THE BIOLOGY OF THE SNARES FERNBIRD

BOWDLERIA PUNCTATA CAUDATA (BULLER, 1894)

A thesis presented for the degree of Master of Science in Zoology in the University of Canterbury, Christchurch, New Zealand.

by

H.A. Best

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CHAPTER 1

INTRODUCTION

Since the arrival of European settlers in New Zealand many species of native birds have declined, become restricted in distribution or even extinct. The New Zealand Fernbird (Bowdleria punctata) is no exception and the population has decreased, mainly because of the draining of its habitat to create farmland (Hamilton, 1885; Kirk, 1895; Handly, 1895). The South Island Fernbird was formerly abundant over most of Canterbury but is now absent (Oliver, 1955). However, fernbirds still remain plentiful in suitable habitats (pers. obs. at Totara River, Buller). Fernbirds typically inhabit dense ground cover of reeds, ferns or scrub growing about swamps, lagoons, or river flats and terraces. Although this habitat may border on rain forest, fernbirds do not penetrate far into the latter (pers. obs. at Virgin Flat and the Totara River, Buller).

Because of the fernbird's inconspicuous appearance and retiring nature it is generally difficult to observe; consequently published reports of its biology are few. Oliver (1968) lists the New Zealand literature from 1843-1900; M'Lean (1906) wrote on the North Island Fernbird, Stead (1948) on the Snares Fernbird, and Blackburn (1967) on the Codfish Fernbird. Unfortunately, M'Lean failed to publish some of his data on nestling development. South Island Fernbirds at Lake Tuakitoto (East Otago) have been studied by Sinclair (1967) but the detailed results are not yet published. Most other accounts of fernbird biology have been anecdotal, describing their general appearance, behaviour and habitat preferences, e.g. Buller (1905), Guthrie-Smith (1914, 1927, 1936), Soper (1965) and Moon (1967).

In this study I set out to describe the general behaviour of the Snares Fernbird, and to compare this information with that published on the other subspecies. Most of the work is concerned with breeding biology, although feeding behaviour and population biology are also considered in some detail.
The advantage of working on the Snares is that at the moment this island group is still in its primeval state and thus the fernbird population has been undisturbed for centuries. A further advantage is that the Snares Fernbird inhabits a relatively uniform, closed universe and thereby is an ideal subject for a study on population regulation.

The Snares are the most suitable place to study fernbirds as they form an isolated community, and the birds are spread throughout the Main Island. Despite the island-wide distribution of the fernbirds, however, it is only in the open Olearia forest that they can be easily observed and followed.

The Snares Fernbird belongs to the endemic monotypic genus Bowdleria (Passeriformes:Sylviidae). The genus shows distinctive characters strong enough to obscure its near relationships to other Sylviidae (Falla, 1953) but it has been considered to be most closely related to the Australian grass bird Megalurus (Oliver, 1955). Oliver (op. cit.) stated that Bowdleria differs from the true Sylviidae in having shorter wings and longer first primaries.

The Annotated Checklist of New Zealand birds (Kinsky, 1970) gives six subspecies of Bowdleria punctata (Quoy and Gaimard, 1830) which are listed below.

b. B.p. punctata (Quoy and Gaimard, 1830). South Island Fernbird.
c. B.p. stewartiana Oliver, 1930. Stewart Island Fernbird.
d. B.p. wilsoni Stead, 1936. Codfish Fernbird, on Codfish Island, off the N.W. coast of Stewart Island.
e. B.p. rufescens (Buller, 1869). Chatham Island Fernbird. Believed extinct since about 1900, but Fleming (quoted by Oliver, 1955) thought it may still exist on Mangere Island, and D.S. Horning (pers. comm.) believed he saw fernbirds on the steep scrub covered slopes there in August 1971.
f. B.p. caudata (Buller, 1894). Snares Fernbird.

No rigorous taxonomic study has been undertaken to support this or other classifications of Bowdleria. Oliver (1955) stated that there are two species of Bowdleria; the Chatham Island Fernbird ("B. rufescens") being specifically distinct from B. punctata as the former lacked any pronounced spots on its undersurface, and had a bright rufous, not brownish,
upper surface. Other authors (e.g. Guthrie-Smith, 1914; Stead, 1936) have suggested that on Stewart Island there are more than one distinct form of B. punctata. The racial status of fernbirds on some offshore islands, e.g. Open Bay Islands, South Westland, has yet to be determined. Thus, to avoid confusion, I shall use the classification outlined in the Annotated Checklist of New Zealand Birds (Kinsky, 1970).

The morphological differences between the subspecies of B. punctata are slight and I found it difficult to detect differences between the Snares and South Island Fernbirds in the field. However, Guthrie-Smith (1936: 193, 198) considered that the South Island Fernbird "is markedly different in colour and other respects from the Snares species" but he did not elaborate further. The differences between the subspecies have been listed by Oliver (1955).

Adult Bowdleria are characterized by light rufous dorsal plumage with the central areas of contour feathers being marked by longitudinal dark brown to black streaks. The outer edges of these feathers have a golden brown appearance. The undersurface is white and the throat and breast is covered with well defined black spots. A white superciliary streak extends from the nostril back over the eye. Soper (1965) stated that the male South Island Fernbird has a more russet crown than the female, particularly during the breeding season, but I found dimorphic differences to be quite subtle and unreliable indications of sex. The most distinctive characteristic of Bowdleria is the long straggling tail (ca 80 mm). This comprises 10 rectrices with pointed tips that are, depending upon the individual, variously abraded; the barbs are separate, giving the tail a frayed appearance. The wings are small (longest primary ca 65 mm) and flight is weak. Flight usually consists of short fluttering glides or laboured direct flight close to the vegetation for only a few metres.

Throughout the remainder of this account, the term "fernbird" refers to the Snares Fernbird only; full names are used when there is a discussion on different forms of B. punctata.
Figure 1: Locational and regional map of the Snares.

The rectangle around Boat Harbour encloses the main study area, shown in Figures 6 and 11.
CHAPTER 2

STUDY AREA AND METHODS

INTRODUCTION

The location, physiography, vegetation and climate of the Snares are described. A short account is given on the main study area. The methods used for capturing, identifying, sexing, and measuring individuals are outlined.

Field work was carried out at the Snares from 18 November 1970 to 10 March 1971 and 20 December 1971 to 24 March 1972. There are no man-introduced vertebrates present at the Snares, and since recent human visits have been few (see McNab, 1907; Chilton, 1909; Warham, 1967; Fleming and Baker, 1973), this group remains one of the few subantarctic-southern cold temperate islands still in a primitive state.

STUDY AREA

General account of the study area

The Snares (48°07'S., 166°36'E.) are a group of small uninhabited islands some 105 km south-west of the South Cape of Stewart Island. Under Holdgate's (1968) classification they lie in the "cold temperate" zone, but in many articles (e.g., Chilton, 1909; Fineran, 1964; Warham, 1967; Gressitt and Wise, 1971) all New Zealand islands south of Stewart Island have been regarded as "subantarctic".

The Main Island, the largest of the group, is triangular with promontories leading off the points of the triangle (Figure 1). The next largest mass is Broughton Island, 180 m south-east of the Main Island. There are many other islets, needles and stacks of which the Western Chain are the largest and most isolated, lying about 4 km to the south-west (Fleming and Baker, 1973). The total area of the Snares has been reported as 2.6 km² (Allan, 1961) and 3.28 km² (pers. comm.)
Figure 2: View of the coast adjacent to Boat Harbour.

Seal Point extends to the extreme right of the photograph and the dinghy is rounding Ho Ho Point. Taken from the south side of Ho Ho Bay.
with C. Hay, who carried out a vegetation survey of the group in the summer of 1969-70). Richdale (n.d.) estimated the area of the Main Island to be "400-500 acres" (1.62 to 2.03 km²), C. Hay reckoned this island to be of 2.80 km², while D. MacPherson, who assisted in a survey on the island in 1890 (Fineran, 1969), thought the Main Island could be "800 acres" - i.e. 3.23 km².

The Snares consist of granite with a gneissic structure and appear to form part of the same plutonic complex as Stewart Island and western Southland (Fleming, 1953). This basement is overlain by peat which, on the Main Island, has an average depth of about 2.4 m (Marshall, 1909a). Deposits up to 6 m thick were recorded in 1890 during excavations for a lighthouse (MacPherson, 1916). The highest point on the Snares is about 190 m above sea level, on the South-west Promontory, Main Island (Fleming, 1953).

Physiography of the Snares

On the west coast the cliffs rise everywhere to a minimum height of 90 m. Declivity is much less on the east coast, and from Skua Point to Ho Ho Bay the rocks slope gently into the sea (Figure 2). The most suitable landing site is Boat Harbour (Figures 1 and 2), believed to be formed from a drowned stream valley (Fleming, 1953). There are a few other isolated areas where a landing could be made. On most of the Main Island the surface slopes gently to the eastward, but it terminates in abrupt cliffs everywhere except in the region of the Boat Harbour. The South-west Promontory is linked with the Main Island by a steep razor-back ridge. The top of this promontory is flat (Figure 3), and almost devoid of surface relief. Small streams draining the surface of the triangular Main Island have cut shallow valleys, separated by broad convex ridges. The general flatness and level surface of the Snares is believed to mark a plain of marine erosion (Marshall, 1909a).

Broughton Island has a similar physiography to the Main Island.

Vegetation of the study area

The flora of the Snares has been well described by Fineran (1964, 1969), and a summary only is given here.
Figure 3: View of steep western coast.

Taken from Signpost Hill, looking across to the South-west Promontory (upper right). Note the fringing coastal tussock, central forest, and flat relief inland. The razor back ridge connecting the South-west Promontory to the remainder of the Main Island appears in the top centre of the photograph.
The vegetation includes 20 vascular plants forming two simple communities - forest and maritime tussock grassland. The central shrub-forest of *Olearia lyallii* is dominant, enclosing a few patches of *Senecio stewartiae*, especially about Boat Harbour on the Main Island and on the eastern half of Broughton Island. *Olearia* and *Senecio* grow up to 9 m in sheltered places but elsewhere the canopy rarely exceeds 6 m. There is generally a paucity of undergrowth beneath the canopy (Figures 7, 8 and 9) except for a few groves of ferns (*Polystichum vestitum*, *Blechnum durum* and *Asplenium obtusatum*) mainly around the moister areas about Boat Harbour. There are two coastal meadow formations; *Poa tennantiana* occurring in the relatively more sheltered gentle slopes, and *Poa astonii* existing on the steeper, more exposed areas. The shrub *Hebe elliptica* grows mainly over abandoned penguin rookeries, or between the forest and meadow communities. The vegetation has been considerably modified by the activities of Sooty Shearwaters (*Puffinus griseus*) and the Snares Crested Penguins (*Eudyptes robustus*). The shearwaters burrow extensively, undermining the vegetation and the daily widespread trampling of some seven million individuals (G.J. Wilson, pers. comm.) during their breeding season has killed off plants in accessible places. Penguins modify the vegetation by concentrated trampling where they congregate and their rich nitrogenous excretory products poison the plant cover.

Climate of the Snares

The climate of the Snares is generally similar to that described for Campbell and Auckland Islands (Marshall, 1909b; De Lisle, 1964, 1965). Data collected in 1961, 1967 (Flint and Fineran, 1969) and 1972 (Figure 4) indicate that the prevailing winds blow from the south-west, west and north-west sectors, and calm days are infrequent (e.g. only three out of 365 days in 1972). Summer is the calmest season of the year (i.e. November - February) (Figure 4). Diurnal and annual temperature variations are low (Figure 4).

The weather is characterized by few hours of sunshine per month (Figure 4) and the humidity is constantly high (Figure 4).
The data were collected from January to December 1972 by D.S. Horning, except for the thermograph trace. The units on the wind rose indicate the number of days in 1972 that the wind blew from that quarter. All observations (except the thermograph trace) were made at 0900 hr each day.
due to winds having travelled considerable distances over water. Consequently, rain is common (Figure 4) mainly occurring as light showers and persistent drizzle, but heavy falls also occur during the passage of rain squalls over the islands. The monthly number of rain-free days is low, although there may be occasional periods during the summer, e.g. January 1971, when there is no rain for 10 or 15 consecutive days and the peat surface becomes quite dry.

**Effect of the vegetation upon microclimate**

The often boisterous weather conditions experienced at the Snares appear to have no effect on the daily activities of fernbirds except that they remain under cover. Even when 60 or 80 km/h gales blow over the Main Island the wind is of low strength, i.e. less than 10 km/h in the forest, in *Hebe* scrub and near the ground in *Poa* meadows. Though the tops of plants are vigorously blown about, the wind cannot penetrate further than 1 m (0.5 m or less in the meadows) into the plant cover, but flows over the top.

Similarly, the vegetation tends to deflect heavy rain and break it into droplets which drip down through the vegetation. Fernbirds inhabiting open forest still forage actively while the ground is quite wet and water steadily patters down from the canopy. Thus, during storms, birds are not subjected to direct wind, rain, or even hail. Some places remain quite dry during rainy spells, e.g. under the dead grass mantles of *Poa tennantiana* and *Poa astonii*, and most nesting sites of petrels.

**Main study area**

The main study area (Figures 1, 6 and 11) occupied approximately 3% (87,000 m²) of the Main Island (area of 279.8 ha, C. Hay, pers. comm.) and contained all types of habitat present at the Snares. However, the study area enclosed more forest undergrowth than was typical of the Main Island and did not include any extensive *Poa* meadows (Figure 6).

The land was generally flat or gently sloping (< 25°), except on *Poa* Slope, Punui Bay (Figures 5 and 11) where the slope was 35° to 45° and terminated abruptly in a sheer cliff.

The distribution of different types and densities of
Figure 5: Poa Slope, Punui Bay.

Note the steepness of the slope, and the shearwater take-off strip (left). The dotted lines indicate the territory borders of Poa Slope (P.Sl.) and South-east Colony 15 (S.E.C.15).
Figure 6: Distribution of vegetation types and densities in the main study area.

The broken lines represent territories mapped in 1971-72.

- **Open *Olearia* forest**

- **Moderately dense *Olearia* forest**

- **Dense *Olearia* forest**

- **Hebe elliptica**

- **Poa meadow**

- **Low ground cover, e.g. *Tillea*, *Callitriche*, *Scirpus* and stunted *Poa***

- **Mixture of *Carex*, *Hebe*, *Stilbocarpa*, *Poa* and *Olearia***

Unmarked areas along the coast are bare rock, whilst the small unmarked areas sited centrally represent penguin colonies.
Figure 7: Dense vegetation in *Olearia* forest.
Figure 8: Moderately dense vegetation in *Olearia* forest.
Figure 9: Open Olearia forest.
vegetation in the study area are shown in Figure 6. Under the Olearia canopy, the density of vegetation varied considerably but was most dense along the coastal fringe, adjacent to streams, and in sheltered basins. The density of vegetation was expressed as (1) very dense, (2) moderately dense, or (3) open forest.

In densely vegetated sections of the forest the undergrowth consisted mainly of closely-spaced Polystichum ferns, with some Asplenium and rarely Blechnum ferns. These ferns provided a dense screen up to 2.3 m above the ground, and above this, cover was formed by the mass of sprawling interlocked Olearia branches from predominantly prostrate trees (Figure 7). Visibility was less than 1 m and rarely exceeded 2 m. Very dense cover was also found in Poa meadows, Hebe shrubbery, Carex trifida, Anisotome acutifolia, Stilbocarpa robusta and thickets of Olearia and Senecio saplings growing at the edges of clearings.

Moderately dense cover existed in areas of forest where ferns were more dispersed. Visibility was mainly 3 to 5 m and rarely exceeded 8 m. Fallen Olearia trees, whose closely packed twigs and leaves extended below the general stratum of the canopy, also provided moderately dense cover. Generally, the Olearia trees were more upright than those in densely vegetated areas. Areas of Hebe habitually penetrated by Hooker's sealions or Sooty Shearwaters provided moderately dense cover (Figure 8).

In open areas of the forest the Olearia trees were upright and the canopy formed an almost level, continuous stratum about half a metre thick and some 6 to 9 m above the ground. In a few places there were wide openings in the canopy where the trees have been wind-thrown. Ground cover, e.g. ferns, Stilbocarpa, was absent. Visibility below the canopy was generally 10 to 15 m and occasionally 25 m (Figure 9).

This cover classification is arbitrary and there was often a transition zone between each type of vegetation. In these areas, the mean distance between the two typical forms was used to plot their common border. Very small pockets of vegetation of a particular density type occurred within another. However, only the distribution of the predominant vegetation density has been mapped in Figure 6.
General field method

The study was based on observations of known individuals that lived mainly in the Olearia - Senecio forest, but that utilized to a lesser degree the Poa Slope of Punui Bay and the supralittoral zone adjacent to Boat Harbour. Fewer observations were made of birds inhabiting the Poa habitat as they were difficult to see or capture.

Fourteen birds were captured by hand, three by mist nest and 67 by a hand net borne on a 1.3 m pole. These birds were marked by a combination of coloured plastic and serially numbered stainless steel bands. Those birds that evaded capture were identified by individual plumage characteristics; their tail feathers providing the most variable feature. Unfortunately, the recognition marks of these unbanded birds were lost after the post-breeding moult, and consequently some unbanded individuals from 1970-71 could have been present, but unrecognized, in 1971-72.

The main study area was visited daily and pairs holding territories observed for at least one hour at one to three day intervals. When each territory had been mapped (see Chapter 3, Physical Aspects of Territories), a concentrated search was made for signs of nesting activity.

Nests were found by a combination of methods. Individual birds were followed continuously for periods of over 40 minutes each week. If they were nesting, such birds would at some time lead me to their nest. Or they might call their mates, whose replies then indicated where the nest was situated. Also, at weekly intervals, all the nesting vegetation in a territory was extensively searched. This technique uncovered eight nests. Three nests were found when I sat quietly amidst a likely nesting area, listening and watching until the birds' centre of activity was determined. This activity centred on the nest.

The type of roosting site used by birds was useful for indicating if nesting was in progress. If a pair had a nest with eggs or young they roosted there together, whereas non-nesting birds chose sheltered sites in dense vegetation.
Pairs of birds which did not appear to be nesting were followed before the onset of darkness until they ceased calling and moving about. The areas in which activity was last seen were noted. The following morning I searched these areas thoroughly for nests or places where the local vegetation had been pushed aside to form a small, nest sized area containing a few fernbird feathers and droppings. The discovery of roosting hollows was taken as confirmation that nesting was not in progress at that time.

In addition, pairs that were not currently nesting did not call or forage as actively as those nesting, and spent more time sunning, bathing and taking short naps than nesting birds. Also, if a pair of birds were seen together for over 30 minutes, it was most unlikely that they had eggs or chicks to attend to.

**Standard measurements of adults**

Seven standard measurements (after Gurr, 1947) were taken on all adults captured. Wing and tail length were measured to the nearest 1 mm with a steel rule, and the remaining parameters, viz. lengths of the bill, tarsus, middle toe (without claw) and bill height to 0.1 mm with steel vernier calipers. Bill width proved to be an unsatisfactory parameter as the basal region of the bill was soft and measurements (to 0.1 mm) unreliable. Measurements of all birds captured (not in moult) are recorded in Appendix 1.

**Method of sexing adults**

The sexes could not be positively distinguished in the field on morphological characters. I found it possible to use only behaviour and vocalizations to sex live birds provisionally. "Males" were taken to be the more aggressive members of a pair and uttered a wider variety of calls (see Vocal Communication, Chapter 3) than "females". "Females" answered calls emanating from their mate's territories. "Females" were usually submissive to an aggressive bird even if on her mate's territory, while a "male" on his territory was always the aggressor.

The attitude of different birds during copulation was
Figure 10: Wing/tail lengths of males and females.

Solid circles are measurements of "females", while open squares are those of "males" (sexed by behaviour). Open squares with dots are measurements from male study skins in the Canterbury Museum. No female skins were available.
of limited value as a technique for determining sex, as only two attempts were observed. However, in both attempts, the bird which moulted was of the "male" type described above, while the subordinate bird's behaviour was consistent with that of a "female". Also, two known birds found dead in February 1971 proved to be males when dissected. Records of their previous behaviour showed they exhibited "male" type behaviour described above. As the Snares are a stringently protected wildlife sanctuary I was not allowed to collect several birds to confirm my diagnoses by dissection.

Morphological measurements are of limited use for verifying differences between the sexes. The sexes (determined by behaviour) could not be consistently separated by plotting any one of the seven standard body measurements against another. Plotting tail length against wing length of non-moulting adults produces the best separation of males from females but some overlap remains (Figure 10). All seven variates that I measured were used in a multiple discriminate function analysis, program (DISCRIM) of Cooley and Lohnes (1962) run by A.J. Baker. This showed that there was almost perfect discrimination between the two sexes on morphological characteristics by using just the first discriminate equation of the reduced spaced matrix. In the field though, I could use only behaviour and vocalizations to sex live territorial birds. As the behavioural and vocal differences (mentioned above) between the two sexes were consistent, only rarely was a bird's sex incorrectly diagnosed.
CHAPTER 3

TERRITORIAL BIOLOGY

INTRODUCTION

The territorial biology of fernbirds is considered under two categories. The first gives a brief account on the physical concept of "territory" and its relevance to fernbirds, and also describes the yearly cycle of territorial activity. The second and major section of this chapter describes and depicts the characteristic postures and calls used in displays associated with territorial behaviour. This is followed by detailed discussions of the origin and function of the various postures, and descriptions of sounds produced during calling, the types of calls and their role in territorial biology.

Although postures and vocalisations are described separately for clarity, it is artificial to set visible and audible components apart as they reinforce each other and express fully the displaying bird's intentions.

PHYSICAL ASPECTS OF TERRITORIES

Throughout this account the term "territory" is used to mean "any defended area" (Noble, 1939). Fernbirds occupy well-defined territories for breeding. The borders of these territories remain constant from at least mid-November to the beginning of April. These territories correspond to Noble's (1939) sexual and nesting territory, or Hinde's (1956) type A territory, i.e. a large breeding area in which nesting, courtship, mating, and most food seeking usually occur.

The behaviour events involved in the establishment and maintenance of such a territory appear to fall into two or three categories as outlined by Hinde (1956):

a) Restriction of some or all types of behaviour into a more or less clearly defined area.
b) Defense of that area.
c) Self advertisement in that area.

Component (a) appears in the young after they have become independent, for they generally frequent a home range (i.e. an area covered in normal daily activities) that includes their parents' territory.

During early April component (b) is present as many vicious fights occur, with some birds even pulling out each other's feathers (D.S. Horning, pers. comm.). In contrast, plumage pulling rarely occurs during border disputes in the breeding season. It is likely that the breeding territories for the following season are determined by fighting in autumn. Throughout the winter territorial border fighting is not apparent, although occasionally birds forage in pairs and call in duet. Territory-owning birds of the previous breeding season tend to remain about their former territories. From early October (D.S. Horning, pers. comm.) through to late March intruding birds are evicted as territory claims are reasserted. During this period aggressive expression appears to be more ritualised as the physical clashes observed were less violent than those observed in autumn.

Self advertisement in the defended area occurs from October to March.

Territory boundaries were plotted on to large scale aerial photographs (scale 10 mm:10 m). Positions of ridges, rock outcrops, creeks and penguin colonies within the main study area were drawn on to these photographs. From these points, and from examination of stereo aerial photographs (taken for the University of Canterbury by the R.N.Z.A.F. in 1967), positions of border displays or fights were recorded to the nearest 4 m, and often to within 2 m. In places where no distinct landmarks were available, distances to the nearest three landmarks were paced out.

Boundaries of territories were regarded as those places where both males, or females, of adjacent territories fought or aggressively displayed at one another.

Sometimes I initiated border disputes by playing taped recordings of fernbird calls while walking through the
study area. The male of the territory I was in often rushed across to my position and followed the calls. I continued to attract the aggressively acting male until he converged on neighbouring males who were also attracted to my calls. Fighting broke out usually when the neighbouring males first met. In this way I could plot some territory borders in a relatively short time. However, this method could not be used too frequently in any area as the males soon ceased to act aggressively to my calls (see The main properties of calls, Section 6). Sites of border disputes were also found during my daily wanderings throughout the study area. In places where few border clashes were observed, both foraging behaviour and ranges of known birds were used to define territory borders. Where a bird ceased calling and acted stealthily it was regarded as being off its territory. These sections of territory borders are marked by dotted lines (Figure 11 a and b).

Territory areas were estimated by weighing card templates of territories and comparing these weights with a square template representing a known area. These areas are given in Table 1. Measurement of the horizontal territory area does not fully represent the total surface area available, since such territories are three-dimensional units and each has a different density of vegetation and other surfaces (e.g., burrows of nesting petrels) upon which fernbirds forage.

In the study area, territories were generally small along the coast (with the exception of Seal Point) but they became larger further into the forest (Table 2, Figure 6). Vegetation density and diversity were higher around the coast (with the exception of Seal Point) and decreased to open stands of Olearia lyallii towards the centre of the island. Although no quantitative data were collected, Sinkhole Flat, the east coast of the North and South Promontories, and the razor back ridge on the South-west Promontory probably had the highest density of territories as these areas contained the most diverse plant communities present on the Main Island of the Snares.

Territorial disputes were heard all over the vegetated tracts of the Main Island in the breeding season. I have no evidence that large areas of barren rock were defended against
Figure 11: Territory maps.

B. 1971-72 territories.

Dashed lines indicate sites of territorial disputes, dotted lines show probable territory borders (where no fights were observed). Heavily stippled circular areas represent penguin colonies. Lightly stippled areas around Boat Harbour mark the beaches, and coast where overhung by trees.
<table>
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<tr>
<th>Name of Territory</th>
<th>1970-71 area (m²)</th>
<th>1971-72 area (m²)</th>
<th>Change in area (%)</th>
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Table 2: TERRITORY SIZE IN DIFFERENT HABITATS
(Data from 1971-72 season)

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<th></th>
<th>Description</th>
<th>Territory Sizes (m²)</th>
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<td>1</td>
<td>In <em>Poa tennantiana</em>, <em>P. astonii</em></td>
<td>1640, 1790 (2530)</td>
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<td>2</td>
<td>In a variety of dense cover</td>
<td>1130, 2050 (1030), 2510 (1260), 2150 (1070), 2560 (1280)</td>
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<tr>
<td>3</td>
<td>In thick <em>Olearia</em> (i.e. moderately dense and dense <em>Olearia</em>, definition in Chapter 2)</td>
<td>1640, 1950, 2050, 2050</td>
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<tr>
<td>4</td>
<td>In open <em>Olearia</em> (as defined in Chapter 2).</td>
<td>3000, 3070, 3230, 3330, 3690, 4100, 4870, 5320, 7170, 7420</td>
</tr>
</tbody>
</table>

Note: In 1) the area 1790 m² refers to horizontal area. Territory on a 45° slope, so flat area = 1.414 x 1790 = 2530 m²

In 2) a "variety of dense cover" indicates territories having small clumps of *Hebe*, *Olearia*, *Carex*, *Poa*, and *Stilbocarpa* all mixed together.

In 2) the areas 2050 - 2560 m² give the total area of territories which bordered on the sea. Figures in brackets indicate the vegetated, and thus the defended areas of territories.
other fernbirds, although they foraged along crevices containing organic debris on steep rocky faces. The two pairs of birds occupying Seal Point during the 1971-72 breeding season strongly defended their border adjacent to vegetated areas, but elsewhere, on bare rock, little aggressive behaviour was seen (Figure 11 b). In the main study area there was no waste land between territories and all territory borders were sharply defined except at penguin colonies (see below and Figure 11). Therefore, at the Snares, fernbirds probably occupied all vegetated habitat.

