were given to captive Priolo they were readily taken.

The timing of flower bud-feeding was most influenced by the developmental stage of the buds; only when they reached a size of 2.8-3.0 mm were they taken in quantity. Similarly, Newton (1964) and Summers (1982) observed that when feeding on wild flower buds of hawthorn, *Crataegus monogyna*, British Bullfinches first selected the largest ones. Newton argued that Bullfinches should prefer cultivated flower buds because they are larger than wild flower buds and both types can be taken at similar rates. Birds should benefit more by concentrating on Conference (*Pyrus*) flower buds because their edible portion is consistently larger than that of Comice (Summers, 1982; Matthews, 1983). However, Matthews & Flegg (1982) reasoned that wild buds can be taken at a faster rate which enables Bullfinches to compensate for their smaller size. Crocker's observations supported their idea. Such compensation is likely to be small because small buds have reduced nutrient concentrations (Greig-Smith *et al*, 1983).

The importance of shape (Summers & Huson, 1984) and flavour (Greig-Smith, 1985a) have also been examined. Summers and Huson measured size and shape of pear cultivars and used linear discriminant analysis to classify them as favoured or unfavoured. Flowe buds that were shorter and in which relative volume of the edible core was greater were preferred. Greig-Smith examined the role of flavour cues by feeding captive Bullfinches with hemp seeds coated with extracts of Conference and Comice buds. Each flavour was given to the birds with a control dish, which were seeds coated with acetone. Bullfinches ate similar numbers of flavoured and control seeds but showed behavioural differences when feeding on each type. Notably, they dropped more flavoured seeds than acetone seeds and took less time in husking them suggesting that they were contacting less with flavoured seeds. Such changes in feeding behaviour were more pronounced for seeds flavoured with Comice extract which matches the avoidance of Comice pear trees by wild birds.

Similarly, the strong flavour of both *P. undulatum* and *L. azorica* might be offensive to the Priolo, but this needs to be investigated. According to these studies both

physical characteristics and flavour may play a part in explaining flower bud preferences by bullfinches. The digestibility of the various flower bud tissues is also likely to be important since this affects the proportion of material that will be absorbed. These variables may be intercorrelated which makes it difficult to know the relative importance of each one.

Summers and Jones (1976) showed that Comice buds have lower protein content and obtained a positive correlation between nitrogen content and the strength of damage induced by bullfinches to pear trees. A detailed chemical analysis by Wilson *et al* (1983) and Greig- Smith *et al* (1983) showed slight differences between these two varieties with reference to total nitrogen, free amino acid, protein hydrolysate amino acid, glyceride-glycerol, glucose, fructose, sucrose, starch, phosphorus and cation contents. Greig-Smith *et al* (1983) showed also that levels of nutrients rose sharply in mid-March coinciding with an increase in the size of the flower buds. According to Greig-Smith *et al* any consistent chemical difference can be regarded as a potential factor determining bud selection. It is, however, very difficult to prove which factor, or combination of factors, is most important in driving the birds selection mechanism.

Priolo foraged on *I. perado* flower buds only when they reached a certain developmental stage. From studies quoted above it is expected that a sharp increase in length in Spring will coincide with an increase in nutrient content. Although there was no shortage of seeds this was the time when there was a switch in the importance of feeding items from seeds to flower buds. Newton (1964) and Crocker (1987) presented similar results for Bullfinches in Britain. My study showed also that bud development can vary considerably between years, which is probably a result of weather conditions. This must influence levels of flower bud feeding and contributes to the explanation of why damage to fruit buds in British orchards fluctuated considerably between years (Summers, 1981).

If *I. perado* flower buds do not increase in size before *C. arborea* seeds get very dry and the stock of fern sporangia runs out, starvation is likely to be common amongst Priolos. Alternative foods, fern fronds and mosses are less preferred. Birds fed on fern

fronds and moss mainly when other foods except old seeds of *C. arborea* were not available. Similarly, Newton (1964) and Summers (1982) demonstrated that if the winter seed stock runs out before the increase in flower bud length, British Bullfinches may starve: captive birds feeding on a hawthorn and pear bud diet, exhibited symptoms of starvation, in January and February, even after only 24 h. Moreover, Newton's captive birds spent three times longer feeding, when on a bud diet than they did on a seed diet. In March birds were able to maintain their weights either on a diet of hawthorn or pear buds.

4.4.5 Fern selection

The Priolo was highly selective when feeding on fern sori. The larger sori were invariably selected both within and between species and the smaller ones ignored. There was thus consistency in its choice, which indicates that the Priolo was optimising based on a maximisation of a currency (McCleery, 1978). This is likely to involve net rate of energy intake, especially because ferns were consumed during the winter.

Within patches of *W. radicans* the preference ranking of sizes was dynamic as it was influenced by the relative variability of sizes encountered within a patch, though sori smaller than 2.2 mm did not seem to be taken. Both observations agree well with optimal foraging theory which predicts that: a) animals should choose food items that provide higher energy intake per unit time and b) an item is taken or not depending on the availability of more favoured items. This has been well established theoretically and empirically (Pulliam, 1974; Charnov, 1976, Stephens & Krebs, 1986).

Although eaten significantly faster than seeds of *C. arborea* , fern sori did not comprise the large majority of the diet. Various reasons may explain why sporangia were taken: as a nutritious balance to the diet, because they were easier to handle; contained less concentrations of toxic or distasteful chemicals; were more digestible or due to a combination of these reasons. The fact that below the threshold size of 2.5 mm sori were ignored suggests that energetic rewards were probably involved. Feeding experiments

showed that, in early winter, when given the option between seeds of *C. arborea* and fern sori, Priolo did not show a clear preference for one of the options. If sporangia provide less energy than seeds then only larger sori would be worth taking. On the other hand, in late winter, sori were preferred to seeds of *C. arborea* although more birds should have been tested. Nonetheless, both feeding choice experiments and diet showed that, as winter progressed, fern sporangia should have become more profitable for feeding Priolos than seeds of *C. arborea.*

In April and May, when sporangia were not available, young fern fronds were consumed. *O. regalis* was actively selected, although other species were more abundant, presumably because this species was the only one about to produce spores. If *O. regalis* shows similar developmental growth characteristics to *P. aquilinum*, young fronds should be more profitable as they have a higher carbohydrate content (Williams & Foley, 1976).

Carcinogens in *P. aquilinum* might prevent the birds from feeding on the tips of young fronds, where the concentrations of these components have been found to be higher (Cooper-Driver, 1976). It should be advantageous for the plant to concentrate its toxin defence mechanisms on the tips because, if the lower parts of the frond are taken, the plant can still grow. A large number of carcinogenic substances have been isolated from *P. aquilinum* (Cooper-Driver, 1976) and Evans (1976) demonstrated experimentally that this fern is carcinogenic for the Japanese quail. *O. regalis*, on the other hand, is acyanogenic (Harper *et al*, 1976). This may help to explain why the Priolo stopped feeding on fronds of *P. aquilinum* when *O. regalis* became available.

Fronds did not seem to constitute a good food source because, as soon as sporangia became available, birds stopped feeding on them. Wild birds feeding on moss and fronds produced large quantities of faeces, implying that little material was digested. Small fronds of *P. aquilinum* had up to ten faeces on top and more underneath whereas large fronds of *C. macrocarpa* had only two to four faeces at the most. This suggests that a great quantity of frond and moss material had passed straight through the gut, perhaps corroborating the

view that a diet of fronds is not adequate for Priolos. According to Garton (1979) a food source that provides nutrients at a rate less than the rate at which they are being used should never be taken. However, if better foods are scarce, fronds should be taken, enabling the birds to survive until better foods became common (Greenwood, 1984).

Thus, the timing of fern-frond feeding should be coincident with the timing of food shortage. Although seeds of *C. arborea* were still present, by the end of the winter, they may be so dry and indigestible that fern fronds, although poor, may be a more profitable alternative. In April, one captive Priolo did not exhibit a clear preference when given the option between *C. arborea* and *P. aquilinum.*

For a better appreciation of the importance of ferns for feeding Priolo future studies should : (1) provide detailed analysis of fern nutrients and their secondary components, (2) use more birds in feeding choice experiments and (3) see whether it is possible for the Priolo to maintain weight solely on fern sporangia and fronds.

CHAPTER 5
ANNUAL CYCLE

5.1 INTRODUCTION

The Azores archipelago has an extreme oceanic climate with small seasonal fluctuations in temperature and water regime (Sjogren, 1984, Medeiros, 1987). Physiognomically, Azorean cloud forests resemble tropical montane forests (Haggar, 1988). Moreau (1950) and Serle (1981) observed that breeding is seasonal in tropical montane forests. For lowland forests, however, they were not able to define a universal breeding season, although most families had a preferred nesting season. Very little is known about the ecology of Azorean cloud forests. For example, it is not known whether the Priolo annual cycle resembles that of tropical montane forest birds. This may not be expected because, for instance, seasonal variations of daylength in the Azores are much more pronounced than those of the tropics. The evaluation of this question would provide a primary step in understanding the ecology of terrestrial birds in these native forests. This would also be of crucial importance on practical grounds because the conservation of the Priolo requires a knowledge of seasonal rhythms and of connections between habitat and food resources.

Both breeding and moulting are energetically costly and are expected to occur when food is abundant (Lack, 1966, Perrins, 1970). Although insular habitats can be regarded as relatively equable throughout the year when compared with similar mainland areas, these activities still often present a strong seasonal component (Snow & Snow, 1964; Diamond, 1980; Greig-Smith, 1980; Brooke, 1985). Generally, the distribution and abundance of food are expected to influence overall seasonal rhythms of birds (Wiens, 1989) and will be used here as a basis for an examination of seasonal activity patterns.

