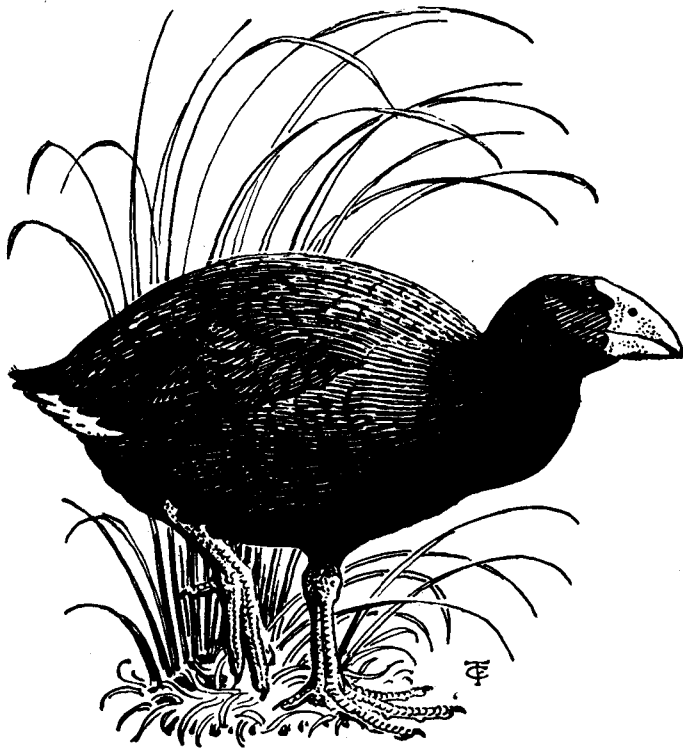


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## INTRASPECIFIC VARIATION IN THE NEW ZEALAND BELLBIRD *Anthornis melanura*

By J. A. BARTLE and P. M. SAGAR

### ABSTRACT

Intraspecific variation in morphometrics, plumage colouration, moult and breeding is described and its taxonomic significance assessed. There is a latitudinal cline in morphometrics and colouration among mainland, nearshore island, and Auckland Is populations. Southern bellbirds are larger and more brightly coloured, but they have shorter bills. Intensity and hue of the iridescent head and olive-green plumage colouration are determined by the degree of melanism, which increases southward and on all isolated islands but the Three Kings. Age and sex differences in plumage colouration are also caused by the different degrees of melanism. The degree of melanism may be reduced by the dryness of the environment, particularly in the period before moult.

Overlain on this cline are insular trends in morphometrics, colouration, moult, and breeding pattern. Bellbirds, particularly males, from isolated islands are larger than those on the mainland, whereas clutches are fewer and smaller, and breeding seasons and adult moult earlier. The size increase occurs whether other species of honeyeater are present or not and may result from high densities and the increased tendency of males and females to use different feeding niches. The relative body proportions of island populations vary and wing length does not increase as rapidly as body size.

A new subspecies is described from the Poor Knights Is. It is characterised by a distinctly blue rather than violet iridescent head in males, an immature plumage phase, and other differences in size, relative proportions, breeding, and time of moult. The nomenclature and taxonomic status of other island subspecies and of the extinct Northland bellbird *A. dumerilii* are reviewed. *A. dumerilii* and *A. incoronata* are regarded as synonyms of *A. m. melanura*.

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## INTRODUCTION

Of the 19 indigenous passerine bird species still living in New Zealand, three are honeyeaters (*Meliphagidae*). Each of these honeyeaters represents a different endemic genus. They eat somewhat different foods obtained by different foraging habits (Craig *et al.* 1981a). All three are sympatric, but the Stitchbird (*Notiomystis cincta*) is now confined to Hen, Cuvier, and Little Barrier Islands.

Bellbirds (*Anthornis melanura*) are widespread in New Zealand, from the subtropical Three Kings Islands in the north to the windswept subantarctic Auckland Islands in the south. They have been a well-known and much-loved component of the fauna since the earliest days of European discovery and settlement. In one frequently quoted passage, Sir Joseph Banks described their dawn chorus at Queen Charlotte Sound on 17 January 1770, on Cook's first voyage, as "certainly the most melodious wild musick I have ever heard, almost imitating small bells but with the most tuneable silver sound imaginable". For the early settlers their "powerful song . . . brighten(ed) the melancholy stillness of New Zealand forests" (Reischek 1887).

It was, therefore, with great concern that Buller (1873, 1878) noted a sharp fall in abundance of bellbirds in the 1860s, and fears were held for the survival of this previously common species. Bellbirds disappeared from Northland by 1870, and although they declined throughout the main islands of New Zealand, birds in the North Island were most noticeably affected. In the South Island, bellbirds did not reach their lowest ebb in Canterbury until 1900, but their numbers increased rapidly after 1910 (Stead 1932). There was a similar, but somewhat earlier recovery in most North Island districts (Best 1909, Myers 1923, Stead 1932, Phillipps & Lindsay 1948).

The causes of this population crash remain a mystery but are likely to differ from those which precipitated the disappearance of many other New Zealand forest birds later in the century (Turbott 1961). Myers (1923, pp. 72-73) suggested that the decline of many native species might have been caused by diseases, such as avian malaria, brought in by birds introduced from Europe. Support for this idea, with particular reference to bellbirds, may be found in Lack (1954, pp. 168-9) and Turbott (1957, 1961, 1965). Introduced diseases, including avian malaria and birdpox, have been held responsible for the catastrophic decline and extinction of most of the endemic forest birds on the Hawaiian Islands (Munro 1944, Warner 1968). However, recent reviews have shown that such explanations could not be used for the many early extinctions (Olson & James 1982) or for the major decline of 1892-1910 (Atkinson 1977), as the probable disease organisms and their vectors had been present since the 1820s. The pattern of geographical variation in the timing and extent of the decline and recovery of the New Zealand bellbird would seem to exclude the explanations (predation and habitat change) which best fit Hawaii. A noteworthy feature of the change in bellbird abundance is that it did not occur on forested offshore islands or on islands in lakes, such as Mokoia Island in Lake Rotorua. The exception was the large and heavily modified island of Great Barrier, from where bellbirds disappeared between 1868 and 1878 (Buller 1888).

Today bellbirds are relatively abundant in even quite small areas of indigenous forest throughout the three main islands of New Zealand, except for Northland and the Waikato district north of Hamilton. A few small pockets of bellbirds appear to have re-established in Northland (Turbott 1953), perhaps by colonising from nearby islands, but numbers remain low and distribution limited (Bull *et al.* 1985). Bellbirds are on most forested offshore islands, sometimes at great densities, but are not on The Snares and Kermadec Islands. Although they occasionally reach The Snares (Reischek 1888), bellbirds are almost certainly prevented from establishing because of the absence of nectar-producing trees (Fineran 1969). In contrast, the forest on the Auckland Is is dominated by southern rata *Metrosideros umbellata*, an abundant nectar-producer in summer.

The Chatham Island bellbird fared less well than the mainland form and was last seen at the Chatham Is on Little Mangere I. in 1906 (Fleming 1939). Intensive collecting during the late 19th century by dealers such as Travers, Dannefaerd, Palmer, and Hawkins – spurred on by the desires of Buller, Rothschild, Newton and others to build up collections of endemic Chatham Is birds – may have hastened their decline, but other factors must also have been at work.