**Influence of natural features on territory borders**

Most territories had at least some part of their border closely following natural features such as vegetation borders, rock outcrops, ridges, creeks, penguin colonies and main penguin (and human) tracks. However, some sections of borders did not appear to follow natural features but adjacent birds appeared to know exactly where their border lay.

Many territories had common borders meeting at penguin colonies, which probably formed fixed geographical border landmarks rather than essential foraging sites, for these colonies did not appear to belong to any particular pair of fernbirds. No aggressive intra-specific fernbird activity was observed in penguin colonies even when these were deserted by penguins in late February (pers. obs.). However, fernbird border disputes occurred a metre or two outside penguin colonies.

Territory size appeared to coincide with the area that can be effectively defended by a male. I interpret this as a consequence of the influence of vegetation density upon a male's ability to see (and be seen). In dense vegetation he could not see far and his calls carried only a short distance. Therefore, he could police only a relatively small area. As cover decreased visible and audible signals would carry further, and intruders would be visible over longer distances.

It was not likely that a change in food abundance was a prime determinant of territory sizes of fernbirds in the two seasons of study. Although insects were notably less abundant in the 1971-72 season than in 1970-71 (pers. obs. supported by pers. comm. from D.S. Horning), most territories remained the same size, and some decreased. At Seal Point, during 1970-71
there was only one territory and one brood of young were fledged. However, in 1971-72, there were two territories, and both pairs of birds fledged two broods. This indicated that even in this rather sparsely vegetated area there was still adequate food for raising offspring.

Changes in territories between the two breeding seasons

Sixteen (out of 19) territories mapped in 1970-71 were the same in 1971-72 (Figures 11 a and b). In 10 territories, the same male held the same territory for both seasons, and in 1971-72 seven new males occupied territories that had belonged to other males in 1970-71. Males of the remaining four territories mapped in 1970-71 evaded capture and thus tail configuration was used to identify them. As their identifying marks would have been lost in the post-breeding moult, it was not known if these males had survived until the 1971-72 season.

The main changes occurring in territories were (1) Seal Point became two territories, (2) East Colony 5 territory changed its shape slightly and, in 1971-72, extended down to Seal Cove, and (3) North Colony 2 territory was reduced from 3580 m² to 1950 m² (decrease of 45%) due to a new territory having been established on its western border.

In two territories (Colony 1 and East Colony 3) a new male had taken over the territory while the previous season's owner was still alive. Only in the Huts territory did a change of ownership occur within a season.

Females in eight of the 1970-71 season territories were banded, and six were present on the same territories in 1971-72. The other two females were not seen in 1971-72. There were seven territories in 1970-71 where both mates were banded, and in the 1971-72 season four territories were held by the same pairs. Of the remaining three pairs, one pair (East Colony 3 territory) had divorced but occupied neighbouring territories in 1971-72, one pair had disappeared (the Huts territory), while the male of South Colony 3 territory had mated with his daughter (Bird 46) of the previous season. His former mate was not seen in 1971-72. Bird 46's sibling also frequented the Colony 3 to 34 area and although it was a non-territorial bird, its father never drove it off his territory as vigorously as he did other intruders. The divorced pair of
birds may have separated because they did not breed successfully in 1970-71 (as Coulson and White, 1958 found for Kittiwakes Rissa tridactyla). However, two other pairs of fernbirds mated for both seasons also failed to raise any young.

BEHAVIOUR EMPLOYED IN TERRITORIAL MAINTENANCE

Territorial maintenance involves a number of displays consisting of various postures and calls. In the section on displays, a description of the calls used is included, but their significance is discussed more fully in a later section on vocal communication.

The displays associated with territorial behaviour

The following displays are used during territorial maintenance. In these descriptions, references to the attitude of the bird's body or tail are in respect of the horizontal plane.

A. Territorial Defense Display.

The Territorial Defense Display is given by territorial males and females. While displaying, the bird stands upright on straight legs facing its opponent who is generally 1 or 2 m away. The displayer's plumage is fully sleeked and its white chest with black spots is prominently exhibited. The partly opened wings, with spread primaries, almost touch the ground. Both wings are quivered rapidly through 10 to 15 mm, and the bird's slightly spread tail is held at 30 to 40 degrees declination (Figure 12).

At the same time, the bird moves back and forward a few rapid, short steps. This motion is followed in reverse by the opponent so that the birds remain equidistant from each other. When such displays are given on horizontally or steeply inclined parallel branches, both birds run rapidly a few steps from one side to the other.

While the short rushes and retreats are in progress each bird either yaws (pivots) or rolls from side to side, through an arc of 30 degrees.

Territorial Defense Displays are directed at the
TERRITORIAL DEFENSE DISPLAY

SUBMISSIVE DISPLAY

BEGGING DISPLAY
Figure 12: Postures associated with territorial behaviour.
opponent(s), for when one bird is above the other, the lower bird tilts its body back further so that it displays at the higher bird, and vice versa. This display also varies in intensity. During low intensity displays, movements and calls are delivered slowly. Often the nape feathers remain sleeked, the wings are quivered slowly and the body plumage is not fully sleeked. Advance and retreat are at a walking pace, and yawning or rolling are reduced. The displayer's body is inclined at 45 degrees and its legs are slightly bent.

A medium intensity Territorial Defense Display indicates a higher aggressive motivation but is unlikely to lead to fighting. At this intensity the body is inclined at 50 to 60 degrees while the legs are usually straight. Wing and feet movements are more rapid than in low intensity displaying, nape feathers are partly raised and Territorial Defense Calls are given at a higher rate.

During high intensity displaying all calling and body movements are extremely rapid. Birds also rapidly change displaying sites, e.g. run up and down branches, flit from tree to tree, and over the tops of fern fronds and other conspicuous places. Nape feathers are fully raised and the body is inclined at 60 to 70 degrees.

Females are less active than their mates in severe border disputes, but tend to remain in the same place, 1 or 2 m behind their mates' original displaying positions. Although high intensity disputes sometimes last as long as six minutes, the females rarely stay longer than two minutes after the start of a dispute.

Territorial Defense Displays are adopted in response to several stimuli, and the intensity of the response depends on the motivation of the bird, and subsequent behaviour of the other bird(s).

Fighting occurs only during border disputes, and begins most frequently when two neighbouring males first meet, or during the highest intensity of Territorial Defense Displays. Fights rarely last more than five seconds, but are fast and furious. It is not easy to determine which bird starts a fight because the antagonists simultaneously rush forward and often rise in a steep climb, meeting feet first about a metre above the ground or branches from which they were displaying.
Furious pecking and grappling ensues, most blows being aimed at the opponent's breast and throat plumage (i.e. where black spotting is most highly concentrated on the white ventral plumage). The birds are often locked together for a few seconds, tumbling over on the ground, but on disengagement aggressive displaying is resumed. Also, while circling around each other the birds may jump up and grapple at one another, even as they fall back to the ground. These jumps are sometimes repeated in rapid succession for about 10 to 15 seconds. Less often, the two opponents leap up and down out of phase, without grappling. Birds are rarely harmed during fighting, although one female was dazed for 30 seconds after a particularly violent attack from a male.

All border disputes end suddenly, when both birds cease their aggressive displaying, and then they usually move off quietly in opposite directions and begin foraging. Foraging behaviour probably serves to inhibit further aggression; both birds have demonstrated their willingness to defend their territories and further displaying is probably unnecessary.

B. Submissive Display.

The Submissive Display is performed by all post-fledging birds except males in their territories. It is seen most commonly in fledglings and juveniles when they first meet another fernbird, or in a novel situation (e.g. humans approaching).

Typically, the Submissive Display involves synchronous wing and tail flicking but the attitude of the body varies. The displaying bird commonly remains silent unless it is the male or offspring of the territorial male. The raised tail with closed rectrices is held rigidly at 30 to 45 degrees inclination. The wing primaries are spread and the wing opened in a drooped fashion identical with the Territorial Defense Display. When the wings are opened, the tail is flicked rapidly down to 0 to 15 degrees declination. Then, as the wings are snapped against the body, the tail is raised, but at a slower rate than when flicked down. Body plumage typically remains sleeked (Figure 12).

Displaying birds sometimes stand still but more commonly move about in short hops. After such "hesitant" jerky paces the displayer stops suddenly and jumps about, often on the
same spot ("jerk jump") facing one way, then another. Jerk jumps occur only when the wings are snapped against the body and the tail is raised.

Initially the submissive bird crouches in a "frozen" horizontal posture with its neck fully contracted. If attack is not forthcoming the bird cocks its head from side to side peering all about. The submissive bird often stands fully upright with its neck fully extended, leaning from side to side, then crouches low to look under branches, in search of the disturbing influence and a path to flee along. Wing and tail flicking continue during this searching phase of the display.

The intensity of Submissive Displays varies and appears to depend on the strength of initiating stimuli, and the displaying bird's motivation. When used in response to a bird giving the Territorial Defense Display, the intensities of the two displays match.

Low intensity display: the submissive bird spends much of its time peering around and either approaching or retreating jerkily. Jerk jumping and hopping about in a small area are of low frequency. Wing and tail flicking occur about once every two seconds, and the tail is inclined at only 15 to 25 degrees before being flicked down.

Medium intensity display: frequency of wing and tail flicking increases to about once per second. The tail is held at 30 to 40 degrees inclination. While the searching-peering phase is reduced, jerk jumps and hopping about rapidly in a small area increase in frequency.

High intensity display: all movements are rapid and the display is marked by very jerky sequences. Wing and tail flicking occur once every half second or less and the head is cocked rapidly about. The searching phase is almost absent.

C. Pre-copulatory Display.

The Pre-copulatory Display was observed only twice, and was given by a male and female immediately before copulation.

In the first observation, the previously foraging female hopped onto a branch and adopted a crouched horizontal posture. She flapped her extended wings slowly up and down. Her tail was held rigidly at 50 to 55 degrees inclination. A nearby male landed alongside her, gave the same display, and
then mounted for two to three seconds, fluttering his wings to maintain balance. Coition however was not attempted.

On the second occasion, the female's display differed from the above in that she was giving low intensity Territorial Defense Calls, her wings were rapidly quivering as in the Territorial Defense Display with her tail feathers spread and inclined at 15 to 20 degrees. The male stood about half a metre away, facing her, and gave the Territorial Defense Display and Territorial Defense Calls of low intensity. He landed beside the female, adopted a similar posture to hers for a moment, and then mounted for two to three seconds. After dismounting he preened. She continued to call and display for 30 seconds after the male dismounted, and then both birds went foraging in different directions.

D. Begging Display.

This display was adopted by fledged young in response to the appearance of a parent. The fledgling crouched low with its head drawn into the shoulders and directed its begging upwards (Figure 12). During begging, the half extended wings were quivered up and down rapidly and the chick uttered a soft harsh "uurr" begging call. This begging posture was somewhat different from that of nestlings, which stood up and stretched their necks out fully towards an approaching parent.

The use of these displays is extremely variable but the sequence of possible events when two birds meet has been summarized in Figures 13, 14 and 15.

Sequence of events when two birds meet.

No reaction occurs in most cases when two mates, two young, or an adult and young meet, and very occasionally when an intruding adult is met by the territorial male (Figure 13). Disregarding the latter case, lack of action by the territorial male when meeting its mate or any fledgling indicates that he recognizes them as inoffensive subordinates. An occasional intruder foraging unmolested within sight of the territorial male indicates that at that time the territorial male has a very low aggressive motivation. This is more likely to occur after the young have fledged.
**Figure 13. Reactions of a male to other fernbirds on his territory**

**Type 1: No reaction**
- Territorial male seen by other bird
- No reaction

**Type 2: Eviction**
- Other bird immediately leaves territory, stealthy departure
- Type 2: Both birds resume foraging

**Type 3: Submissive territory adoption**
- Other bird immediately adopts Submissive Display but remains in the same place
- Type 3: Submissive territory adoption
- Other bird adopts Pre-copulatory Display
- Copulation attempted
- Type 3: Copulation attempted

**Type 4: Territorial Defense Display**
- Other bird rushes slowly ahead, adopting Territorial Defense Display and Calls, and rushes at other bird
- Type 4: Territorial Defense Display
- Other bird runs up to territorial male and also adopts Territorial Defense Display and Calls
- Type 5: FIGHT
- Both birds have a bout of Territorial Defense Displays and Calls of varying length and intensity
- Both birds resume foraging

**Type 5: Border disputes**
- Both birds face away from each other, but stand close together continuing Territorial Defense Displays and Calls
- Territorial Defense Displaying and Calls cease
- Both birds resume foraging

**Type 1: No reaction**
- Territorial male seen by other bird
- No reaction

**Type 2: Eviction**
- Other bird immediately leaves territory, stealthy departure
- Type 2: Both birds resume foraging

**Type 3: Submissive territory adoption**
- Other bird immediately adopts Submissive Display but remains in the same place
- Type 3: Submissive territory adoption
- Other bird adopts Pre-copulatory Display
- Copulation attempted
- Type 3: Copulation attempted

**Type 4: Territorial Defense Display**
- Other bird rushes slowly ahead, adopting Territorial Defense Display and Calls, and rushes at other bird
- Type 4: Territorial Defense Display
- Other bird runs up to territorial male and also adopts Territorial Defense Display and Calls
- Type 5: FIGHT
- Both birds have a bout of Territorial Defense Displays and Calls of varying length and intensity
- Both birds resume foraging

**Type 5: Border disputes**
- Both birds face away from each other, but stand close together continuing Territorial Defense Displays and Calls
- Territorial Defense Displaying and Calls cease
- Both birds resume foraging

**Types:**
- Type 1: No reaction
- Type 2: Eviction
- Type 3: Submissive territory adoption
- Type 4: Territorial Defense Display
- Type 5: Border disputes
Type 2 behaviour (Figure 13) is exhibited by trespassing adults only, and their reactions indicate that they know they are on "claimed" ground. Their immediate withdrawal from such territories upon sighting the territorial male, or (if the intruders are females or non-territorial birds*) the territorial female, indicates that they can recognise the status of territory owners. In many cases, the intruder stealthily leaves the territory without any signal from the owners.

Type 3 (Figure 13) behaviour occurs mainly when the submissive bird is the male's mate or any fledgling. The submissive role is adopted most often in response to sudden meetings with the male. At such times, the male commonly acts aggressively, and the submissive display serves to inhibit his aggression. This behaviour probably assists the male to recognise a member of his family group, as he usually halts his aggression shortly after submissive activity begins. Submissive action indicates that the displaying bird poses no threat to the male's dominance, and that it does not want to leave.

Less often, submissive action is used by non-territorial birds, other trespassers, and stray fledglings and juveniles. Of these, non-territorial birds least commonly adopt submissive action as they usually flee at the first sign of the territory owners. Submissive displays are used most commonly by stray young birds who initially act submissively to any sudden disturbance. Submissive non-territorial and intruding territorial birds are usually slowly chased off the territory by the male, while submissive stray fledglings or juveniles are chased only a short distance.

Through the male's response to these different classes of submissive birds it is probable that he can recognise his mate, his offspring, foreign offspring and intruding territorial birds. Non-territorial birds are probably also recognised as they are usually poorly groomed and frequent the same area.

Type 4 (Figure 13) behaviour sequences occur only between mates, mainly when they are close to, or changing duty.

* Non-territorial bird: an adult bird lacking a territory.
Figure 12. Reactions of a female to other fernbirds on her mate's territory

Territorial female meets neighbouring territorial male → No reaction

Terrestrial female calls 'Cheep' loudly and rapidly

Female adopts Pre-copulatory Display

Her mate is attracted → Figure 13, type 5 behaviour follows

Figure 13, type 2 behaviour follows

Figure 13, type 5 behaviour ensues. This often attracts the males and a vigorous dispute follows

Figure 13, type 3A and 3B behaviour follows

Figure 15. Reactions of fledged young to other fernbirds

Fledgling or juvenile meets another bird → No reaction

Commonly

Young bird adopts Figure 13, type 3B behaviour

Young bird adopts Territorial Defense Displays and Calls
at their nest. This pattern happens infrequently when they meet unexpectedly while foraging indicating that both mates do not recognise each other initially, for displaying is momentary. On one occasion however, the mates attacked one another and fought for three seconds before parting and reducing their aggression by facing away from each other as they displayed. Aggressive behaviour during nest duty changeovers indicates that the area around the nest is the centre of the strongest offensive motivation, and of highest priority for defense. Thus the presence of another bird near the nest, even its own mate, is likely to trigger off aggressive responses. The members of a pair must recognise each other at this moment, and behaviour and vocalization may assist identification. As this aggressive behaviour is often carried out by male and female standing together and facing outwards, it seems likely that it may also serve to strengthen the pair bond.

Type 5 behaviour (Figure 13) occurs in border disputes; the only exception seen is mentioned in Type 4 behaviour, when two mates fight each other. Border disputes are most frequent and spirited when both neighbours have their nests only a few metres apart. In contrast, along well established borders where nests are well separated, most disputes are generally of low intensity. For example, on several occasions neighbouring birds came within sight of each other and while stationed 5 to 8 m apart they gave low intensity aggressive chittering calls for about five seconds, then continued on their separate ways. This was observed between neighbouring males, females, and a male and female.

The responses of territorial females to intruding birds are similar to those of the male (Figure 14) except when the intruding bird is a territorial male. In the latter case, the female appears to have conflicting tendencies to flee from the strange male and to remain in her territory. Her adoption of the pre-copulatory display probably inhibits any attack by the intruding male, i.e. it is used as a submissive posture.

Young birds either do not respond to one another, or act submissively (Figure 15). As young birds are lowest in the hierarchy it is probably advantageous to them to act submissively following the sudden appearance of any strange
Analysis of territorial displays

The following account breaks the above mentioned displays down to their simplest components. This allows for subsequent discussion of the probable origin of the display components, and their inherent signal function.

A. Components of territorial displays.

See Table 3.

B. Origin of territorial display components.

There have been many studies involving the interpretation of behaviour and the origin of displays, e.g. van Tets (1965), Marler and Hamilton (1966), Hinde (1970), and Morris (1970). However, in most cases the physiological changes within the animals are not known and it becomes necessary to construct abstract models which serve to interpret the causal relationships of behavioural sequences. Even though these models are abstract the consequences they predict are concrete and can be verified by experiments (see Morris, 1970).

Tinbergen (1952) showed that threat behaviour could be better understood if it were assumed to depend on the simultaneous arousal of tendencies to attack and flee, i.e. aggression and fear. Each component of a display depends on one, two, or more drives. Hence, a change in the intensity of one drive results in a change in only some components of the display. The presence of two, or more, drives in a display produces a conflict situation where rapid alternations of attack and fleeing tendencies occur. These hypothetical drives are expressed overtly by means of intention movements.

Intention movements consist of the initial phases of movements or movement sequences derived from direct behavioural responses to stimuli. For example, one of the responses of an intruding bird following the appearance of the territorial male is to immediately fly away. However, the intruding bird instead sometimes retreats slowly, making flight intention movements. These movements have been derived from the take-off leap of a bird before flying. Take-off leaps consist of two
THE CROUCH

THE LEAP
Figure 16: Flight intention postures (after Daanje, 1950).
### Table 3: COMPONENTS OF TERRITORIAL DISPLAYS

<table>
<thead>
<tr>
<th>Component</th>
<th>Territorial Defense</th>
<th>Submissive</th>
<th>Pre-copulatory</th>
<th>Begging</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing quivering</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Bill raising</td>
<td>present</td>
<td>--</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Neck extended, head forward</td>
<td>always</td>
<td>sometimes</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Nape feathers raised</td>
<td>at highest intensity only</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Tail lowered and slightly spread</td>
<td>present</td>
<td>--</td>
<td>--</td>
<td>present</td>
</tr>
<tr>
<td>Short advancing and retreating steps</td>
<td>only</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Jerk jumps and hesitant jerky steps</td>
<td>--</td>
<td>only</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Sleeked body plumage</td>
<td>present (except nape)</td>
<td>present</td>
<td>present</td>
<td>--</td>
</tr>
<tr>
<td>Pivoting and rolling</td>
<td>only</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Territorial Defense Calls</td>
<td>present (and nest-duty changes)</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Alarm calls</td>
<td>--</td>
<td>sometimes</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Facing another bird</td>
<td>present</td>
<td>--</td>
<td>--</td>
<td>present</td>
</tr>
<tr>
<td>Facing away from another bird</td>
<td>present in special cases only</td>
<td>present</td>
<td>present</td>
<td>--</td>
</tr>
<tr>
<td>Crouched-hunched posture</td>
<td>--</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Wing and tail flicking</td>
<td>--</td>
<td>present</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Alert posture, peering</td>
<td>--</td>
<td>present</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>&quot;Frozen&quot; posture</td>
<td>--</td>
<td>--</td>
<td>present</td>
<td>--</td>
</tr>
<tr>
<td>Fluffed feathers</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>only</td>
</tr>
</tbody>
</table>
phases (Daanje, 1950): first the bird crouches, withdraws its head and raises its tail, and then reverses these motions as it springs into the air (Figure 16). This source display has been modified to consist of the initial phases of movements or movement sequences and these incomplete movements may be repeated several times before take-off. Flight intention movements occur repeatedly for much of the time that the bird remains in conflict. This conflict is signalled by the flight intention movements coinciding with a slow retreat, indicating a desire to remain.

From the above discussion, I classify the following components of territorial displays as indicators of flight intention: wing quivering, bill raising, extension of the neck with the head forward, the lowered and spread tail, sleeked body plumage, jerk jumps and steps, crouched-hunched posture, wing and tail flicking. The first five components listed here are prominent in the Territorial Defense Display. Escape intention is indicated by alarm calls and facing away from another bird.

Wing quivering has been recorded as a common component of courtship by male passerines and, with the exception of a few carduelines (listed on p322, Andrew, 1961) is never closely associated with aggressive responses (Andrew, op. cit.). Since in fernbirds wing quivering is also a component of the Pre-copulatory and Begging Displays, it would be unlikely to include any signals of aggression, at least in those contexts. Therefore, it is also unlikely to be correlated with aggressive intent in other contexts. Coombs (1960) noticed that rooks (Corvus frugilegus) increase wing and tail flicking when under some degree of alarm short of the actual intention to fly, i.e. these motions indicate an increased motivation to fly. This is also the case for fernbirds.

Those components that appear to indicate attack are: raised nape feathers, facing another bird, Territorial Defense Calls, bill raising, and the head forward and neck extended. Although bill raising and head forward with neck extended components are listed under flight intention movements, these components also indicate attack when combined with facing another bird, as the bill (weapon) is exposed to the other bird, whereas a fleeing bird faced the other way, hiding its
bill. This is similar to the way in which the submissive female Lesser Black-backed Gull (*Larus fuscus*) faces away from her mate, hiding her bill, during courtship (Tinbergen, 1969).

Marler (1958) stated that "bill pointing" or "head up" postures of many birds during fighting can be regarded as postures combining elements of preparation for attack and elements of incipient withdrawal. In fernbirds, flight intention movements such as wing quivering, and the depression and spreading of the tail may indicate flight towards the opponent, thus attack, for these movements are directed towards the opponent. Therefore, the orientation of the displaying bird relative to the other may be the overriding factor indicating attack or submission. In support of this idea, the attack motivation signalled by both mates' actions during a change-over in nesting duty soon becomes directed away from the partner. In the one case when both mates continued to face each other they attacked and fought briefly before facing away from each other.

Conflicting attack and flee tendencies are shown by the following territorial display components: (1) short advancing and retreating steps, and (2) pivoting and rolling. These two components probably represent ambivalent behaviour as they consist of strong attack and retreat drives apparently combined in equal quantities, for a pair of Territorial Defense Displaying birds remain equidistant. Pivoting and rolling are found in the courtship displays of many passerines, e.g. Crimson Backed Tanager, *Ramphocelus dimidiatus* (Moynihan, 1962); Zebra Finch, *Poephila guttata* (Morris, 1954) and the American Redstart *Setophaga ruticilla* (Ficken, 1962), and in these species appears to represent ambivalent behaviour in conflict situations.

Conflicting tendencies are possibly also indicated by jerk jumps and steps, but here the motivations appear to be to approach and flee rather than "attack" and flee. In jerk jumps and steps, the movements are of short distance and during them the bird often changes direction, once edging a little closer, pausing, then backing off hesitantly, and peering about all the time in an exaggerated fashion.

This completes the description and analysis of the displays used in the territorial biology of the fernbird.
Figure 17: Different forms of "Tcherp" type calls.

A. "Tcherp" call from male.
B. "Tchorp" call from male.

The male call is the unhatched section of the sonagram. The vertical slash represents the "Tc", whilst the horizontal slash depicts "herp". In B the "horp" is shown by the descending horizontal stripe. The hatched portion of both duet sequences represents the female's slurred "Teort" reply.

Figure 18: Variation in duet sequence.

The series of closely spaced pulses are clicks (chittering) produced in Territorial Defense Calls. The rate of delivery and pitch can be fairly constant as in A, or both can vary as in B. A typical male-female duet of "Tcherp-teort" is also shown.

Figure 19: Typical female duet calls.

The first two calls are "Tchep" and the third is "Teort".

Figure 20: Example of a "Tee-oo" type call.

In this example, a single clear "Thwee" call is produced. As this sound carries far and is readily located it is probably a contact call.

Figure 21: Typical "U-tick" type calls.

The male call consists of two closely spaced vertical pulses ("Whuddit" sound). This is followed by a typical "Teort" female response.

Figure 22: Different forms of "U-tick" calls.

A. "Whee-teort".
B. "Whu-teort".

Notice that "ee" sounding calls are of higher pitch (A) than "u" calls (B). Although these calls were given by different males, one male often gave both variants.

N.B. Sonagrams of South Island Fernbirds were used in Figures 17, 18 and 21. Calls of Snares Fernbirds were used in Figures 20, 22 (both supplied by J. Warham) and 19.
Further analysis with the present data would be extremely tenuous.

**VOCAL COMMUNICATION**

Fernbirds have no song, but communicate vocally by brief and subtly varied calls. The volume, pronunciation (Figure 17) duration and rate of calls (Figure 18) may alter, even within one bird's typical calling sequence.

At the Snares, on calm days, I could hear loud calls at over 70 m if uttered above the vegetation, about 40 m in open forest, and 20 m or less in thicker undergrowth. Calls are heard least well when they originate amongst the basal vegetation of *Poa* meadows. Wind noise markedly reduces the carrying distance of calls, but in addition, blustery conditions confine fernbirds to sheltered places. The late evening chorus of courting shearwaters often reduces the range of fernbird calls. Sometimes fernbirds can successfully duet only within 5 m of each other, even though the nearest shearwater may be more than 12 m away.

Moderately loudly calling birds can be heard when up to 40 m from me, and soft calls for up to 20 m under optimum conditions, i.e. on calm days and above the vegetation.

Although the carrying distance of calls is restricted in dense vegetation, the frequency of calling is higher than in open *Olearia* forest. In the 1970-71 season two 180 m long line transects were set up. One transect was situated in open *Olearia* forest, starting by Colony 2 and passing by Colony 3, while the other ran through the dense *Poa astonii* meadow between Sinkhole and Sinkhole Gut. Each traverse took four to four and a half minutes and the number of birds calling within 10 m to either side of my path were recorded. Traverses over the two transects were carried out within 30 minutes of each other, at two to four day intervals from 1 December 1970 to 23 February 1971, and the results summarised in Table 4.

The greater frequency of birds calling in *Poa astonii* is partly due to the greater density of fernbirds living therein (2.83 times more fernbirds inhabit denser vegetation, than in a similar area of open *Olearia* forest - data from
Table 4: MEAN NUMBER OF CALLS IN DIFFERENT DENSITIES OF VEGETATION

<table>
<thead>
<tr>
<th></th>
<th>In open Olearia</th>
<th>In dense Poa astonii</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of traverses</td>
<td>20</td>
<td>21</td>
</tr>
<tr>
<td>Mean no. of birds calling/traverse</td>
<td>0.58</td>
<td>3.14</td>
</tr>
<tr>
<td>Variance</td>
<td>0.98</td>
<td>4.12</td>
</tr>
</tbody>
</table>

\[ ts = 4.99, \text{ with } 20 \text{ d.f., } p < 0.001, \]
i.e. very highly significant difference.