This chapter provides information on annual cycle events and, to a lesser extent, the population dynamics of the Priolo. Previously, it was only known that juveniles occur in September (Bibby & Charlton, 1991) and females with brood patches from June to August

(Bibby *et al*, 1992). This chapter, therefore, can be viewed as an attempt to begin to fill in the gaps.

The following questions were asked: (1) Do breeding and moulting show seasonal occurrence and are they correlated with food abundance? (2) Are mortality levels correlated with food abundance?

5.2 METHODS

Mist netting was carried out at several sites both within and at the edge of the Laurel forest. Three nets (6, 12 and 18 m) were used at any one time: the nets were placed at feeding sites, especially patches of *Polygonum capitatum* and *Leontodon filii*, on up to four days a week.

Birds were examined for differences between male and female plumage, were colour-ringed, weighed with a 50 g Pesola spring balance and measured. The following measurements were taken: (a) wing length, measured by folding the wing and pressing it flat on a millimetre ruler; (b) tail length, measured by pressing a ruler against the skin under the base of the tail and pressing the tail feathers flat on the ruler, (c) bill length, from bill tip to the front of the skull using dividers; (d) bill depth, using a pair of callipers at the deepest point of the bill (Svenson, 1982); total head, from the back of head to bill tip; tarsus length, folding the tarsus on a stopped ruler. At the start of the study, May and June of 1991, measurements were taken three times and an average calculated.

All birds were examined for presence of a brood patch, presence or absence of primary moult, fat score (0 to 4 according to Spencer (1975), odd marks or injuries and presence or absence of throat pouches.

Recruitment into the population was estimated by counting the number of juveniles (with brown heads) during route walks (routes indicated in chapter two) made every ten days. To assess mortality rates, colour-ringed birds were sought widely along all marked routes.

5.3 RESULTS

5.3.1 Sexing

In the field sexes were indistinguishable. In hand, some birds could be sexed by colour differences. Cocks had the abdomen and flanks suffused with a reddish-tawny tinge as stated by Goodwin (1985) and never possessed brood patches. When this criteria was used for sexing I obtained a sample size of 22 males (with reddish tinge) and 28 females (with brood patch). Wing and tail length were significantly different between males and females. The remaining male and female measurements overlapped extensively (Table 1).

A further 23 birds could not be sexed with this method. The amount of red varied between individuals; in some birds only 2 or 3 feathers had a reddish tinge and, 15 birds caught between May and July had no reddish tinge at all. At first sight, it did not seem realistic to classify all these birds as females because some young males might not develop the reddish-tinge until late in the season. From these 23 birds, 12 could be sexed because they were seen paired with ringed birds of known sex. However, as they had neither reddish-tinge nor brood patch (although it was too early for much of the period; see 5.3.2 breeding and moult) and, were probably mostly first year birds, were not used in calculations of biometrics.

The traditional method of ageing bullfinches, colour differences in their greater coverts (Newton, 1966), was difficult to apply to Priolos because adults have buffish edged coverts too, unlike the greyish mainland bullfinches. Some birds seemed definitely first-years (four birds captured in June still had a few brown feathers on their heads) but, for others this was difficult to determine. Therefore, for the analysis of overall mortality rates I did not attempt to distinguish between first years and older birds.

Table 1. Priolo Biometrics: comparison between sexes of wild birds.

	Sex	n	Range (mm)	Mean (mm)	SD	T-test
Wing	m	22	86.0-93.0	90.0	1.67	2.83**
	f	28	85.0-92.0	88.7	1.49	
Tail	m	21	65.0-75.0	72.8	2.48	2.56**
	f	28	66.0-74.0	71.2	1.68	
Bill L	m	22	12.0-14.0	12.8	0.48	0.12 NS
	f	28	12.0-13.0	12.7	0.39	
Bill D	m	22	9.7-11.0	10.4	0.33	0.86 NS
	f	28	9.5-11.5	10.4	0.52	
Total head	m	21	30.5-32.2	31.0	0.51	0.29 NS
	f	22	29.3-31.8	30.8	0.54	
Tarsus	m	22	23.5-25.5	24.5	0.57	0.96 NS
	f	28	22.0-25.7	24.5	0.92	

** P<0.01 NS=Not significant

5.3.2 Breeding and Moult

The first female with a brood patch was caught on the 10th of June, about three weeks after fresh *P.capitatum* seeds became available. The birds' behaviour in late April, May and early June indicated pre-breeding activity. The male's dance and bill caressing (Hinde, 1955; Nicolai, 1965) were common in May and early June; a twig display was observed in late April and courtship feeding (see Newton, 1972) was commonly seen in late May and early June. In the last week of May two birds were seen flying with dry twigs in their beaks.

In 1992 two nests were found. The first, on the 6th of July, was being built. Two birds were watched for two hours on two consecutive days. They were seen to be carrying twigs, stems of dry grass and moss but no eggs were laid on this nest. The second, found on the 26 of July, had one chick of about 10 days old. Twelve faecal sacs (see Newton, 1967) were present on the edge of the nest. The first nest was located within short *Cryptomeria japonica* and the second within *Clethra arborea* and laurel but both were placed on a *C. japonica* tree at about 3 m height. Nests were alike, consisting of an outer layer of

twigs of *C. arborea* and *Erica azorica* and an inner layer of rootlets, grass and a few bits of moss

(Fig. 1).

Figure 2 shows that although breeding commenced in June a significantly higher proportion of birds started only in July (χ^2=10.06 P<0.001, df=1 with Yates' correction). There were positive correlations between the monthly percentage of females with brood patch and food abundance, as indicated by (1) the number of plant species providing food (rs=0.975, P<0.05, n=5) and (2) the number of seed heads and fruits in transects (rs=0.8, P<0.10, n=5; Fig. 3). This indicates that Priolo bred when food abundance was high. The relatively extended time period that females were found with brood patches (Fig. 2) e.g. one captured on the 10th of June with a brood patch, and again on the 3rd of August still with a brood patch, perhaps suggests a second breeding attempt by some birds. A small proportion of birds could still be breeding in early September, but no adults were caught (Fig. 2) which verified this.

The progressive appearance of juveniles into the population (% of juveniles seen during route walks) is shown in figure 4. Juveniles reached 50% of the birds by the last ten days of August in 1991 and by the first ten days of September in 1992. However, this figure could be biased in September owing to the fact that adults, undergoing a full body moult, were probably less likely to be seen than juveniles. Further increases in the proportion of juveniles were not significant (χ^2:1991=0.34, 1992=0.15, df=1 with Yates correction). Therefore, breeding productivity seemed relatively low: about two young per pair.

Adult moulting followed breeding (Fig. 5). It occurred when the abundance of fleshy fruits was increasing (see Chapter 3). Also, two juveniles caught in September were moulting head feathers and, some juveniles were observed from late August to October with partially black caps.

Fig. 1. Nest of the Priolo. Note the occurrence of two layers.

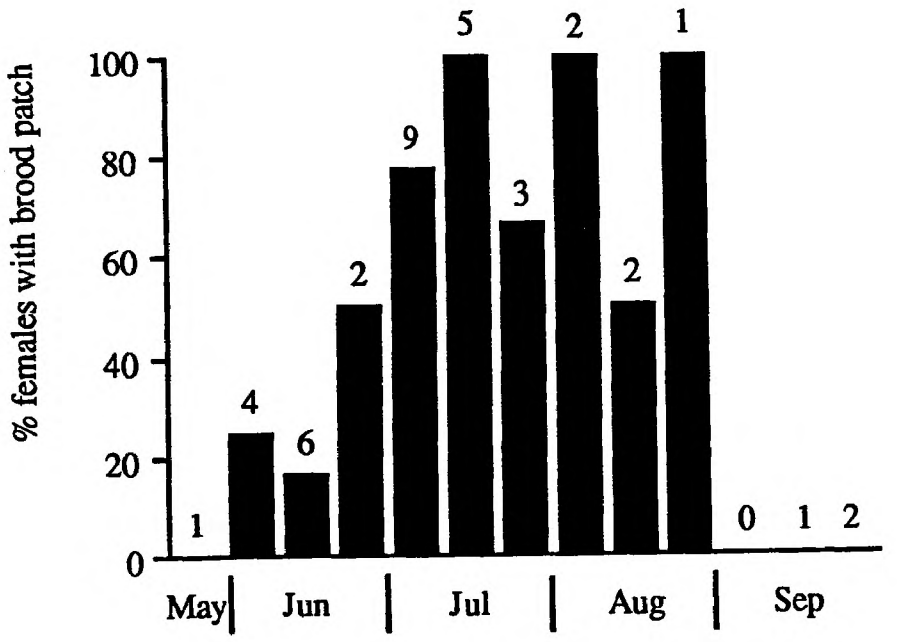


Fig. 2. Seasonal pattern of nesting, shown by the percentage of females with brood patch in 10 day periods. Numbers above bars indicate the total number of females caught. Data from 1991 and 1992 were combined. It should be noted that some birds were difficult to sex (see section 5.3). This may explain the decrease in the percentage of females with brood patch in July (some of these birds could actually be males) when, presumably, the whole population should be breeding.