Our review of intraspecific variation in New Zealand bellbirds developed from a seven-year ecological study of bellbirds on the Poor Knights Islands, off northern New Zealand (see Fig. 1). A paper on breeding has been completed (Sagar 1985) and other papers on food and feeding and population dynamics of Poor Knights bellbirds are in preparation. Information on weights, measurements, plumages and moult of the Poor Knights population was collected during the ecological studies and is compared here with data from mainland and other populations. This revealed some marked differences between the Poor Knights and other bellbird populations, and so we made further investigations to discover whether these differences warranted subspecific status for the Poor Knights birds. In the course of this study we re-examined the status of other named subspecies of bellbird.

### MATERIAL AND METHODS

The birds were grouped from the following localities, which are shown in Fig. 1:

1. Three Kings Is (Great I.) 34°10'S 172°08'E, museum specimens
2. Poor Knights Is (Aorangi I.) 35°28'S 174°44'E, live specimens
3. Northland (population extinct since 1860s): museum specimens from the Bay of Islands (35°16'S 174°08'E) and Waitemata Harbour
4. Hauraki Gulf Is (Hen and Chicken Is, Little Barrier I., Cuvier I., Motuihe I.), museum specimens
5. Tiritiri Matangi I. (slightly north of Waitemata Harbour and Motuihe I.) 36°36'S 174°53'E, live specimens
6. North I. (Rotorua and Wairoa south to Kapiti I. and Upper Hutt), museum specimens
7. Orongorongo Va. (DSIR Ecology Div. Intensive Study Area) 41°21'S 175°01'E, live specimens (Robertson *et al.* 1983)
8. Western South I. (Tasman Bay south to Preservation Inlet, west of the Alpine Fault), museum specimens
9. Punakaiki-Charleston 42°07'S 171°20'E, live specimens
10. Geraldine (Pleasant Valley) 44°05'S 171°15'E, live specimens
11. Eastern South I. (Kaikoura south to Catlins), museum specimens
12. Stewart I. 46°45'S 168°10'E, museum specimens
12. Auckland Is (Ocean I., Adams I., main island) 50°35'S 166°00'E, museum specimens
14. Chatham Is (Pitt I.) 44°00'S 176°30'W, museum specimens

Measurements of bellbirds from Kowhai Bush, Kaikoura (Gill 1980) were not included because they seemed to have been recorded by techniques different from ours.

Specimens of bellbirds from the following museums were measured, and special thanks are due to the curators and to the staff mentioned. All examples were measured of *A. m. melanura* from known localities in the American and New Zealand museums listed.

American Museum of Natural History, New York (AMNH): Mrs Mary LeCroy

Carnegie Museum of Natural History, Pittsburgh (CMNH): Mr J. Loughlin  
Sub-Department of Ornithology, British Museum, Natural History (BM):

Mr I. C. J. Galbraith, Dr P. R. Colston  
University Museum of Zoology, Cambridge (UMZC): the late Mr C. W. Benson



Laboratoire d'Ornithologie, Museum National d'Histoire Naturelle, Paris  
(MNHN): Dr C. Erard

Auckland Institute and Museum (AIM): the late Mrs Sylvia Reed

National Museum of New Zealand (NMNZ)

Canterbury Museum, Christchurch (CM): Mr G. A. Tunnicliffe

Otago Museum, Dunedin (OM): Mr J. T. Darby

Most live birds were weighed with Pesola 50 g spring balances graduated in 0.5 g divisions, and measurements were taken as specified by Baldwin *et*

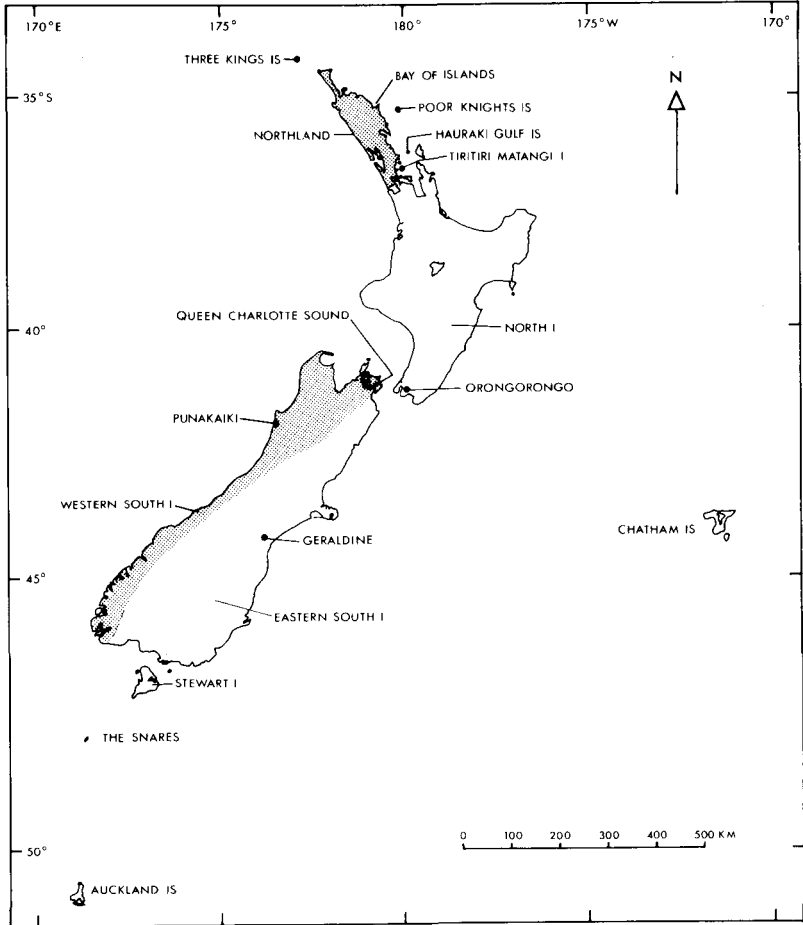


FIGURE 1 — New Zealand and outlying islands where bellbirds have occurred. Localities from which morphometric data were obtained are shown. Northland and the western South I. are stippled to distinguish them from other parts of the North and South Is

*al.* (1931) and Gurr (1947). J. L. Craig (pers. comm.) suggested an additional measurement for use in sexing birds, and this was also taken. This was the overall length of the bill plus head (from the tip of the bill to the back of the skull). Some museum specimens could also be measured in this way, but most had damaged skulls.

Weights and measurements were grouped according to locality. Measurements from each locality were obtained either from live birds or from museum specimens, but within each locality, measurements and weights from these two sources have not been combined. Large samples of both live and museum specimens were not available from the same locality, and so no direct comparison has been possible. However, the bill, tarsus, and mid-toe plus claw measurements are relatively longer in the live-caught birds, reflecting some shrinkage in museum specimens. The weights of birds in museum collections are those recorded immediately after the birds were collected.

Another potential source of bias lies in the number of people who measured birds. However, most museum specimens were measured by J. A. Bartle and most live birds on the Poor Knights Islands and at Geraldine were measured by P. M. Sagar. Measurements of live birds from Tiritiri Matangi Island and Cuvier Island in the Hauraki Gulf were kindly supplied by J. L. Craig and M. E. Douglas (including many measurements additional to those of Craig *et al.* 1981b). In the Tiritiri project several workers took measurements. In the Orongorongo study (Robertson *et al.* 1983) most measurements other than those of weight and wing length were done by A. H. Whitaker. Finally, a small series of measurements of live bellbirds from the Punakaiki-Charleston area was supplied by D. J. Onley, who also helped with measurement of some Poor Knights and museum specimens.