Chapter 10). If this differential population density is taken into account the mean numbers of calls in open Olearia is still half that recorded for dense Poa astonii, e.g. 0.58 x 2.83 = 1.64 which is approximately half of 3.14. Thus fernbird vocal activity in dense Poa astonii, where visibility is greatly limited, is twice as high as that in open Olearia forest.

Fernbird calls are either of long (0.3 - 0.5 sec), medium (0.1 - 0.3 sec) or short duration (< 0.1 sec). Long calls are typically clear bell-like sounds, while many of the moderate and short calls are harsher.

The different sounds of calls

The main sounds produced by fernbirds are given below. These descriptive titles must suffice until a further study of the calls can be carried out.

A. "Tcherp" type calls.

Territorial males, their mates, and fledged offspring use this call while foraging (Figure 17). It is of moderate volume and medium length, with constant pitch.

At other times, this sound is used in contact calls (Thorpe, 1961) given only by territorial males. Then it is of loud volume and long duration. In those variations having an "er" or "ee" pronunciation, the pitch remains constant until the "e" is reached, when the pitch rises sharply. With those variants having an "or" sound, the pitch descends at the "o"...
giving the call a slur (compare Figures 17 a and b).

Similar calls are given by South Island Fernbirds at the Totara River, Buller (pers. obs.).

B. "Tchip" type calls.

"Tchip" sounds are mainly abbreviated versions of "Tcherp". Typically they are abrupt, short calls, varying from soft to loud, and used by all except non-territorial birds.

Variations fall into three groups, (a) those uttered only by males; "Blut", "Bluck", "Took", (b) those typically used by females during duets; "Tchep", "Teort", "Tep", "Tet" (Figures 17, 19), and (c) those uttered by males, females and offspring; "Tchic", "Tchap", "Toup", "Tchop".

Moon (1967) and M'Lean (1906) describe some calls of the North Island Fernbird at "Zrup" and "Tu-\'t" respectively. Moon's "Zrup" call appears to correspond to male "Blut" type calls, and M'Lean's "Tu-\'t" similar to male and female duet calls. South Island (pers. obs.), Codfish (Blackburn, 1967) and Stewart Island Fernbirds (Wildlife Service, Dept of Internal Affairs, recording 1970) utter "Tchip" type calls that sound identical with those of Snares Fernbirds, variations (b) and (c).

C. "Tee-oo" type calls.

"Tee-oo" calls are produced only by territorial males. They are given at soft to loud volume, and short to long duration.

Variations include "Tee-touw", "Blee-touw", "Ee-ouw", "Thwee-ouw", "Tou-ee". Sometimes only the first part of the call is given (e.g. Figure 20). As with other calls, the "ee" sounds corresponds to high pitch, and "oo" sounds to falling or lower pitch. As the form of the call shown in Figure 20 is penetrative, of long duration, and "pure" it is well suited for location when used as a contact call. M'Lean (1906) describes calls of "Tu-ult" and "Ki-po-ki" for North Island fernbirds; the former appears to correspond to "Tou-ee" while the latter sounds similar to a male-female duet of "Too-ee-tet".

There is no record of these calls from other forms of B. punctata.
D. "U-tick" type calls.

This is regarded as the "traditional" fernbird call, as many authors (Potts, 1869; Buller, 1882; M'Lean, 1906; Soper, 1965) call B. punctata the "U-tick". "U-tick" calls are given by males alone, or male or female in duet. In duet the female usually calls the "tick" section (actually, any type 2b calls), although on occasions her response comes after the male has called "U-tick". Most often this call is heard at medium speed and moderate to loud volume, although at border disputes the calls become abrupt.

Variations of this call include; "Dtew-tchick", "Whudd-tick", and "Whuddit" (Figure 21). I have heard these variations from both Snares and South Island Fernbirds.

Other authors (cited by Oliver, 1955; Oliver, 1968) record this call for all forms of B. punctata.

E. "Tching" type calls.

Only males give "Tching" type calls, which are always at loud volume and of long duration. Each call has a very distinct, clear, metallic sound with slightly rising pitch in the "ing" variation. The other form given is "Tcheong" where pitch rises up to "e", and levels out or falls on the "ong". Blackburn (1967) originally recorded this call for Codfish Fernbirds, and it is also produced by South Island Fernbirds (pers. obs.).

F. Scream type calls.

These are uttered by fernbirds over 19 days old (i.e. nearly fully fledged) when captured by the author, or (in one observation) when a female was clawed and grasped by a territorial male during a border dispute.

The different uses of calls

Calls of fernbirds are used for at least eight purposes. The categories used here are adopted from Thorpe (1961).

A. Foraging Calls.

Foraging birds are generally silent, even when members of a pair are close together. However, when a bird gives foraging calls there is no change in its relaxed foraging behaviour and calls are soft to moderate, and of medium duration.
The role of foraging calls is not clear, for the calls are not apparently directed at any object. They may indicate the caller's position to its mate but this does not appear to be their primary function, as calling often continues when the mate replies. Also, mated birds may give foraging calls when they are only a few metres apart and still visible to each other.

Foraging calls may possibly inform nearby birds that the territory is still occupied, but lack of loud calls means that territory advertisement is not their main function either.

As foraging calls are given only when a bird slowly hops about (if it is actively seeking food it would be running about) looking amongst debris, or when perched, resting with relaxed feathers and in a hunched posture, it appears that the callers have a low response to environmental stimuli.

Calls used during foraging are types 1 to 4.

B. Contact Calls.

These are given when a male is seeking his mate, for he stops his previous activity, stands semi-upright and raises his head during calling. His plumage usually remains relaxed and at the end of each call his head droops back towards his shoulders. Between calls the male often continues to forage, but sometimes he hops up into the branches, or on top of a Poa tussock, to call from there. All calls are loud and long, predominantly of types 1, 3 and 5 which are penetrative (see Figure 20). These types of calls are distinct, clear-cut, and thereby more suited for long distance signals, than the less distinct disyllabic type 4 calls.

Contact calling usually stops either as soon as the mate replies, or when both birds are together after one has joined the other. Less often the male continues calling for a minute after his responding mate has joined him.

C. "Pleasure" Calls.

Thorpe (1961:17) regarded pleasure calls as being characteristic of young birds. He cites Collias and Joos (1953) who describe this in the domestic chicken. Its "pleasure" calling consists of a frequently repeated simple musical figure. Chicks give these notes "generally in the presence of other chicks and in the absence of obviously harmful or alarming stimuli" (Thorpe, op. cit.:18). From
these details, the "Tsip", "Tsap" and "Tschip" calls of fledgling fernbirds can be classified as "pleasure" calls. Although "Tsip" calls sound soft, they are audible, though not conspicuous, up to 40 m over open ground. Fledglings give "pleasure" calls when stationary or mobile sometimes for periods in excess of 30 minutes.

Although calling fledglings are often close together they may ignore each other. "Pleasure" calls may inform the parents of their offspring's whereabouts for the young appear to give "pleasure" calls less often when in the company of an adult. Fledglings use "pleasure" calls progressively less often as they grow older, and by the time they reach independence "pleasure" calling is rarely heard.

D. Aggressive Calls.

Male and female territorial birds use aggressive calls mainly in conjunction with the Territorial Defense Display. In addition, both birds sometimes give low or moderate intensity aggressive calls during nest duty changes. The characteristic feature of aggressive calls is a series of rapid clicks (Figure 18), subsequently named "chittering". Chittering is interspersed with loud, short type 1 to 4 calls from the male, and only type 2 replies from his mate. The intensity of the aggressive drive is indicated by the frequency of chittering for fighting occurs most commonly during highest intensity chittering, but is rare at low intensity chittering. Thus aggressive calling, combined with the Territorial Defense Display, appear to be substitutes for fighting, for only at their highest intensities does fighting occur.

E. Escape Calls.

All classes of fernbird (male, female, offspring and non-territorial) give escape calls when disturbed while trespassing. Escape calls are associated with direct flight, or sometimes with flight intention movements present in the submissive display. The fleeing bird calls with loud, sharp "Tcheep"s that are repeated rapidly and at highest frequency with highest intensity submissive displaying.

F. Distress Calls.

Distress calls uttered as screams are given by birds
when they are captured, and often bring the mate or parents quickly upon the scene. This call appears to elicit a mobbing response in the presence of a predator.

G. Alarm Calls.

Alarm calls are produced by territorial birds when eggs break during incubation, at hatching, or when the offspring are threatened. Parental alarm is indicated by the uneven bursts of chittering and the loud, short "Tcheep"s while the adults appear to be uncertain whether to approach or flee. They tend to approach the source of disturbance as close as protective cover allows.

H. Territorial Advertising Calls.

Territorial Advertising Calls are characteristically long, moderately loud to loud calls of types 1, 3 and 4. Only males give Territorial Advertising Calls. The caller stands in a prominent place and raises his head during calling. After each call his head is slightly drawn into the shoulders and his bill and head tilted downwards. For the first few minutes of calling the female sometimes responds in duet, but afterwards responds infrequently. Her mate often continues calling for well over half an hour. The calling bird does not appear to be directing his vocalizations at any physical object, for during each address he tilts his head skywards, and between calls gazes at the ground below him.

These calls are heard throughout the day but most commonly at between 0600-0800 hr and 1800-2000 hr, and mainly from birds without nestlings or fledglings. The role of Territorial Advertising Calls is discussed more fully in The main properties of calls, Section 3.

The main properties of calls

The great advantage of using calls as signals is that "sound carries far and fast and readily by-passes obstacles, there is a great spectrum of frequency and intensity available for use, it is extremely economical to produce, and - since sounds vanish as quickly as they are produced - the items of information do not accumulate so as to prevent the sending of further messages" (Thorpe, 1961).

Vocal communication in the Snares Fernbird has the
following features.

1) Most calls are readily localizable.

2) Calls have variable carrying power.
   (See the Introduction to Vocal Communication).

3) Calls assist in territorial maintenance.
   Calls appear to be most important in delineating and
   maintaining territories and territorial males are the most
   vocal class. The importance of a territory owner's call in
   keeping his territory is indicated by an episode involving
   Bird 32. In the 1971-72 season he held the "Huts territory"
   when we arrived in late December, and his Territorial
   Advertising Calls were often heard from the Hebe beside the
   upper hut. On 13 January 1972 he disappeared and was replaced
   by a new male. Many border disputes then ensued between the
   new male and neighbouring males. Bird 32 was later seldom
   seen and remained silent. However, the new male was suddenly
   replaced by Bird 32 on 28 January 1972 and again territorial
   disputes followed for two to three days. Then territorial
   interactions decreased, indicating that stability between
   neighbours had returned.

   Similarly, Armstrong (1963) reported that with many
   passerines, a territory that becomes silent through accident
   to the owner is soon invaded. This indicates the importance
   of the territory owner's vocalizations in keeping a territory
   inviolate.

   Advertising territorial fernbirds are conspicuous and
   their calls give plenty of clues for location. Their calls
   discourage the entry, or speed the departure, of intruders,
   often without any other form of aggressive display, and attack
   is not necessary (see Figure 13).

   Thus, the information conveyed by a male calling
   conspicuously appears to be that the caller is (i) a fernbird,
   (ii) a male, (iii) within his territory, (iv) in a particular
   place, and (v) ready to drive off intruders. It is likely
   that information on the identity of the caller is also
   transmitted - see Section 6 below.

4) Calls indicate the status of the caller.

   Only territorial males give Territorial Advertising
   Calls; females and offspring reply to male calls and give
   foraging calls. Non-territorial birds remain silent, as they
have no territory and no pair-bond to maintain; any conspicuous behaviour on their part invites attack from the territory owners.

5) Calls assist pair-bond maintenance in the breeding cycle. It is likely that calls, in the form of antiphonal duetting, contribute greatly to maintenance of the pair-bond. Duetting has been defined as when "both members of a pair sing, either more or less together, or antiphonally, each making a distinct contribution to the duet" (Hooker and Hooker, 1969). Antiphonal duetting is a specialized form of duetting in which male and female use different notes and sing alternately, often with marked precision in timing.

The following conclusions can be made on duetting of the Snares Fernbird (and probably apply also to other forms of *B. punctata*.)

(i) In duetting each individual has his own part which is not exchanged during the duet.

(ii) The contribution is sex-specific; males always call first in my experience.

(iii) In any duet pattern timing varies with (a) the distance between duetting birds, and (b) the current activity of the responding bird.

(iv) Duetting occurs regularly between adults of an established pair whilst on their territory. Duetting between adults and their fledglings seldom occurs. No other form of duetting has been heard.

(v) Although duetting does not occur between members of adjacent territories, sometimes when aggressive displays at border disputes become intense, timing falls out of phase and both females respond to the calls of each male. During these times females exhibit conflict behaviour and adopt submissive displays rather than aggressive displays.

(vi) In many cases there seems to be no signal, other than the production of the first note, for initiating a duet sequence. Frequently the male is not answered for several calls, though just as often the first note is answered with nearly perfect timing irrespective of the time lapse since the previous bout of duetting.

(vii) Any disturbance increases vocal activity. The rate of
duetting increases when eggs are broken, or hatching, and during border disputes. Duetting is also common while a pair build their nest and probably serves to co-ordinate their activities.

(viii) Either bird can stop a duet by not calling, but no signal for stopping was detected. The male sometimes continues to call long after the female ceases replying, or she may answer his calls only sporadically.

(ix) The number of consecutive duets in a sequence varies considerably. Monotonous performances lasting over 30 minutes occur, at a rate of one duet each one to five seconds. The longer duet sequences occur most often as evening approaches, or in response to played back recordings of fernbird calls.

These observations almost exactly agree with those described for the tropical bou-bou shrike, *Lanaru aethiopicus*, the black headed gonolek, *L. erythrogaster* and the gonolek, *L. barbarus* by Hooker and Hooker (1969).

Similarities between fernbirds and tropical shrikes (as described by Hooker and Hooker, op. cit.) extend beyond their duetting behaviour, and the two groups provide a good example of convergent evolution. For example in both birds:-

(a) Evidence suggests they pair for life and hold the same territories for long periods.

(b) Duetting continues throughout the year though it increases when the birds nest as the need to co-ordinate activities is then greater.

(c) These birds characteristically inhabit dense vegetation and their behaviour is cryptic.

(d) During territorial disputes the birds become conspicuous, both visually and vocally.

(e) The precision of timing of duets indicates that these birds have well developed auditory and vocal reactions (e.g. Figure 22 a).

(f) These birds frequently duet from extremely dense foliage where members of a pair are out of visual contact. Therefore, in some cases it would not be possible for visual clues to assist the response of the second caller.

(g) It seems likely that the more rapid response of birds
close enough to be in visual contact is a combination of auditory and visual signals. The cue would be intention movements made by the initiator as his neck swells and head rises vertically during calling. In the tropical shrikes evidence that the answering bird responds to the intention movements, and not to the sound of the first note was confirmed on several occasions when it made intention movements before the first bird had produced a sound. This could account for differences in timing of duets (of shrikes and fernbirds) as well as the time taken for the initiator's signal to reach its mate.

(h) Duetting appears to function in maintaining the pair bond between family groups in dense vegetation, and in joint aggressive displays during territorial disputes. The manner in which duetting can contribute to maintenance of the pair bond is apparent from the above information. Thorpe and North (1965) concluded for tropical shrikes that in order to develop and maintain the adult duet pattern, each contributor must have learned its partner's phase in relation to its own. The male is the bird which answers with the correct contribution and the appropriate time interval following the preceding contribution.

6) Calls provided individual recognition marks.

In many avian species, individual vocalizations are recognized by other members of that species. Harris and Lemon (1972) list 10 passerine species in which dialects have been shown to exist; where individuals from the same locality share similar vocal patterns, and where these patterns are not shared with individuals of the same species from other localities.

Falls (1969) showed that territorial male White-throated Sparrows (Zonotrichia albicollis) can recognize each other's songs, but they respond more strongly to songs of strangers than to those of neighbours. The response is not only at a higher rate but it also lasts longer. In 1970-71, when I began calling to fernbirds in my study area, territorial males reacted very strongly, and my calls often initiated long, high intensity border disputes between neighbours. Within a week or two the strength and length of
aggressive responses to my calls decreased. This was not due to a decline in the motivation to defend their territories for as soon as I started calling outside the main study area to "strange" birds there was again an extremely vigorous, long response. Male Snares Fernbirds reacted to played back recordings of South Island Fernbird males as if the calls were uttered by strange Snares males. Initially the Snares males to whom the recordings were regularly played reacted most aggressively, but in a few days their aggressive response to such reproduced calls declined. Thus it is likely that Snares Fernbirds can recognize other individual's calls. Established birds would be of little threat to each other as they recognize each other's claims, whilst strange birds would be a challenge to the status quo.

There was no obvious decline in the response of female Snares Fernbirds to strangers' calls (even of different subspecies) indicating their discrimination of individual's calls is probably low. However, as her mate would be the only male calling in the territory, any male-type calls must come from him. Also, during some border disputes females lose synchrony in duetting and exhibit conflict behaviour showing they are not certain which male is calling, although their respective mates may be visible to them.

7) Calls communicate the motivation of the sender.

Aggressive motivation is indicated by Territorial Defense Calls, alarm by alarm calls, and so on.

8) Calls function as a specific recognition mark.

The Snares Fernbird responds only to calls of other fernbirds, or human imitations of fernbird calls in my experience. However, at the subspecific level it is unlikely that fernbirds can distinguish vocalizations of other forms of B. punctata per se for the reasons described above in 6). This lack of differentiation has probably arisen because all populations of B. punctata are well separated and it would be highly improbable that at present there is any interchange of genes between any two subspecifically distinct populations. Due to this condition, there would be no selective advantage for subspecific distinctness and this could allow for greater freedom in individual differences.

Lack and Southern (1949) found that the song of the
Blue Tit is fairly stereotyped and provided good specific character in Britain where it has to co-exist with four or five members of the same genus. But on Tenerife, where it is the only *Parus* species, it has a wide variety of utterances. It was as if, with specific distinctness no longer required, individual distinctiveness had become valuable, or at least allowable. Marler and Boatman (1951) found a similar situation in regard to vocalizations in the goldcrest.

This concludes the account of the territorial biology of the Snares Fernbird.
CHAPTER 4

NEST BUILDING

INTRODUCTION

Nest building is considered under the categories of the nest site and its selection followed by a description of nest construction. A brief discussion of nests and nesting vegetation concludes this chapter.

NEST SITE SELECTION

I was able to observe the selection of only one nest site, viz. nest 20, 1970-71. On 16 January 1971, two days before building started, bird 25 and his mate were heard duetting from the potential nest site, in a clump of Carex trifida. Both birds moved in and out of the Carex at short intervals, chittering sporadically. They occasionally picked up Poa astonii leaves from nearby, but dropped them short of the potential nest site. No other material was gathered.

I have no further knowledge of the pre-constructional history of this site. Two days later, on 18 January 1971, the skeleton of the nest base had been laid down and further construction followed rapidly.

NEST SITES

Fernbirds utilize a wide range of nest sites but apparently prefer to build in the fern Asplenium obtusatum; 34% of all nests located were found in the fronds of this plant (Table 5). Stead (1948) also noted this preference in his visit to the Snares. Another fern, Polystichum vestitum, of similar growth habit to that of A. obtusatum, was less popular (containing only 8% of all nests) even though it was at least twice as abundant in the study area. Both ferns
Table 5: NESTING SITES OF THE SNARES FERNBIRD

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Nest situation in vegetation</th>
<th>percent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>In</td>
<td>Under</td>
</tr>
<tr>
<td></td>
<td>base</td>
<td>head</td>
</tr>
<tr>
<td>A. Ferns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asplenium obtusatum</td>
<td>17</td>
<td>-</td>
</tr>
<tr>
<td>Polystichum vestitum</td>
<td>4</td>
<td>-</td>
</tr>
<tr>
<td>Blechnum durum</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>B. Tussocks* and Sedges+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carex trifida*</td>
<td>9</td>
<td>-</td>
</tr>
<tr>
<td>Poa tennantiana*</td>
<td>-</td>
<td>9</td>
</tr>
<tr>
<td>Poa astonii*</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>C. Other sites</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hollow Olearia trunks</td>
<td>2</td>
<td>-</td>
</tr>
</tbody>
</table>

often grew in dense thickets with closely packed basal stems which provide strong foundations and protection from mechanical damage, e.g. the landing of shearwaters at late evening. The other fern occurring at the Snares, Blechnum durum, was less plentiful and, because of its low growth habit (up to 0.4 m; cf. Asplenium up to 1.25 m and Polystichum 2.0 m plus) and thin stems, it did not provide as much protection as the other fern species.

All three ferns occupied similar niches on the forest floor and were predominantly found around the east coast from Skua Point to Ho Ho Bay. Only Asplenium occurred outside the forest, as small patches in Poa meadows and on cliff areas. However, some birds appeared to prefer Polystichum for nest sites. Five nests were built in this fern even though suitable Asplenium ferns were available in the respective
Tussocks and sedges were the next most popular nesting sites; *Poa tennantiana* provided 24% of the nesting sites, *Carex trifida* 18%, and *Poa astonii* 12%. These three species grew in forest clearings or in bogs, but only *P. astonii* and *P. tennantiana* occurred in coastal meadows. These plants were similar in that they provided dense cover and generally good support for the nests. Protection from wind and rain was adequate in well developed specimens. However, six nests in small *P. tennantiana* (0.5 m high and 0.25 m diameter) were poorly protected and clearly visible 5 m away, once the nest sites were known.

Only two of the nests found (4%) were built in hollows of rotten trees. Both were completely protected from the elements and animal disturbance. The use of hollow trees for nesting sites was probably quite frequent deeper in the forest, for here there were extensive areas which were devoid of other forms of nesting vegetation and only *Olearia lyallii* was available. Birds nesting in these regions must use either dead *Olearia* leaves, bark and twigs, with Sooty Shearwater feathers, or *Poa astonii* to line their nests. If such birds used *Poa astonii*, trips of several hundred metres would be necessary and they would have to know a large area intimately in order to find the nearest of these tussocks. Their fastest method of gathering *Poa* would be to fly over the forest on calm days and thereby avoid detection by neighbouring territorial birds. This is feasible as fernbirds were seen taking flights of over 150 m long, maintaining a direct line of travel at a constant height without apparent strain.

One bird was seen to cut across 120 m of Comma Bay. Two other birds carrying tussock leaves in their bills flew 50 m across *Poa* meadows and up to 100 m over the forest before fluttering down through breaks in the *Olearia* canopy. Stead (1948) also saw fernbirds flying with nest building material for "over 100 yards". In contrast, fernbirds that I disturbed while walking through *Poa* meadows flew only a few metres before dropping back into cover.

Fernbird nests are generally built within half a metre of the ground (Table 6), although exceptionally three out of the 50 nests found were between 1 and 2 m above the ground.
Table 6: NEST MEASUREMENTS*

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean (mm)</th>
<th>Variance</th>
<th>Range (mm)</th>
<th>No. in sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height above ground</td>
<td>330</td>
<td>1810.1</td>
<td>0 - 2000</td>
<td>50</td>
</tr>
<tr>
<td>Internal diameter</td>
<td>69</td>
<td>29.4</td>
<td>60 - 85</td>
<td>30</td>
</tr>
<tr>
<td>Internal depth</td>
<td>66</td>
<td>102.8</td>
<td>40 - 90</td>
<td>30</td>
</tr>
<tr>
<td>Wall thickness</td>
<td>26</td>
<td>52.8</td>
<td>10 - 40</td>
<td>30</td>
</tr>
</tbody>
</table>

* Details of measurements in Figure 23. Raw data in Appendix 2.

These latter three nests were in Asplenium clumps growing on horizontal wind toppled Olearia trunks, situated on sloping ground. Nest measurements (Table 6) closely agree with those recorded by Stead (1948), i.e. "the cup measures 55 m.m. in inside diameter, by 65 m.m. deep, the walls being from one to three c.m. thick".

NEST CONSTRUCTION

Fernbirds use a variety of materials and methods for building their nests. Nest form depends mainly on the type and exposure of the vegetation (see Appendix 2), as well as the individuals building the nest. In this account, the terms "nest", "nest base" or "base", "lining" and "nest bowl" are defined as follows. The "nest" refers to the complete structure built by the birds for housing eggs; the "nest base" is that external part which lies closest to the ground, the "lining" refers to the material which forms the internal surface of the nest, and the "bowl" is the area enclosed by the internal surface of the nest.

Methods of Construction

The nest's base was built of dead dry coarse fibrous
material, e.g. Poa tennantiana, Carex trifida and fern rootlets, loosely interwoven into a saucer-shaped structure. The open weave retarded seepage of moisture from the surrounding vegetation into the Poa astonii bowl, and may have helped the nest bowl dry out after rainy spells.

The P. astonii bowl was then built on top of the porous base. Although a little of this grass was woven into the base, the nest bowl was not tied to the base but sat snugly on it. The curved bottom of the bowl was laid down by interweaving of grass strands placed at right angles. Strands often exceed 0.3 m, and usually only one or two were brought each trip. The circular walls were then built of P. astonii leaves arranged latitudinally. The long, needle-like leaves of this tussock made it a most suitable material for weaving the bowl. The leaves were laced into a rigid, closely packed structure that retained its shape and was quite weatherproof.

In six nests, building of the walls followed rapidly on that done to the bottom of the bowl. When the walls were completed, feathers and more P. astonii were added to finish the bottom of the nest bowl. The feathers were lightly fixed to the nest by the bases of their shafts and were easily displaced. In some nests the largest proportion of the nest material consisted of Southern Skua (Catharacta skua lonnbergi) feathers about 80 to 100 mm long, neatly arranged so that they pushed against the nest walls and were not fixed in any other fashion. In these nests, the eggs or young were completely hidden when the adult left the nest.

Most nests contained 30 to 40 feathers although three nests had only five to 10 feathers lining the nest bowl. Sooty Shearwater feathers most commonly lined nests, but some nests were lined with those of Antarctic Tern (Sterna vittata), Red-billed Gull (Larus novaehollandiae) and Mottled Petrel (Pterodroma inexpectata). This lining provided insulation when the adults were absent. During wet spells, the waterproof feathers also protected the eggs or young from chilling. Nests placed in even the thickest vegetation became quite damp after a few hours of heavy rain and their contents cooled more rapidly if adults and feather lining were not present.

During construction, an adult fernbird stood on the edge of the nest and pushed one end of a P. astonii strand
into the nest's framework, with its bill. Then the bird sat
down and shuffled around, pushing the strand into the walls
with its bill. Pressure from the breast and fluffed up flank
feathers consolidated the structure. Strands of grass
displaced while shuffling about were pushed back into place
until all loose ends had been tucked in.

Completed nests were neatly woven and had smooth
interiors. They were strong and unless built around the
supporting vegetation stems, retained their shape after being
lifted out of the vegetation.

Nests built in ferns were often not hemispherical,
especially where the basal areas of fern fronds could not be
pushed aside. In such instances, *P. astonii* was bent sharply
around the resistant fronds, giving an oval or squared nest.

Fernbirds probably completed nests within three days
when not interrupted by rain. Nest building activities were
greatest in fine weather following long periods of rain.
However, after prolonged periods of fine weather building
became sporadic, occurring most commonly between 0500-0900 hrs
and 1700-2000 hrs. Nest making activity continued in dull
weather during dry spells, but was infrequent or non-existent
on dull days between rainfalls.