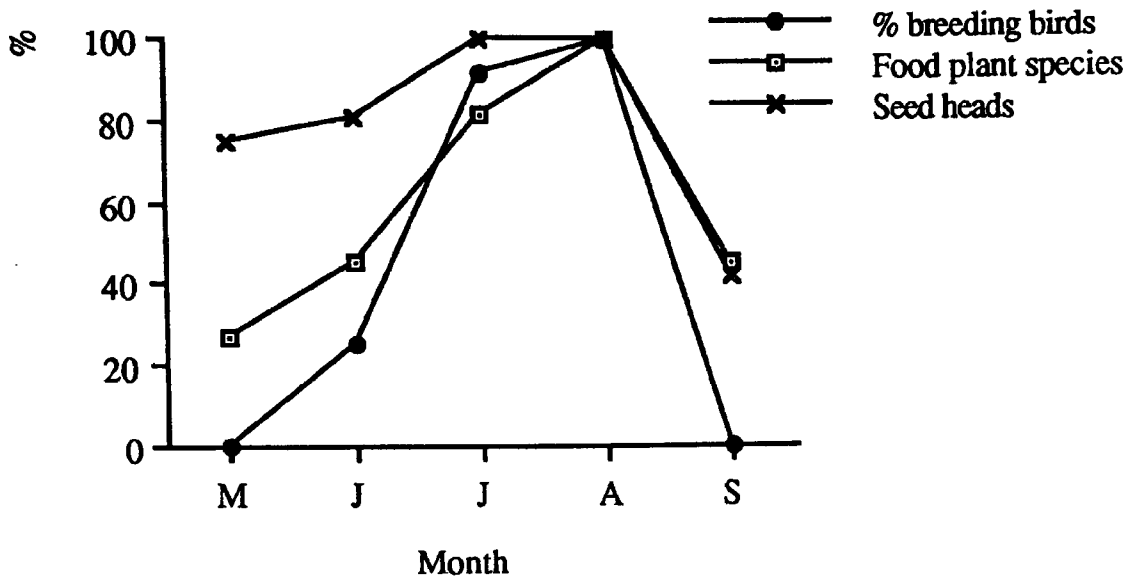


Fig. 3. Relation between the number of breeding birds (as % of females with brood patch) and two measures of food abundance (number of food plant species and seed heads in transect counts along established routes, see Chpter 3). The data is presented as follows: the largest value of each categorie was given a value of 100% and the rest were scaled accordingly (Grant & Grant, 1980).

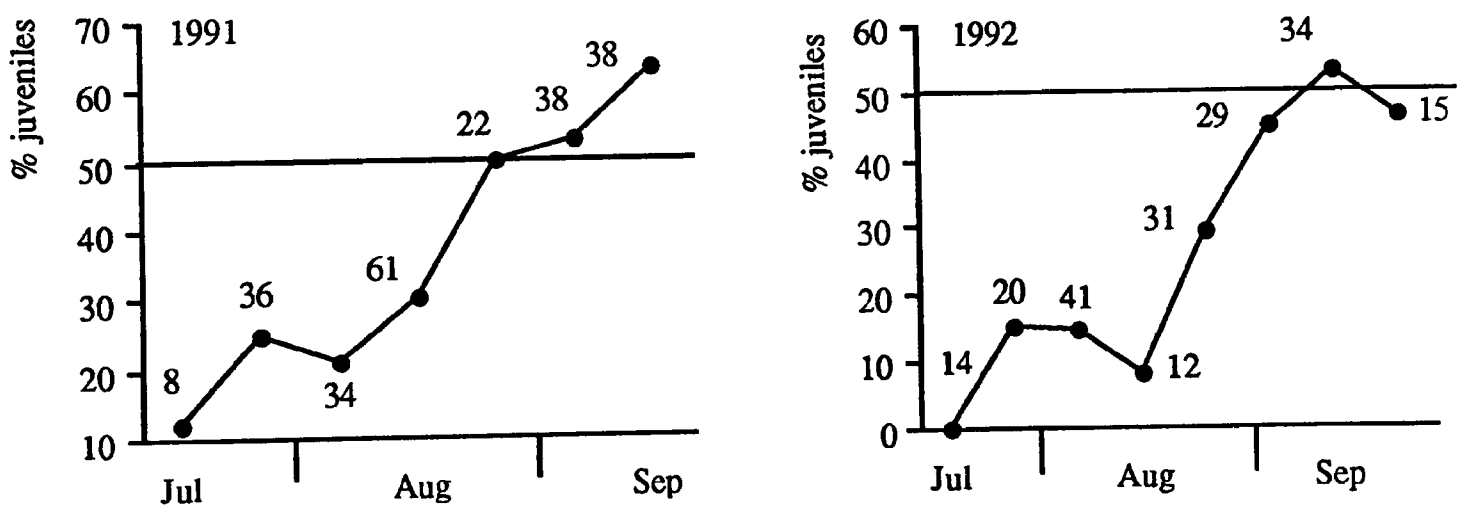


Fig. 4. Proportion of juveniles seen during route walks in 1991 and 1992. Sample sizes are indicated beside the points.

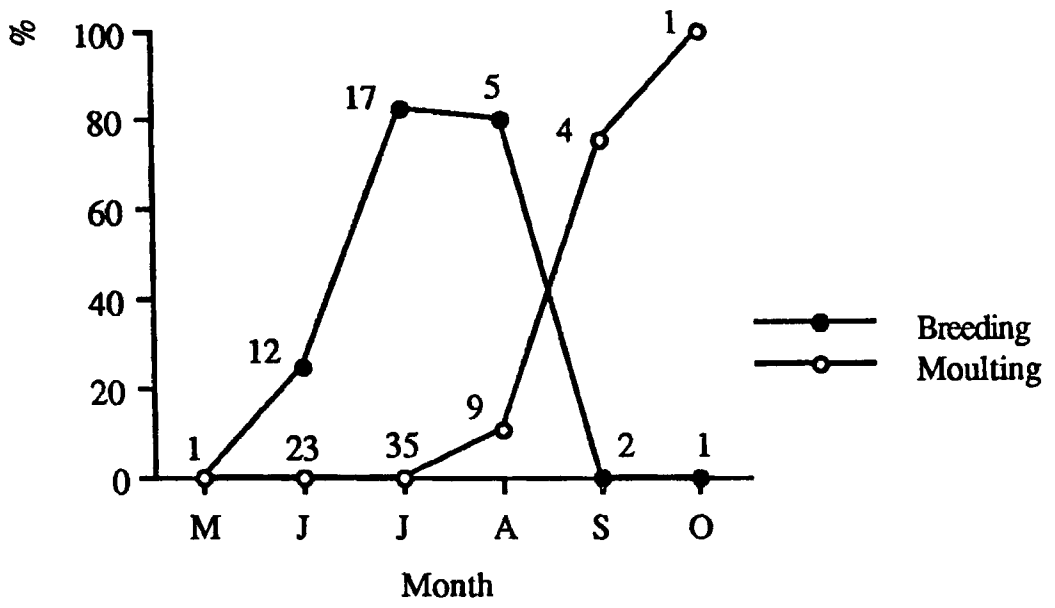


Fig. 5. Monthly comparison between the percentage of breeding and moulting adult birds. Breeding is presented as the percentage of females with brood patch and moulting as the percentage of adults undergoing primary moult. Sample size is indicated beside the points.

5.3.3 Body weight and fat scores

Overall, the mean monthly weight of the Priolo varied from 29.6 g in August to 31.4 g in January, a difference of 1.8 g (Fig. 6). Average female body weight was higher than average male body-weight in June (mean=31.49, n=10 vs mean=29.58, n=10), July (mean=30.37, n=18 vs mean=28.96, n=17) and August (mean=30.22, n=5 vs mean=28.15, n=2). In June the difference was almost significant ($t=2.07$, $P<0.053$, $df=18$) and in July it was significant ($t=2.52$, $P<0.017$, $df=33$). The monthly winter body weight comparison between males and females is precluded due to very small sample sizes. However, one should expect the weight variations between winter and summer to be less pronounced for females since they were heavier in summer (Newton, 1966). In fact, when the weights were divided into summer (May-September) and winter (December-April) only males showed a significant difference between seasons (males: $t=2.7$, $P<0.01$, $df=38$; females: $t=0.7$, NS, $df=44$). Although seasonal changes in body weight appeared to be

small there was considerable diurnal variation: birds caught in winter before 12:00 h were, on average, 1.3 g lighter than birds caught after 14:00 h. Though sample sizes were small, this difference was significant (t=2.75, P<0.02, df=16).

Fat scores higher than two were recorded only twice (Fig. 6). When fat scores were divided into =0 and ≥1, winter-birds (December-April) had significantly more fat (P<0.001) than summer-birds (May-October; χ^2=13.78, df=1 with Yates correction; Fig. 7). The correlation between monthly mean fat scores and weights was slight (rs= 0.17, n=10, no birds were captured in both November nad April) but when calculated without May and October (in which only two and one birds were captured, respectively) it improved strongly (rs=0.64, P<0.05, n=8).Thus, as expected, increased fat deposits help to explain why birds in winter were heavier.

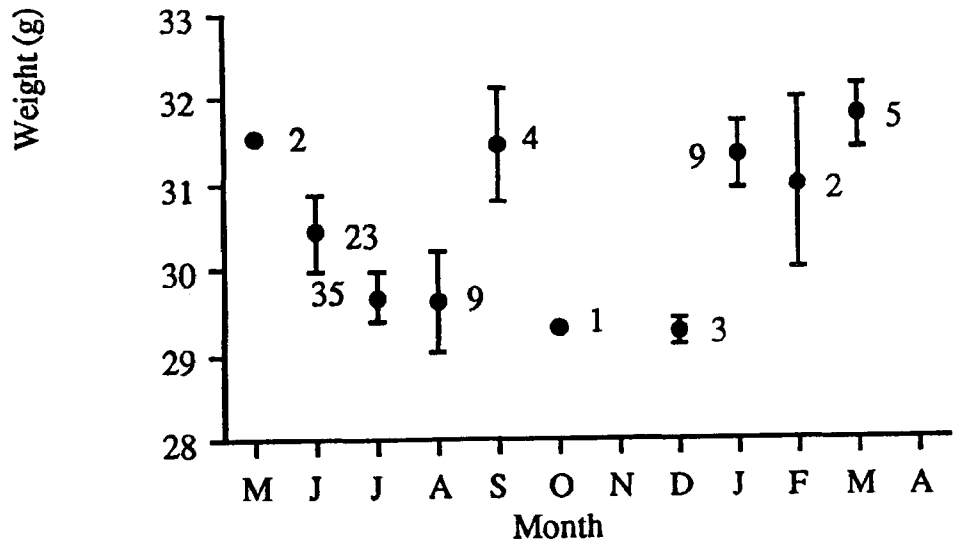


Fig. 6. Seasonal pattern of body-weight, shown by monthly means ± S.E. of birds mist-netted. Sample sizes are indicated beside the points. Data from 1991, 1992 and 1993 were combined.