Although differences in technique contributed to few biases in the weight data, on the Poor Knights Islands the weights showed marked seasonal and year-to-year variations (Sagar, in prep.). These variations could not be studied for other localities because adequate data were not available. However, because most birds were weighed in late summer and autumn (immediately after adult moult) we did not attempt to correct weights for seasonal variation.

Birds were sexed and aged by plumage characters, except for those on Tiritiri Matangi Island, where many birds were sexed and aged retrospectively by morphometric methods. Robertson *et al.* (1983) confirmed that sexual differences in adult weight and measurements are always highly significant ( $P < 0.001$ ).

Ageing of bellbirds was more difficult, partly because of geographical variation in the pattern and timing of moult. During the study we found that on the Poor Knights first-winter birds could be identified by the weak degree of emargination on the ninth primary (Fig. 2), and many birds were later aged by this method. With the Tiritiri birds, which were aged by us on morphometric criteria, it seemed probable that some which had been aged as subadult females were actually adult females.

The term adult is used for birds with an emarginated ninth primary (Fig. 2). Subadults include birds in immature and juvenile body plumages that do not have an emarginate ninth primary. Immatures and juveniles were

not at first separated because the flight feathers are not moulted between the two phases, and the differences have only recently been recognised. Juvenile birds with incompletely grown flight feathers and fleshy gapes which were clearly fledglings were not included in Tables 2-14.

Bellbirds (both live and museum specimens) were placed in one of the eight following moult categories:

1. Newly moulted. Flight and contour feathers immaculate
2. Fresh plumage. No significant sign of wear
3. Little wear. Wear definitely visible
4. Worn. Emargination on ninth primary gone, sheen on contour and flight feathers lost
5. Very worn. Extensive wear on contour and flight feathers and loss of iridescence on head
6. Moulting. (a) Flight feathers  
(b) Contour feathers  
(a) + (b) Flight and contour feathers

The percentages of adult males and females and subadult males and females in each category during visits to the Poor Knights Islands were calculated (Table 1). The seasonal cycle of moult on the Poor Knights could then be compared with that of bellbirds at Geraldine, the Auckland Islands, and the Chatham Islands (based on museum specimens).

Bellbird plumages were described according to the colour terminology rigorously defined by Smithe (1974, p.12) and, where possible, Smithe's colour swatches (1975, 1981). However, when there was no satisfactory match between feather colour and swatch, Ridgway's (1912) colour standards were used, despite some reservations (Smithe 1974, pp. 5-7). A library datestamp of 26 May 1919 shows that the National Museum library copy of Ridgway is not an unauthorised reprint (Zimmer 1948). With bellbirds complexity is added by the importance of iridescence and structural colours (for discussion of terminology refer Fox & Vevers 1960). Colours determined after comparison with standard swatches are capitalised in the text and, unless otherwise indicated, are as used by Smithe (1975). A more informal description is shown by the lack of an initial capital.

## NOMENCLATURE

Several names have been applied to New Zealand bellbirds.

***Certhia melanura* Sparrman, 1786, *Mus. Carlsonianum*, fasc. 1, No. 5.**

Although Banks described the calls of bellbirds at Ship Cove, Queen Charlotte Sound (South Island) during Cook's first voyage, the first specimens were not collected until Cook returned to this anchorage with Forster and Sparrman, a young Swedish naturalist, in 1773. These were described by Latham (1782) under the name Mocking Creeper, but the first Latin binomial was applied to them by Sparrman (reference above). Unfortunately Sparrman erred in giving the type locality as *Promontorium Bonae Spei*, the Cape of Good Hope. No type specimen exists (Medway 1976, p.53), and the Leverian Museum specimen on which Latham's (1782) description was based was probably lost when this huge collection was broken up and auctioned in 1806 (Stresemann 1975).

A new genus, *Anthornis*, was erected by G. R. Gray in 1840 (*List Gen. Birds*, ed.1., p.15), with its designated type species as *Certhia melanura* Sparrman. Since then, *Anthornis* has been consistently used for the New Zealand bellbirds.

***Philedon dumerilii* Lesson & Garnot, 1828, *Voy. La Coquille, Zool.*, 1, atlas livr. 6, pl.21, fig. 1.**

The French naval corvette *La Coquille* (later to become even more famous when renamed *Astrolabe*) visited the Bay of Islands from 3 to 17 April 1824, during a round-the-world cruise. The vessel was under the command of Duperry, but Dumont d'Urville was also aboard as First Lieutenant. The surgeon-naturalists assigned to the expedition were the young French ornithologists R. P. Lesson and P. Garnot, but Garnot had already been sent back to France after having contracted dysentery in South America (Dunmore 1969, p.115). Extensive observations on natural history were made (Lesson 1839), and an account of the zoology was published (Lesson & Garnot 1828-30) which included the description of a number of new forms, including the North Island Robin and Pied Tit. Kiwi, Tui, New Zealand Pigeon, parakeets, Kaka and various seabirds were also seen, and specimens were collected.

Five bellbirds ("koko-i-mako") were collected and figured in the *Atlas* (1828). The subsequent description (1829, livr. 9, p.416 and footnote; 1830, livr. 14, pp. 644-645) was far more comprehensive than that of Sparrman. Four syntypes are known (Benson, in press), and JAB examined them all in 1980. The type locality is the Bay of Islands.

***Anthornis melanocephala* G. R. Gray, 1843, in Dieffenbach, *Travels in New Zealand*, 2, p.188.**

Ernst Dieffenbach, naturalist to the New Zealand Company, made the first collection of birds on the Chatham Islands in 1839. Gray gave an account of these specimens in an appendix to Dieffenbach's *Travels* and, later, in the *Zoology of the Erebus and Terror* expedition (1845).

The distinctive Chatham Island form of the bellbird (treated last century as a full species by Buller, Rothschild, Gadow and others) was first figured by Gray (1845, *Zool., Erebus Terr.*, Birds, pt. 4, p.1.2). Following the review by Mathews & Iredale (1913), *A. melanocephala* has usually been treated as a subspecies of *A. melanura*.

The HOLOTYPE (BM 1842.9.29.26) is in the British Museum (Natural History) at Tring (Warren & Harrison 1971), and the type locality is the Chatham Islands. Specimens have been recorded from Wharekauri (main island), Pitt I., Mangere I., and Little Mangere I.

***Anthornis incoronata* Bangs, 1911, *Proc. Biol. Soc. Wash.* 24, pp. 23-24.**

Buller, Gadow and others were content to list Auckland Island bellbirds under *A. melanura*, although Gray (1845) had already commented on the larger size of the Auckland Is birds. However, on the basis of only two specimens (HOLOTYPE, Mus. Comp. Zool., Harv., No. 40,008, ad.male, Auckland Is, H. H. Travers; PARATYPE, U.S. Nat. Mus. No. 175,193, ad.male, Auckland Is), Bangs (1911) described the Auckland Island bird as a full species. Few subsequent authors have admitted *incoronata* as a valid

taxon, even at the subspecific level. Neither Oliver (1930, 1955) nor the Checklist Committee, Ornithological Society of New Zealand (1953, 1970, 1980) listed *incoronata* as a separate form, although Salomonsen (1967: Checklist of the Birds of the World, Harvard), perhaps following Mathews & Iredale (1913) and Mathews (1930), treated it as a subspecies of *A. melanura* (Sparrman).