Unfavourable weather extended the construction period
for upwards of two weeks, e.g. Nest 20, 1970-71 season. Here
site selection occurred about 16 January 1971, and building
started within two days. The nest was finished on 4 February
1971 (20 days later) and during this time there were five rain-
free days. Unfavourable weather sometimes continued for
several weeks on end, and during such periods nest fabrication
was inhibited. Five other nests with known construction times
took five to 10 days for completion. Two of those (Nest 3 and
6, 1970-71) were built in two to three rain-free days. The
time taken in nest construction appeared to have little effect
on breeding success. Two nestlings were fledged from Nest 20,
1970-71, while the eggs laid in Nests 3 and 6, 1970-71 were
infrequently incubated.

Members of a pair worked together while making the nest.
Flights of 30 to 40 m to and from the nest site and duetting
were common during active nest building. During two hours
observation of construction activity at Nest 22, 1970-71, each
Figure 23: Nests: measurements and types.
TYPE 3 NEST

SUPPORTING FERN

BASE OF FIBROUS MATERIAL

TYPE 2D NEST

AREA BUILT BY BIRDS

TYPE 4 NEST
Figure 24: Views of type 2a and 2b nests.

The *Poa tennentiana* containing the type 2a nest has had part of the mantle cut away to show the underlying base. Also a considerable amount of grass has been trimmed from the head of the tussock to reveal the nest, which was formerly well concealed.

Note the simple construction of the type 2b nest. The woven grass collar forming part of the nest walls has been detached from the tussock to show the base (B). The base is a hollow excavated in the side of the tussock and lined with feathers.
bird spent mainly 20 to 60 seconds at the nest per visit, although on three occasions, two or three minutes were spent getting material bedded in satisfactorily. Intervals between visits ranged from 20 seconds to nine minutes, but two minute intervals were most common. As nesting materials were placed low intensity chittering calls were given indicating the birds were excited. Building stopped abruptly when a short rain squall passed over, and did not resume until a few hours later.

Types of nest constructed

I classified the nests as follows:-

A. Type 1 Nests.

These are characteristically built into hollow Olearia trunks. The nest base consists of a plug of dead Poa astonii and P. tennantiana packed together without any semblance of weaving. All the nest support is provided by the cylindrical hollow trunk. In Nest 13, 1970-71 this plug was about 160 mm long and 80 mm in diameter. Dead Senecio inflorescences, dead Olearia leaf fragments and over 100 Sooty Shearwater feathers made up the remainder of this nest. The top of this wad was lined with a layer of about 60 Sooty Shearwater feathers, 25 mm thick and 70 mm in diameter (Figure 23).

B. Type 2 Nests.

This type is ingeniously made using a minimum amount of materials and effort to produce a strong and well concealed nest. Two forms of this nest are produced.

Form A: A simple scoop is made in the head of a Poa tennantiana or P. astonii tussock which may be lined with dead woven P. tennantiana leaves plus a few feathers. Inside the scoop, varying amounts of P. astonii are made up into the typical neat hemispherical bowl containing a few (10) to many (50) feathers. For some type 2A nests the inner nest lining of P. astonii and feathers is placed at the bottom of a hollow in the nesting tussock so that the walls of the nest are formed from the head of the tussock (Figures 23 and 24).

Form B: The outer edge of a simple scoop on the side of the basal region of P. tennantiana or P. astonii is shored up with a semicylindrical wall of woven dry Poa. Nests built in P. tennantiana have an outer lining of P. tennantiana but
those in P. astonii tussocks are built entirely of P. astonii. In some nests the inner, hemispherical bowl is made of very little P. astonii but the simple hollow is lined with large numbers of feathers. At the other extreme, some type 2B nests have well built P. astonii structures with walls some 30 mm thick, e.g. Nest 13, 1971-72.

In type 2 nests the nesting vegetation is used as the foundation and moulded into a hollow that requires only little modification to produce good nests. One such example is Nest 22, 1971-72, on Seal Point. This nest was situated between two P. astonii tussocks, one growing immediately above the other so that its leaves drooped over the lower. The nest was placed against a rock wall and so well concealed that it was found only after a five minute's search around the two tussocks.

Type 2B nests are slightly more sheltered than type 2A, as type 2B's are under the mantle of dead grass which covers the bases of Poa tussocks (Figure 24). Type 2A nests are open to rain falling from straight above, although most rain in exposed areas is driven obliquely by strong winds.

C. Type 3 Nests.

There are three parts to this kind of nest - a saucer-shaped base of coarse fibrous materials, a hemispherical P. astonii nest bowl and a feather lining. These nests are all set in the basal regions of ferns where there is a firm foundation. The basal saucer varies from 10 to 20 mm in thickness, while the P. astonii hemisphere ranges from less than 10 mm thick up to 25 mm thick.

D. Type 4 Nests.

These are the most elaborately constructed nests. They have thick walls (up to 30 mm thick) and are built almost entirely of P. astonii. There are few, if any, coarse materials such as dry, dead P. tennantiana or Carex trifida used to construct a saucer-shaped base. Some of these nests have features that are not usually present in any other types of nests. These features are -

Feature A, Hoods: These are built up as a high wall on one side of the nest (Figure 23). Hoods range from 100 to 140 mm from the internal bottom of the nest to the top of the
hood, compared to normal walls which are about 60 to 70 mm. Nests with hoods are orientated so that the hooded side faces the prevailing westerly winds (pers. obs. and Guthrie Smith, 1936).

Feature B, Ring-shaped bases: A base of P. astonii is built to form a ring of approximately 100 mm external diameter and 50 mm internal diameter. These bases are made where drainage is poor (as in the bottom of Carex trifida clumps growing in boggy areas) and when little support is provided by the nesting vegetation. The hemispherical bowl, with or without a hood, is built on this skilfully woven base and held about 20 mm above the ground.

Discussion of nest types

Although nests of fernbirds are divisible into these four main types some overlap occurs, e.g. Nests 11 and 13, 1971-72 are typical of type 2 nests built into Poa tussocks, but they also have hoods constructed on one half of the nest.

Each type of nest is found in a certain form of vegetation (Appendix 2). Type 1 nest sites provide maximum support and only minimum skill is needed in construction. Progressively less support is provided by the nest site as the number of the nest type increases. Nests in Poa need only to be lined; those in ferns (except for the one in Blechnum durum) are supported by rods but need material to fill in the areas between the reinforcing stems. Finally, nests found in Carex and one in Blechnum have to be mainly self-supporting as the nesting vegetation provides concealment but little mechanical support. Type 4B nests occur in relatively open nesting vegetation, where the nest bowl has to be raised above the damp ground.
Figure 25: Distribution of egg laying, hatching and fledging of young.

Open bars show first clutches, stippled areas represent replacement clutches, and striped areas depict second clutches.
CHAPTER 5

EGG STAGE

INTRODUCTION

In this chapter, descriptions of egg shape, laying dates, clutch sizes and incubation are given.

EGG-LAYING DATES

Laying dates were recorded at only 14 (28%) nests due to the difficulty of finding nests before the eggs had been laid. However, from known incubation periods (see Incubation section, end of this chapter) and the ability to determine ages of nestlings (section on the Development of nestlings Chapter 6), it was possible to construct histograms of laying dates (Figure 25). Nests found with one or two nestlings are presumed to have contained two-egg clutches, rather than three-egg clutches. In 1970-71, laying was spread over 16 weeks, from the first week of November to the third week of February. The number of eggs laid per week reached a maximum during the fifth week (29 November - 5 December 1970) and slowly declined thereafter. Fifty-five percent of the eggs were laid by the end of the second week of December 1970, six weeks after laying began.

In contrast, egg laying in the 1971-72 season was over a period of only 13 weeks. Laying began suddenly in the second and third weeks of November, declined, and then peaked in the third week of December, and again in the second week in January. After this, the laying rate rapidly declined. Fifty-three percent of eggs were laid by the first week of January, i.e. two weeks later than in the preceding season, and eight weeks after laying began.

It is not likely that eggs were laid before November in either season. Although I did not arrive on the Snares until
18 November 1970, the absence of fledglings or juveniles suggests that laying had not occurred earlier than stated above. Similarly, during the last week of December 1971, (the date of arrival for the second season) only one-week-old fledglings were found. Extensive searches through the vegetation revealed no signs of deserted nests containing rotten eggs.

However, in the first week of November 1972, D.S. Horning saw only one one-week-old fledgling on the west coast of the Main Island. No more fledglings were seen until early December 1972. This record of early breeding, after an extended period of settled weather, may be unusual.

Dunnet (1955) and Gibb (1950), from their work on Starlings *Sturnus vulgaris* and Great and Blue Tits *Parus major* and *P. caeruleus* respectively, stress the phenomenon of simultaneous laying of first clutches by different females and, with the tits, synchrony between the species. Laying in these three passerines is timed so that the maximum number of nests containing young are present during the period of maximum abundance of nestling foods. Starlings laid their first clutches within a 10 day period, Great and Blue Tits produced eggs over a three week period, whilst fernbird first clutches were laid during an eight to 11 week period. The breeding timetable of the Snares Fernbird, however, does not demonstrate such synchronous laying; in fact egg production in both seasons was spread over a considerable period (13 to 16 weeks). This indicates that nestling foods were readily available throughout the two breeding seasons. Similarly, Coleman (1972) found that Starlings in Canterbury, New Zealand, produced their first clutches over a period of one to two months for three consecutive breeding seasons. Available nesting sites, not food, were a limiting factor in their breeding.

**TIME OF EGG-LAYING**

All occupied nests were checked daily at 0800 - 1000 hrs, and 1900 - 2100 hrs. In addition, nests found before egg-laying were checked every two or three hours of daylight to
Table 7: TIME OF DAY EGGS WERE LAID

<table>
<thead>
<tr>
<th>Time</th>
<th>No. eggs laid</th>
</tr>
</thead>
<tbody>
<tr>
<td>pre 0800</td>
<td>2</td>
</tr>
<tr>
<td>pre 0900</td>
<td>8</td>
</tr>
<tr>
<td>pre 1000</td>
<td>5 (2)</td>
</tr>
<tr>
<td>pre 1100</td>
<td>1 (1)</td>
</tr>
<tr>
<td>post 1100</td>
<td>4 (4; 1440-1550; 1400-1550; 1205-1405; - 1700-1830).</td>
</tr>
</tbody>
</table>

Brackets around figures indicate that time of egg laying was known within the hour, e.g. record 5 (2) indicated five eggs were laid sometime before 1000 hr, and two of these between 0900 and 1000 hrs.

determine more precisely when eggs were laid. Table 7 shows that most eggs (N = 15, or 75%) were laid before 1000 hr and 50% (N = 10) before 0900 hrs. Twenty percent of the eggs were laid in the afternoon, with the latest egg being produced probably a few minutes before 1830 hr, when it was found, damp and sticky.

Intervals between the laying of eggs varied from one to three days. In 10 clutches, eggs were laid at daily intervals. There was a two day interval between laying of first and second eggs of one clutch, and a three day interval in another clutch. These two clutches were not incubated and the nest owners made infrequent visits to roost.

Some birds varied their time of laying, e.g. at Nest 2, 1971-72, the first egg was laid just before 1830 hr and the second was produced before 0940 hr the following day.

INTERVAL BETWEEN LAYING OF FIRST, REPLACEMENT AND SECOND CLUTCHES

A first clutch is defined as the first clutch produced by a pair of birds in that breeding season; a replacement clutch is that laid after the total failure of a first clutch; while a second clutch is that produced after the young have fledged from the first clutch.
Laying of replacement clutches occurred from five to 43 days after desertion of the first clutch (Table 8). There was no apparent relationship between the period that the birds attended to the first clutch before failure, and the subsequent interval before the replacement clutch (if any) was laid. For instance, on record 5 (Table 8), a replacement clutch was laid 43 days after the loss of the first, which was attended to for approximately 28 days. Nonetheless, in record 6 (first clutch lost after 36 days attendance) and record 4 (first clutch lost after 23 days attendance) replacement clutches had been laid 24 and 20 days later respectively. The time taken to lay replacement clutches probably depends greatly upon individual pairs, rather than on weather conditions, for records 4 and 6 extended over a similar time of the same season (and thus similar weather conditions) to record 5. Even in record 11 (where the East Colony 5 pair produced three clutches in 1970-71) the interval between loss of the first replacement clutch and the laying of the second replacement clutch was 15 days.

CLUTCH SIZES

Clutch sizes ranged from one to three eggs. Only one one-egg clutch was found, and after this egg was laid the nest was deserted. Eighteen two-egg clutches were found, in 14 of which it is known that only two eggs were laid. The other four nests were not found until all the eggs had been laid, but as they contained typical first and second eggs (see Egg Colour and Dimensions) it is assumed that no third eggs had been laid and subsequently lost. Thirteen three-egg clutches were found.

Only nests found with eggs were used to determine average clutch size. Nests with nestlings only could have suffered loss of eggs and even nestlings before their discovery.

Thus for 32 clutches of known size 3.2% contained one egg, 56.3% contained two eggs and 40.5% contained three eggs. The fernbird is a determinate layer: new eggs are laid only as new clutches in new nests, but not to replace eggs lost by accident from one clutch.
Table 8: INTERVAL BETWEEN LAYING OF FIRST, REPLACEMENT AND SECOND CLUTCHES

<table>
<thead>
<tr>
<th>1st Clutch laid</th>
<th>1st Clutch deserted (days after clutch laid)</th>
<th>Replacement laid (days after loss of 1st)</th>
<th>2nd laid (days after 1st fledged)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) ♀. 27 Nov 1970</td>
<td>38</td>
<td>-</td>
<td>43 (8)</td>
</tr>
<tr>
<td>2) ♂. 14 Nov 1971</td>
<td>38</td>
<td>-</td>
<td>43 (8)</td>
</tr>
<tr>
<td>3) ♀. 22 Nov 1971</td>
<td>38</td>
<td>-</td>
<td>37 (2)</td>
</tr>
<tr>
<td>4) ♀. 16 Nov 1970</td>
<td>23</td>
<td>20</td>
<td>-</td>
</tr>
<tr>
<td>5) 25 Nov 1970</td>
<td>28</td>
<td>43</td>
<td>-</td>
</tr>
<tr>
<td>6) 9 Dec 1970</td>
<td>36</td>
<td>24</td>
<td>-</td>
</tr>
<tr>
<td>7) 8 Jan 1971</td>
<td>0</td>
<td>17</td>
<td>-</td>
</tr>
<tr>
<td>8) 12 Dec 1971</td>
<td>21</td>
<td>13</td>
<td>-</td>
</tr>
<tr>
<td>9) No data</td>
<td>No data</td>
<td>16</td>
<td>-</td>
</tr>
<tr>
<td>10) No data</td>
<td>No data</td>
<td>5</td>
<td>-</td>
</tr>
<tr>
<td>11) No data</td>
<td>20 Nov 1970</td>
<td>No data</td>
<td></td>
</tr>
</tbody>
</table>

Clutch lost 8 Jan 1971.
2nd Replacement laid
15 days later.

N.B. 

a) In records 9 and 10 the date of loss of the first clutch was known, but the laying date of the first clutch could not be estimated.

b) Figures in brackets for first three records indicate the time taken to relay after first brood had become independent.
VARIATION IN CLUTCH SIZE WITH SEASON

If the data from each season are considered separately, there is no well defined seasonal variation in the frequency of occurrence of various clutch sizes. When the two seasons' data are grouped, however, it may be seen that three-egg clutches were few in proportion to two-egg clutches in November, but in January were double the number of two-egg clutches (Table 9). The reason for this trend is not obvious, but if this fernbird is to raise the maximum number of young it can feed, one would expect larger clutches to be relatively more common than smaller clutches at the peak of laying, rather than later. Indeed, the numbers of two-egg clutches tended to follow the general laying pattern more closely than did three-egg clutches. The former were most numerous in December (the peak of egg laying) and then became progressively less common, whilst three-egg clutches were equally common in December and January. However, the sample size may be too small to exhibit clearly any real trends.

Table 9: VARIATION IN CLUTCH SIZE WITH SEASON

<table>
<thead>
<tr>
<th>Two Seasons' Data Summed</th>
<th>1 egg</th>
<th>2 egg</th>
<th>3 egg</th>
<th>Ratio of 2 egg : 3 egg clutches</th>
</tr>
</thead>
<tbody>
<tr>
<td>November</td>
<td>-</td>
<td>3</td>
<td>1</td>
<td>3 : 1</td>
</tr>
<tr>
<td>December</td>
<td>-</td>
<td>8</td>
<td>6</td>
<td>1.5 : 1</td>
</tr>
<tr>
<td>January</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>0.5 : 1</td>
</tr>
<tr>
<td>February</td>
<td>-</td>
<td>2</td>
<td>1</td>
<td>2 : 1</td>
</tr>
<tr>
<td>No. of Clutches</td>
<td>1</td>
<td>16</td>
<td>14</td>
<td></td>
</tr>
</tbody>
</table>
EGG COLOUR AND DIMENSIONS

Snares Fernbird eggs vary in colour with sequence of laying. Egg pigmentation becomes paler with successive eggs of the same clutch. Differences in pigmentation between first, second and third laid eggs are consistent and pronounced. Eggs have a background colour of pale mauvy pink although one infertile egg had an almost white background.

First laid eggs are heavily spotted with mauvy-brown to purple-brown flecks. Most flecks are minute, but on some eggs the majority are nearly 1 mm in diameter. Flecking is concentrated at the broader end of the egg, often forming a complete purple-brown band, although the polar region of the broad end is almost devoid of spots. Second laid eggs are similarly marked, but fleck pigmentation is paler and intermediate to first and third laid eggs. The pigment band at the broad end of the egg is also paler than in first laid eggs. Third laid eggs have very pale purple-brown flecks almost evenly distributed over the egg's surface.

In general appearance, eggs of the Snares Fernbird differ little from those of the other forms of *P. punctata* (M'Lean, 1906; Oliver, 1955; Blackburn, 1967), i.e. a light pink background covered with purple-brown or reddish-brown spots, often concentrated in a band about the broad end of the egg.

All 73 fernbird eggs examined were ovoid. The maximum length and breadth of these eggs were measured to the nearest 0.1 mm with steel vernier calipers. Mean egg length was 22.9 mm (Range = 20.7 - 24.2 mm; variance = 0.457) and mean egg breadth was 16.7 mm (Range = 15.8 - 17.9 mm; variance = 0.234). Data on all eggs measured is in Appendix 3.

Egg sizes and shape indices were compared by calculating values for length x breadth^2, and breadth/length x 100 respectively. I did not weigh or measure the volumetric displacement of any eggs. Mean egg sizes and shape indices do not vary significantly with laying sequence or clutch size (Tables 10 and 11).
Table 10: COMPARISON OF LENGTH (mm) X BREADTH$^2$ (mm) OF TWO AND THREE-EGG CLUTCHES

<table>
<thead>
<tr>
<th>Sequence</th>
<th>2-egg clutches</th>
<th></th>
<th>3-egg clutches</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Variance</td>
<td>Sample size</td>
<td>Mean</td>
</tr>
<tr>
<td>First egg</td>
<td>6535</td>
<td>202406</td>
<td>18</td>
<td>6370</td>
</tr>
<tr>
<td>Second egg</td>
<td>6454</td>
<td>255108</td>
<td>18</td>
<td>6368</td>
</tr>
<tr>
<td>Third egg</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6295</td>
</tr>
</tbody>
</table>

Significance tests:
First laid eggs of two and three-egg clutches, $ts = 0.9432$
Second laid eggs of two and three-egg clutches, $ts = 0.3621$
First and second laid eggs of three-egg clutches, $ts = 0.0074$
Second and third laid eggs of three-egg clutches, $ts = 0.2814$

There are no significant differences at the 5% level.

Table 11: COMPARISON OF EGG SHAPE INDICES (BREADTH/LENGTH X 100) OF TWO AND THREE-EGG CLUTCHES

<table>
<thead>
<tr>
<th>Sequence</th>
<th>2-egg clutches</th>
<th></th>
<th>3-egg clutches</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Variance</td>
<td>Sample size</td>
<td>Mean</td>
</tr>
<tr>
<td>First egg</td>
<td>73.4</td>
<td>4.788</td>
<td>18</td>
<td>72.8</td>
</tr>
<tr>
<td>Second egg</td>
<td>73.3</td>
<td>5.004</td>
<td>18</td>
<td>72.8</td>
</tr>
<tr>
<td>Third egg</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>72.7</td>
</tr>
</tbody>
</table>

Significance tests:
First laid eggs of two and three-egg clutches, $ts = 0.6905$
Second laid eggs of two and three-egg clutches, $ts = 0.4901$
First and second laid eggs of three-egg clutches, $ts = 0.000$
Second and third laid eggs of three-egg clutches, $ts = 0.0839$

There are no significant differences at the 5% level.
INCUBATION BEHAVIOUR

Incubation, or the application of heat to eggs by the brood patch, is carried out by both males and females. Both have well developed brood patches and share incubation equally (see Table 12).

Several factors influence incubation behaviour. Sometimes, while approaching the nest site, a bird ruffles its feathers in anticipation of settling on the eggs, indicating that sighting the nesting area can initiate the preliminary phases of incubation behaviour. An adult may also move hesitantly towards the nest as if uncertain whether to incubate or forage, and chitters in low intensity excitement. Factors influencing incubation include the arrival of the relieving mate and the prevailing weather conditions. The arrival of the mate generally decreases the sitter's motivation to incubate. It often leaves the nest as soon as the calls of its approaching mate are heard, or sits up alerted until its mate arrives at the nest. On occasions, the bird at the nest appears reluctant to move and its partner comes to and from the nest several times in rapid succession until the bird on duty leaves. During these movements the pair chitter and duet. Weather influences incubation behaviour in the following ways. During rainy weather a bird sits tightly over its eggs, with the wings spread against the sides of the nest, so that any rain falling into the nest runs off the adult's back into the grass lining. The bird usually does not vacate the nest until its mate is beside it. On fine days, the adult often sits with its dorsal feathers fluffed up and more readily leaves the nest before its mate appears.

Egg breakage also influences incubation behaviour. The bird present at the nest calls to its mate by chittering and makes sporadic, harsh, low volume "Tchup" cries (Figure 19). Both birds continue calling while they make conflicting movements to remove spilt fluid, egg fragments and damp nesting material, and sit on the remaining egg or eggs. Change-overs are frequent during this period, but the birds' excitement generally dies down and their usual incubation routine is re-established some 30 or 40 minutes after their
Figure 26: A pair of fernbirds changing nest duty.

Figure 27: View of an incubating bird.
Table 12: LENGTH OF INCUBATION SPELLS
(Data from Nest 9, 1970-71).

<table>
<thead>
<tr>
<th>No. of incubation spells</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>31</td>
<td>28</td>
</tr>
<tr>
<td>Mean length of spells</td>
<td>14 min 37 sec</td>
<td>15 min 52 sec</td>
</tr>
<tr>
<td>Variance (calculated from time in seconds)</td>
<td>417,242</td>
<td>261,553</td>
</tr>
<tr>
<td>Range</td>
<td>6 sec to 35 min 4 sec</td>
<td>2 min to 33 min 5 sec</td>
</tr>
</tbody>
</table>

There was no significant difference in the mean period of incubation duty between male and female

\[ t_s = 0.4973, \, 30 \text{ d.f.}, \, p > 0.05. \]

mishap.

During most change-overs of incubation duty (Figure 26) there is a period of soft muttering and chittering from one or both birds. Usually about five to eight seconds elapse before the relieved bird leaves the nest, though on odd occasions change-overs take longer than 20 seconds. Least often change-overs are only one or two seconds long and no vocalizations are heard.

Nest building activities occur sometimes at change-over and can be exhibited by the relieved bird, and/or the newcomer. The latter bird may subsequently carry out the following stereotyped behaviour (Baerends, 1959) while it settles on the eggs: stooping, ruffling the belly feathers, shifting eggs and settling, which all serve to make contact with the brood patch and thermal isolation from the environment as perfect as possible.

Throughout much of an incubation spell, the bird remains motionless, with its head and tail held upright by the vertical nest walls (Figure 27). Sometimes, as a bird re-positions itself on the nest, its long straggling tail is deflected about the inside of the nest. Often the bird goes
to sleep with its bill tucked under a wing. Intermittent periods are spent yawning, preening breast and wing feathers, and carrying out nest building activities. These latter activities indicate that the motivation to incubate is low, for the bird often leaves the nest soon after beginning to move about, without its mate having indicated its approach.

After a bird leaves the nest, it often pauses in the nearest open patch of ground to yawn, stretch, preen or scratch briefly before going foraging.

**INCUBATION PERIOD**

The incubation period is the time elapsing between laying and hatching of the last egg of a clutch. This period was ascertained for seven nests (Table 13). Another seven clutches were found for which the laying dates of the last eggs were known but unfortunately these clutches were subsequently lost.

**Table 13: INCUBATION PERIOD OF LAST LAID EGGS**

<table>
<thead>
<tr>
<th>Incubation Period</th>
<th>Range of each period (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>15.38 - 15.96</td>
</tr>
<tr>
<td>2</td>
<td>15.17 - 16.08</td>
</tr>
<tr>
<td>3</td>
<td>15.25 - 16.79</td>
</tr>
<tr>
<td>4</td>
<td>15.79 - 16.29</td>
</tr>
<tr>
<td>5</td>
<td>16.00 - 16.88</td>
</tr>
<tr>
<td>6</td>
<td>16.04 - 16.58</td>
</tr>
<tr>
<td>7</td>
<td>17.17 - 17.54</td>
</tr>
</tbody>
</table>

Summed Data.

Mean (max + min/2 of the seven records) = 16.13 days

(i.e. 16 days 3 hours).

Variance = 0.4095

Range = 15.38 - 17.54 days
The incubation period of 16 days is significantly greater than that of the sole record (M'Lean, 1906) of 12.5 days for the North Island Fernbird (ts = 5.306, 6 d.f., p = < 0.01 but > 0.001, "t" test in Sokal and Rohlf, 1969: 223-225). The longer incubation period for the Snares Fernbird is probably due mainly to their greater size, i.e. 73 Snares eggs average 22.9 x 16.7 mm compared to five North Island Fernbird eggs with a mean of 19.5 x 14.5 mm (data from M'Lean, 1906 and Oliver, 1955).
In this chapter hatching, parental care and feeding of young, food of nestlings and the physical and behavioural development of nestlings are dealt with.

HATCHING

The length of time over which the eggs hatch (hatching period) for entire clutches ranges from less than six hours to 26 hours (Table 14). The eggs hatch asynchronously, in the order laid, but the time taken for an egg to hatch was not determined. Approximate hatching times can be deduced by comparing the nestlings with respect to size, strength and posture. This information indicates whether a nestling has hatched within (i) six hours, or (ii) six to 12 hours. Once the first nestling hatched I visited the nest every two or three hours during daylight until the remaining young had hatched.

During hatching, both adults frequently duet and chitter to each other, making frequent trips to and from the nest, but they generally do not move far off. Their behaviour is similar to that occurring when an egg is broken during incubation. This period of high activity dies down about 20 to 30 minutes after a nestling has hatched.

Egg shells are carried about 10 to 20 m from the nest after a nestling has fully emerged. Examination of discarded shells shows that fracturing occurs latitudinally around the broadest part of the egg.
During Incubation

During Nestling Phase

Young Fledged

A. MINS PER HOUR

B. NO. OF VISITS PER HOUR

DAYS
Figure 28: Role of male and female in tending their young. Data from Nest 9, 1970-71.

Part A: Mean period per day that the nest was (i) unattended by an adult (solid line), (ii) occupied by the male (dashed line), and (iii) occupied by the female (dotted line).