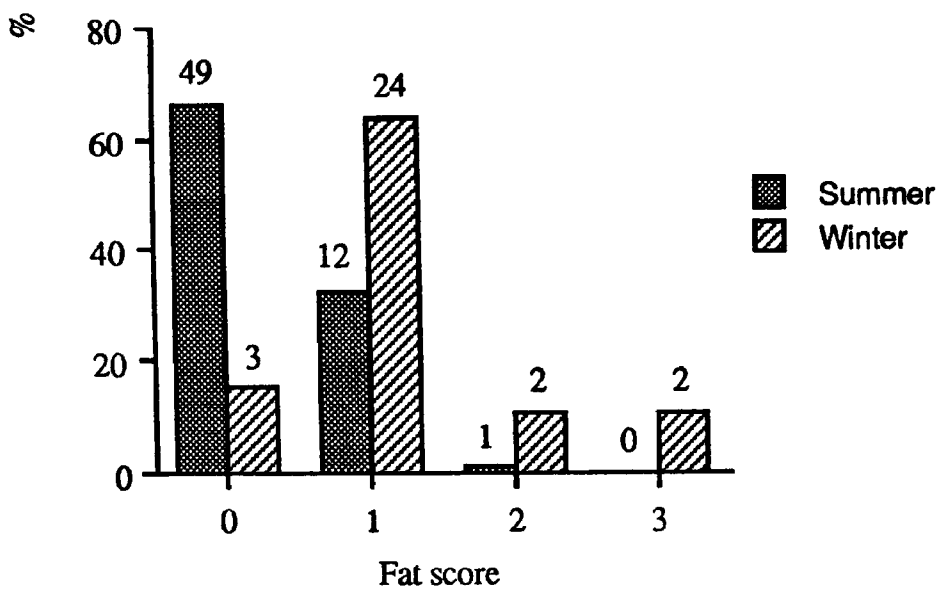


Fig. 7. Comparison between fat scores in summer (May-September) and winter (December-April). Numbers above bars indicate sample size. Data from 1991, 1992 and 1993 were combined.

5.3.4 Mortality and recruitment

A total of 37 and 31 birds were caught in 1991 and 1992, respectively. Of these, only 23 (62%) and 17 (55%) were seen subsequently during the year of capture. The other 14 were presumed mainly transient visitors (see mobility, Chapter 2) or unestablished first-year birds (as judged by their greater coverts). Of the 23 birds that were recorded again at least once in 1991, 11 and 4 were known to be alive, respectively in 1992 and 1993, which gives a maximum annual mortality rate of 58% (52% in 1991/92 and 64% in 1992/93). The mortality figure for birds caught in 1992 is 59%. These figures are almost certainly overestimates since it is likely that some settled individuals in the study area escaped being seen. For example, if only two and one more birds were seen, respectively in 1992 and 1993 the mortality rate figure would be 48%. In order to compensate for small sample sizes I considered also the birds that were not recorded again during their year of capture. Only four were seen in subsequent years. If these had been seen at a similar rate to the settled individuals, the figures would be seven for 1991 and six for 1992. When calculations are

based on the grand totals, the mortality rate is 51% for 1991 and 58% for 1992. Thus, although accurate mortality rates cannot be calculated, a figure of about 50% showed up. This fits the 1:1 ratio of adults:juveniles after breeding (Fig. 4).

In a stable population, the number of juveniles surviving to enter the breeding population can be expected to be similar to adult mortality. Recruitment can be evaluated using the ratio: first years/adult birds, captured before the breeding season. Unfortunately, an accurate figure of recruitment was impossible to determine because some birds were difficult to age (see sexing section above). In June and July of 1992, I captured 22 birds. Of these, ten to twelve seemed definitely first years which gives a recruitment figure between 45% and 59%. The comparison between this figure and the mortality figure for 1991/92 indicates that the Priolo population might be stable or, at least, does not seem to be declining; however, the sample sizes are too small to draw any firm conclusions.

I tried also to use a GLIM program developed by Cormack (1985) to analyse my capture-recapture data. Of the models calculated, those including birth and death seemed satisfactory but one outlier was present and one birth estimate was negative. When birth was set to zero and the outlier eliminated, other large positive residuals occurred. A similar result was obtained by considering winter and summer or 15 day periods over summer (captures in winter were too few) as capture periods. This analysis suggests that birds left the area being sampled temporarily (Cormack, 1985). Large movements and transient visitors were common over summer (see mobility, Chapter 2). This behaviour simply invalidates all capture-recapture analyses (Seber, 1982) and survival estimates should not be quoted. Thus, population estimates derived from Lincoln indices (Chapter 2), especially those obtained over a larger area, should be viewed with great caution.

The proportion of birds ringed as adults in 1991 along route 1 (n=17) that were seen in the winter of 1992 increased from 17.6% in January and 11.8% in February to 41.2% in March and 35.3% in April. Moreover, in 1992, of 11 birds ringed in January/February, I did not see five (45.5%) after April. Of these, four were first year

birds. These results indicate either differential mortality or movements of younger, less experienced birds. The last explanation is the least likely because the area along route 1 had a high density of *Ilex perado* (which provides the main food in April; Chapter 3) and also because adult birds did not seem to move out of these area. A single *I. perado* tree was visited by at least 6 marked birds (of which two were definitely first-years). In addition, aggression between feeding Priolos was very infrequent (see also Wilkinson, 1982) and caused only momentary interruptions of foraging. Field and laboratory observations of feeding birds and radio-tracking to plot home ranges, together suggested that first-year British Bullfinches were neither excluded from ash trees nor suffered direct interference while feeding (Greig-Smith, 1985). Because first-years had less ash in their gut contents and were less efficient in dealing with ash seeds than adults, Greig-Smith (1985) attributed their poor winter survival mainly to relative incompetence in foraging.

5.3.5 Group size

Direct records of Priolo group sizes showed that the median group size was always one or two and that there was little monthly change (Fig. 8). This shows that most individuals foraged independently or in pairs. In May and June the proportion of birds seen in pairs was significantly higher than the proportion of birds seen singly ($\chi 2$=7.5 and 10.5, $P<0.01$, df=1 with Yates correction), whereas in July and August, the majority of the birds were seen singly, but only in August was this significant ($\chi 2$=5.3, $P<0.05$. df=1 with Yates correction). This suggests that in May and June birds were pairing up, and in August most females were incubating. There was a very slight tendency for larger groups (> 4 birds) to be encountered in May/June and November. The largest group of birds (8) was seen in May at about 340 m of altitude, when seeds were very rare at high altitudes (Chapter 3). In August and September most groups larger than two consisted solely of juveniles. This possibly applies to November as well.

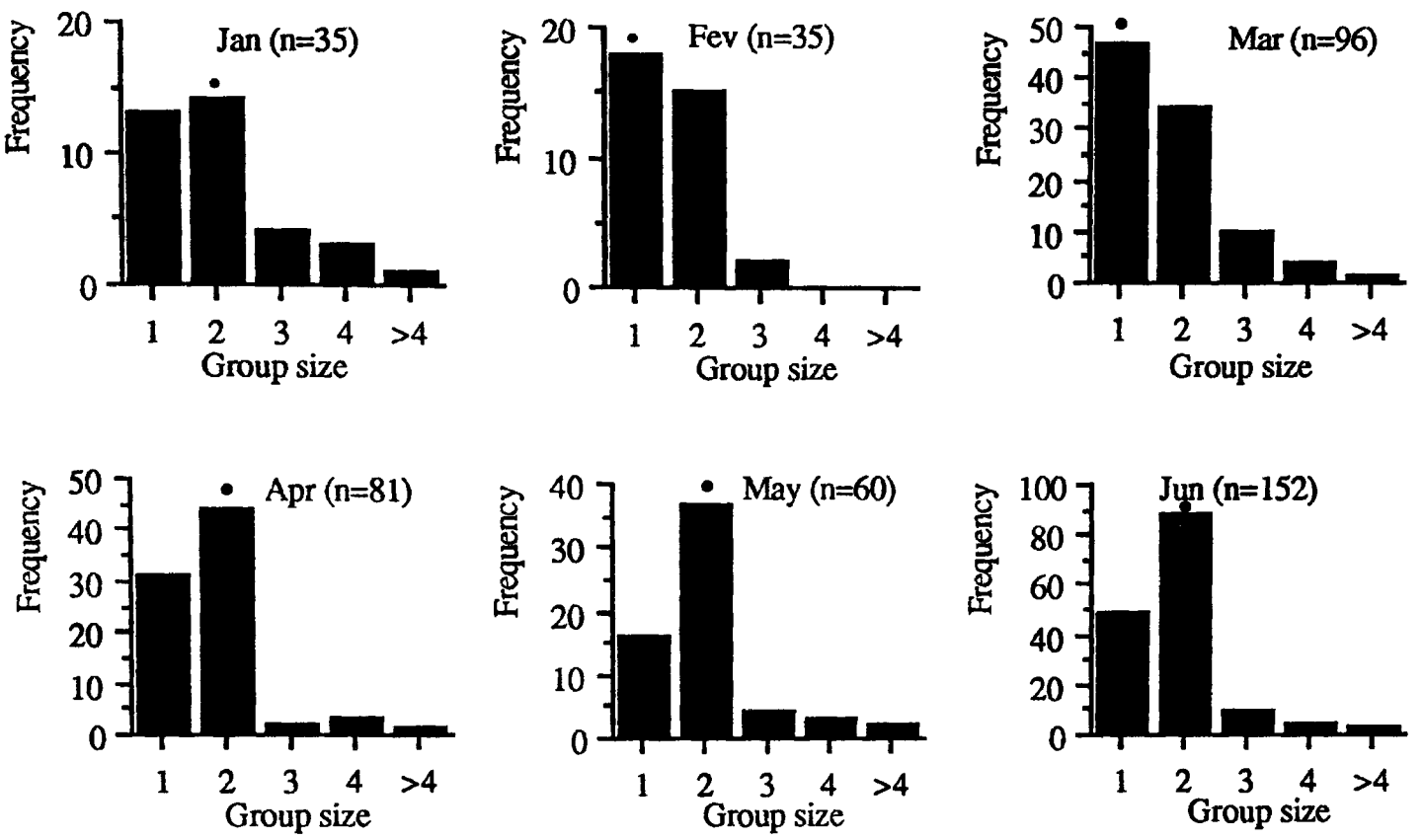


Fig. 8. Monthly distribution of Priolo group sizes observed within the study area between April 1991 and May 1993. Dots indicate monthly median group sizes.