***Anthornis melanura obscura* Falla, 1948, *Rec. Auck. Inst. Mus.*, 3, pp. 337-338.**

Falla showed a more modern approach by including a range of measurements of mainland bellbirds in his delineation of a subspecies on the isolated Three Kings Islands, to the north of New Zealand. The separate identity of the Three Kings birds had been suspected since Cheeseman (1888) visited the islands, and Falla's treatment of *obscura* as a subspecies of *A. melanura* (Sparrman) has been widely accepted.

There are only two study skins of Three Kings bellbirds in collections: the HOLOTYPE (AIM Av. No. 15.22), and another adult male collected on 3 December 1945 (AIM Av. No. 15.29) but not mentioned in Falla's paper. Unfortunately the two PARATYPES (AIM Av. No. 15.23 and 15.24) are mounted and are now very faded, as are two mounted TOPOTYPES (NMNZ No. 14050 and 14051), collected on the same day as the holotype and paratypes. These six specimens, which JAB has examined, are thought to be the only ones ever collected.

## BREEDING

### Three Kings Islands

Turbott & Buddle (1948) recorded that bellbird nesting is over by early December, when newly fledged young are common. The timing of breeding seems similar to that on the Poor Knights Is.

### Poor Knights Islands

A breeding season extending from late September to late December was inferred from our observations of the earliest bellbirds fledging in late October and the last eggs being laid in late November. Although these extremes extend the breeding season to 90 days on the Poor Knights Is, laying is at a peak between mid-October and mid-November. Only one clutch of 2-4 eggs (mean 2.9,  $n = 37$ ) is laid.

### Mainland New Zealand

Oliver (1955) stated that the breeding season of *A. m. melanura* extends from September to January (inclusive) and that two broods may be reared. However, later breeding has been recorded. Potts (1871) recorded finding a nest on 10 March which contained "four young birds, 2-3 days old; the latest brood ever encountered". At Punakaiki, D. J. Onley (pers. comm.) saw fledgings being fed in mid-April and so, on the mainland, laying must continue in some localities until the middle of March.

It is likely that part of the reason for extended breeding on the mainland is to allow the raising of two (or more) broods. Regular observations on the monthly distribution of laying by mainland bellbirds are not available, but there are numerous records both of laying and of fledging in December and

January. Stidolph (1971) found eggs in two of three bellbird nests on Kapiti I. in late December-early January, whereas the third contained well-feathered nestlings. Near Queen Charlotte Sound, Sparrow (1982) found a recently fledged brood on 1 January, and the female built another nest and began incubating a new clutch in mid-January. This is firm evidence of double clutching, and recent observations of D. J. Onley (unpubl.) suggest that at least two broods are normal on the mainland. This contrasts with the situation on the Poor Knights, where the compressed breeding period permits only a single clutch. A similar pattern is found when mainland Grey Warblers (*Gerygone igata*) are compared with Chatham Island Warblers (*Gerygone albofrontata*) (Dennison *et al.* 1984).

The clutch size of mainland bellbirds is 3-4 (Oliver 1955), and this is borne out by the results of J. L. Craig and M. E. Douglas (pers. comm.) on Tiritiri I., where 11 nests contained 3-4 eggs each (mean 3.6). Potts (1884) said that the clutch size of bellbirds is "more constant than many species in keeping to its complement of eggs, namely four; only once in 30 years have I known this number to be exceeded"; this was a nest containing 5 eggs on 9 December. Other 5-egg clutches were noted by Reischek (1887), who recorded that 4-5 eggs are laid on Little Barrier I., and Sparrow (1982), who observed a brood of 5 fledglings.

### **Chatham Islands**

The little available information is contradictory. Whereas Travers (1873) said that breeding began in October, Potts (1884) gave the breeding season as August-October inclusive. The usual clutch was three eggs (Travers 1873), but a nest in the Canterbury Museum contained two. The nest itself is much larger than in *A.m.melanura* and had a much more loosely formed bowl. (Buller 1876).

### **Conclusion**

Poor Knights Is bellbirds differ from mainland birds in having a much shorter breeding season and a single, smaller clutch. On the Chatham Is the clutch size may have been even further reduced and the nests and eggs were much larger than on the mainland. No published data are available for the Auckland Is, but fledglings have been collected in November (CM Av. 21278) and January (CM Av. 1036).

## **PLUMAGES AND MOULT CYCLES IN BELLBIRDS**

### **Poor Knights Islands**

The annual cycle of moult in bellbirds on the Poor Knights Islands varies with age (Table 1). Juveniles fledge in a distinctive plumage. Males have Buffy Olive contour feathers (all of the following colours from Ridgway 1912) and Blackish Green-Gray wing and tail feathers, and females Buffy Olive contour feathers, paler underparts, and Brownish Olive wing and tail feathers. Both sexes have a Primrose Yellow cheek stripe from the point of the gape, Glaucous tarsi, toes and claws, brown eyes, and black bills, with a yellow fleshy gape. This plumage is retained throughout January before the birds undergo contour feather moult in February-March, when they assume a distinct immature plumage.

TABLE 1 — Seasonal variation in the percentages of adult and subadult bellbirds in different moult categories on the Poor Knights Is

Moult Category	Adults (both sexes)								Subadults (both sexes)							
	Jan	Feb-Mar	May	Sept	early Oct	late Oct	Nov	Dec	Jan	Feb-Mar	May	Sept	early Oct	late Oct	Nov	Dec
1	-	98	-	-	-	-	-	-	-	1	-	-	-	-	-	-
2	-	-	85	-	-	4	-	-	-	-	-	-	-	-	-	-
3	-	-	15	94	90	83	83	45	100	70	58	37	16	49	10	-
4	7	-	-	4	10	-	4	-	-	-	16	17	29	-	3	-
5	8	-	-	1	-	2	-	-	-	8	21	46	52	8	5	-
6(a)	57	1	-	-	-	-	-	-	-	3	-	-	-	4	-	-
(b)	-	1	-	1	-	11	13	55	-	18	5	-	3	38	79	79
(a & b)	28	-	-	-	-	-	-	-	-	-	-	-	-	1	3	21
n	136	397	137	184	49	193	70	29	90	156	62	48	31	72	40	19

The new contour feathers of immature males are mostly Warbler Green, and the crown and forehead are dull Hyacinth Blue, lacking the bright and extensive iridescence of adults. Not only are the retained wing and tail feathers a slightly duller black than the jet black of adult males, but these feathers are also shorter; the mean wing length of immature males is 84.0 mm as against 87.7 mm for adult males, and tail length 83.1 mm and 88.1 mm respectively (Tables 6, 7, 12 and 13). However, only the tail lengths are significantly different (Student's t-test,  $P < 0.001$ ). Immature females are Buffy Olive above and paler below. The cheek stripe becomes Pale Olive-Buff, and a faint Niagara Green iridescence is sometimes visible on the forehead and crown. Wings of immature females are shorter than those of adults — averaging 74.3 mm compared with 77.0 mm — but the difference is not significant (Student's t-test,  $P > 0.05$ ). Immatures of both sexes have brown eyes and black bills.