Part B: The mean visiting frequency per hour of the male and female during incubation and throughout the nestling phase.
Table 14: HATCHING PERIOD IN RELATION TO CLUTCH SIZE

<table>
<thead>
<tr>
<th>Clutch Size</th>
<th>No.</th>
<th>Mean hatching period</th>
<th>Range</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>6</td>
<td>12-14 hrs (12.83)</td>
<td>6-22 (±3 hr)</td>
<td>7.080</td>
</tr>
<tr>
<td>3</td>
<td>6</td>
<td>11-15 hrs (13.33)</td>
<td>6-23 (±3 hr)</td>
<td>6.394</td>
</tr>
</tbody>
</table>

PARENTAL CARE OF THE YOUNG

A quantitative study of the contribution made by each sex in tending the young was carried out at three nests, Numbers 2, 9, and 17 in 1970-71. During this study, I kept a four hour daily watch while 3 m from the nest. A hide was not used as the birds were indifferent to a quiet observer. Nest 9 was observed for 25 and Nest 17 for four consecutive days, in spells from 0400-0800 hr, 0800-1200 hr, 1200-1600 hr, and 1600-2130 hr. Nest 2 was observed for four out of five days. Thus in four days observation there was a composite record for one day-block. The following data were recorded during an observation period; sex of the birds approaching and leaving the nest, the nature and duration of any calls used, and type of material brought to the nest during change-overs. A quantitative study of food brought to the nest was abandoned for it was difficult to identify food items held in the parents' beaks. The use of feeding collars on nestlings was attempted but proved unsuccessful as adults took food from nestlings which did not completely swallow the prey given to them, and fed it to another nestling. The data presented here give only an indication of the roles of sexes during raising of offspring. Much more prolonged observation is needed to provide a full account.

The mean period spent on the nest (Nest 9, only) per hour, by each adult is shown on Figure 28 a. Both adults spent, on average, similar amounts of time on the nest, from incubation up until the fourth day after hatching. After the
fourth day, both parents spent progressively less time per hour on the nest. It is unlikely that this increasing neglect of Nest 9 is directly related to the food requirements of the young, for as indicated on Figure 28b the number of feeding visits to the nest did not increase greatly after the fourth day. The subsequent peaks and troughs in the rate of feeding visits were diurnal variations reflecting observation times. It is not understood why only the male visited the nest in the last day's observation - his mate was still alive.

Although feeding rate increased only slightly after the sixth day, nestling weight kept increasing until 11 to 16 days after hatching. This indicated that nestlings were fed on larger prey as they grew older. It was unlikely that the adult birds experienced difficulty in finding and despatching larger prey as indicated by the following two examples. The adult female brought three wetas (Insulanoplectron spinosum) to the nest within two minutes, while on another occasion the male brought four wetas (two Insulanoplectron, and two Zealandosandrus subantarcticus) within seven minutes. This feeding activity was observed commonly when nestlings were over 10 days old.

The adults' increased neglect of the nest from the fourth day after hatching indicates that the nestlings had begun to develop thermoregulatory ability. After 11 days this ability was probably complete, aided by the developing nestling feathers. The survival curve for nestlings (Figure 35, Chapter 8), which shows a great improvement in survival after 11 to 12 days, supports this hypothesis.

Also, if the mean period of adult nest attendance per hour for one nestling (Nest 2, 1970-71), two nestling (Nest 9, 1970-71) and three nestling (Nest 17, 1970-71) broods are compared (Figure 29), the effect of brood size upon parental attentiveness is clearly exhibited. A single nestling was brooded for at least 50 minutes per hour, two nestlings for 22 to 58 minutes per hour, whilst three nestlings were brooded for less than half of each hour throughout the period observed.

Work by Mertens (1969) on the energy metabolism of nestling Great Tits demonstrated that with increased brood
Figure 29: Parental attendance/hour at one, two and three nestling broods.

Nest unattended (solid line); male on the nest (dashed line); female on the nest (dotted line).
A. VISITS PER HOUR

'DAY' 1 Incubation

'DAY' 2 Nestlings age, 0 to 3 days

'DAY' 3 Nestlings age, 4 to 7 days

'DAY' 4 Nestlings age, 8 to 11 days

'DAY' 5 Nestlings age, 12 to 15 days

'DAY' 6 Nestlings age, 16 to 19 days

B. 3 Nestling Brood, age 5 to 8 days
Figure 30: Feeding rates of nestlings.

Part A: Record for a two nestling brood. The first day-block shows parental visiting frequency during incubation, subsequent day-blocks show feeding rates of nestlings.

Part B: One day-block of feeding frequency of the three nestling brood.
size each nestling lost less heat. If this is also applicable to the fernbird, adults with three nestling broods (and probably higher food requirements) would have more available time per hour to forage and patrol their territories than other adults with smaller broods. The higher food requirements of three nestlings is indicated by a one day-block of nestling feeding rate at Nest 17, 1970-71. During the observation period the nestlings were five to eight days old, and their feeding frequency (Figure 30 b) should be compared with that of day-block 3, Figure 30 a, for a brood containing two nestlings of four to seven days age. The three nestling brood received about one and a half times more food items (220 per day-block) than the two nestling brood (160 items per day-block). Even in day-block 4, when the two nestling brood was aged eight to 11 days, the young received 192 food items per day. Both nests were situated in similar habitat, viz. dense Olearia forest, and were 40 m apart.

FEEDING RATES

Feeding rates of two nestlings at Nest 9 (1970-71) over six day-blocks (composite of 23 days observations) are illustrated in Figure 30 a. "Day" 1 shows the visiting rate per hour during incubation, and the subsequent day-blocks demonstrate feeding rates of nestlings (aged 0 to 19 days). Feeding rates are extremely variable, both within and between days. The only features common to all day-blocks are a peak in feeding rate at 0500-0600 hrs, a trough in mid-afternoon (1500-1600 hrs), and a second peak late in the evening. This second peak tends to become greater with nestling age. The early morning peak is probably due to all the birds being hungry at daybreak, and the late evening feeding peak is a final burst to last the birds overnight, when they stop foraging. The variability of intervening feeding rates may be partly due to the strength of nestling begging. High intensity begging means that the nestlings are hungry, low intensity begging indicates they are nearly satiated.

Feeding continues at a steady rate during short rainfalls (one to two hours) but it is not known whether it does
so in prolonged rain (several hours or days). However, as adults can readily dig out prey sheltering under bark, or from loose organic debris on the ground, it is not likely that longer rain periods interfere with feeding of nestlings.

Gibb (1955), while studying Great Tits, also found that feeding rates varied considerably in similar environmental conditions. Thus a detailed study over several seasons would probably be necessary before any valid conclusions could be drawn on fernbird feeding rates. Also, feeding frequency alone is not a good measure of the total amount of food brought to the nest, as food may vary considerably in size and nature (see also Gibb, 1955 and Royama, 1966 on Great Tit feeding biology; and Dunnet, 1955 on Starling feeding biology).

NESTLING FEEDING BEHAVIOUR

Adults bring only one food item per visit to the nest (cf. South Island Fernbirds, which may bring several items per visit, M.F. Soper, pers. comm.). When prey is very large (over 20 mm long), e.g. weta *Zealandosandrus subantarcticus*, a nestling often has difficulty in swallowing it, and the adult may remove the prey and refeed it to the nestling several times. If the first nestling still cannot eat the food, the latter is thrust down another younger's throat. If none of the chicks can ingest the oversized prey the parent removes it and, after a few moments of conflicting motions and chittering, swallows the prey or, holding it down with one foot, tears portions off the arthropod which are then fed to the nestlings.

Occasionally, the usual rapid feeding sequence is upset by abnormal responses from the nestlings. For example, at Nest 21A, 1970-71, two 11 day old nestlings were asleep when the adult came to the nest with food. When the nestlings did not instantly rear up to be fed, the adult called "Tchup" softly. Both nestlings woke up and begged directly forward, but they were not immediately fed as they faced away from the adult. They soon redirected their begging at the adult and one nestling was fed. At another feeding visit, the two nestlings did not beg when the female brought food. Both
Table 15: SOME FOODS OF NESTLING FERNBIRDS

ARANEAE
Dictynidae, Oramia rubrioides (Hogg).

ORTHOPTERA
Rhaphidophoridae, Insulanoplectron spinosum Richards.
Stenopelmatidae, Zealandosandrus subantarcticus Salmon.

COLEOPTERA
Tenebrionidae, Psuedhelops quadricollis Broun. Larvae.

DIPTERA
Coelopidae, Chaetocoelopa littoralis (Hutton).
Coelopa debillis Lamb.
Larvae and adults of both species.
Calliphoridae, Calliphora huttoni Miller. Larvae and adults.
Calliphora sp. indet. Harrison. Adults.
Muscidae, Fannia fuliginosa sensu Harrison. Adults.
Limnophora, four species, undet. Adults.
Tipulidae, Leptotarsus (Macromastix) n.sp. Adults.
Limouia (Dicranomyia) arthuri (Alexander). Adults.
Helomyzidae, Allophylopsis laquei (Hutton). Adults.
Syrphidae, Helophilus hochstetteri Nowicki. Adults.

LEPIDOPTERA
Noctuidae, Graphia insignis pagaia Hudson. Adults and larvae.
Tortricidae, Planotortrix syntona laquaerum Dugdale. Adults.
Psychidae, Cryptotheca horningae MS Dugdale. Adults and larvae.
Oecophoridae, Izatha oleariae Dugdale. Uncertain identification.
Tineidae, Proterodesma bysopola Meyrick, Uncertain identification.

PHALANGIDIDA
Several species, Gen et sp. undet.

AMPHIPODA
Orchestia aucklandiae (marine).
Gen et sp. undet (terrestrial).
looked up at the female, but remained huddled together in the nest. During the following three minutes the female came up to and left the nest hesitantly 12 times, chittering softly. She even prodded both nestlings with her bill but they would not beg. Finally she made her way slowly from the nest, and swallowed the tipulid prey as she went into the forest. Apparently both nestlings were satiated and were fed only twice during the subsequent 45 minutes.

On another occasion during a feeding visit, the two nestlings vigorously lunged forward at the male, begging loudly. The male appeared to be in a quandary for eight seconds, turning from one gape to the other, before feeding a nestling. Both nestlings must have had equally strong begging responses when the male appeared.

NESTLING FOODS

Nestlings were fed on a wide variety of arthropods, some of which are listed on Table 15. Many food items brought to the nests could not be seen clearly before they were devoured by the nestlings. The data were collected from observation of five nests in the Olearia forest, and also from sightings of food carried to inaccessible nests on the steep Poa astonii clothed walls of Sinkhole and Sinkhole Gut. In other places other prey species are probably used.

In the forest and Hebe-clad eastern coastal territories, nestlings less than eight days old were fed mainly on small soft-bodied prey (flies, moths, spiders and various larvae). As nestlings approached full weight (when 12 to 16 days old), wetas (Orthoptera) were commonly offered, and in the Sinkhole Gut area large nestlings were fed predominantly on the superabundant supply of large (over 20 mm long) marine amphipods (Orchestia aucklandiae) found amongst flotsam on the boulder beaches. Some wetas and marine amphipods offered were too large for even the oldest nestlings to swallow.

Some prey, e.g. moths and tipulids, are brought to the nest most often during early morning and late evening when these cryptic insects become more mobile. Other prey, such
as wetas, are brought at about the same rate throughout the day as they can be readily found in Sooty Shearwater burrows.

NEST SANITATION

Almost without exception, the parent pauses after feeding a nestling in anticipation of a fecal sac being produced. The young usually defecate a few seconds after being fed and the adult sometimes lingers and peers around for up to 30 seconds after completion of feeding. Occasionally, the parent even prods the nestling's cloaca with its bill if a fecal sac is not immediately produced.

Often a chick turns 180° from where it is fed and raises its cloaca up to the nest's edge before defecating. On other occasions it turns only a few degrees before raising its cloaca to defecate. The parent either lunges across the nest to take the fecal sac directly from the cloaca, or moves more slowly if the sac is deposited at the nest's edge. The fecal material is then carefully raised above the edge of the nest and carried off slowly for up to 25 m. After the adult drops the pellet it wipes both sides of its bill on the ground or a nearby branch. If a fecal sac is broken during handling the parent makes several trips to carry off as much spilt material as it can— even moving soiled nesting material. The adult also usually removes any fecal pellets that are deposited whilst it, or its mate, is away foraging.

Only during the nestlings' last three or four days in the nest does nest sanitation decline, and a ring of damp fecal sacs accumulates about its edge. The reason for this lapse of parental cleanliness is not clear. It could be that towards the end of the nestling period it becomes less important to conceal the whereabouts of the nest by removing conspicuous fecal matter.

Nest sanitation behaviour of fernbirds is similar to that described for Great Tits (Betts, 1955).

NEST MAINTENANCE

At various intervals during feeding visits, one of the
Figure 31: Stages of nestling development.

Feathered areas are shown by stippling.
adults remains on the nest and probes about in the lining. This occurs more frequently as nestlings grow older (and was observed once two hours after the young had left the nest) as there is more wear and tear through increased movements of adults and young on the nest. While the parent probes about the offspring are pushed aside, or if older than seven to nine days, are forced up on to the parent's back. The adult often disappears completely except for its vertically inclined tail. The passive nestlings are jostled about considerably as the parent rearranges the feather lining and tucks projecting pieces of Poa back into the nest walls. Some strands of Poa are pulled out of the nest and rewoven into the walls. Periodically the adult surfaces between the nestlings for a brief spell before resuming nest maintenance. Rearranged material is consolidated into the smooth nest bowl by typical nest building motions (see Chapter 4). Both parents carry out nest maintenance for periods of up to five minutes. Fouled material is removed and sometimes replaced with fresh material gathered by the adults while out foraging.

Nest probing activities may be a reaction against the activities of ectoparasites. Some fernbird nests have an extremely high parasite load. D.S. Horning found as many as 1698 flea larvae in one nest and 129 flea adults in another nest (pers. comm.).

DEVELOPMENT OF NESTLINGS

The morphological and behavioural development of nestlings of known age from hatching to departure are described below. The number of young birds examined at each stage of development is shown by \( N = \). Only the main changes and those features indicating the relative age of the young are recorded here. The age of the chicks is expressed in days after hatching. Descriptions of the nestlings are given at 24 hour intervals after the day of hatching.

Morphological development of nestlings

Age 0 days \( N = 11 \)

A newly hatched nestling is naked, with its viscera
visible through the pink-red skin. The chick's abdomen is large, while the wing buds and clawed legs are small. The relatively small head contains two blind eyes which appear as large slate-grey bulbs, and the bill is short but has a broad gape. The mouth is pink-red with yellow bill margins. Only small prey such as tipulids, spiders, Diptera and Lepidoptera (larvae and adults) can be swallowed. Six hours after hatching the nestlings are noticeably larger than the eggs they hatched from, and they have partly lost their embryonic posture.

The first signs of feather tracts appear in nestlings about 12 hours after hatching. These tracts are represented by diffuse areas of very fine pores through which hair-like processes just project above the skin.

Age 1 day (N = 8)

A dark red-brown zone along the dorsal surface marks the position of the future dorsal feather tract. Three black "begging spots" (absent at day 0), one at the front of the tongue, two at the back, have appeared on the now yellow tongue. There is a colour gradation in the mouth. The yellow bill margins tend to orange near the tongue, then red at the beginning of the oesophagus. The gape remains wider than the bill's length. Nestlings have grown appreciably since hatching.

Age 2 days (N = 13)

Slits are just forming along the equators of the eye bulbs. Feather tract areas on the future dorsal, alar, capital and abdominal tracts (in that order of conspicuousness) are well defined, slate-grey waxy patches (terminology after Saunders, 1956).

Age 3 days (M = 9)

The abdominal region (i.e. gut) continues to develop at a greater rate than other parts of the body. The viscera are still visible through the abdominal wall. Body proportions remain similar to those when the nestling hatched, except the head has increased in relative size. Small waxy sheaths are beginning to push up from the slate-grey tracts.

Age 4 days (N = 11)

Splits are starting to form along the eye slits, as well
as at the tips of dorsal and alar feather sheaths, exposing the distal ends of developing feathers. The remaining sheaths are still capped with short hair-like processes. Primary alar sheaths are about 1.5 mm long, while dorsal and secondary alar sheaths are 1.0 mm long.

Age 5 days (N = 8)

The eye splits have advanced a little more than on day 4, and moist mucus is present along the splits. Primary alar tract sheaths plus feathers are 3.0 - 4.0 mm long, while those of the secondary alar and dorsal tract measure 1.5 - 2.5 mm, and the caudal and femural tract sheaths are about 0.5 mm long.

Age 6 days (N = 7)

The eye slits are fully split but vision probably remains non-existent as mucus covers the eyes. Feather and sheath measurements are: primaries 4.0 - 5.0 mm, dorsal 2.5 - 3.5 mm, lateral and abdominal 2.0 - 2.5 mm, and caudal 1.0 - 1.5 mm.

Age 7 days (N = 14)

Vision may exist for some young, but is probably poor for a thin mucus film covers the eyes. Primary and secondary feathers have begun to differentiate in length and the third, fourth, and fifth primaries are longer than any other feathers. Combined sheath and feather measurements are: primaries, 5.5 - 7.5 mm, dorsal and lateral 3.5 - 4.5 mm, tail 1.0 - 2.0 mm. The pink leg flesh is tinged with grey and the bill is a slightly darker grey.

Age 8 days (N = 7)

The eyes are fully open and functional. Sheath and feather measurements are: primaries 7.0 - 9.5 mm, dorsal and abdominal 4.0 - 5.0 mm, caudal 2.0 - 3.0 mm.

Age 9 days (N = 6)

Sheath and feather measurements are: primaries 9.0 - 10.0 mm, dorsal and abdominal 5.0 - 6.0 mm, caudal 2.5 - 4.0 mm.

Age 11 days (N = 10)

Sheath and feather measurements are: primaries 14.0 - 17.5 mm, dorsal and abdominal 7.0 - 8.5 mm, and caudal
When nestlings remain in a crouched posture at the bottom of the nest, the rapidly erupting feathers cover most of the body and small fleshy strips are present only between the dorsal and abdominal tracts. The ventral surface remains naked from the heart region to the cloaca. A ring of small feathers is present around the cloaca.

Age 13 days (N = 9)

Much of the legs (crural tract) and an area 2 mm wide and 5 mm long behind the eye remain naked. The ventral bare area is about 35 mm long and 15 mm wide.

Age 14 days (N = 9)

The area behind the eyes is covered by feathers. Only a 10 x 30 mm belly strip of flesh remains naked.

Age 15 days (N = 10)

There are considerable holes in the wings between the primary and secondary feathers. The wing coverts are just beginning to grow over these gaps.

Age 16 days (N = 5)

The gaps between the primary and secondary feathers are partly covered by the wing coverts.

Age 17 days (N = 13)

The belly is completely covered by feathers.

Age 18 days (N = 11)

The gaps between primary and secondary feathers are almost completely covered.

Age 20 days (N = 8)

Nestlings of this age are similar to recently fledged young.

Behavioural development of nestlings

Age 0 days (N = 11)

Newly hatched nestlings lie huddled in a clump at the bottom of the nest with their heads turned inwards. When touched, they shakily disengage themselves and weakly raise their heads on trembling necks. After about three seconds,
the upward displayed gapes slowly close and the heads subside back against the huddled bodies. The nestlings' legs cannot grasp, or brace their bodies. If turned over, they experience great difficulty in righting themselves, and sometimes fail to do so. Unbrooded nestlings cool rapidly.

Age 1 day (N = 8)

Begging occurs in response to tactile and sound (any sound) stimuli. As soon as an adult stands up on the nest begging begins for at this time feeding was most likely to occur. Nestlings spend most of their time passively huddled together as they are too weak to do much moving about. Constant brooding indicated that nestlings are not homeothermic.

Age 2 days (N = 13)

The begging response is sustained and stronger, than previously, to sound and touch.

Age 7 days (N = 14)

There is a weak grasping tendency with the clawed feet when a nestling is tipped over, or the undersides of the toes touched.

Age 8 days (N = 7)

Begging is directed at visual stimuli, viz. the presence of any approaching object. This is the first day that vision is operational. There is a less sustained begging response to touch and sound.

Age 10 days (N = 12)

Begging occurs only at quivering vegetation beside the nest, or the appearance of an adult fernbird. Slight wing quivering during begging occurs for the first time. Many nestlings cower low in the nest when any other objects approach.

Age 11 days (N = 10)

If an adult does not appear within two or three seconds after vegetation beside the nest has been disturbed, the nestlings begin to cower. In this posture, a nestling retracts its head and legs hard against the body so that a flat "frozen" profile is presented. This response probably has evolved as an anti-predator device, for cowered nestlings
are quite inconspicuous. Two or three nestlings huddled together in a nest "merge" into one another and are less obvious than a single nestling.

Age 12 days (N = 9)

Nestlings can just manage to grip strongly enough to perch unsteadily on a finger. However, their balance is poor and they have to flap their wings in an effort to retain their position. Sometimes nestlings lean forward and give short begging calls at blowflies walking near the nest.

Age 13 days (N = 9)

Chicks removed from their nest for measurement tend to crawl into dark corners. Most of the young's begging is directed at the frontal view of an adult, and begging intensity falls as soon as an adult turns to leave the nest. During high intensity begging, nestlings stand up and quiver their wings rapidly.

Age 14 days (N = 9)

The young commonly stand up while begging and lunge vigorously at the incoming adult. Frequently handled chicks make no attempts to escape, although those not handled before do.

Age 16 days (N = 5)

Nestlings are liable to abandon their nest at the first sign of any unusual disturbance. When handled, the young restlessly squirm about, especially if their parents call.

Age 17 days (N = 13)

"Tsip" calls are given by nestlings. Captured nestlings also utter distress calls if their parents call in alarm. Some young even scream when caught (typical adult reaction).

Nestlings older than 17 days after hatching cannot be accurately aged (to my knowledge) by the appearance of any new behavioural traits.

The sequence of behavioural and morphological development of fernbird nestlings is typical of that described for other passerines, e.g. Tree Sparrows *Spizella arborea* (Baumgartner, 1938), White-crowned Sparrows *Zonotrichia*
leucophrys (Banks, 1959), Cactus Wrens Campylorhynchus brunneicapillus (Anderson and Anderson, 1961), and several other passerines described by Saunders (1956) and Barraud (1961).

Abnormal nestlings

Two abnormal nestlings were found during this study, one in each season. The young were progeny of the same male. It is not known if his mate was the same in both seasons as she was not banded in the first summer. The abnormalities were consistent. In both chicks the right eye was absent and the tip of the upper mandible was deflected sinistrally 2 or 3 mm. In the eldest surviving chick (who lived for 36 days) the upper mandible's tip lay 2 mm below the tip of the lower mandible. Both offspring hatched from second-laid eggs of three-egg clutches.

Growth rates of nestlings

Ten nestlings were measured (three broods in 1970-71, and one brood in 1971-72) at 24 hour intervals, starting at the age of four to eight days. Five parameters were used to determine nestling growth: wing, bill, tarsal and tail lengths, and body weight. These were measured in the same manner as adults (see Chapter 2). During periods of heavy rain younger nestlings were not disturbed in case they became wet and chilled, and then died. Daily increments of the five parameters expressing nestling growth are given in Figure 32.

Feather growth and bill length increase in a linear fashion. Body weight and tarsal length tend to follow a sigmoid growth pattern. There is considerable variation in the size of a given parameter for a given age. This is typical of other passerines, e.g. Robins Erithacus rubecula (Lack and Silva, 1949), White-crowned Sparrows (Banks, 1959) and Cactus Wrens (Anderson and Anderson, 1961). Thus, these parameters cannot be used to accurately determine nestling ages. I conclude, as did Lack and Silva (1949) for nestling robins, that physical appearance and behaviour are far better indicators of age.

The daily increase in weight of nestlings is fairly
Figure 32: Growth rates of nestlings.

Note. In the N16, 1971-72 nestling graphs only the second nestling's growth has been delineated for clarity.
uniform but growth begins to level off at different ages for different broods, the range being 11 to 15 days (Figure 32, a, b, c and d). However, between members of the same brood, body weights are similar. Lack (1949) found for robins that there are marked differences in weight even between members of the same brood. In fernbirds, the only sudden decrease in weight of a chick occurred for the third offspring (C10004) of Nest 17, 1970-71. This nestling's weight dropped suddenly after the death of its sibling who was a freak (see section on Abnormal nestlings). It is interesting to note that in spite of the weight change of nestling C10004, growth of its other elements continued at a steady rate. Lack (1949) also reported that the weight of a nestling robin has scarcely any influence on the rate of its feather development. Thus, in both the fernbird and the robin these elements must have fixed rates of development irrespective of the amount of food supplied to the young.

Fluctuations in the weights of chicks after the growth curve has levelled out have been noted by other authors, e.g. Anderson and Anderson (1961), Banks (1961), Coleman (1968), Dunnet (1955), Lack (1966), Lack and Silva (1949). These changes may be due to the amount of food taken by the young before being weighed, and the amount of fecal material retained within the nestling.

Tarsal growth follows a similar pattern to increases in weight, with age. Levelling out of tarsal growth also occurs on different days for different broods (see Figure 32, a, b, c and d). As this is a skeletal element there are no decreases in size with nestling age (cf. with body weight) and it is not influenced by fluctuations in body weight. Tarsal length of young ready to fledge ranges from 93 to over 100% of the mean adult tarsal length.

Bill length increases at a relatively constant rate throughout nestling development, and this is the last of the five elements measured to reach adult proportions (see Figure 34, Chapter 7). Twenty to 21 day old nestlings have bill lengths ranging from 78 to 90% of the mean adult length.

Up to the age of four days after hatching, the growth rate of the bare manus (wing) is rather slow. Once the primaries and secondaries begin to split the tips of their
sheaths at the age of four to five days, the rate of growth of the wing rises at a fairly constant rate and levels off after fledging (see Figure 34, Chapter 7). Chicks 19 days old can fly 12 to 15 m. Wing length of 20 day old young is 77 to 89% of the mean adult length.

Initially, the rectrices are merely hair-like wisps no longer than 0.5 mm, but they soon begin to grow. Growth rate of the tail feathers increases when the young are seven to eight days old, but the feathers do not reach full size until the young are independent of their parents (see Chapter 7). At age 20 days, nestling rectrices are 22 to 49% of the mean adult size.

Factors affecting growth rates

Variation in intra- and inter-brood growth rates are low and their growth curves follow a similar pattern, with the exception of nestling C10004, of Nest 17, 1970-71. The temporal displacement of growth rates indicates that some broods develop a day or two ahead of others and retain their lead. It seems likely that individual nestlings in a brood receive similar amounts of food, as increases in weight are similar for all nestlings (except nestling C10004 mentioned above). As fernbird brood sizes are low, the adults would not be as hard pressed to find food as birds with larger broods such as Great Tits (with ten or more young/brood; Lack, 1966) everything else being equal. Due to the nature of this study, I was not permitted to place additional chicks into nests to find out how many young a pair of adult fernbirds could raise.

Hatching sequence appears to have little influence on the development of fernbird young, as members of a brood hatch within a 26-hour period (see Table 14). In passerines with larger clutches, the hatching sequence does have an effect on nestling development rates: the older offspring grow faster than younger ones, e.g. robins (Lack and Silva, 1949) and tits Parus spp (Gibb, 1955). Gibb considered that the different growth rates of different sized tit broods results from an inverse relationship between brood size and the amount of food brought to the nest.
CHAPTER 7

POST-FLEDGING ACTIVITIES OF ADULTS AND YOUNG

INTRODUCTION

In this chapter, a general description of daily activities of fledglings is given. This is followed by a chronological account of the initial account of the initial appearance of morphological and behavioural traits, as in the preceding chapter on nestlings. A summary of the characters for distinguishing between adults and young in the field is given. A brief account of post-breeding moult and dispersion concludes this chapter.

All fledglings and their parents were observed for up to two hours at a time, at one to five day intervals. The birds morphology, behaviour and movements were recorded.