5.4 DISCUSSION

Despite strong preferences for native vegetation, (Chapter 2) the two nests that were located were in *C. japonica.* At present there is no evidence to suggest that the Priolo should be specialised in terms of nest site selection. Both native and exotic forests provide an enormous amount of cover and predators were not common in the study area. Nonetheless, a few cats were present at low altitudes and head, wings and leg remains of an individual were found at a *P. capitatum* patch; the bird was presumably predated by cats. Newton (1964a) and Bijlsma (1982) studied the breeding of Bullfinches in England and Holland, respectively, and do not report specialisation in the choice of nest sites.

The decrease in the number of singletons and increased frequency of pairs in late spring and early summer can readily be explained by birds pairing up prior to the breeding season (Wilkinson, 1982). Breeding was highly seasonal and occurred when food abundance was high. The breeding season was considerably later (mid June/August : May/August) and shorter than that of European (but not Northern) Bullfinches (2 to 2, 5 months : 3 to 3, 5 months). Breeding in early summer may be advantageous because young fledge and disperse when fleshy fruits, a highly preferred food (Chapter 4) are abundant (Lack, 1966). In September and October, all birds observed above Furnas, approximately 7 - 10 Km from the main core of native vegetation, were juveniles feeding on a field of *Leicesteria formosa.* Also, the availability of protein may have an important role in enabling females to come into breeding condition (Perrins, 1970) and to feed young (Newton, 1967). Nymphs of *Hemiptera* emerging on leaves of *Laurus azorica* (Chapter 3) represent a readily available source of protein in June and July. Significantly higher female than male weights at this time may reflect a marked period of ovary action and egg formation (Newton, 1966a).

Breeding and moulting were strongly seasonal but variations in weights and fat scores between summer and winter were slight. Winter birds were, on average, just 1.8 g

heavier. This value is quite small when compared with the 4 to 5 g difference between summer and winter for the slightly smaller Bullfinches in England (Newton, 1966a; Greig-Smith & Wilson, 1984). The slight seasonal changes in body-weight and fat scores of the Priolo more closely resemble those of tropical birds (Ward, 1969, 1969a; Fodgen, 1972). These subtle changes are difficult to follow meaningfully by plotting mean weights of small samples (Ward, 1969). Similar diurnal changes in body weight to those of the Priolo have been documented for tropical birds (Ward, 1969). These variations could be caused by changes in fat, water, protein or the amount of food in the gut (Ward, 1969). British Bullfinches caught in the evening were, on average, just over 1 g heavier than those caught in the early morning (Newton, 1969).

Both Priolos (this study) and British Bullfinches (Newton, 1969) are heavier in the winter due to accumulation of fat. Winter nights in Britain are much longer and colder than those in the Azores, which may largely explain the higher winter fat scores of British bullfinches. The ability to accumulate sufficient fat each day, as an over night energy source, critically affects survival (Newton, 1969). Similarly, in less seasonal environments, most of the fat that birds deposit during the day is needed for overnight metabolism (Ward, 1969, 1969a). If preferred seeds are not available, other plants may be taken for their particular nutrient values. However, it must be born in mind that carbohydrates and fat are probably more important than nutrients such as minerals during late autumn and winter, because high energy sources are needed to meet the birds' metabolic requirements. This could help to explain why fern fronds were taken only when other foods were not available.

Higher mortality rates in 1992/93 are probably a result of later availability of large buds and herbaceous seeds (Chapters 3, 4). The consumption of moss tips and fern fronds was significantly higher in 1993 than in 1992 (Chapter 3) which corroborates this view. Some evidence was found for higher juvenile than adult mortality in late winter. This is common in many species e.g. the Great tit, *Parus major*, (Krebs & Perrins, 1978). British

national ringing recoveries also suggest highest Bullfinch mortality in late winter (Flegg, 1980) although Newton (1964) recorded heavy mortality from October to December in Wytham woods, Oxford. Bibby (1973) estimated that about 50% of British Bullfinches die each year, which is similar to the values obtained in this study.

Overall, the Priolo presents a strong seasonal pattern similar to that of Western European Bullfinches. There appeared to be slight variations upon this pattern, e.g. the slight variations in weight and fat, which could be an environmental correlate of a temperate oceanic island. Comparisons with the annual cycle of passerines of other North Atlantic islands may reveal further interesting points but, at present, no data are available. The phenology of most native plants of the montane forest was highly seasonal (a few individuals of certain species had two flowering periods in some areas; Chapter 3) meaning that there would be no scope for a different annual cycle pattern.

CHAPTER 6
GENERAL DISCUSSION AND CONSERVATION

6.1 General discussion

This study was aimed at evaluating the ecological factors which explain the distribution and abundance of the Priolo. I have shown that this question can best be analysed by a hierarchy of scale levels: general (range), broad (habitat), large (food supply) and small (food preference). Each scale allows certain types of questions to be answered and prevents unwarranted generalisations across inappropriate levels (Wiens, 1981). My results indicate that factors which may control the distribution and abundance of the Priolo (and perhaps those of most granivorous birds) will only be partially analysed unless all scale levels are taken into consideration.

Point counts showed that the distribution of the Priolo was highly associated with native vegetation and its margins all year round. Therefore, at an island level it is fair to say that the present range of this species is largely a reflection of the available area of native forest, though there are a few patches of native vegetation to the West where birds do not occur. Apparently, the Priolo has not been able to adapt to cope with a wide range of environmental changes, including the large-scale invasion of exotic plant species. This may partly be a result of historical factors (O'Connor & Fuller, 1985) but my study was not designed to evaluate this question.

On a broad scale, habitat types, and habitat structure and vegetation composition variables were used to correlate with the number of birds detected at marked stations. The density of Priolos was much higher in areas of native vegetation than in areas of exotic (plantations of *Cryptomeria japonica* and copses of *Pittosporum undulatum*) vegetation. Nevertheless, the degree of habitat selection and habitat discriminators varied seasonally. In summer, birds were less selective and used more habitats but in winter birds were more selective and used far fewer habitats.

Analysis at a large scale (food supply) showed that such shifts could be explained by dramatic seasonal changes in resource levels between habitats (Wiens, 1989). During the summer season birds relied mainly on herbaceous seeds obtained in forest openings but as winter progressed tree seeds, fern sporangia and flower buds available in areas of mature Laurel forest became increasingly important. Sightings of colour-ringed birds indicated that marked altitudinal movements occurred in spring and early summer, when food levels were lowest at higher altitudes.

Many of the landslides now present were created by a severe storm in 1986, which may have favoured breeding Priolos. In some areas the ground is so steep that new openings may be formed every year. Severe storms are mentioned in 1543 (Fructuoso, 1926) and local inhabitants remember a great storm in the 1960's. Several studies have shown that disturbances play an important role in the organisation of forest communities (Denslow, 1980; Guariguata, 1990; Sousa, 1984; Thompson and Wilson, 1978 amongst others). Openings seemed important in maintaining the community diversity of endemic flora through its positive influence upon *Leontodon filii* and *Luzula purpureo splendens* occurrence. Gaps and openings are known to be major foraging habitats in other montane forests (Gradwohl & Greeberg, 1980; Levey, 1988; Wunderle *et al* , 1987).

Therefore, because of its diet pattern, the Priolo requires a mosaic of habitat types to complete its annual cycle. Several studies have shown that seasonal changes in resource levels and habitat conditions mean that resident herbivores and frugivores require extensive areas of different habitats in order to complete their annual cycle (Karr & Freemark, 1983; Garrot *et al*, 1987; Levey, 1988; Rabenold & Bromer, 1989; Loiselle & Blake, 1990, 1991).

In contrast to all other habitat types, the native forest provides food and cover all year round. Due to this complete overlap of resources in time and space this forest is the Priolo's optimal habitat. In winter it provides the vast majority of food resources which enables the Priolo to minimise the costs of movements in search of food. The strict

dependence on buds of *Ilex perado* in April and the considerable use of large ferns from January to May are undoubtedly of great importance in understanding the present distribution of the Priolo. Above Furnas, where birds neither occur over winter nor breed, these foods were present in significantly lower densities than in the eastern part of the range, where birds occur throughout the year (Chapter 2). The western patch of native vegetation may also be relatively unsuitable in summer because the ground is less steep and, as a result, landslides and openings are uncommon. Because this is a rare species, habitat quality is readily assessed through the comparison patterns of habitat occupancy (Rosenzweig, 1985). Theoretically, if the population density is low, the Priolo is expected to concentrate in the optimal habitat. If the population increases then, in terms of individual fitness, the quality of the optimal habitat is lowered and Priolo should increasingly use sub-optimal (especially exotic forests) habitats (Fretwell & Lucas, 1970; Fretwell, 1972). However, these are so deficient in food resources that their occupation throughout the year is very unlikely.