During an examination of Tui (*Prothemadera novaeseelandiae*) specimens, Onley (1986) noted that Tuis have a narrow eighth primary with a notch out of the inner web. He considered this to be associated with the loud whirring noise made by that species. Juveniles lack the notch, and this is a useful feature in ageing Tuis in their first year. Stead (1932) noted that bellbirds "are very pugnacious, chasing their own kind and other birds in and out among the branches with great speed, and making a loud whirring noise with their wings while doing so . . . and they can increase the noise at will". Thus Stead recognised the importance of whirring in the aggressive displays of bellbirds but he did not note the mechanism by which it is made. Craig (1984) suggested that in bellbirds the whirring is probably produced by an emargination of the inner web of the ninth primary, leaving a finger-like process at the outer edge of the feather tip (Fig. 2). This was illustrated by Gadow (1884), and although present in adults of both sexes, it is more pronounced in males. In immature birds of both sexes this process has a different shape, being broader and rounder (Fig. 2). Therefore the main characters distinguishing immature Poor Knights bellbirds from adults are: reduced iridescence on the head; dull colouration overall; shorter wings and tail (the latter in males only); and the shape of the ninth primary.

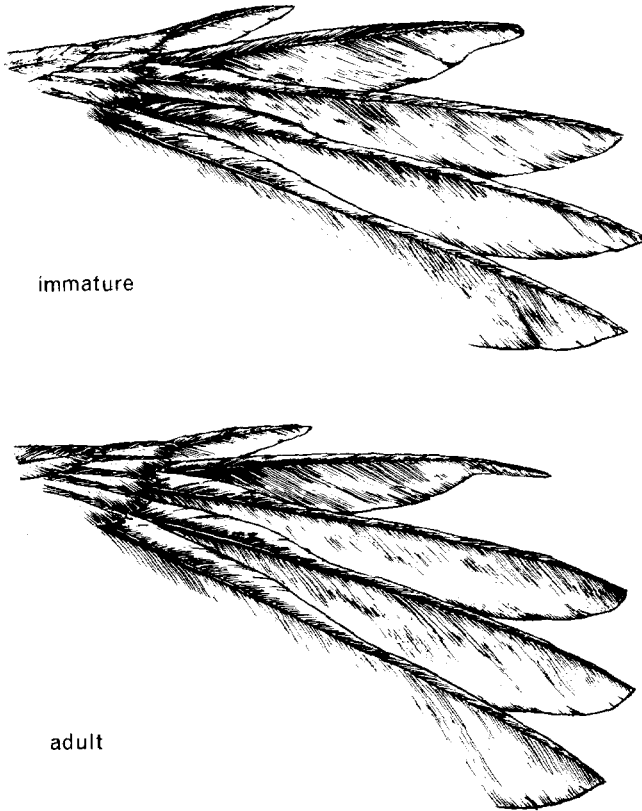


FIGURE 2 — Outer primaries of male Poor Knights bellbirds compared to show the emarginate inner web of the ninth primary of adults

Immature plumage persists until the birds undergo a full moult into adult plumage during November-January (Fig. 3). During their first winter the plumage of immatures shows increasing wear and by September they have very worn wing and tail feathers — in some immature females only the rachis of the outer tail feathers remains. Contour feather moult begins in October and is particularly noticeable about the head, chin, and throat. Wing covert moult starts in late November, and flight feather moult starts in early December. By early January immatures from the previous year are indistinguishable from adults.

In contrast to the prolonged moult of immatures, full adult moult on the Poor Knights Is is compressed into the period from late November to late January but, as with immatures, contour feather moult begins first, head feather moult being the earliest indication. Some body feather moult is under way in early December, but by early January most adults are replacing flight feathers.



### Mainland New Zealand

Adult bellbirds collected in the Bay of Islands in April were freshly moulted (UMZC No. 27/Mel/3/a/6 and 7 and MNHN New Catalogue No. 544 and 545). Birds on Tiritiri moult their flight feathers from February to April (J. L. Craig and M. E. Douglas, pers. comm.). North Island specimens are in active moult in March (NMNZ No. 336) and very fresh plumage in April and May (NMNZ No. 18121; AMNH No. 203028), whereas the plumage of most specimens collected at other times of the year shows some wear. In the South Island, birds at Punakaiki undergo flight and tail feather moult from late February to March and some contour feather moult may continue into April (D. J. Onley, pers. comm.). At Geraldine, slight head moult can be detected in late January, and the flight feathers are moulted from February to April. Most birds have completed moult by early April, but some contour feather moult continues into May. A Stewart Island specimen (AMNH No. 697250) had worn plumage in January, but 10 specimens collected in June and July were in fresh or slightly worn plumage (NMNZ).

Features indicative of immaturity in mainland bellbirds, other than measurements, include:

- (a) A yellow fleshy gape. Although this is most conspicuous in fledglings, some older juvenile bellbirds retain it, perhaps because they are fed by their parents for several weeks after leaving the nest (Sparrow 1982). Fleshy gapes sometimes persist in females even after they have moulted their juvenile contour feathers in January and assumed adult body plumage.
- (b) A yellow cheek stripe. This is present in juveniles of both sexes and disappears in males after their first body moult. It persists in females but becomes whitish during the first head moult.
- (c) Brown irises. Robertson *et al.* (1983) found that the iris colour of known-aged birds of both sexes changes from brown to red between April and June of their first winter.
- (d) Lack of an emarginate ninth primary. The shape of the ninth primary in subadult birds is distinctive (Fig. 2).
- (e) Lack of iridescence on head. Juveniles lack this altogether; it appears in subadult males and females after their first head moult, although always less brilliant and extensive than in adults.

We have not found any immature-plumaged bellbirds in mainland New Zealand populations. The birds described by Oliver (1955) as "immature" males must have been juveniles, for he described them as having a yellowish-white cheek stripe. Observations at Punakaiki suggest that most juveniles moult into adult body plumage before April (D. J. Onley, pers. comm.). At Geraldine, juvenile males caught in late December had vivid black wing and tail feathers (like those of adults) but lacked head iridescence and had a yellow cheek stripe and brown irises. Whereas some subadult females in adult body plumage at Geraldine in early January still had yellow fleshy gapes, others already showed some iridescence on the head. By April, when all birds at Geraldine were in adult body plumage, the subadults could still be identified by their brown and red-brown irises. One bird which had been

colour-banded as a juvenile in late December was seen in adult plumage in October of the following year. Thus juveniles apparently moult into adult body plumage a few months after leaving the nest.

### **Auckland Islands**

The moult cycle of bellbirds on the Auckland Is appears to be similar to that on mainland New Zealand. Two adults collected on 7 February (OM No. A204 and A205) were in active wing, tail, and contour moult, and a bird collected in March (CM Av. 1093.21) had very worn plumage. Birds collected in April (CM Av. 21976 and 21977; NMNZ No. 13161 and 13163) were freshly moulted, except for some slight moult of the dorsal body feathers.

Auckland Is bellbirds have a similar pattern of juvenile moult to that of mainland birds. Fledglings (CM Av. 1036 and 21278) have flight feathers of the same colour as adults. A subadult (NMNZ No. 13166) had already undergone contour feather moult by 28 March and was in adult plumage except that it lacked an emarginate ninth primary. This suggests that juvenile Auckland Is bellbirds also moult into adult body plumage soon after leaving the nest.

### **Chatham Islands**

The month of collection is not recorded for most specimens, and so little information is available. However, two adults collected in December and January (NMNZ No. 5018 and 5019) had worn plumage, indicating that the moult cycles of Chatham Is and mainland New Zealand bellbirds may have been similar.