ACTIVITIES DURING FLEDGING DAY

The young fledge when aged 20 to 21 days. Nest desertion is marked by conflicting tendencies to remain in the nest and to move off into the surrounding vegetation. Typical fledging behaviour is shown by the following example at Nest 18, on 17 February 1971.

At 1030 hr the adult male came to the nest, fed a nestling and then began to rearrange displaced nesting material. Throughout this process both nestlings were jostled to the edge of the nest, and a few seconds later they hopped into the fern adjacent to the nest. Following the male's departure, the younger nestling returned to the nest. During the next 20 minutes, it alone was fed, for the absence of the older nestling apparently went unnoticed. Subsequently, the older chick returned to the nest, but only after spending about 50 seconds peering into the nest. Ten minutes later the female returned and further rearranged the nest lining. Again both offspring left the nest. There they remained, and at the next feeding visit the adult chittered
in low intensity alarm for three seconds when it found the
nest was deserted. Both young responded with "Tsip" calls,
the adult turned and fed the nearest "nestling". After the
adult's departure both young remained crouched in the ferns
for half an hour, calling "Tsip" infrequently, but at 1130 hr
they began to clamber about.

The fledging of broods in 18 out of 20 study families
was completed within one day. In the remaining two broods
fledging extended over a period of 26 to 28 hours. The
young initially remained within 10 m of the nest. They were
reluctant to move out of dense vegetation, and when they did,
were extremely wary and difficult to capture.

The young spent long periods standing still, softly
calling "Tsip". However, some chicks scrambled about in the
sheltering dense vegetation for periods of 10 to 15 minutes
per hour. They were unsteady on their legs and when hopping
about in low branches misjudged distances and had to flap
their wings vigorously to maintain balance. On landing they
teepered, clung tightly, and then relaxed. At fledging, the
young could fly 15 m and clamber up tree trunks in
emergencies. Improvement of motor capabilities and distance
judgement was rapid, for within six days they could follow
their parents all over the territory, from the tops of trees
to the depths of petrel burrows.

Both adults brought food to their offsprings' hiding
place and the young were fed either under cover, or, alerted
by the approaching adult's calls, they moved to the edge
of the concealing vegetation to be fed. The fledglings some-
times followed half a metre behind the adult as it turned to
enter the forest, but usually they returned to shelter after
travelling only a few metres.

At the end of their first day, the young and their
parents roosted together, most commonly in the old nest, but
sometimes in cover nearby. Before roosting, the family group
was more vocal than normal. Adult calls appeared to act as
contact notes, helping to keep the young close at hand. The
roosting ritual usually began 20 to 30 minutes before dark
and could carry on until 10 to 15 minutes after dark, by
which time calls must have been the only means of holding the
family together.
Within two or three days of leaving the nest, the young often settled upon one or two favoured areas where they were often found resting, sun- or dust-bathing or pecking randomly at nearby objects. Many of these areas were away from the nest, in sunny places with suitable cover nearby. The parents also frequented these resting areas when they were not foraging.

In the days following fledging, the young spent progressively more time away from cover and more readily followed adults into the forest. The fledglings appeared to find that food was more readily available if they followed their parents. Adults seemed to encourage this behaviour, as often one landed a few metres from where its offspring was concealed and called. The chick usually ran out to be fed and it would follow as the adult moved off. These adult-fledgling outings are subsequently called "foraging sorties".

The parents generally tended to specific young. With one fledgling in the brood the parents alternated feeding duties; with two young, each parent attended to its own chick; and when there were three offspring the male looked after two much of the time, while the female attended mainly to the third.

Only rarely did adults feed chicks "attached" to the other parent. Thus Male 11 brought some food to where his offspring was usually found. When he did not find his fledgling he called "Ding" softly. His mate's fledgling ran up and begged vigorously at him, but the male stood on tiptoe and peered about, calling loudly. When his chick still failed to appear the male looked at the other and after three seconds of hesitant movements put the food into its gape. Male 11 then spent 60 to 70 seconds searching and calling for his chick around the latter's typical resting area, before hesitantly going foraging. On other occasions, young adopted the wrong parent at the start of a foraging sortie but they soon dropped behind.

Within three days of leaving the nest fledglings undertook foraging sorties lasting 20 to 25 minutes, although a few lasted up to 35 minutes. These sorties were initiated
mainly by the appearance of the adult at the chick's resting site, although on a few occasions a youngster aroused its parent by pecking at the latter's tail or jumping on its back while the adult sun-bathed or slept. Sorties ended when the adult led its charge past its resting area, and the youngster moved off to join its sibling(s) while the adult continued on. If a chick lagged behind and became separated from its parent while some distance from its resting area, the parent called and relocated its offspring by following the latter's replies. This occurred most frequently when the young had been fledged for only a few days and probably did not know their way about. Older fledglings, which had a better knowledge of local geography, were more ready to stop following their parents.

Foraging sorties appeared to serve two main functions: young birds were shown where and how to find food, and the nature of the surrounding environs. Two-week old fledglings often strayed into neighbouring territories alone for 30 to 45 minutes and returned unguided.

It was hard to tell how often the chicks were fed during such sorties. Sometimes the adult and its youngster were hidden by vegetation, or down petrel burrows, and each time an adult slowed or changed course the young bird often begged. Occasionally, a young bird scarcely had time to beg, for as soon as food was caught the adult turned around to thrust the morsel down its offspring's throat. More frequently the chick had time to rush up and beg.

As they grew older fledglings spent more time alone. They hopped about (cf. adult's walk or run) outside their resting areas and investigated their surroundings. Initially, they did not appear to be searching for anything in particular but simply explored all manner of objects, including the anatomy of siblings and adults. One chick was seen to overturn its sibling when it picked up its foot. The first fledgling seemed to be unaware that the foot was attached to anything. At this stage the young were more venturesome and less prone to flee instantly from novel situations than they had been. By the end of the second week of fledging they often investigated large stationary objects such as humans, sleeping sea-lions or penguins, and pecked at the hair or
feathers of these creatures.

It was unlikely that younger fledglings recognized their food, for they caught flies, moths, or tipulids without eating them - the birds merely played with the prey until it ceased to move, and then discarded it. At this stage chicks appeared to relate food to the presence of a parent, and only after trial and error did they find that food could be obtained independently of parents. This awareness first appeared at about 20 days post-fledging, when the young consumed prey they had caught, but the "parent equals food" tendency lingered for many days afterward. Similarly, Anderson and Anderson (1962) reported that young Cactus Wrens (Campylorhynchus brunneicapillus) tended to associate their parents with food, for one fledgling, in its impatience to be served, stood in the middle of a pan of dog food and begged while the parent was feeding its offspring on the soft mash.

Although older fledglings spent periods of 45 minutes foraging (or going through the motions of foraging) they still actively followed their parents on foraging sorties. For example, 32 days after leaving the nest the Tern Point chick and adult male were observed on a foraging sortie lasting 35 minutes. For the following two hours the young bird remained alone, foraging successfully for itself.

Some adults regularly led their young on to neighbouring territories, and often to the same area repeatedly. For example, in both seasons, the Tern Point female was regularly seen taking her young into the thick growth of Carex, Hebe, Poa, and Polystichum growing between Station Cove and the Biological Station. Although the Station Cove male and female often evicted the intruding female, they ignored her fledgling and usually she returned to her offspring within 1 to 2 minutes to continue foraging. On several days the Tern Point female was chased off five or more times, in less than 30 minutes.

Trespassing with the young may have served to show the chicks where neighbouring territories lay. It was not likely that the birds led their chicks into neighbouring territories because their own were "deficient" in food, as shown by the following example. On Seal Point, an area which contained very little vegetation (see vegetation map, Chapter 3) the
female of East Seal Point territory was seen hunting blowflies on a *Poa astonii* patch of only a few square metres, growing 30 m from the nearest vegetation. When she caught a fly, the female ran to her fledging, who was hiding in a thicket of *Hebe* some 40 m away. Her behaviour was not easy to understand, for there were many more blowflies of the same species around the *Hebe* blossoms adjacent to her youngster, and she could have saved many long trips to and from the *P. astonii* patch. This activity was seen on eight occasions within five days, and each session lasted for over 20 minutes.

Adults rarely acted aggressively towards young birds. In one example, a partly concealed 20 day post-fledging bird was fossicking under the basal skirt of a *P. tennantiana* tussock. The adult male rushed up to the tussock and called aggressively. His chick immediately ran out, calling loudly in alarm, and displaying submissively. When the male stopped his aggressive behaviour the youngster ceased displaying and hesitantly resumed its exploration.

Fledglings appeared to be indifferent to each other, although members of the same brood often practised foraging 5 m apart. Most interactions occurred when young birds met unexpectedly. Thus fledgling No. 39 was abruptly woken when his sibling (No. 38) glided down from the canopy and landed on No. 39's resting site. Both chicks ran out of the tussock, faced each other and then displayed submissively. Recognition followed five seconds later, both stopped displaying and began to forage. On other occasions, two youngsters momentarily begged and then peered hesitantly at each other before resuming their foraging-exploring behaviour. Aggressive behaviour was first noted in fledglings 37 days off the nest. For example, two young of Colony 1 territory (1970-71) were foraging independently, but met as they rounded a rock outcrop on the territory border. One bird chased the other, who displayed submissively. The chase extended over 3 m, then both birds stopped and hesitantly peered at one another for about eight seconds. A diagram of all interactions seen to occur between a fledgling and any other fernbird is shown in Figure 15, Chapter 3.
DEVELOPMENT OF THE YOUNG FROM FLEDGING TO INDEPENDENCE

The records used here are compiled from the dossiers of 37 fledglings that were followed for 40 more days after leaving the nest. The number of chicks, from which descriptions of each stage of development are recorded, is signified by \( N = \) at the start of each account. Although many details of body plumage and behaviour were recorded, only those features indicating the relative age of the young have been included here. The behaviour records indicate the earlier sighting of a particular activity, e.g. aggressive behaviour of the young. Some of these activities may occur at an earlier age, but I did not see them.

**Physical development**

**Age 21 days (fledging day) \( N = 10 \)**

Newly fledged fernbirds resemble nestlings 19 or more days old, except that the former have longer tails and wings (Figure 33). The young bird's bill is light grey-brown with a pale yellow tip, while the basal third of the bill margins is soft and yellow. The gape is yellow along the mandible margins, tending to orange on the tongue and almost red at the back of the throat. Three black spots remain on the tongue. The chick's feet and legs are pale grey-brown, and its breast plumage is much less boldly marked than an adult's. The breast of a fledgling is very pale brown, with diffuse spots of light to medium chocolate brown in the central areas of contour feathers. These spotted feathers are concentrated in the lateral regions of the throat and upper breast.

Young birds at this age have short tails with a square-ended appearance as the rectrices are of equal length and have rounded tips. In comparison the tail of an adult has the following shape. The innermost pair of rectrices is longest, with lateral pairs being progressively shorter. The rectrices of adults have pointed tips unless they have undergone considerable abrasion.

For the next few days there is little change in the appearance of fledglings except that their tails grow longer (see Figure 34).
Figure 33: Newly fledged fernbird.

This bird was 23 days old. Note the short tail, short bill, indistinct superciliary streak and erupting flight feathers.
Age 29 (21 + 8) days (N = 6)

Such young are characterized by tails of about 30 - 35 mm long (one-third adult length) and by a change of the soft, yellow material lining the basal margins of the mandibles into pale-grey, hardened bill. The tail still retains its square-ended appearance as all the rectrices remain of similar length and have rounded tips.

Age 35 (21 + 14) days (N = 11)

The fledgling's tail is two-thirds of the mean adult length, viz. about 60 mm long (Figure 31); the six central rectrices are of similar length, but the shorter outer two pairs are already fully grown. Slight abrasion of the distal 2 or 3 mm of the rectrices has occurred in the tails of some chicks.

Age 37 (21 + 16) days (N = 4)

The breast plumage is paler (pale cream-brown) than in newly fledged birds, and the breast spots more distinct. The mouth is pink to red, as in adults, but three diffuse black spots remain on the tongue.

Age 36 (21 + 25) days (N = 3)

The tail is about 70 to 75 mm long, and only the central two pairs of rectrices remain of similar length. All still have rounded, rather than pointed, tips. The black spots have disappeared from the tongue.

Age 53 (21 + 32) days (N = 4)

The crown feathers have started to turn slightly reddish brown, in contrast to the dorsal plumage which is dark brown.

Age 58 (21 + 37) days (N = 7)

The central pair of rectrices is slightly longer than the next pair, and all rectrices have slightly pointed, rather than rounded tips.

Age 76 (21 + 55) days (N = 6)

The tail has now attained adult proportions, and all rectrices have pointed tips which are variously abraded.
Behavioural development

Age 21 days (N = 10)

Chicks peck at many objects with no evident aim. Most of the time they stand in a hunched posture with their feathers fluffed, frequently calling "Tsip" for periods of over 30 minutes at up to 40 calls per minute. One chick lunged at a fly that was buzzing by.

Age 24 (21 + 3) days (N = 5)

The young birds are now a little more active when alone than previously. They investigate loose vegetation, bark and forest floor litter, within 10 m of the nest. Most of the time they stay within 2 m of the ground, although they make the occasional flight up into the forest canopy. On several occasions a fledgling was seen to fly up to, and try to settle on the parent's back, when the latter first appeared. The young may approach or ignore quiet observers, but they are much more frightened than adults by sudden movements or the crackling of twigs.

Age 27 (21 + 6) days (N = 8)

Chicks of this age lift leaves with their feet and peck in the area exposed. Others hop about alone, some distance from their birth site. Exceptionally, one fledgling was seen exploring 35 m from its nest. However, most young birds not on foraging sorties are within 5 or 10 m of their adopted resting sites.

Age 31 (21 + 10) days (N = 3)

The chicks respond to adult calls with typical adult female duet responses of "Tchep", "Teart", and "Tchip", as well as the typical fledgling "Tsip".

Age 35 (21 + 14) days (N = 9)

Young birds now sun- and dust-bathe in typical adult fashion. They still have difficulty in recognising food as such. For example, one novice was snapping at flies in Poa around the Biological Station. Although it caught several it did not eat them, but discarded them after they had ceased moving.

The chicks can at this age duplicate foraging actions of adults. For instance they can fly up, to land upside down
on the undersurfaces of reclining *Olearia* trunks.

**Age 42 (21 + 21) days (N = 16)**

The young birds may now eat the prey they catch. One fledgling was so engrossed in catching flies that it foraged for over five minutes within 1 m of me. Over a period of 30 minutes it caught 10 blowflies in 73 lunges (adults capture *Calliphora huttoni* on sea-lions at a rate of 7 to 10 flies per 10 lunges). This bird had adopted the typical adult habit of walking through the leafy heads of *Poa* tussocks to flush blowflies which then aimlessly flew about. Those flies that came within range were snapped at.

**Age 46 (21 + 25) days (N = 3)**

Three offspring (of Nest 16, 1971-72) were heard calling "Thirao", a long call with falling cadence, while fossicking. Other calls heard were "Thoo" (long call, rising cadence) and "Theoo". This last call was not quite like adult male's "Thee-oo" call, as the fledgling's version was slurred together.

Although fledglings eat food they catch, they readily abandon their efforts when their parents appear and they follow them out on a foraging sortie.

**Age 54 (21 + 33) days (N = 12)**

Typical adult male "Thee-oo" calls are infrequently uttered by some foraging chicks. Only rarely do they follow their parents for foraging sorties, and when they do, they usually lose interest within five minutes and go their own way. Twelve offspring were not fed by their parents during the two hours that I watched them.

**Age 56 (21 + 35) to 61 (21 + 40) days (N = 38)**

All the young are probably independent of their parents by this age, and are thus classified as juveniles. Twenty-three of the 37 young observed since nest desertion foraged alone outside their parent's territory, although they also wandered through the parental territory. The other 15 young may have foraged outside their parent's territory but they were hard to find and I did not observe them elsewhere.

The 23 frequently observed young birds seemed indifferent to the appearance of their parents, now and later.
In grams

BILL LENGTH in mm

WING LENGTH in mm

TAIL LENGTH in mm

TARSUS LENGTH in mm

MID TOE LENGTH in mm
Figure 34: Growth rates of fledglings.

Brackets to the right of each graph show the maximum (upper horizontal bar), mean (middle bar) and minimum (lower bar) measurements of the appropriate adult parameters.

The solid triangles indicate the growth of the abnormal nestling.
To sum up, young birds generally become increasingly more interested in their surroundings, and once they begin to catch food, tend to rely on their parents less. There are no signs that the adults urge their young to leave: the young go when they are ready. Adults make no attempt to resume breeding (contra Stead, 1948) or to moult, until their young cease to follow or to beg from them. Before final independence the young catch their own food for at least two to two and a half weeks.

THE GROWTH OF FLEDDGLINGS AND JUVENILES

Many attempts were made to capture and measure known-age young after they had fledged. Eighteen captures were made by hand net and standard measurements taken (as in Chapter 2) and graphed (Figure 34).

After fledging, increases in bill length do not appear to follow any well defined growth pattern (Figure 34). The only bill length of adult proportions is recorded for a bird 62 days out of the nest (or 83 days old). All other characters measured show similar trends (Figure 34), except for the wing and tail which increase rapidly in length during the first 15 and 30 days after fledging, respectively. The length of the tail is the most accurate single measurement for assessing age after fledging. After the young have been out of the nest for 30 days other less accurate methods were used for indicating a young bird's probable age, viz. behaviour, and occurrence of the plumage patterns described previously.

A SUMMARY OF DIFFERENCES IN APPEARANCE BETWEEN ADULTS AND YOUNG

Young birds up to 16 days after nest desertion have very little spotting on their breasts, and any spots present are light brown and diffuse. At 26 days post-fledging breast spotting is well defined only along the sides of the lower throat and upper breast regions, where the pale cream-brown breast plumage merges into the darker flank plumage. Some
localized smudgy patches on the middle of the lower throat and upper breast regions probably develop later into well defined adult spots.

At 55 days post-fledging, the juvenile's breast plumage is similar to an adult's, and by 76 days after nest desertion is identical to an adult in the breeding season, i.e. the ventral parts are palest centrally (cream) from under the bill down to the tail, and slightly browner laterally (very pale cinnamon brown). The adult breast area is distinctly bordered by the darker flank plumage. The black spots on the breast are more concentrated at the margins of the pale breast area, and centrally from the throat to upper breast. Very few spots are present on the belly.

Fledgling and younger juvenile plumage is darker and duller than that of adults in the breeding season, but the colour of juvenile plumage tends towards the adult's condition with increasing age. The plumage of juveniles, 62 days out of the nest, has the typical adult sheen, though this is not properly developed in young 55 days after fledging. The dorsal feathers of an adult have brown-black centres with a rufous background tending to golden brown at the feather margins. The same feathers of newly fledged young are also dark brown-black centrally, but the remainder of the feather is dark rufous, and lacks the lighter margins.

The superciliary streak of a juvenile is not well defined as in an adult. In the newly fledged young this streak is a short, indistinct, pale tan stripe, but it appears to develop at a similar rate to the paling of breast plumage and darkening of breast spots. Thus for a juvenile 80 days after nest desertion the nearly white superciliary streak extends from just in front of the eye to about 8 mm behind the eye, whilst in an adult the streak begins at the nostril and fades out some 10 to 12 mm past the eye.

The tail feathers are round tipped in young up to the age of 30 to 37 days post-fledging but in young 40 days off the nest, the tail tips have become pointed and even considerably abraded in some individuals.

Although reddish tinting on the crown is first discernable 32 days after fledging the crown is not as
conspicuous as an adult's even in birds 80 days out of the nest. This is partly due to the surrounding head and dorso-lateral plumage of the young being slightly darker (i.e. less contrasting) in comparison to a pre-moult adult's more golden brown plumage. However, juveniles more than 55 days out of the nest are difficult to distinguish from freshly moulted adults.

Thus younger birds can be separated from adults by the former having more diffuse markings and duller plumage. Younger birds also tend to be more jerky in their movements, and more curious, yet wary, of novel situations. I could not differentiate the sexes of live juveniles during my stay at the Snares.

POST-BREEDING MOULT

No birds were seen in post breeding moult before my departure (11 March 1971) in the first season, but post-breeding moult was observed in the second season. While traversing the 2.00 km line transect (described in Chapter 10), adults were scored as whether in moult, or not in moult. Birds were judged to be in moult if there were gaps in the wing feathers, or in the tail. Such birds also had a tattered appearance not seen in non-moulting animals. During 4-11 February 1972, there were no adults in apparent moult, of 80 counted. However, by 29 February - 7 March 1972, there were 126 adults in obvious moult (78%) out of 161 adults counted.

In my study area the post-breeding moult occurred first in those adults that had raised no offspring, or whose young had been independent for some time. Adults with dependent young retained their breeding plumage until their young were independent. The old plumage is replaced gradually by slightly darker plumage which looks very similar to that of advanced juveniles. The new tail feathers of adults are similar in shape, and go through a similar growth pattern, to that described for fledglings. Observation of marked individuals indicates that moult takes five to six weeks per bird. The exact sequence of feather moult was not recorded.
DISPERSION OF ADULTS AND YOUNG

Although juveniles may wander from their parents' territory, the latter appears to be the activity centre of their range. By mid-February in both seasons there was an increasing influx of unbanded young into the main study area, and, in the second season, moulting adults also wandered off their territories quite frequently. For example, Male 32, of "The Huts" territory, and the "Tern Point" territory pair were often seen foraging from Station Point to Seal Point and up towards Colony 5 when they were in moult. When on their own territories they still evicted intruders but usually not very vigorously.

Observations made by D.S. and C.J. Horning during the winter of 1972 indicate that some birds may move as far as 300 m from their territories, though most birds were either on, or within 100 m of their breeding areas.
INTRODUCTION

This chapter considers the breeding biology of fernbirds over two consecutive seasons. Mortality factors are discussed first. This is followed by a section on hatching, nestling and breeding success in relation to clutch size, laying date and first, replacement, and second clutches. A short account of the external factors influencing breeding is given. Conclusions on the clutch size of the Snares Fernbird complete this account on breeding success.

MORTALITY FACTORS

Egg loss

The sources of egg loss are shown in Table 16, and rate of egg loss through the incubation period in Figure 35. Some of the eggs broken or "disappearing" during incubation could also have been infertile and thus the estimate expressed in Table 16 is a minimum. The 20 eggs listed as infertile were incubated for at least 15 days and proved to be rotten when broken open for examination.

Other factors that influence egg loss probably include the chilling of eggs during sudden cold periods associated with passing rain squalls, and the activities of Sooty Shearwaters and Hooker's Sea-lions. The effect of these latter two influences is discussed in the External factors influencing breeding success, at the end of this chapter. Summing the two seasons' data, out of 32 clutches found before any eggs hatched, 13 complete clutches (41%) were lost through infertility, lack of incubation, egg breakage or embryo death.
NO. OF 40 EGGS OR YOUNG ALIVE 20

Egg Phase 16 11 Nestling Phase 22 18 Fledgling Phase 36 Young Independent
Figure 35: Survival of reproductive material.

The units on the horizontal axis indicate the age in days of eggs, nestlings or fledglings at each stage of development.
Table 16: CAUSES OF EGG LOSS

<table>
<thead>
<tr>
<th>Cause</th>
<th>Count</th>
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</thead>
<tbody>
<tr>
<td>Broken during incubation</td>
<td>9</td>
</tr>
<tr>
<td>Infertile</td>
<td>20</td>
</tr>
<tr>
<td>Deserted, containing embryos</td>
<td>2</td>
</tr>
<tr>
<td>Laid, but not incubated</td>
<td>6</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>37</strong></td>
</tr>
</tbody>
</table>

37 eggs, out of 78 laid.

Nestling mortality

Nestling mortality has been considered only for the young produced from the same 32 clutches mentioned in the section on egg mortality. Survival rate of nestlings is shown in Figure 35. Seventeen nestlings (40.5%) succumbed from the 42 eggs that hatched. Most (76.5%) of this mortality occurred within 10 days of hatching. During this period, nestlings were mainly naked, had poorly developed thermoregulation and required brooding more often than older nestlings.

Table 17: CAUSES OF MORTALITY AMONG NESTLINGS

<table>
<thead>
<tr>
<th>Cause</th>
<th>Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Found mutilated, possibly killed by parents</td>
<td>6</td>
</tr>
<tr>
<td>Ruptured gut</td>
<td>1</td>
</tr>
<tr>
<td>Chilling</td>
<td>1</td>
</tr>
<tr>
<td>Nest Collapse</td>
<td>3</td>
</tr>
<tr>
<td>Unknown causes</td>
<td>6</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>17</strong></td>
</tr>
</tbody>
</table>

17 nestlings, out of 42 hatched.
The sources of nestling mortality are shown on Table 17. Nestlings that died of unknown causes probably succumbed through chilling or physiological malfunction, as there were no signs of external or internal damage. Nestling mutilation was the most common of the known mortality factors, and it eliminated three broods containing one, two and three nestlings respectively. The causes of mutilation were not known. For the first two broods there appeared to be no reason for the mutilation. In the third brood of three nestlings both parents were nervous of people and sea-lions moving along the track a few metres from their nest. The most plausible explanation for the mutilation seems to be that it was carried out by the adults during a moment of distress: any opportunistic predators would have eaten the young.

Nest collapse caused the death of a three-nestling brood probably due to shearwater activities. It was not likely that nests would have collapsed as the result of activities of the fernbirds, for all nests that I found were quite strongly built on solid foundations.

Only one nestling was known to have died from chilling. This occurred during a sudden 2.5°C drop in air temperature (within five minutes) as a short rain squall passed by, and the seven-day old nestling was unbrouded. This sudden drop in air temperature was not typical at the Snares.

Another nestling died from a ruptured gut within two hours of hatching. The gut could have been ruptured during hatching, or by the activities of an adult while brooding, or changing brooding duty, e.g. gut punctured by an adult's claw.

Fledgling loss

Only one fledgling died within the first 40 days of nest desertion, compared to a gross total of 37 fledglings which survived until independence. The fledgling that died was a freak (see Chapter 6); it was two-thirds normal fledgling weight, was not very alert, and its flattened corpse indicated it died when rolled on by a sea-lion. I was surprised that this bird survived until fledging.

The extremely low mortality after fledging is apparently due to several factors, including the long period of post-fledgling care by the adults (five weeks), the lack
of predators, the abundance of shelter from wind and rain, readily available food, and the equable climate.

In the following sections, there are several observations that I cannot explain due to insufficient data. Therefore, only the main points have been covered and explained as far as possible, and the conclusions are tentative only.

**Effect of laying sequence upon mortality**

A. Upon eggs

Laying sequence has little effect on the chances of first or second laid eggs hatching in two-egg clutches, but first laid eggs of three-egg clutches have a higher survival than second or third laid eggs (Table 18). The reason for this differential mortality in three-egg clutches is not understood.

**Table 18: EGG MORTALITY WITH ORDER OF LAYING**

<table>
<thead>
<tr>
<th>Laying sequence</th>
<th>1-egg clutch</th>
<th>2-egg clutches</th>
<th>3-egg clutches</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st laid egg</td>
<td>1</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>2nd laid egg</td>
<td>-</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>3rd laid egg</td>
<td>-</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>1(1)</strong></td>
<td><strong>19(36)</strong></td>
<td><strong>17(42)</strong></td>
</tr>
</tbody>
</table>

Note: Numbers in brackets give total number of eggs laid in that clutch size.
B. Upon nestlings

Mortality is equally low for first and second hatched nestlings derived from two-egg clutches (Table 19). However, the first and third hatched nestlings from three-egg clutches had a higher mortality than second hatched nestlings. Again, the reason for this pattern is not understood, but the sample may be too small to exhibit clearly the overall mortality pattern.