Although the Priolo was highly associated with native vegetation at all months, a food supply hypothesis was better in explaining patterns of distribution and abundance than a habitat structure hypothesis: (1) Seasonal changes in the abundance of foods in habitats were matched by shifts in the distribution of Priolos. (2) Areas of exotic forest were little used because they were scarce in food resources. They were of some importance in summer and autumn when micro-habitats (openings) within them contained relatively high levels of herbaceous and fleshy fruit seeds. (3) The native vegetation on the western part of the range was not occupied throughout the year, but their feeding resources were apparently much lower than those on the eastern part of the range. (4) In addition, the Priolo was apparently unspecialised in nest site placement.

Fields were virtually unused but, again, their feeding resources, mainly grasses, were much lower. However, some had high crops of fleshy fruits and the fact that they were not used suggests that cover also play a part in habitat selection. Newton (1967)

reported that seed crops in open fields are also not exploited by British Bullfinches. This may be explained by predation reduced pressure (Newton, 1964a) whereas such explanation cannot be invoked for the Priolo.

Priolos did not specialise on native foods. These comprised the vast majority of the diet in August/September and April when introduced species were least abundant. In the last century and early this century, orchards were common in Eastern S. Miguel and the Priolo was commonly located feeding on buds of fruit trees (Bannerman & Bannerman, 1966). This is a typical Bullfinch feeding behaviour throughout Europe (Wright & Summers, 1960; Newton, 1967, Matthews, 1983). These observations corroborate the view that seasonal variations in habitat occupancy largely reflect variation in levels of abundance of foods that can be exploited by Priolos. The Priolo showed a narrower foraging niche when food was least abundant.

Finally, there was some evidence that food may be limiting this population. Mortality of first-year birds appeared to have been greatest in late winter when seeds and sporangia were scarcest.

The role of a food supply hypothesis in explaining patterns of island bird abundance has been invoked in several studies e.g. Galapagos finches (Schluter, 1982; Grant & Grant, 1986) and the Hawaiian honeycreeper Palila, *Loxioides bailleui* (Scott *et al*, 1984). With food resources being less diverse on islands and other factors such as predation and weather being relatively unimportant (Schluter & Repasky, 1991), this seems a logical explanation. However, all studies, including mine, are observational and rely mostly on correlations; experimental manipulation of food levels on islands are necessary to demonstrate this hypothesis.

Although total food abundance largely explained patterns of Priolo distribution and abundance, some points needed further explanation. Seeds of *Hedychium gardneranum* were virtually not exploited. *Clethra arborea* fruited in October and produced a large crop size but was not consumed in quantity until December. Oddly, the crop was never depleted

and, in mid-April, around 30% of it was still present (Chapter 3). Even with this food source present birds altered their foraging behaviour, ignoring these seeds and exploiting alternative, non-granivorous, foods such as flower buds, moss tips and fern fronds. Newton (1964), Matthews (1983) and Crocker (1987) obtained similar diet shifts for Bullfinches in Britain.

Food preferences (local scale) were examined to explain these patterns. Birds showed strong size selectivity amongst most food types: herbaceous seeds, sori, fruits of *C. arborea* and flower buds. Seasonal changes of phenols of winter seeds failed to explain winter changes in diet. Nutrient contents were not examined but foods that were expected to show high levels of important nutients for the winter, especially fat (seeds of fleshy fruits) were over by late November. This picture is quite different from that for British Bullfinches because their main winter food are ash seeds, which are much larger than seeds taken by Priolos and costly in terms of handling time (Greig-Smith & Crocker, 1986). On the other hand, phenolic content was important in explaining tree preference (Greig-Smith & Wilson, 1985). Therefore it may be that, within a large resource spectrum, birds are more discriminating and so several factors play an important part in determining food preference. For instance, phenolics may become important in seed selection only if available foods provide enough energy, needed to maintain basic metabolic requirements, relatively easily. Therefore, I tentatively conclude that energy was the most important factor in driving the Priolos food selection mechanism over winter.

Such behavioural differences between relatively abundant and scarce food environments may be a major difference between island and mainland species and can be regarded as a prediction of foraging theory (Stephens & Krebs, 1986) to population ecology. Within this line of reasoning, Loiselle and Blake (1990) showed that Costa-Rican frugivores were more selective in areas with high fruit-abundance (second-growth) than in areas with low fruit abundance (forest).

In a scarcer food environment, seasonal variations in food availability may largely account for seasonal variation in diet (Grant & Grant, 1986; Loiselle & Blake, 1990, this study) but this may vary among bird species. In the case of the American Robin, Wheelwright (1988) demonstrated that even when fruit availability was held constant, the birds showed seasonal variation in fruit use, which indicates that physiological needs, and not fruit availability, influenced that seasonal variation. The winter food selection pattern of Priolo can be viewed in a similar manner. A switch in preference from seeds to flower buds can best be viewed graphically (Fig. 1).There is a point in spring (A) when buds increase sharply in size and so preference for these overcomes that of seeds. A similar mechanism occurs in British Bullfinches (Greig-Smith *et al*, 1983; Matthews, 1983). In May, ash seeds are as indigestible as the husks of pear buds and these are rejected by Bullfinches (Matthews, 1983). In the case of the Priolo, fern sporangia, although important, may be mainly a "stand-by" food.

Thus, the crop size of "good quality food" (fleshy fruits in autumn, large tree seeds and sori in winter and large flower buds in spring) should be important in controlling the Priolo's population size. An experiment with enclosures showed that the Priolo foraging pressure significantly reduced the number of flower buds. Because this is largely the only food available in April, it is probably the most important food in limiting the present population of Priolos. It should be noted that one type of food will be of only minor use in replacing the other. For instance, seeds of *C. arborea* may not replace those of fleshy fruits in autumn because their phenolic levels are extremely high. Likewise, large seeds of *C. arborea* cannot replace flower buds in spring because they may be too indigestible. A shortage of preferred foods may limit this population in late winter. In 1992/93, the mortality was higher than in 1991/92 and large buds became available later. Then, the consumption of fern fronds and moss tips was much higher. The intake of these " low quality foods" should coincide with the timing of food shortage.

In summary, in S. Miguel as a whole, the range of the Priolo depends largely on the availability of native vegetation. Different micro-habitats of this forest are selected seasonally, leading to changes in bird distribution. Within each micro-habitat, birds discriminate on the basis of available foods. First of all, foods must be relatively easy to handle i.e. neither too large or hard. Acceptable foods can be further discriminated on the basis of their sizes although for specific food types feeding deterrents and/or accessibility may be of some importance. Overall, total food abundance appeared more important than habitat structure in accounting for bird distribution and abundance but "food quality" should be brought into this scenario for a full understanding of these factors.

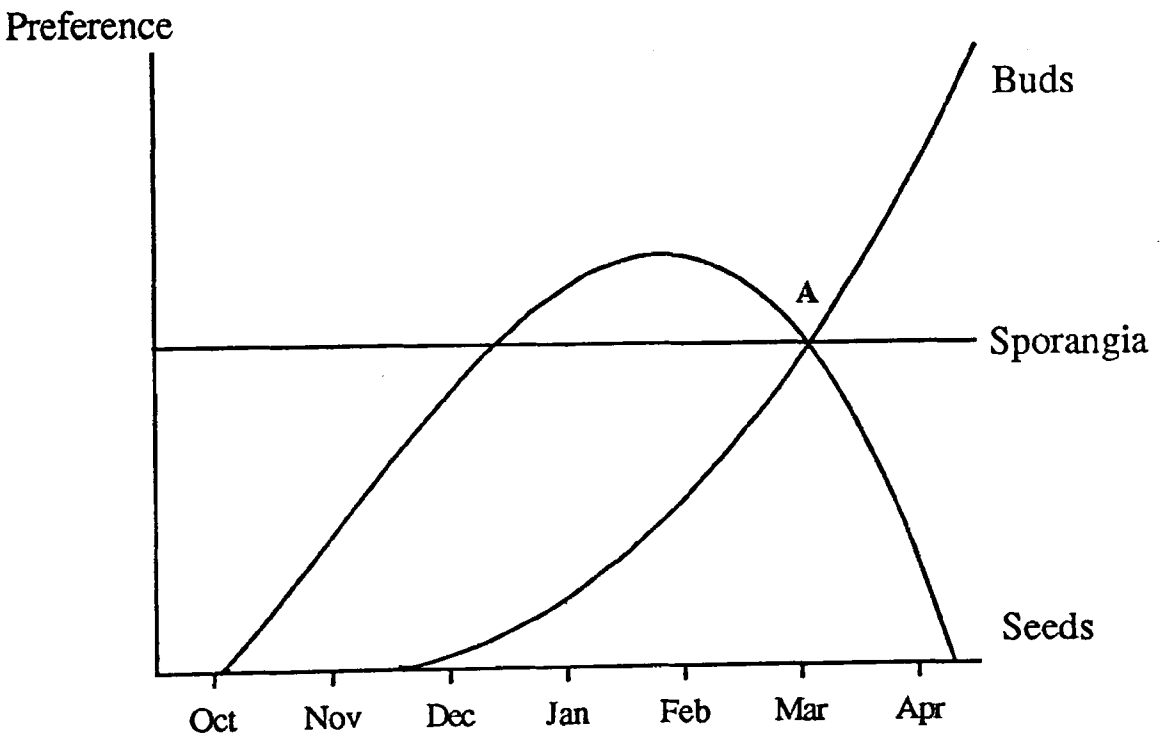


Fig. 1. Model showing temporal switches in food preference over winter. From October to December, seeds seemed less preferred than fern sporangia because of their phenolic levels. Once flower buds showed a sharp increase in size, at point A in spring, preference for these overcame that for seeds. After March, seeds, although with lower phenolic levels, are too dry and, presumably, less digestible. Fern sporangia may be mainly a "stand-by" food. The point A or the whole bud line may be shifted backwards and forwards according to weather conditions. This may lead to different mortality levels in different years.