Immature plumage may have been present in Chatham Is bellbirds. One specimen (NMNZ No. 2461) was replacing juvenile contour feathers while retaining brown wing and tail feathers. These old wing and tail feathers showed only moderate wear, and there was no emargination of the ninth primary. The timing of this moult is unknown, but we suspect that it occurred in late summer. The holotype (BM No. 1842.9.29.26) is an immature specimen (Buller 1873; P. R. Colston, pers. comm.) moulting into fully adult plumage. The brownish juvenile contour feathers on the head have been replaced by dark iridescent feathers, and the yellowish-margined brown rectrices and secondaries are being replaced (asymmetrically) by jet black flight feathers (P. R. Colston, pers. comm.). This bird was collected between May and July 1840 (Dieffenbach 1841) and the early timing of this moult is more in accordance with the August-October breeding season described by Potts (1884) than with the later breeding mentioned by Travers (1873).

### **Three Kings Islands**

An adult collected on 3 December (AIM Av. 15.29) was in worn plumage, but others collected on 20 February (AIM Av. 15.22; NMNZ No. 14050 and 14051) were freshly moulted. Turbott & Bull (1954) found "most adults [were] moulting" during the last days of December and first week in January. The moult cycles of adult Three Kings and Poor Knights bellbirds are thus very similar.

No specimens of subadult birds from the Three Kings Is are available.

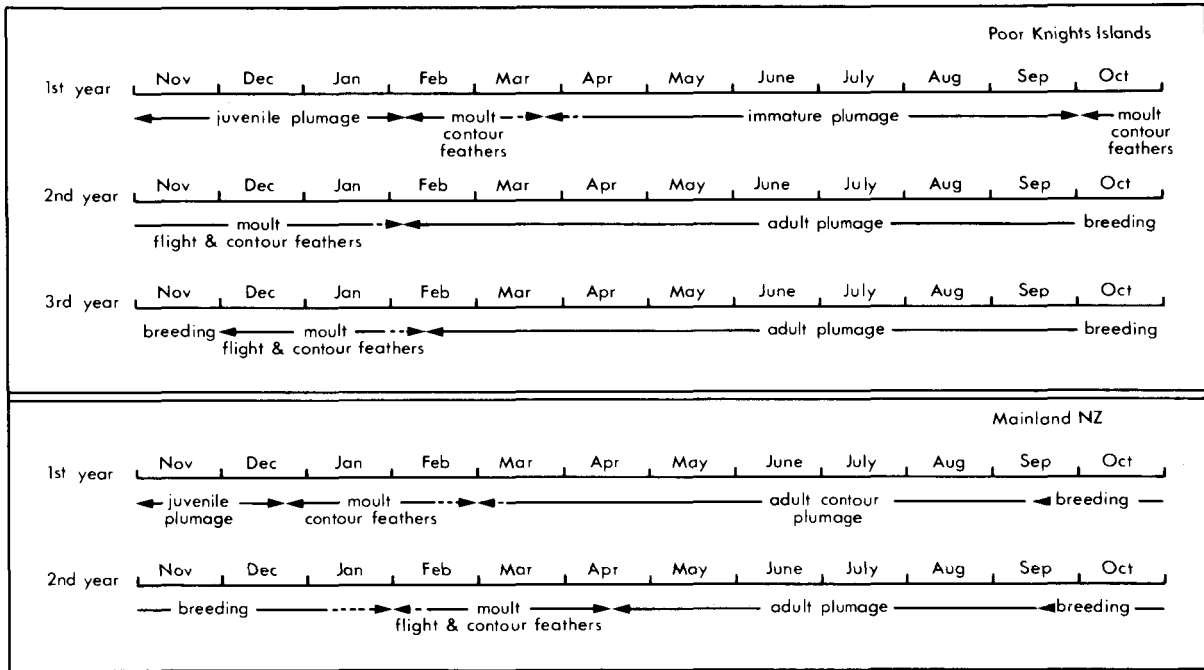


FIGURE 3 — A diagrammatic representation of the life cycles of Poor Knights and mainland bellbird populations

## Conclusion

Poor Knights bellbirds differ from mainland and nearshore island bellbirds in having an immature plumage. They also differ, except for the Three Kings bellbirds, in the timing and duration of moult. These dissimilarities are easily seen in Fig. 3.

The presence of a distinct immature plumage in the dense population on the Poor Knights Is should reduce conflict between aggressive territorial adult males and the non-territorial immature birds (which cannot therefore breed in their first year, unlike mainland birds). The long-term advantage of these differences to Poor Knights bellbirds is probably linked with a tendency towards K-selection on islands (Sagar 1985).

## PLUMAGE COLOURATION IN BELLBIRDS

### Plumage colouration and the role of melanin

The subtle changes in hue, chroma and colour value of bellbird contour feathers are very difficult to describe accurately. However, the task is easier if the colours are analysed according to feather structure as well as pigmentation. The key to understanding age, sexual, and geographical variation in the colour of bellbird plumages is the varying distribution of melanin. Iridescence (a structural colour) is caused by interference of incident light by melanin granules of different specific shapes in the barbules (Fox & Vevers 1960). Even the distinctive olive-green of the contour feathers is produced by the juxtaposition of yellow carotenoid pigments and melanin, and no green pigment is involved.

Microscopic examination of bellbird contour feathers revealed that all contain yellow pigment in the barbs, and that the shafts and barbules contain no coloured pigment, only various amounts of melanin. The olive-green feathers on the head exhibit brilliant violet iridescence in adult males and blue-green iridescence in females. Heavy deposits of melanin in the shafts and barbules are easily seen, and the barbules are well developed and somewhat widened. Schmidt (1949) has shown that the shape of the highly refractive melanin granules in the barbules determines the interference colour.

The olive-green contour feathers of bellbirds have intensely pigmented yellowish barbs with various amounts of melanin in the shafts and barbules. The juxtaposition of yellowish barbs and black barbules and shafts is perceived as olive-green, and the hue, chroma and colour value alter according to the degree of melanisation. Even Ridgway's Citrine and Warbler Green colour swatches contain no truly green pigment. The green colour was derived from the amount of grey in the yellow pigment used (Smithe 1974).

The paler contour feathers on the bellies of bellbirds have pigmented barbs identical in hue and chroma to those of the olive-green contour feathers. The belly feathers appear as Primrose Yellow (Ridgway) or even paler because their shafts and barbules lack melanin. In contrast, the greenish hue on the outer webs of the inner primaries, secondaries and greater coverts is caused by yellow pigments in the barbs of these otherwise black feathers.

### Variation with age and sex

In adult bellbirds the barbules of the head feathers are set more closely together and are thicker than in the juveniles and immatures, and they contain more eumelanin. Melanin increases the iridescence on the head of adults and, because it strengthens feathers, the head plumage of adult bellbirds wears more slowly than that of juveniles.

The flight feathers of immature bellbirds from northern New Zealand are less melanistic than those of adults, and they therefore wear faster. The barbules of all immature contour feathers contain less melanin than in adults, which results in a reduced colour value and, in juveniles, the breast feathers may be olive-brown rather than green. The pigmentation of the shafts and barbs does not appear to increase with age, and so the heightened colour values of immature and adult plumages are the result of increased melanisation and thicker barbules.

The colour value and chroma of the female plumage are also less than those of the male because the shafts and barbules of female feathers have less melanin. Melanin production is controlled by male hormones in many birds (Fox & Vevers 1960).