Table 19: NESTLING MORTALITY WITH ORDER OF LAYING

<table>
<thead>
<tr>
<th>Laying sequence</th>
<th>2-egg clutches</th>
<th>3-egg clutches</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st laid</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>2nd laid</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>3rd laid</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Total nestlings lost</td>
<td>2</td>
<td>17</td>
</tr>
</tbody>
</table>

For some birds that have an uncertain food supply, such as owls, storks or eagles (Ward, 1965:348) and swifts (Lack and Lack, 1952) it has been found that the first hatched nestlings have a better chance of survival than subsequent nestlings, as many more young are produced than can be fed, except under unusually favourable conditions. "The youngest member, or members, of the brood can only obtain food when their much larger nest mates are satisfied; if food is short they die at an early age and the survivors continue normal development" (Ward, 1965:348).

This trend is not exhibited amongst fernbird nestlings, indicating that all nestlings were well fed, and thus food supply was plentiful. Further evidence for this is given by the nestling growth curves (Chapter 6, Figure 32)
where all nestlings within a brood generally have similar increases in weight.

C. Upon total mortality of young.

There is no preferential survival of juveniles produced from first, second or third laid eggs when egg, nestling, and fledgling mortality are summed (Table 20). This further suggests that all chicks within a brood, and fledglings, are adequately fed. In those nests where nestlings die, the whole brood is more commonly lost (seven broods) within a few days, rather than one nestling (three broods) or two nestlings (no broods), from a total of 21 broods of known size.

<table>
<thead>
<tr>
<th>Laying sequence</th>
<th>2-egg clutches</th>
<th>3-egg clutches</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st laid eggs</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>2nd laid eggs</td>
<td>10</td>
<td>12</td>
</tr>
<tr>
<td>3rd laid eggs</td>
<td>-</td>
<td>12</td>
</tr>
<tr>
<td>Total reproductive material lost</td>
<td>21 (36) 58% loss</td>
<td>35 (42) 83% loss</td>
</tr>
</tbody>
</table>

Note: Numbers in brackets indicate total number of eggs laid in that clutch size.

**Influence of human disturbance on mortality**

It is difficult to measure the influence of human disturbance on the mortality of breeding fernbirds. However, I do not think that human activities during this study had much effect on the breeding success. Most adults silently left their nests when I came within 2 m, and returned soon after I had moved off a few metres. A few pairs of birds at
first appeared nervous of my presence near their nests and therefore I checked only how many eggs or nestlings were present. After a few days of regular visits the adults generally lingered in cover near their nests until I had gone, and then immediately resumed incubating or brooding. Incubating fernbirds reacted similarly to sea-lions or humans moving close by their nests. At first the birds sat up in alert fashion, cocking their heads about, and usually left the nests only when the adjacent vegetation was disturbed. Those birds with nests situated alongside commonly used sea-lion and human paths were generally very tolerant of mammals moving by.

Further indication of the birds’ tolerance to regular disturbances is shown by the fact that only one nestling (a freak), out of 10 regularly handled, died (see Nestling growth, Chapter 6).

HATCHING, NESTLING AND BREEDING SUCCESS
IN RELATION TO CLUTCH SIZE

During the 1970-71 season, hatching success for two- and three-egg clutches was similar, but nestling, and consequently breeding success in two-egg clutches was twice that of three-egg clutches (Table 21). It is not likely that lower nesting success in three-egg clutches was due to starvation of nestlings as this would have resulted in higher mortality of younger nestlings in the brood, thereby producing more first hatched young that developed into juveniles. This did not occur (Table 20).

However, adults with three nestling broods spent less time per hour on the nest, than those whose nests contained one or two nestlings (see Chapter 6). Three nestling broods housed in relatively open nests may be more susceptible to cooling during cold rain squalls than nestlings in smaller broods who would be brooded more often.

When data from the 1971-72 season are examined, difficulties arise in interpretation. While hatching, nestling and breeding success for three-egg clutches are similar to those recorded for 1970-71, there is a considerable difference in these parameters between the two seasons for two-
Table 21: HATCHING, NESTLING AND BREEDING SUCCESS IN RELATION TO CLUTCH SIZE

<table>
<thead>
<tr>
<th></th>
<th>Hatching success</th>
<th>Nestling success</th>
<th>Breeding success</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. 1970-71</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-egg clutches</td>
<td>65.0%</td>
<td>84.6%</td>
<td>55.0%</td>
</tr>
<tr>
<td>3-egg clutches</td>
<td>66.0%</td>
<td>40.0%</td>
<td>26.6%</td>
</tr>
<tr>
<td>Data based on</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10, two-egg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>clutches</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5, three-egg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>clutches</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>B. 1971-72</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-egg clutches</td>
<td>25.0%</td>
<td>100.0%</td>
<td>25.0%</td>
</tr>
<tr>
<td>3-egg clutches</td>
<td>55.5%</td>
<td>40.0%</td>
<td>22.2%</td>
</tr>
<tr>
<td>Data based on</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8, two-egg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>clutches</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9, three-egg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>clutches</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>C. Both Seasons</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-egg clutches</td>
<td>47.3%</td>
<td>88.3%</td>
<td>41.8%</td>
</tr>
<tr>
<td>3-egg clutches</td>
<td>59.5%</td>
<td>40.0%</td>
<td>23.8%</td>
</tr>
<tr>
<td><strong>D. Total of all 32</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>clutches (78 eggs)</td>
<td>53.9%</td>
<td>59.5%</td>
<td>32.1%</td>
</tr>
</tbody>
</table>

Note: Hatching success = no. nestlings produced/no. of eggs produced x 100.

Nestling success = no. of nestlings fledged/no. of nestlings produced x 100.

Breeding success = no. of nestlings fledged/no. of eggs produced x 100.
egg clutches.

In 1971-72, insects were noticeably less abundant (D.S. Horning, pers. comm. and pers. obs.), but there were more three-egg clutches produced (9) than in 1970-71 (5). One would have expected that in years of higher insect abundance three-egg clutches would predominate over two-egg clutches, rather than the reverse, if breeding of the Snares Fernbird is directly related to raising the maximum number of young on the given food resources. Possibly the decrease in food abundance was of little influence because food was actually in excess of requirements in both seasons.

HATCHING, NESTLING AND BREEDING SUCCESS IN RELATION TO LAYING DATE

In both seasons the highest hatching, nestling and breeding successes were obtained in November, and lowest successes in these parameters occurred in December (Table 22). There were considerable monthly variations within each season, and also between the same month in two seasons. Most first clutches were laid in November, perhaps by more experienced breeders.

BREEDING SUCCESS IN RELATION TO FIRST, REPLACEMENT AND SECOND CLUTCHES

Replacement and second clutches were more successful than first clutches, with second clutches having the greatest success (Table 23). Data from Table 23 are limited to known clutch sizes only. The success of second clutches is further illustrated by the birds of the 1971-72 Seal Point territories. Although the number of eggs laid, and the original number of nestlings hatched from their second clutches is not known, both pairs fledged two second clutch offspring each, so they had at least 66.6% and possibly 100% success.

The higher breeding success of fernbird replacement and second clutches compared with first clutches, contrasts with results for other passerines where food supply during breeding
Table 22: HATCHING, NESTLING AND BREEDING SUCCESS IN RELATION TO LAYING DATE

<table>
<thead>
<tr>
<th></th>
<th>No. eggs laid</th>
<th>Hatching Success (%)</th>
<th>Nestling Success (%)</th>
<th>Breeding Success (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. 1970-71</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>4</td>
<td>100</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>December</td>
<td>18</td>
<td>61</td>
<td>55</td>
<td>33</td>
</tr>
<tr>
<td>January</td>
<td>8</td>
<td>88</td>
<td>86</td>
<td>75</td>
</tr>
<tr>
<td>February</td>
<td>7</td>
<td>57</td>
<td>75</td>
<td>43</td>
</tr>
<tr>
<td><strong>B. 1971-72</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>3</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>December</td>
<td>10</td>
<td>40</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>January</td>
<td>20</td>
<td>60</td>
<td>50</td>
<td>30</td>
</tr>
<tr>
<td>February</td>
<td>2</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td><strong>C. Both Seasons</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>7</td>
<td>100</td>
<td>71</td>
<td>71</td>
</tr>
<tr>
<td>December</td>
<td>28</td>
<td>54</td>
<td>40</td>
<td>21</td>
</tr>
<tr>
<td>January</td>
<td>28</td>
<td>68</td>
<td>63</td>
<td>43</td>
</tr>
<tr>
<td>February</td>
<td>9</td>
<td>67</td>
<td>50</td>
<td>33</td>
</tr>
</tbody>
</table>
Table 23: BREEDING SUCCESS IN RELATION TO FIRST, REPLACEMENT AND SECOND CLUTCHES

<table>
<thead>
<tr>
<th>Clutches Type</th>
<th>Eggs</th>
<th>Clutches</th>
<th>Hatching Success (%)</th>
<th>Nestling Success (%)</th>
<th>Breeding Success (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A: 1970-71</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st clutches</td>
<td>23</td>
<td>10</td>
<td>65.2</td>
<td>53.3</td>
<td>34.8</td>
</tr>
<tr>
<td>Replacement</td>
<td>14</td>
<td>6</td>
<td>71.3</td>
<td>80.0</td>
<td>57.2</td>
</tr>
<tr>
<td>2nd clutches</td>
<td>2</td>
<td>1</td>
<td>50.0</td>
<td>100.0</td>
<td>50.0</td>
</tr>
<tr>
<td>B: 1971-72</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st clutches</td>
<td>33</td>
<td>13</td>
<td>45.5</td>
<td>53.3</td>
<td>24.3</td>
</tr>
<tr>
<td>Replacement</td>
<td>11</td>
<td>4</td>
<td>45.5</td>
<td>60.0</td>
<td>27.3</td>
</tr>
<tr>
<td>2nd clutches</td>
<td>2</td>
<td>1</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>C: Both Seasons</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st clutches</td>
<td>56</td>
<td>23</td>
<td>53.6</td>
<td>53.3</td>
<td>28.6</td>
</tr>
<tr>
<td>Replacement</td>
<td>25</td>
<td>10</td>
<td>60.0</td>
<td>73.3</td>
<td>44.0</td>
</tr>
<tr>
<td>2nd clutches</td>
<td>4</td>
<td>2</td>
<td>75.0</td>
<td>100.0</td>
<td>75.0</td>
</tr>
</tbody>
</table>

becomes restricted. Lack, Gibb and Owen (1957) working on Great Tits, and Dunnet's (1955) work on starlings, demonstrated that replacement and second broods were produced under less favourable breeding conditions due to decreased food availability. Consequently breeding success was much lower than in earlier broods when food was more plentiful. The food supply of fernbirds, however, appears to remain adequate for later breeders in the season.

EXTERNAL FACTORS INFLUENCING BREEDING SUCCESS

Both Hooker's Sea-lions and Sooty Shearwaters influenced the breeding success of fernbirds. Each evening, millions of shearwaters returned to the Snares and crash-landed heavily at high speed. Each dawn a similar multitude of shearwaters departed from traditional launching sites.
overlooking the sea. In the process they clambered onto ferns, tussocks and rock outcrops to gain early height for take-off, and then often crash-landed again before finally becoming airborne. Activity on this scale posed grave threats to exposed fernbird nests.

Seven nests (out of 50 found) appeared to have no protection from Sooty Shearwater activities and those nests built on the Poa slope, Punui Bay (a favoured shearwater landing and launching site) were placed at least 0.2 m into the heads of Poa tennantiana tussocks. However, one of the nests on Poa slope collapsed, as it was semi-exposed on the northern side of the tussock and was probably struck by a landing shearwater.

Hooker's Sea-lions hauled out from the sea and sought out flat areas near the east coast. They often rolled about whilst asleep, scratching and rubbing themselves against the vegetation. Nests 2 and 3, 1970-71 were completely devastated by a bull sea-lion, although both sites had been deserted for a few weeks. Two other nests were threatened while the birds continued incubating. Another four nests were situated on often frequented sea-lion "highways". Although the sea-lions usually brushed the nesting vegetation of these latter nests while passing by, the nests were quite safe as they were set above the ground and protected by stout overhanging branches.

CONCLUSIONS ON THE CLUTCH SIZE OF THE SNARES FERNBIRD

The most widely accepted theory on clutch size is that it is adapted to limited food supply (Lack, 1966) and that parents raise the maximum number of young possible. A great deal of evidence indicates that clutch size, or subsequent brood size, varies directly with food availability, and that the breeding season is closely linked with the period of maximum food availability, e.g. Lack, Gibb and Owen (1957), Lack (1966), Southern (1970). In these circumstances, Lack's thesis provides a good explanation of average clutch size and its variations throughout the years in many birds.

Data collected during this study suggest that in the
case of the Snares Fernbird, clutch size is not adapted to producing the maximum number of young that can be fed in each breeding season. This conclusion is based on the following points. Although insects were much more abundant in the first season (D.S. Horning, pers. comm., and pers. obs.), there was little difference in the nestling and fledgling success between the two seasons. Also, in the second season three-egg clutches were slightly more plentiful than two-egg clutches (compare with the first season, Table 21) and produced more surviving offspring per clutch than did two-egg clutches. If food availability does limit the number of surviving offspring, surely three-egg clutches would have proved less productive than two-egg clutches in the second season. It would appear then that clutch size is not directly related to food availability.

Clutch size of the Snares Fernbird is probably low due to the stable environment on this small oceanic island group. The matter is further discussed in Chapter 10.
CHAPTER 9

FEEDING BIOLOGY

INTRODUCTION

The methods employed and the areas searched during foraging are recorded. A list of prey species eaten is given. Descriptions of four postures associated with feeding complete this account.

FORAGING METHODS

Fernbirds usually forage alone, but a territorial pair, or an adult with young, sometimes feed together. Fernbirds search for food in sites as diverse as floating kelp fronds in the littoral zone at low tide, to the outer surface of the forest canopy on calmer days. The methods employed while foraging in different situations are outlined below.

Fernbirds spend much of their time foraging in areas of detritus. Detritus includes leaf litter on the forest floor, washed-up debris on the beaches about Boat Harbour and the West Coast, and petrel bones in skua middens. Dead leaves often become concentrated into shallow basins on the floor of the open forest, especially after periods of gales. Often the leafy "carpet" is 0.2 m deep and fernbirds commonly rummage through the loose leaves. A bird first grasps the edge of a leaf with its foot and raises the leaf laterally. The uncovered area is scrutinized rapidly and often the bird pecks about in the exposed area to disturb potential prey. If nothing attracts the hunter's attention, it releases the leaf which falls back to its former position. This behaviour is often repeated, first with one foot, then the other, raising and dropping leaves in rapid succession.

If something of interest is seen, leaves, twigs and other debris are flicked or thrown, sometimes for over half a
metre, by alternate strokes of the left and right legs. Loose clods of peat, or small stones are pushed aside, or raked over with the feet to expose prey. As a bird moves along throwing material aside it often clears a path through the leaf litter down to the bare peat. The cleared litter forms small mounds bordering these pathways. A bird may disappear completely under the leaves and its position is marked by a small, localized, trembling hummock of leaves from the rear of which loose material is vigorously tossed aside. At odd intervals during burrowing, the bird pushes its head above the leaf litter, looks about briefly and then resubmerges.

In penguin colonies, Fernbirds feed on maggots and flies (Calliphora spp) around dead penguins. Even though maggots are plentiful the birds take only a few, but concentrate on adult flies buzzing above the debris and mud. Fernbirds spend much time whilst in these colonies fossicking amongst the loose twigs and leaf litter that constitute penguin nests. Similarly, in streams draining penguin colonies, Fernbirds turn sticks, stones and plant fragments over in search of food. On occasions, the birds eat food spilt by adult penguins while feeding their chicks (J. Warham, pers. comm.). However, they do not appear to use penguin colonies as preferential foraging sites as suggested by Stead (1948).

In open parts of the forest, Fernbirds spend most of their time on the ground searching through the abundant petrel breeding burrows for weevils and wetas. Birds usually remain 15 to 30 seconds in each burrow although one bird stayed underground for at least four minutes.

When hunting amongst mat plants (e.g. Tillea moschata, Callitriche antarctica, Stellaria media, S. decipiens) Fernbirds either strut about on top of the mats (see Figure 39) or delve down among the basal vegetation, some 0.2 m below. Birds on top of the mats search for insects flying just above the vegetation or for others resting on top of the plants. Foraging behaviour amongst the basal vegetation of these mats is similar to that adopted when birds burrow through piles of Olearia leaves on the forest floor. Plant stems are grasped with one or both feet, parted, and the bird
Figure 36: Foraging attitudes.
peers down into the exposed lower regions of the plants. The plants may then be parted further down to allow the bird to hop into the separated vegetation and probe about with its bill. While the bird remains in the lower vegetation, overlying material slowly springs back to its former position so that often only the tail of the bird is visible. The searching bird sometimes tunnels through the loosely packed lower vegetation, leaving the upper vegetation undisturbed, and only small tremblings indicate the bird's whereabouts.

The loose skirt of dead leaves drooped over the basal regions of *P. tennantiana* tussocks provides another commonly frequented foraging area. A bird climbs onto the skirt and pushes it aside with one or both feet to expose the tussock's well protected base (Figure 36, c). One foot is sometimes used for flicking or pushing aside sections of the mantle. The bird may even circumnavigate the tussock base while it investigates all the dead leaves for prey. While pushing aside loose material the bird may move under it to examine the tussock's stalk-like base for arthropods. The now-concealed bird also shakes the mantle from inside to flush insects. Similar food seeking behaviour is adopted under *P. astonii* tussock heads.

Birds search for prey from around the exposed root systems of *Olearia* and *Senecio* trees up into the leaf axils amongst the forest canopy. However, most foraging on *Olearia* and *Senecio* is carried out on the trunk or larger branches. On *Hebe* shrubs though, birds concentrate on the outer surfaces of thickets, where most of the flies are found.

On trees and shrubs, birds move mainly in a strutting, stooped fashion over branches, with their heads jerking continually up and down or from side to side while examining crevices in the vegetation. Birds walk up near-vertical branches and tree trunks either directly or sideways. Where two branches grow close together the bird grasps a branch with each foot and walks up or down examining the bark for food. This stance is frequently adopted when a bird wishes to examine debris lodged in the crutch of a branch system.

Birds also cling upside down looking for prey on overhanging parts of the trees, but they apparently cannot
walk along in this position. Several methods are employed to examine overhanging places. Overhangs near the ground, or less than 0.1 m above other branches can be searched by the bird standing underneath and pecking into crevices to dislodge insects. Slightly higher overhangs are investigated by the bird standing on tip toe, stretching fully upwards and rocking from side to side.

Those overhangs not near lower perches are examined by other methods. Birds sometimes jump from lower sites and peck at loose debris thrown up into the bark by burrowing shearwaters. On occasions these leaps are repeated several times, but more often birds fly up and land upside down by executing a sudden backflip before landing.

While hanging upside down, food is sought in the same fashion as when on level branches, and the sound of the bird's claws digging into the bark is sometimes audible up to 5 m. When scratching off the loose bark with one foot, an inverted bird flaps its wings to maintain its balance.

As soon as a bird has finished its upside-down inspection it releases itself, flips over to right itself and then glides down on to a suitable perch, or the ground. Birds can right themselves after falling less than 0.1 m.

If a bird stands on the side of a branch it can usually reach the undersurface of the branch and still clamber back on top of the branch when it has finished looking about (Figure 35 a).

In the other vegetation (ferns, Carex, heads of P. astonii, P. tennantiana, P. poppelwellii and P. annua) birds thread their way through even the closest set stems with ease, grasping surrounding stems with either foot. Birds adopt a sleek, streamlined posture similar to the slink (see below). As the foliage becomes more open (at the end of fern fronds) birds tend to adopt a more upright stance. Many crevices are examined cursorily as the birds move by.

In the main study area, birds whose territories extended to the sea sometimes foraged extensively on the rocky lichen-encrusted supralittoral zone. The following data were collected by K.J. Sainsbury from 14 minutes' observation of Bird 32, in 1971-72. On average, this bird had 19.7 successful strikes (i.e. food caught) per minute,
Figure 37: Fernbird foraging on a sea-lion.
Figure 38: Fernbird resting on a sea-lion.
and he was consuming mainly beetle species found on the supralittoral lichen down to minute mites less than 0.5 mm long. He also foraged along the small crevices found along quartz veins and tension gashes in the weathered granite basement rock. He was ignoring all flies, even though several times he ran through clouds of Calliphorids flying or settled on seal and sea-lion feces.

At other times (pers. obs.) fernbirds ignore all the minute lichen dwelling arthropods and concentrate on flies, or forage through small patches of Tillea or Callitriche growing in hollows in the granite. This indicates that fernbirds tend to concentrate on one form of prey at a time and ignore all others. This specific search image (Tinbergen, 1960) may allow for more efficient foraging instead of chasing all manner of prey that come their way and consequently having to rapidly change their hunting techniques.

Fernbirds sometimes roam in the Durvillea antarctica (bull kelp) zone at low tide, grasping smaller fronds and lifting them with their feet in the same fashion described for Olearia leaves. On the boulder beaches of Sinkhole and Sinkhole Gut (west coast) fernbirds often run over washed up kelp, either snapping at the adult coelopid flies buzzing about above the seaweed, or digging into the kelp for larvae. In the latter two sites, fernbirds hunt the large red marine amphipods (Orchestia aucklandiae) which are found between the boulders and crawling over washed up flotsam dumped by westerly swells. On the east coast, exposed sea lettuce and coralline algae on Seal Point and Station Cove are also examined. In steep, cliff areas (e.g. the walls of Sinkhole and Sinkhole Gut) the birds run along narrow rock ledges, digging amongst any accumulated debris for pseudoscorpions, mites, harvestmen and terrestrial amphipods.

Blowflies (Calliphora huttoni) are plentiful around fur seals (Arctocephalus forsteri) and sea-lions. The birds hunt mainly for flies on and around sea-lions as they prove less reactive to the birds' activities than do seals. Sea-lions have either no reaction to fernbirds running over them (Figure 37), or they lose interest as soon as they find out what is running over their backs. The birds even search
THE STRUT

THE STOOP

THE SLINK

THE LUNGE
Figure 39: Postures adopted during foraging.
around the muzzle and jowls of sea-lions, picking flies off their snouts. In 35 minutes Bird 9 caught 31 blowflies (Calliphora huttoni) in 36 attempts. Birds also forage close to sea-lions that roll and toss about while asleep, but the birds never appear to be in danger of being flattened as they move more rapidly than sea-lions. Several times between bouts of catching flies a fernbird beds down in the thick mane fur of a bull sea-lion and rests (Figure 38).

Fur seals are generally indifferent to fernbirds foraging close by, but are intolerant of birds moving along their backs. Fernbirds that persist in their efforts to run over seals are threatened with snorts, huffs and growls.

Fernbirds use their tails in the following ways during foraging. In situations where the feet are used to lift or dig debris the tail is held on the ground with the rectrices spread 60 to 70 mm like a partly opened fan. When a bird tilts its body laterally to lift an Olearia leaf, the rectrices on the "uphill" side of its body are raised off the ground, but the "downhill" rectrices are pressed down even harder. The rectrices are depressed hardest when the claws are clasped strongly, e.g. while a bird clings to vertical or overhanging surfaces (Figure 36 b). When the bird moves backwards the tail feather shafts are bent and often pushed sideways, skewing the disconnected barbs out of sequence. After the rectrices are lifted off the ground, the barbs soon re-align.

While fernbirds forage in shallow streams or slushy rain-soaked peat, the tail is always held in a horizontal position regardless of the attitude of the bird's body. Usually, in drier sites, the tail is held in line with the body axis, as in the strut, slink and stoop (Figure 39).

**POSTURES ADOPTED DURING FORAGING**

Four postures are frequently used by fernbirds while hunting for prey. The adoption of these postures by a bird appears to occur when it has a high motivation to forage. In all the postures the body plumage is sleeked. The postures are ...
The Strut

This posture was most noticeable when a bird moves about on the tips of *Hebe* branches, on sea-lions and in penguin colonies. The bird adopts an upright posture with its neck extended and the bill declined five to 10 degrees. The legs are almost fully extended, and as the bird walks (does not run) each foot is carefully raised in a "goose-stepping" fashion. As each leg is moved forward, the body and head jerk forwards. When the leg is put down the body and head jerk upright again before another step is taken. Thus, the bird progresses in an upright, jerky walk (Figure 39).

The strut is employed apparently to find the approximate positions of prey, for it is an upright stance and the head is held high, scanning for quarry. The high goose-stepping walk is often hesitant, as if the hunter is in conflict as to which fly to pursue next.

The Slink

In this attitude the bird crouches so that its body, bill and tail lie along a horizontal axis, pointing directly at a victim. The bird appears to be staring and fixing its gaze on one insect only. The legs are moved in the same careful fashion described for the strut, but at a higher speed. Slinking birds usually run, but on occasions walk rapidly.

Slinking is used when prey is sighted and only a few more steps are required to come within striking distance. As the strut changes into the slink the bird often pauses, and does a number of short steps on the spot. It appears that the hunter is trying to get the right footing, and is judging the number of steps required to reach its prey.

The Stoop

Sometimes the strut and slink are combined into an intermediary posture, which I have called the stoop (Figure 39). The body axis is inclined at 30 to 40 degrees to the horizontal (cf. in the strut, 50 to 60 degrees) and the legs are moved in the typical slink-strut fashion. The head is
held forward of the body axis with the bill declined at five degrees, giving a stooped appearance. Stooping birds move mainly in a partly crouched attitude and at a walking pace.

**The Lunge**

Slinking, strutting, or stooping birds suddenly stop walking and then lunge forward. In a vigorous lunge the body is thrust forward and tilted down head first. The tail and wing flick up momentarily to help the bird maintain balance and regain its upright posture. At the furthest extent of the lunge, a loud "snip" is heard as the then opened mandibles are closed.

**FOODS TAKEN**

Fernbirds feed on the largest arthropods present at the Snares (marine amphipods *Orchestia aucklandiae*) down to minute beetles and mites on the supralittoral zone. As there is little need for specialization in feeding methods or food taken (through lack of environmental pressure), probably all arthropods at the Snares falling within this macroscopic size range are eaten. My determination of fernbird diet is based on examination of (1) crop castings of independent birds, (2) crops of dead nestlings, (3) food brought to the nests, and (4) food caught by foraging fledglings, juveniles and adults. A list of prey species eaten is in Table 24.

Of the prey listed, wetas, and especially weevils, form the bulk (over 75%) of the food taken in the forest (pers. obs.). Throughout penguin colonies, *Hebe elliptica*, and the supralittoral zone where seals are, Diptera, especially *Calliphora huttoni*, probably form a significant part of the diet. In Poa meadows, smaller prey such as aphids, small spiders, tipulids, Lepidoptera larvae, pseudoscorpions and harvestmen are probably predominantly taken. This list, along with the methods and sites used in foraging, suggests that the fernbird is an opportunistic feeder, although sometimes it tends to concentrate on one prey until satiated before going after another.

Terrestrial amphipods are taken only occasionally even
Table 24: SOME FOODS OF FERNBIRDS

AHANEAE

Dictynidae, Oramia rubrioides (Hogg).
Three other species, gen et spp. undet.

ORTHOPTERA

Rhaphidophoridae, Insulanoplectron spinosum Richards.
Stenopelmatidae, Zealadosandrus subantarcticus Salmon.

HOMOPTERA

Psyllidae, gen et sp. undet. Common about Senecio stewartiae and Hebe elliptica.

COLEOPTERA

Tenebrionidae, Pseudhelops quadrir~ollis Brown.
Curculionidae, Exeiratus laqueorum Kuschel.
Gromilus laqueorum Kuschel.
Pentarthurum spadiceum Brown.
Phryuixus laqueorum Kuschel.
Oclandius vestitus (Broun).
Anthribidae, Cacophatus propinguus aucklandicus (Brookes)
Staphylinidae, Gen et sp. undet, in shearwater burrows.
Carabidae, Necadema hudsoni
Colydiidae, Pristoderus sp.
Chrysomelidae, Gen et sp; undet, alytra orange with black diagonal stripes.