6.2 Niche expansion on islands. Niche expansion (broader spectrum of occupied habitats and changes in feeding habits) of insular populations have been documented by many authors (Crowell, 1962; MacArthur *et al*, 1972; Lack, 1976; Wright, 1980; Blondel, 1985, Blondel *et al*, 1988 amongst others). By niche I mean microhabitat structure of the vegetation and food supply as well as other features such as foraging techniques (Blondel, 1985). The classical explanation for niche expansion is that extra-resources become available because of the lack of competitors (Crowell, 1962; MacArthur *et al*, 1972, MacArthur & Wilson, 1967, Case *et al*, 1967). However, the importance of competition has been increasingly challenged (Simberloff, 1983; Strong *et al*, 1983; Arthur, 1987; Blondel *et al*, 1988) and the need to consider alternative hypotheses, involving bioclimatic factors and life history parameters of the populations, have been put forward.

I shall consider here, at a population level, some aspects of the comparative ecology of bullfinches on the mainland and in S. Miguel. At a habitat level, the Priolo has certainly not expanded its niche as most available habitats were little used throughout the year. Open and suburban habitats, have been recently occupied by bullfinches on the mainland (Newton, 1967; Maheo, 1965, Yeatman, 1971), but on S. Miguel, they were not used at all. Also, apart from fruit tree orchards, historical records only suggest the occupancy of native vegetation. At the scale of food resources, the Priolo showed niche expansion. Despite larger beaks, the Priolo consumed a higher proportion of small size foods, exploited a wider range of food types (Chapter 3) and showed wider local movements than mainland bullfinches (Chapter 2). Larger bills would confer an advantage by increasing the amount of food gained per unit time when dealing with fern sporangia and non-granivorous material such as fern fronds. This is important because these foods are taken when seeds are scarcest.

Are these niche differentiations evolutionary adaptations to broaden the niche or are they simply an ecological adjustment to differences in the plant community and abundance

of foods? Changes in diet may be accompanied by a change in bill structure and body size. An expanded diet is often related to increases in bill and body size (Cody, 1974; Grant, 1986). The Priolo and other Atlantic passerines (Grant, 1979, 1979a) followed this pattern. Sexual dimorphism in size suggests that intraspecific competition (Blondel, 1985) might play a role in this case but sexual dimorphism in food selection needs to be investigated. Interspecific competition, on the other hand, does not seem to have any role. Most foods exploited by Priolos when food was scarcest: fern sporangia, fern fronds, flower buds, moss tips and seeds of *C. arborea,* are either very little or not exploited by other species. It appears that potential competitors, such as chaffinches and blackcaps, possess quite different foraging techniques and/or exploit different foods from those of the Priolo.

It seems that the niche differentiation of Priolo is an evolutionary adaptation with a possible role for intraspecific competition. Intraspecific competition tends to broaden the spectrum of resource utilisation whereas interspecific competition tends to contract (Svardson, 1949; Blondel, 1985). Speculating, part of the niche expansion may have occurred immediately after a small founder population arrived on S. Miguel. Further niche broadening may have occurred once the population grew and intraspecific competition (due to low food availability) became an important selection pressure.

Differences in the spatial and temporal patterns of resource abundance may largely explain changes in foods and foraging habits without taking into account release from competition pressure (Recher, 1990). Therefore, the bioclimatic factors of the environment and the species concerned should be important to explain the extent and/or direction of the niche expansion of insular populations. Three examples from this study are:
(1) the sedentariness of island species needs to be evaluated critically. Although long distance movements are precluded, local movements may be more extensive than those of mainland conspecifics; (2) if insular seed predators, such as the Priolo, have evolved to exploit a wider food spectrum they may be less discriminating in terms of seed chemistry. It is thus possible that they may show behavioural and/or physiological modifications in

order to deal with foods with relatively high levels of toxins and/or low levels of nutrients. These hypotheses need to be investigated; (3) The Priolo has complex diet requirements depending on many plant types. The colonisation of exotic forests and hedges is improbable because these habitats do not possess suitable feeding resources.

6.3 Conservation

6.3.1 Introduction

It is important to consider what the natural foods of the Priolo might have been through the year before the exotic species appeared. Presumably the native species that are now important in the diet provided the majority of the food over extended periods of time.

In summer the birds probably fed on seeds of native herbaceous species such as *L. p. splendens* and *L. filii*, and also on *Chaerophyllum azoricum* and *Lactuca watsoniana* (both now rare). As most of these plants fruit only in July and August, the introduction of *Polygonum capitatum* has probably advanced the breeding season for about 1,5 months. Originally, the life history of the Priolo may have been partly a response to disturbance effects. These would provide suitable habitats for herbaceous species and were probably important to account for variations in the population of these plant species.

From September to March, seeds of native fleshy fruits (*Vaccinium cylindraceum* and *Rubus hochstetterorum*) might have provided a large proportion of the diet. Sporangia were also probably very important. The population of both fleshy-fruit producing species and ferns should have been much greater in an undisturbed forest. Presumably, fleshy fruits were not depleted before February or March. Other plants, such as *Euphorbia stygiana*, now rare, might also have been important.

In April and May, flower buds of *Prunus lusitanica* ssp *azorica* (now extremely rare) may have been very important in the diet. This species provides much larger buds (5.0 - 6.0 mm) than *I. perado* (3.0 - 3.5 mm) and was readily taken by captive Priolos. Buds of *Prunus* trees are important for bullfinches throughout Europe and Japan. As its

wood is much appreciated it may have declined sharply soon after colonisation. The use of orchards in the second half of last century may have been partly a result of the decline of the *Prunus* population.

I. perado and *V. cylindraceum* are much appreciated by livestock and may also have declined strongly. Overall, there was a large demand for hard wood (*Juniperus brevifolia*, *P. lusitanica* and *I. perado*) by humans, which means that mature areas of the forest were disturbed more intensively. At Salto do Cavalo, this mosaic of the forest has almost vanished.

The apparent historical absence of the Priolo from western S. Miguel might have been a consequence of the absence of important feeding resources or some other reason that prevented the birds from disperse to or established a population in that area (i.e. vulcanism).

Therefore, the present distribution pattern suggests a relict population. The Priolo seems to be restricted to the best remaining areas of native cloud forests. It was probably never a regular inhabitant of the once-present lowland native forests (Godman, 1870). Lowland forests form a closed canopy and an understorey does not develop (Sjogren, 1984). An understorey with shrubs and ferns seems important for over-winter survival.

Three annual time periods can be devised for Priolo: breeding (Jun-Sep.), over-winter survival (Oct-Mar) and the timing of food shortage (late March - mid May). The availability of preferred foods is the major factor underlining all Priolo movements. Thus, wider ranging behaviour in summer than in winter may be explained by the heterogeneous nature of Priolo feeding habitat over summer: this consists of openings, streams, and landslides that are separated by plantations of *C. japonica*, copses of *P. undulatum* and areas of mature laurel forest that are unsuitable for foraging.

My results contradict Matthews (1983) view that in winter Bullfinches should have a wider foraging range. Certainly one should expect winter food (tree seeds and buds) to be

regularly distributed whereas summer foods (herbaceous seeds) will have a more clumped distribution.

At the time of minimum food availability, Priolo movements were more pronounced and birds reached areas where, in the past, there were orchards nearby. Bullfinches in Western Europe behave in a similar way (Greig-Smith & Wilson, 1984; Newton, 1967 and Noval, 1971). Sightings of colour-ringed birds showed that these movements are carried out predominantly along streams. Noval (1971) reports similar observations for bullfinches in Northern Spain.

Although the extent and timing of the Priolo movements throughout the year appears to be consistent with that of Western European Bullfinches, post-1960 ringing recoveries of the British population showed an increase in movements (Summers, 1979). This seemed likely to be the result of a recent behavioural change in this species (Newton, 1967) and therefore a greater tolerance to feed and breed in more open habitats. In the middle of the last century, French birds were known chiefly from mountainous areas, but in this century their numbers in lowland areas (Yeatman, 1971) and suburban habitat (Maheo, 1965) have increased.

The Priolo does not seem to show such behavioural relaxation. On the contrary, its distribution has apparently been gradually contracting since the middle of the last century. This seems to be a consequence of habitat quality: once the birds leave the laurel forest and its margins, the habitats remaining, pasture with hedges of *Hydrangea macrophyla*, copses of *P. undulatum* and thick plantations of *C. japonica*, are so poor in feeding resources that their colonisation is unlikely. They could provide some food only in the summer season.

A diverse mosaic of vegetation types and structures within a small area is typical of Azorean Cloud forests (Haggar, 1988). Seasonal variations in diet showed that Priolo needs the several mosaics of the forest in order to complete its annual cycle. Though birds rely on foods that also occur on disturbed sites, in summer and autumn, in winter and early spring they depend heavily on well developed forests with a canopy of *I. perado* (and now

also of *C. arborea*) and an understorey of large ferns. It is possible that this population has recently increased slightly due to the introduction of *C. arborea*, which might have relieved the bottleneck caused by the decrease of the population of fleshy-fruit producing species.

However, an apparent abundance of *C. arborea* fruits in March does not necessarily mean that Priolos have a good food supply. Larger and easily accessible fruits have presumably already been taken (Chapter 3). Even if these are abundant, seeds may be so dry and indigestible that Priolos gain little by feeding on them (Chapter 4). Alternative foods should be considered at this time of the year. As an apparent favoured alternative to dry *C. arborea* seeds, fern sporangia are especially relevant to Priolos in March (Chapter 4). However, in April most sporangia no longer have any nutritional value because spores have been shed from sporangia (Chapter 3). As a result of these, flower buds of *I. perado* are, to a high degree, the only food available for Priolos in April.