### Patterns of clinal and insular variation

Clinal variation in plumage colouration is evident among mainland and nearshore island bellbirds. Males tend towards more intense chroma on the underparts, brighter yellow pectoral plumes and more saturated green upperparts southwards, apparently in contradiction to Gloger's rule, which generalises that warm-blooded animal races living in warm and humid areas are more heavily pigmented than those in cool, dry areas. However, the higher intensity of bellbird plumage colouration in the south is caused by the feather shafts and barbules having more melanin, not by an increase in yellow pigment. Little geographical variation in the yellow pigment occurs, except on the Three Kings Is, where the yellow is less intense.

Moreau (1957) showed that variation in the green colour of African *Zosteropidae* was also caused by various degrees of melanisation. He found that the degree and type of melanisation of *Zosterops* varied clinally (even within subspecies) with the humidity of the environment and that, on the whole, the more richly coloured green birds were in the more humid areas. The richer colouration was linked to a greater degree of melanisation whereby the melanin granules are larger, are more regular in shape, and lie parallel with the axis of the barbule. Earlier, Beebe (1907) had demonstrated that intraspecific variation in the amount of melanin in birds is not necessarily under direct genetic control, but is affected by the humidity prevailing before moult. Inca Doves (*Scardafella inca*), kept in a humid atmosphere (84% relative humidity) by Beebe, became darker with each successive moult, and even developed brilliantly iridescent feathers where none had been before. Thus geographical variation of melanism in bellbirds, which is responsible for all observed differences in plumage colouration, is probably of little taxonomic significance. Moreau (1957, 1967) reached a similar conclusion when he recommended that the number of *Zosterops* species in Africa and its islands be reduced from 18 to 13 (all alleged specific differences having been based on colour alone) and the number of subspecies from 82 to 47.

The climate of New Zealand is often classified as warm temperate, but it varies more than is generally appreciated because of the interaction of oceanic and physiographic effects. Nevertheless, sea-level temperatures differ significantly between the North and South I. only in winter (Garnier 1958), and at the Auckland Is the annual average of mean daily temperatures is only 2.3 °C lower than that at Wellington (De Lisle 1965; NZ Meteorological Service 1973). Similarly, latitudinal variation in precipitation is negligible (NZ Met. Serv. 1973). Physiography rather than latitude influences rainfall in New Zealand, and precipitation is very much higher and less seasonal to the west of the main ranges. The low-lying islands to the north and east of northern New Zealand are drought prone (NZ Met. Serv. 1973 and unpublished), in contrast to those south and east of New Zealand, where rainfall is heavier and less seasonal (De Lisle 1965, NZ Met. Serv. 1973).

Moreau (1957) found that in Zosteropidae the degree of melanism varied with the seasonal distribution of rain rather than with the total rainfall; he classed as humid those climates with more than 1524 mm of rain per year and no long dry season. The average annual relative humidity does not vary with latitude in New Zealand. Kerikeri (80%) is much the same as Wellington (81%), Westport (80%), and Invercargill (81%) (NZ Met. Serv. 1973). Changes in relative humidity cannot therefore account for the clinal increase in bellbird melanisation southwards.

The dryness of any locality is determined by many factors, such as the balance between rainfall and temperature, absolute humidity, wind strength, and evenness of rainfall. Oceanic influences result in high and even relative humidities throughout New Zealand and on the offshore islands, except for the dry areas east of the main ranges. Thus, in New Zealand, the average deficit in water balance at each locality is a more sensitive measure of dryness than relative humidity. A deficit occurs when the combined rainfall and available soil moisture are less than the potential evapotranspiration.

The deficit in water balance is highest in Northland and at localities east of the main ranges on both islands. If conditions on the Three Kings Is are similar to those at Cape Reinga, 56 km to the southeast, the average annual deficit of 116 mm (for 28 years up to 1970; NZ Met. Serv. 1973) is nearly twice as high as for any other locality from which both bellbirds and water balance deficit data are available, and it occurs entirely during the months of December-April, when bellbirds are moulting. Deficits at or near other places where bellbirds were sampled, or which are typical of sample areas are as follows: at Kerikeri (near the Bay of Islands) 54 mm; Rotoehu Forest (typical of the North I. localities from which bellbirds were available) 39 mm; Wellington, 37 mm; Fairlie (near Geraldine) 68 mm; Musselburgh (Dunedin) 59 mm; Westport (near Punakaiki) 3 mm; Greymouth, 0; Haast, 0; and Milford Sound, 0. Comparable data are not available for Stewart I., the Auckland Is, and the Chatham Is, but water balance deficits should be close to zero because of the high and evenly distributed rainfall and cool temperatures in these islands.

Melanism in bellbirds is noticeably higher in the wettest places (western South I., Stewart I., Auckland Is, and the Chatham Is) where the average annual deficit in water balance is close to zero. Where the deficit in water

balance in summer is significant (Northland, North I., eastern South I.), melanisation is less advanced. *Anthornis m. obscura* represents an end-point in the northward trend towards reduced melanin deposition, and this probably reflects the higher deficit in water balance and the frequency of droughts on the Three Kings Is. Melanism increases in warmer climates only when rainfall is not reduced (Mayr 1942), and thus the increased melanism of bellbirds from southern and western mainland areas and the southern islands is not in contradiction to Gloger's rule.

A strong correlation between degree of plumage pigmentation, humidity and substrate colour was found by Bowers (1960) in Wrentits (*Chamaea fasciata*) in the San Francisco Bay area. In humid areas with luxuriant vegetation dark soils with abundant humus are formed, and Bowers suggested that, under these conditions, selection would favour darker plumage. Under different circumstances, Johnston (1966) found darkness of the breast in female House Sparrows (*Passer domesticus*) to be correlated with soil colour.

### Discussion

A trend towards drab plumage colours of birds on islands was described by Grant (1965a) but not thought to have adaptive significance. Perhaps he had not adequately taken into account that dense island populations need to reduce intraspecific aggression. Ewald & Rohwer (1980) experimentally demonstrated that reduction in bright colouration, particularly iridescence on the crown, reduced conflict between young and old birds. This helped the older birds establish territories, and the young gained by being attacked less by territory holders and were thus more successful at stealing food from adult territories. These benefits would be especially great for K-selected dense island populations such as the Three Kings (Turbott & Buddle 1948) and Poor Knights bellbirds (Sagar 1985, 1986 and in prep.).

In Poor Knights and Chatham Is bellbirds conflict is reduced by the development of an immature plumage. Consequent increased subadult survivorship in good years, and decreased subadult survivorship during hard times (cf. Kikkawa 1980) will buffer Poor Knights and Chatham Is breeding adult bellbirds against population fluctuations, and reduce their need to expend energy on territorial defence (Stamps & Buechner 1985).

Female bellbirds exploit different foods from males (Craig *et al.* 1981a; Angehr 1986; Sagar 1986 and in prep.), but there is intense rivalry, with females using their (smaller) emarginate processes to defend favoured feeding sites against other females (Craig 1984). Marler (1955) showed how the dull plumage of female Chaffinches (*Fringilla coelebs*) prevents them dominating males. Decreased sexual dimorphism and dichromatism in the Auckland Island Tit *Petroica macrocephala marrineri* and Snares Black Tit *P.m. dannefaerdi* (Fleming 1950) must also reduce interpair competition. The frontal spot, which normally serves as an aggressive signal in New Zealand tits (Flack 1976), is also small or absent in these island forms.