ACARINA

Several species, gen et spp. undet.

DIPTERA

Tipulidae, Leptotarsus (Macromastix) n.sp, Limouia (Dicranomyia) arthuriana (Alexander).
Mycetophilidae, Zygo~via trifosciata Tonnoir.
Stratiomyidae, Bereis sp. nr. micans (Hutton).
Psychodidae, Gen et sp. undet, on Hebe elliptica
Empididae, Cholopida sp. undet.
Hilarempis sp. undet.
Syrphidae, Helophilus hochstetteri Nowicki.
Syrphus (Melangyra) novaezelandiae MacQuart.
Coelopidae, Chaeto~olopa iittoralis (Hutton).
Coelopa debilis Lamb.
Protocoelopa philpotti Nallock.
Helomyzidae, Allaphyllopsis laquei (Hutton).
Helocclusia antipoda Harrison.
Sciomyzidae, *Polytoma costata* Harrison MS.
Calliphoridae, *Calliphora huttoni* Miller.

*Calliphora* sp. undet.
Muscidae, *Limnophora*, four sp. undet, from *Hebe elliptica*

*Limnophelina* sp.
*Fannia fuliginosa* (Hutton)


**LEPIDOPTERA**

Noctuidae, *Graphnia insignis pagana* Hudson.
Tortricidae, *Planotortrix syntona laqueorum*
Psychidae, *Cryptotheca horningae* MS Dugdale.
Oecophoridae, *Izatha cleariae* Dugdale.


**HEMIPTERA**


*Brachycaudus helichrysi* (Kaltenbach).

**PHALANGIDA**

Several gen et spp. undet.

**HYMENOPTERA**

though they are readily accessible amongst any damp litter. However, those birds with access to marine amphipods crawling over washed up wrack on western boulder beaches, gorged themselves.

Small items of food are picked up and swallowed alive. Larger and tougher prey, e.g. the beetle *Mecodema hudsoni*, wetas, marine amphipods and large weevils (e.g. *Oclandius vestitus*) are dashed on the ground, or against rocks or trees until dead. During this process, the appendages are torn off and sometimes devoured. Most prey are incapacitated within 30 seconds although on one occasion a fernbird continued to knock a large weta *Z. subantarcticus* on the ground for five minutes after it was caught. The weta appeared to have died within 20 seconds of being dragged out of a shearwater burrow. It was held on the ground by the birds' foot and pieces torn off and eaten. Generally, all larger prey are swallowed whole after the appendages have been removed.

Fernbirds have quite acute eyesight for often they run directly 3 to 5 m at stationary tipulids and at moths on cryptic backgrounds and capture them. Only twice in eight month's observations was a fernbird seen to capture prey while it held other food in its mandibles. Otherwise all individual prey are consumed before seeking out new food.
Figure 40: Diagram of transect path around the Main Island.

The solid line represents the transect path, and the dashed line shows the remainder of the track around the Main Island. The figures on the transect path indicate the distance covered from the north beach of Boat Harbour.
CHAPTER 10

POPULATION BIOLOGY

INTRODUCTION

This chapter describes how a population estimate of the Snares Fernbird was made for the 1971-72 breeding season. A brief discussion of the population of the Snares Fernbird, and the survival of adults and young over one year ensues. From this discussion some interesting questions are posed on the mechanisms of population regulation for which, with the present limited information, no precise answers can be given.

POPULATION ESTIMATES

The fernbird population on the Main Island was estimated from periodic counts of birds seen on a line transect. In the 1971-72 season, a 2.00 km transect was marked along the main track around the island (Figure 40). It started beside the north beach of Boat Harbour and was marked at 150 m intervals with fluorescent orange painted tin squares.

After three trial runs each 150 m sector could be traversed at a constant pace (4 minutes ± 15 seconds) which gave sufficient time to search for birds and record their presence. A strip 8 m wide was scrutinized each time, this being the maximum width which could be monitored accurately in the time available. If there was any doubt as to whether a bird had approached within the 8 m strip, I stopped briefly and paced out the distance to its closest position.

The transect was traversed nine times between 4 - 11 February 1972 inclusive, and 15 times during 29 February - 7 March 1972 inclusive, between 1500 to 1730 hrs. Throughout this period the weather remained fine, except for three days of prolonged rain. During the rainy
days no counts were made. The following data were recorded in each traverse: the time at the start, at each 150 m interval, and at the end of the transect and the number of adult and young fernbirds seen in each 150 m sector within the 8 m strip. The summarized data for each transect are presented in Table 25.

Table 25: SUMMARIZED TRANSECT DATA: SNARES FERNBIRD

<table>
<thead>
<tr>
<th></th>
<th>4 - 11 Feb 1972</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of trials</td>
<td>9</td>
</tr>
<tr>
<td>Mean No. birds seen per trial</td>
<td>10.8 (Range = 9-14)</td>
</tr>
<tr>
<td>&quot; &quot; adults &quot; &quot; &quot; &quot;</td>
<td>8.9</td>
</tr>
<tr>
<td>&quot; &quot; young &quot; &quot; &quot; &quot;</td>
<td>1.9</td>
</tr>
<tr>
<td>Mean adult : young ratios</td>
<td>4.7:1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>29 Feb - 7 March 1972</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of trials</td>
<td>15</td>
</tr>
<tr>
<td>Mean No. birds seen per trial</td>
<td>16.5 (Range = 13-20)</td>
</tr>
<tr>
<td>&quot; &quot; adults &quot; &quot; &quot; &quot;</td>
<td>10.7</td>
</tr>
<tr>
<td>&quot; &quot; young &quot; &quot; &quot; &quot;</td>
<td>5.7</td>
</tr>
<tr>
<td>Mean adult : young ratios</td>
<td>1.9:1</td>
</tr>
</tbody>
</table>

Note: "young" refers only to fledglings and juveniles

Fernbirds in open Olearia forest are ideal subjects for transect studies as they neither move away or towards an observer. The birds generally progress slowly and are readily sighted. However, it is not practicable to estimate the numbers of fernbirds living in denser vegetation by line transect. In Poa meadows the birds cannot be seen until a fraction of a metre away and counting the number of birds calling along a transect is unsatisfactory as it is greatly influenced by variations in wind force and weather.

Several factors have to be taken into account before population estimates can be made from transect data; these are the influence of habitat on territory size, the area of vegetation on the Main Island, and the proportion of the fernbird population available for counting.

The mean areas of territories in different densities of vegetation in my study area were calculated (see Table 26). Territories in areas of Poa, in thick Olearia and in other
Table 26: COMPARISON OF THE SIZES OF SNARES FERNBIRD TERRITORIES IN DENSE VEGETATION AND OPEN OLEARIA FOREST

<table>
<thead>
<tr>
<th></th>
<th>Dense vegetation*</th>
<th>open Olearia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample size</td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td>Mean area</td>
<td>1 600 m²</td>
<td>4 520 m²</td>
</tr>
<tr>
<td>Range</td>
<td>1 024 - 2 508 m²</td>
<td>3 000 - 7 424 m²</td>
</tr>
<tr>
<td>Variance</td>
<td>218 359</td>
<td>2 459 018</td>
</tr>
</tbody>
</table>

* Figures here are those in brackets in Table 2 (Chapter 3)

dense cover are generally about 2920 m² smaller than those in open Olearia forest.

Territories in the Poa, the thick Olearia and in other dense vegetation are not significantly different in size, and may therefore be grouped together. The territories in open Olearia forest are significantly larger than those in the more densely vegetated habitats (ts = 5.908 with 10 d.f., p = < 0.001). The ratio of territory area in dense : open vegetation is 2.83 : 1 (calculated from data on Table 26).

As much of the land occupied by fernbirds is sloping it is necessary to correct estimates of area to make allowance for this. A map of the Main Island (based on a vegetation map of the Snares prepared by C. Hay in 1970 from R.N.Z.A.F. aerial photographs) was drawn up with areas of rock, steep land and open or dense vegetation plotted. The various zones were cut off the map and weighed to give an estimate of their horizontal area. From the estimated slope of the various zones it was possible to estimate the total area of habitat available to fernbirds (Table 27).

During transect traverses some of the fernbird population was not available for counting, viz. incubating or brooding adults. Similarly fledglings less than one week off the nest, would not be detected as they were mainly hidden away. In the period 4 - 11 February 1972, nine (17%) out of 54 adults in my study area were incubating or brooding, and
Table 27: AREAS OF VARIOUS HABITATS USED BY FERNBIRDS ON THE MAIN ISLAND

<table>
<thead>
<tr>
<th>Habitat</th>
<th>horizontal area</th>
<th>Estimated available area</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Open forest (on flat ground)</td>
<td>153.3 ha</td>
<td>No change</td>
</tr>
<tr>
<td>2. Flat, densely vegetated land</td>
<td>29.5 ha</td>
<td>No change</td>
</tr>
<tr>
<td>3. 45° to 75°, densely vegetated slopes</td>
<td>62.5 ha</td>
<td>106.3 ha (x 1.7 horizontal area)</td>
</tr>
<tr>
<td>4. Rock slopes, 70° and steeper</td>
<td>34.4 ha</td>
<td>99.7 ha (x 2.9 horizontal area)</td>
</tr>
<tr>
<td></td>
<td>279.7 ha</td>
<td>388.8 ha</td>
</tr>
</tbody>
</table>

Note: Estimated total area of densely vegetated habitat available to fernbirds = 135.8 ha.

Total vegetated habitat on the Main Island available to fernbirds = 289.1 ha.

two (15%) of 13 fledglings then present (of a total of 27 fledglings produced) were less than one week off the nest. During 29 February to 7 March 1972 all adults would have been available for counting, although four (15%) out of the net 27 fledglings produced in my study area, would not have left their nests.

The population size of the Snares Fernbird was estimated as follows. The number of birds available for counting in -

1) Open Olearia = mean no. observed/area of open Olearia searched x total area of open Olearia.

2) Dense vegetation = mean no. observed/area of open Olearia searched x total area of dense vegetation x 2.83.

From this information:-

3) The total adult population = total number of birds of all categories available for counting x proportion of
adults in the population (Table 25) + percent of adults at nests.

4) And similarly for the fledgling and juvenile population.

During 4 - 11 February 1973.

No. of birds available for counting:

in open *Olearia* = \(10.8/16\ 000 \times 1\ 533\ 000\)

= 1 073

in dense vegetation = \(10.8/16\ 000 \times 1\ 358\ 000 \times 2.83\)

= 2 716

Total no. of birds available for counting

= 3 789 (Range = 3 226 - 4 775)

Total adult population = \((3\ 789 \times 4.7/5.7) + 17\%\)

= 3 655 (Range = 3 112 - 4 607)

Total fledgling and juvenile population

= \((3\ 789 \times 1.0/5.7) + 15\%\)

= 764 (Range = 651 - 963)

Total no. of fernbirds present at this time

= 4 419 (Range = 3 763 - 5 570)

During 29 February - 7 March 1973

No. of birds available for counting:

in open *Olearia* = \(16.5/16\ 000 \times 1\ 533\ 000\)

= 1 533

in dense vegetation = \(16.5/16\ 000 \times 1\ 358\ 000 \times 2.83\)

= 3 843

Total no. of birds available for counting

= 5 376 (Range = 4 300 - 7 018)

Total adult population = \((5\ 376 \times 1.9/2.9) + 0\%\)

= 3 522 (Range = 2 817 - 4 598)

Total fledgling and juvenile population

= \((5\ 376 \times 1.0/2.9) + 15\%\)

= 2 132 (Range = 1 705 - 2 783)

Total population of fernbirds present on the Main Island at the end of the 1971-72 breeding season

= 5 654 (Range = 4 522 - 7 381)
The estimate of the population of fernbirds on the Main Island, given above, appears to be of the right order of magnitude. A simple calculation, shown below, checks this.

At the end of the 1971-72 breeding season there were 24 adults and 12 young (36 birds) in 4.88 ha of open forest, as well as 29 adults and 15 young (44 birds) in 2.05 ha of densely vegetated habitat.

Thus in 153.3 ha of open forest there would be $35/4.88 \times 153.3$ birds = 1130
and in 135.8 ha of dense vegetation there were $44/2.05 \times 135.8$ birds = 2915
Total = 4045

This estimate is about 30% less than the population reckoned from line transects.

The precision of the line transect method used here, under these ideal conditions is indicated by the close agreement of the two estimates of the number of adults present. After the appropriate factors have been taken into consideration, the calculated adult population of 4 to 11 February 1972 very closely agrees with that derived for 29 February to 7 March 1972, viz 3655 and 3522 respectively (error of 1% magnitude).

SURVIVAL RATE OVER ONE YEAR

Fernbirds survived well between the 1970-71 and 1971-72 breeding seasons. Twenty-three of the 35 adults (63.9%) and seven out of 12 juveniles (58.5%) marked in 1970-71 were sighted in 1971-72. Other banded birds could have been alive in 1971-72 elsewhere, having dispersed from the study area during the non-breeding season (as happened in March, 1972). Thus the survival rates determined from marked birds are minimum rates.

Minimum survival rates were not far below the expected survival values (66.6%) as derived from the percentage of adults in the total population of my study area at the end of the 1970-71 (65.6%) and 1971-72 (68.8%) breeding seasons (for actual figures see adult : fledgling ratios in Population Discussion). At 66.6% yearly survival rate, population
levels would be maintained at a constant level, losses exactly countered by gains.

The high survival rate of juveniles through one year is in great contrast to that recorded for Great Tits in Britain. In the latter, juvenile : adult ratios generally varies from 2.1 to 5.0 juveniles : 1 adult, before the winter and death rate of juveniles is far greater than that of adults over winter due to cold weather and/or food shortage (Lack, 1966). Equal survival of adult and juvenile Snares Fernbirds indicates that equable conditions were maintained throughout the year and food remained plentiful, otherwise the (presumably) less efficient young would have suffered through competition with adults.

**POPULATION DISCUSSION**

The Snares Fernbird is an interesting subject for a long term population study as it is confined to a small oceanic island group, interspecific competition is extremely low as there are few other species of insectivorous birds (see Warham, 1967; Warham and Keeley, 1969). During the study shelter was plentiful and the climate (see Chapter 2) was relatively equable. I have no definite knowledge of food being a limiting factor for the fernbird population on the Snares. Even so, I believe that food shortage over winter is not as important in maintaining fernbird population levels as it is with tit populations in Britain (see Lack, 1966). Factors that tentatively suggest that it is unlikely for food to limit the Snares Fernbird population are:

1) There was no evidence to suggest that nestlings were not receiving sufficient food. Sometimes the chicks refused to beg, indicating they were satiated.

2) Parents with three nestling broods showed no signs of being worn out in their efforts to feed their young. Also the male of Nest 9, 1970-71 fed both his fully grown nestlings for over four hours without the help of his mate. This male showed no signs of tiredness.

3) Only one fledgling (a freak), out of 38 observed, died within 40 days of leaving the nest. The remaining 37 young
showed no signs of being undernourished. Those fledged young I captured had similar body weights to adults (Figure 34).

4) The production of young per adult was similar in both seasons (see p 125) although insects were notably less abundant in the second season (pers. obs. and pers. comm. D.S. Horning).

5) Insects remained plentiful throughout the winter of 1972 (pers. comm. D.S. Horning).

6) The survival of young over one year was similar to that of adults with two thirds of both population classes surviving for 12 months.

7) The wide food spectrum and diverse foraging methods, combined with low interspecific pressures on food, would allow fernbirds to very efficiently utilize low stocks of prey.

However, as space is limited, it would seem that intraspecific factors must play a significant role in maintaining optimum population levels. Factors that restricted population growth included:

1) Only territory-owning birds bred, and by maintaining territories they were assured of undisputed access to a set quantity of resources.

2) Most territories in my study area (16 out of 19, or 84%) remained essentially the same size during two breeding seasons, indicating that the available land was fully "stocked", although some territorial compression occurred locally (see Chapter 3).

3) Not all territory holding birds bred. The breeding performance of territorial birds in 1970-71, and 1971-72 territories is shown in Table 28. Why some territorial pairs did not breed is not understood. In the Huts territory, in both seasons, the territory holders did not even build a nest, although numerous suitable nest sites were available. Male 25, and his mate, of the West Colony 3 territory, produced two clutches in 1970-71, but the same pair failed to produce any eggs in the second season. There are several other examples of unexplained failure to breed (Table 28).
Table 28: BREEDING PERFORMANCE OF PAIRS OF FERNBIRDS IN THE MAIN STUDY AREA

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of territories diligently searched for nesting activity</th>
<th>No. of first clutches</th>
<th>No. of replacement clutches</th>
<th>No. of second clutches</th>
<th>No. of pairs not breeding</th>
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</thead>
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<td>1970-71</td>
<td>19</td>
<td>16</td>
<td>4</td>
<td>2</td>
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<tr>
<td>1971-72</td>
<td>24</td>
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The production of young appears to depend greatly on the motivation of individual pairs, for although many adjacent territories contained virtually identical habitat, the breeding performance varied considerably from neighbour to neighbour and from season to season.

4) Few offspring were produced. With a maximum clutch size and 100% breeding success, one pair of Snares Fernbirds could raise only six nestlings, compared with a potential 20 or more young for a pair of Great Tits (Lack, 1966).

Actual fernbird breeding success was, of course, much lower than the theoretical maximum, and expressed as the total number of fledglings produced per adult present in my study area we have:

In 1970-71 22 fledglings : 18 territorial pairs plus 5 non-territorial birds or 1 fledgling : 1.87 adults.

In 1971-72 27 fledglings : 24 territorial pairs and 4 non-territorial birds or 1 fledgling : 1.92 adults.

The number of non-territorial birds present in the main study area indicated above was a minimum value only: there were a few unbanded adults wandering in mapped territories - these were either intruding territorial birds from outside my study area, or non-territorial adults. Even so, I do not think that there were many unaccounted adults in my study area, as a similar young : adult ratio was
corded in transect counts in March 1972, i.e. 1 fledgling: .9 adults.

It was very unlikely that birds I listed as not breeding (Table 28), did breed. If these birds laid eggs and raised nestlings, they would have roosted in their nest at night, they would have been more active and vocal than birds not nesting currently, and only one bird of the pair would be foraging alone for any length of time. Nesting birds had a distinct centre of activity (around the nest) in their territories, whilst those not nesting (for example, those adults with newly independent young) were relatively idle.

As it took 37 to 38 days from egg laying to fledging of young, I am positive that I did not underestimate the number of fledged offspring, for during the 38 day nesting period I would have detected some signs of nesting activity. If I did miss any nesting activity it would have most likely been during the egg stage, for during the nestling stage the adults were busy carrying food to their young.

5) As 70 days are required to raise a brood to independence, only early breeders have enough time to fledge two broods.

From the above considerations it is apparent that the Snares Fernbird is breeding below its potential, but the mechanisms influencing this lowered potential are not understood. However, a situation is maintained whereby the level of recruitment is low, and mortality of adults and juveniles equally low. It is likely that the Snares Fernbird population is maintained by density-dependent regulation.

According to Lack (1949:457) "my general theory is that the normal clutch size is that which results in the maximum number of young surviving to become parents." This is the optimum clutch size for any population, including the Snares Fernbird. However, for the latter, it is not correct to say that "birds......raise not only all the offspring that they need, but also all that they can" (Lack, 1949:455-56). This would give a reproductive rate above the optimum, for although it would produce more young it would not maintain the population at a higher level because the excess individuals would soon be removed by mortality. The surplus
would have nowhere to emigrate to and are wasted reproductive effort.

My conclusions from this very short term population study are similar to those of Skutch (1967) and Cody (1966) for birds inhabiting stable environments. "It is obvious that, in order to avoid extinction, a species must, on the average, produce enough offspring to replace its annual losses, with perhaps a small surplus to meet emergencies.... From this it may be deduced that a species which reproduces slowly does so simply because its mortality is low and because it has no need to beget more offspring, whereas a rapid rate of reproduction is an indication of high annual losses" (Skutch, 1967:580).

Thus "maximum reproduction is to be expected in a region of pronounced seasonal changes in climate, with accompanying fluctuations in the abundance of food; whereas adjusted reproduction would be expected in a more equable climate", Skutch (loc. cit: 581).
CHAPTER 11

CONCLUDING COMMENT

This study has served several purposes. Firstly, it has provided a broad account of the biology of the genus Bowdleria. Details of territorial behaviour, vocal communication and feeding behaviour described for the Snares Fernbird probably also apply to the other forms of B. punctata.

Secondly, this study has shown that there is a great potential for research on animal populations inhabiting small offshore islands. Many offshore islands around New Zealand, e.g. the muttonbird islands, south-west Stewart Island (Blackburn, 1965) have a relatively stable environment, where floral and faunal diversity is low, and the wildlife is relatively tame. These islands form discrete communities where factors such as immigration and emigration, and predation are minimal. In a situation such as exists at the Snares, long term population studies could pose some interesting questions to current theories (Wynne-Edwards, 1962; Lack, 1966) on population regulation.

Thirdly, this study is important as it was carried out on a population of birds living in an unmodified (by man) environment. It is imperative that groups such as the Snares are intensively studied for sometime in the future there may be undesirable introductions, such as rats, that would radically change the flora and fauna. Although there are stringent controls to ensure this is unlikely (the Snares are gazetted as a "Flora and Fauna Reserve", the highest priority for reserves in New Zealand), some insurance in the form of documented reports is highly desirable.
SUMMARY

1. This account outlines the breeding, feeding and population biology of the Snares Fernbird.

2. The Snares are a small isolated group of islands lying 105 km southward of Stewart Island, New Zealand. Fernbirds were studied on the Main Island of the group. The vegetation of this island consists basically of coastal tussock meadows and a central daisy tree (Olearia and Senecio) forest.

3. The study was based on observation of known individuals over two consecutive seasons. Live adults with territories were sexed by behaviour.

4. Breeding territories were mapped by plotting the positions where neighbouring pairs of birds had disputes. Territories were smallest in dense vegetation (1100 to 2000 m²) and largest in open Olearia forest (up to 7600 m²). In places territory borders coincided with vegetation borders or other landmarks such as ridges or valleys.

5. Sixteen out of 19 territories mapped in 1970-71 were the same in 1971-72. There was a tendency for individual males to maintain the same territory, with the same mate, during the two seasons.

6. Postures and vocalizations played important roles in the maintenance of territories.

7. Fernbirds in the study area apparently preferred to build their nests in the fern Asplenium obtusatum. The tussocks Poa tennantiana and P. astonii, and the sedge Carex trifida were the next most popular nesting sites.

8. Nest construction is described in detail. Fernbirds built four types of nest, each type being built in a characteristic vegetation form.

9. Fernbirds laid eggs over a 13 to 16 week period, and produced clutches containing one to three eggs. Fifty-six percent of 32 clutches found contained two eggs while 40
percent were three-egg clutches.

10. Both adults share in the incubation of eggs. The incubation period was 16 days. Eggs of one brood hatched within 24 hours of each other.

11. At hatching the young were naked and were constantly brooded. Nestling thermoregulatory ability probably started to develop four days after hatching and chicks 10 to 11 days old could apparently maintain their own temperature.

12. Nestling feeding rate varied considerably. However, in all records, there was a peak in feeding activity during early morning and late evening, whereas feeding rate was lower during mid-afternoon. The late evening peak in feeding activity increased with the age of the nestlings.

13. The morphological and behavioural development of young through the nestling phase is described.

14. Chicks fledged when aged 20 to 21 days. The young remained hidden in cover about the nest during fledging day. As they grew older they more readily left cover to follow their parents on foraging trips. About 20 days after leaving the nest, young birds were eating food they had caught. The young were independent about 36 days after fledging.

15. The development of the behaviour of fledged young, and their changes in morphology are described. A summary of the differences in appearance between adults and fledged young is given - basically the young have more diffuse markings on their plumage than adults.

16. Adults began their moult after their young had become independent. The moult appeared to take about five weeks per bird. During the post-breeding moult adults tended to wander from their territories. Defense of territories during the moult was not as strong as during the breeding months.

17. From a total of 78 eggs laid, 37 were lost during incubation, 42 hatched and 25 nestlings survived until fledging. Only one fledgling (a freak), of 38 observed
until independence, died. There was no evidence that predation was a mortality factor during this study. Some nests though were destroyed by the trampling and crashing about of Sooty Shearwaters and Hooker's Seals.

18. Fernbirds are opportunistic feeders, examining a wide range of substrates for arthropod prey. The birds eat all manner of prey from large amphipods and carabid beetles (about 20 mm long) down to mites (less than 1 mm long). The diverse foraging methods of fernbirds allows them to utilize a wide food spectrum.

19. The fernbird population on the Main Island was estimated from a 2.00 km line transect. At the end of the 1971-72 breeding season there were about 3500 adults and 2100 fledged young, giving a total post-breeding population of 5600 fernbirds.

20. Adults and young appeared to have similar survival rates over one year. Two thirds of each class live for at least 12 months.

21. Snares Fernbirds are maintaining a low level of recruitment. One juvenile is produced for every two adults in the population. The mechanisms controlling this low recruitment are not understood, but warrant detailed investigation.
Without the encouragement of Professor G.A. Knox and my supervisor, J. Warham, this study would not have been possible. My thanks go to other expedition members, viz. M.C. Crawley, O.R. Wilkes, G.J. Wilson, K.J. Sainsbury, D.S. Horning and C.J. Horning, for their companionship and advice. D.S. Horning kindly identified insect material and gave entomological advice. Special thanks go to Gordon Crowther, Fisheries Research Institute, Bluff, for his ceaseless efforts to secure sea transport, and to J.T. Kay, of this department, for preparing equipment to go to the Snares. Transport to and from the Snares was provided by G.M.V. "James Cook", H.M.N.Z.S. "Endeavour", M.V. "Sandra Kaye", and "R.V. Acheron".

The numerous drafts were criticized by A.J. Baker, V. Benzie, J.D. Coleman, M.C. Crawley, and J. Warham. Finance for the Snares Expeditions of 1970-71 and 1971-72 was provided by the University Grants Committee and the Nuffield Foundation.
REFERENCES


HAMILTON, A. 1885. A list of the native birds of the Petane
district, Hawke's Bay, with notes and observations.
Transactions of the Royal Society of New Zealand,
18: 123-128.

HANDLY, J.W. 1895. Notes on some species of New Zealand
birds. Transactions of the Royal Society of New
Zealand, 28: 360-367.

HARRIS, Margaret A. and LEMON, Robert E. 1972. Songs of
Song Sparrows (Melospiza melodia): individual
variation and dialects. Canadian Journal of Zoology,
50: 301-309.

HINDE, R.A. 1956. The biological significance of the

and comparative psychology. 2nd edition.

HOLDGATE, M.W. 1968. The influence of introduced species
on the ecosystems of temperate oceanic islands. IUCN

pp 185-205 in "Bird vocalizations, their relations to
current problems in biology and psychology",

KINSKY, F.C. (Convenor) 1970. Annotated checklist of the
birds of New Zealand including the birds of the Ross
Dependency. The Checklist Committee, Ornithological
Society of New Zealand, Inc. A.H. and A.W. Reed,
Wellington. 96pp.

KIRK, T. 1895. The displacement of species in New Zealand.
Transactions of the Royal Society of New Zealand,

LACK, D. 1949. Comments on Mr Skutch's paper on clutch


### APPENDIX 1

#### MEASUREMENTS OF ADULTS

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<th>Bill Length</th>
<th>Bill Height</th>
<th>Tarsus Length</th>
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### APPENDIX 2

**NEST MEASUREMENTS AND SITES**

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**A. 1970-71 Season**

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* These nests were built on horizontal Olearia trunks situated on steep slopes.
### APPENDIX 3

**EGG MEASUREMENTS AND MONTH OF LAYING**

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