6.3.2 The influence of *C. arborea* on the production of *I. perado* flower buds

Although *C. arborea* is now an important food supply, especially in January and February, it might be outcompeting native plants that provide important food sources in other months. Of special concern is the apparent negative influence of *C. arborea* on the production of flower buds by *I. perado*. *C. arborea* grows taller (6-8 m) than *I. perado* (4-5 m) and is also present in much higher densities (Chapter 2). Under a canopy of *C. arborea* the understorey seems to be less diverse and dense, especially in terms of large ferns (pers. observations). In areas with high density of *C. arborea* most of the *I. perado* trees are partially or totally overshaded by *C. arborea*.

In order to throw some light on this question two 50 m transects, one in an area with an apparent high density of *C. arborea* and other in an area with an apparently low density of *C. arborea* were made through the forest and points located every 2 m. The

closest *I. perado* tree to each point was marked and the number of flower buds was counted on the first branch encountered above 2 m in late April 1992.

The number of flower buds per branch of *I. perado* was significantly different between areas with (mean=47, SE=13.6) and without (mean=212, SE=29.9)*C. arborea* ((t=3.7, P<0.001, df=48, data was log (x+1) transformed)) which agreed with expectation. Although no firm conclusions can be drawn from these data a trend was obtained suggesting, although tentatively, that *I. perado* overshaded by *C. arborea* produce significantly less flower buds. Experimental work is necessary to demonstrate this hypothesis: *C. arborea* trees that are shading *I. perado* should be removed before the beginning of leaf bud formation (June/July) to see whether the production of flower buds increases in subsequent years.

6.3.3 Management plan

The deterioration and fragmentation of the cloud forest must have contributed to the reduction in range and abundance of the Priolo. This study suggests that conservation measures should be considered at two inter-related levels: (1) enhance the suitability and/or restore habitat areas and (2) ease the factors that limit this population.

(1) It is clear from this study that all exotic plant species, with the exception of *C. arborea,* do have a strong negative impact on Priolo. Thus, the expansion of *P. undulatum* and *H. gardneranum* into areas of native forest should be controlled and afforestation with *C. japonica* should be severely restricted. *P. undulatum* and *H. gardneranum* could be controlled manually over several years to allow native seedlings and saplings to develop. In the long term further, problems will arise because, as the forest matures and opens its canopy, it may be easier for recruits of exotic plants to become established (Chapter 2). However, because suckering is an important means of regeneration for most native trees (Haggar, 1988), once a forest is established most species might perpetuate themselves, to a certain extent. Research on this topic would be most valuable.

Restricted *C. japonica* afforestation does not necessarily lead to a conflict between conservation and local economy. Many areas that have been afforestated with *C. japonica* are unsuitable for tall trees due to exposure to cyclonic winds and, perhaps, also because of the high altitudes. Entire afforestated areas have been knocked down by strong winds and in other areas, trees have grown only to 2-3 m tall, after 30 years. A preliminary assessment showed that 150-200 ha, at least, are subjected to these conditions. In other areas, the costs of logging may be prohibitive. Clearly, afforestation should have been planed in accordance with the ecological characteristics of the area. Undoubtedly, these and other areas should be converted to their primitive vegetation, although the aggressive *H. gardneranum* is a further threat to habitat restoration.

Populations of native plants should be re-established in these areas by planting seedlings. It is expected that the range and numbers of the Priolo will increase with such measures, although the response will be delayed until plants reach suitable sizes. Because native trees are slow-growing, control of *H. gardneranum* must be done in planted areas over several years (10-15) until the native trees are well established.

(2) Fidelity of adults to the same area and the apparent lack of adult dispersal suggests that they would be slow in colonising new areas or ones enhanced by habitat management. Therefore, the increase of this population may be largely dependent on juvenile dispersal or population growth.

Because the Priolo feeds on many vegetation types, a mosaic composed of openings, shrubs and ferns and mature forest must be present in any one area. Being a granivorous bird, the Priolo relies on unpredictable food sources. Therefore, it would be expensive to become attached to a particular area (Wiens, 1976). Furthermore, differences in the spatial distribution and abundance of foods between years may be pronounced, as a consequence of different climatological conditions. Wide home ranges around an habitual base, as suggested in this study, may be the best strategy, enabling the birds to explore landslides and stream banks that are separated by large areas of forest. Under conditions of

unpredictable food and disturbance, a bird should show a capacity for plasticity. Thus, areas with low densities of resources or those that are situated quite far from the main core of native vegetation may be important foraging habitats at certain times. Any possible future orchard plans for such areas should consider that these may be used as a food source.

For the moment it seems especially important to consider the food supply between January and April. It is extremely difficult, if not impossible, to calculate the true supply of suitable food for Priolos at this time. Very extensive data on the quantity, sizes, digestibility and chemistry of seeds of *C. arborea*, fern sporangia and flower buds, would be necessary every month (Matthews, 1983).

Because flower buds are largely the only food available in April and because Priolos significantly reduce the number of flower buds in trees, it is urgent to increase the population of *I. perado* and *P. lusitanica* (now extremely rare), the only flower-bud species exploited by the birds. Since Priolos only take large flower buds, restoration of lower altitude areas must include these species. There, trees will produce larger flower buds earlier.

The restoration and rehabilitation of the habitat must also include fleshy-fruit producing shrubs (mainly *V. cylindraceum* and *R. hochstetterorum)* and large ferns (*Woodwardia radicans*, *Culcita macrocarpa* and *Osmunda regalis*). Fleshy-fruit crops are now available only until late November but fruits that may remain on plants over winter may provide essential diet supplements of good quality (Newton, 1964). The fact that two seed fragments were identified in faeces in March and April suggests a potential importance of these foods after January if plant populations are allowed to increase. In such a forest the Priolo density should increase. Population densities of *V. cylindraceum* recorded in S. Miguel are much smaller than levels recorded in an apparently less disturbed forest in Pico island (Haggar, 1988). It should be interesting to mark plants there and investigate predation rates by local passerines.

The exotic *C. arborea* constitutes the most controversial food plant available in winter. Although not preferred it seems to constitute the best option for the birds in January and February. The expansion of *C. arborea* must be controlled in some areas but caution must be taken before one decides to control *C. arborea* over large areas. Possibly the best approach would be a progressive control as areas of native vegetation are progressively restored.

In order to reduce winter mortality artificial food could be provided over the winter (January-April) at some specific places. Like British Bullfinches (Greig-Smith & Crocker, 1986), one Priolo kept in captivity for 35 days much preferred sunflower seeds to all other commercial seeds. Population monitoring should be implemented to trigger possible action if the population decreases markedly (i.e. captive breeding).

Habitat management should be carried out in a way as to connect native vegetation fragments. This could either create one large area consisting purely of native vegetation or of several native vegetation areas connected with large corridors of suitable vegetation. This should facilitate colonisation and allow gene-flow between areas, by the highly mobile Priolo.

Finally, habitat restoration should firstly be carried out along the main valley of Ribeira do Guilherme (below route 11, see Fig. 2 of Chapter 2) because this area is fairly accessible and within the main range of the bird. Plantations of *C. japonica* have been knocked down by strong winds and these areas could be replaced with native vegetation. In other areas, *P. undulatum* should be felled. Habitat restoration should progressively expand to the west, especially around routes 13 to 17 (Fig. 2 of Chapter 2).

Appendix 1

Monthly list of all plant species that were recorded in the diet of Priolos. A distinction is made between months in which plants comprised less than 5% (*) or more than 5% (**) in the diet

	M	J	J	A	S	O	N	D	J	F	M	A
Seeds												
Polygonum capitatum	**	**	**	*	*	*	*	**				
Luzula purpureo-splendens	*	*	*	*								
Sonchus sp		*	*									
Prunella vulgaris			**	**	*							
Sagina sp		*	*									
Hypericum humifusum		*	**	**	*							
Scrophularia auriculata			*	*								
Potentilla erecta			**	*	*							
Rumex sp			*	*								
Leontodon filii			*	**	**	*	*					
Epilobium obscurum			*									
Duchesnea indica			*									
Gunnera tinctoria			*									
Erica azorica			*									
Cyperaceae			*									
Rubus hochstetterorum			*	**	**	**						
Rubus ulmifolius			*	**	**	**						
Vaccinium cylindraceum			*	**	**	**	*				*	*
Leicesteria formosa			*	**	**	**	**	**				
Clethra arborea				*	**	**	**	**	**	**	**	**
Hedychium gardneranum								*			*	
Cryptomeria japonica (ground)										*	*	
Calluna vulgaris									*	*		
Carex peregrina (?)			*									
Holcus rigidus		*	*									
Aira sp		*	*									
Sporangia												
Woodwardia radicans					*	*	**	**	**	**	*	
Culcita macrocarpa							**	**	**	**	**	**
Osmunda regalis	**	**	**									
Flower buds									*	*	**	**
Ilex perado spp *azorica*												*
Prunus lusitanica spp *azorica*												
Leaves and ovules												**
Pteridium aquilinum	**	*										
Osmunda regalis	**	*										
Woodwardia radicans	*											
Scrophularia auriculata	*	*										
Potentilla erecta		*										
Cryptomeria japonica		*		*	*						*	*
Hydrangea macrophylla		*										
Juniperus brevifolia		*										
Laurus azorica	*	*										
Vaccinium cylindraceum	*											*
Rubus hochstetterorum		*										
Rubus ulmifolius		*										
Prunella vulgaris		*										
Leicesteria formosa		*	*						*	*	*	
Pinus thunbergii				*	*		*	*				
Pinus radiata				*	*		*					
Clethra arborea			*	*	*						*	
Polythrichum sp										*	**	
Tree trunk moss			*									*

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