## MORPHOMETRIC VARIATION IN BELLBIRDS

### Variation with sex and age

Craig *et al.* (1981b) identified morphometric characters that could be used to discriminate the sexes in the three New Zealand honeyeaters.

They found that the measurements of head plus bill or of tail length could be used for bellbirds of all ages, and our results generally agree. For head plus bill length we found no overlap between sexes in any samples south of Tiritiri (Tables 3 and 10), and negligible overlap between male and female Poor Knights and Hauraki Gulf birds. We also found the value of 40 mm for head plus bill length to be a boundary value for all populations except those on the Three Kings and Chathams. The other discriminator, tail length (Tables 7 and 13), provided wider separation of males and females from all localities except the Orongorongo Valley, where seasonal variations in wear may have blurred the sexual difference. For bellbirds of known age, wing length can also be used to identify sex (Tables 6 and 12) in all localities except Northland and the Poor Knights. The overlap noted by Craig *et al.* for Tiritiri was caused by the inclusion of subadults in the sample.

Many species of passerine birds are sexually dimorphic in size, partly because this may reduce competition for food between males and females (Selander 1966). Seven of the species of forest passerine in the Orongorongo Valley are sexually dimorphic in size (Robertson *et al.* 1983), including the six that are sexually dichromatic. The male is the larger, except for the Rifleman (*Acanthisitta chloris*), and the degree of dimorphism was noticeably more marked in honeyeaters than in other birds. There are major differences in food and in foraging behaviour between adult male and female bellbirds, and between adults and subadults, on the Poor Knights Islands (Sagar in prep.).

Tables 2-14 give weights and measurements of bellbirds from the 14 localities sampled (Fig. 1). For each locality, we calculated the degree of sexual dimorphism and the degree of difference in size between adults and subadults. Percentage differences between adult males and adult females,

TABLE 2 — Bill length of adults (mm)

	Adult ♂♂				Adult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Three Kings Is	17.1	1.05	15.9-18.3	4	14.7	0.49	14.3-15.0	2
Poor Knights Is	15.4	0.60	14.0-17.4	48	14.8	0.76	13.4-16.8	33
Northland	14.3	0.15	14.2-14.5	3	13.3	0.84	11.8-13.8	5
Hauraki Gulf Is	14.2	0.62	13.4-15.4	13	-	-	-	-
Tiritiri Matangi I.	14.5	0.50	13.3-15.5	17	13.9	0.39	13.1-14.4	19
North I.	13.6	0.65	12.9-14.6	7	12.0	0.35	11.6-12.3	3
Orongorongo	14.2	0.79	13-17	148	13.3	0.83	12-16	61
Western South I.	13.7	0.67	12.3-14.6	19	12.5	0.60	11.3-13.5	11
Geraldine	14.6	0.98	13.4-17.1	26	14.1	0.54	13.2-15.2	19
Eastern South I.	13.6	0.69	12.3-14.4	10	13.1	0.79	12.0-13.9	4
Stewart I.	13.4	0.77	12.4-14.7	9	13.4	0.44	13.1-13.9	3
Auckland Is	13.2	0.38	12.6-14.0	15	12.1	0.76	11.6-13.2	4
Chatham Is	15.2	1.28	13.3-16.8	7	13.3	0.51	12.7-13.8	5



subadult males and subadult females, and between adults and subadults of the same sex were calculated from the mean measurements. Finally, a mean value for the differences with age and sex in all measurements at each locality was obtained.

An intriguing result of this analysis was that both sexual dimorphism and the relative difference in size between adult and subadult bellbirds vary geographically. Within the central group of localities (Northland south to the Auckland Is), the between-locality difference in overall sexual dimorphism was very low. Females were 91% the size of males (mean difference between females and males in all measurements, expressed as a percentage of mean male size) and the range varied only from 89% to 92% over all 11 localities. Similarly, females weighed 77% as much as males (range 75% to 80% over all localities). The degree of sexual dimorphism on the Poor Knights was very similar to that on the mainland (average of all female measurements 91% those of males, and of weight 74%). The size difference between the sexes was greater, however, in the larger island races, Three Kings females being 88% the size of males and Chathams females 86%.

There is, therefore, some insular variation in sexual dimorphism, but no clinal variation with latitude. Despite the clinal variation (see next section) in the absolute size of bellbirds through the 11 localities in the central group in the tables (Northland south to the Auckland Is), the relativity in size and weight of females to males is constant. Thus it appears that there is an advantage in maintaining a constant size ratio between sexes on the mainland and on nearshore and southern islands.

Selection pressures on offshore islands, although favouring larger birds of both sexes, have had a greater effect on the size of males. For instance, the wing length of adult male Chatham Island bellbirds was 17% longer, but of females only 13% longer, than for mainland birds of the same latitude (Table 6). It is this process which has resulted in the increased sexual dimorphism in size on offshore islands.

The pattern of a constant ratio of sexual dimorphism in size irrespective of latitude can also be seen in subadult birds. Values for the mean difference in all measurements between subadult males and females are available from fewer localities (4), but again females were 92% of the size of males (range 91-92%) and 74% of the weight (range 72-75%). Sexual differences in mean weights and measurements on the Poor Knights were the same (92% for size and 74% for weight), but no values for subadult sexual dimorphism are available from the Three Kings or Chathams.

When subadults are compared with adults of the same sex, the reduction in mean size and weight (1.5%) is the same, regardless of sex. This does not vary with latitude. However, the mean difference in weight and lineal measurements is 3% on the Poor Knights, and it was 5% on the Chathams. Apparently slower growth and delayed maturity are selected for on offshore islands. This fits with previously described differences in subadult plumage (Poor Knights and probably Chathams), clutch size and frequency (Poor Knights and probably Chathams), and population density (Three Kings – Turbott & Buddle 1948; Poor Knights – Sagar 1985, 1986 and in prep.).

TABLE 3 — Head &amp; bill length of adults (mm)

	Adult ♂♂				Adult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Three Kings Is	44.9	-	-	1	40.0	-	-	1
Poor Knights Is	42.0	0.76	40.2-43.5	144	38.9	0.63	37.5-40.5	64
Hauraki Gulf Is	40.5	0.94	39.2-41.2	4	38.0	0.77	37.0-39.3	9
Tiritiri Matangi I.	41.1	0.63	40.1-42.2	40	38.3	0.52	37.3-39.5	23
North I.	40.0	0.75	39.3-40.8	3	36.3	-	-	1
Western South I.	41.2	0.88	40-42	7	37.0	1.11	35.3-38.7	7
Punakaiki	41.6	0.71	40.5-42.7	13	38.5	0.64	37.2-39.3	7
Geraldine	41.0	0.58	39.6-42.2	27	38.3	0.56	37.3-39.5	21
Eastern South I.	40.7	0.66	40.2-41.6	4	38.3	-	-	1
Stewart I.	41.1	0.70	40.2-42.3	9	38.7	0.42	38.2-39.0	3
Auckland Is	40.6	0.34	40.2-41.3	8	37.1	0.70	36-38	5
Chatham Is	45.9	1.14	44.7-47.5	5	41.4	1.02	39.9-42.7	5

TABLE 4 — Tarsus length of adults (mm)

	Adult ♂♂				Adult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Three Kings Is	27.9	1.01	26.8-29.2	4	25.9	1.2	25.0-26.7	2
Poor Knights Is	27.4	1.05	23.2-30.0	115	25.6	1.13	22.3-27.2	73
Northland	27.0	1.73	26-29	3	25.5	3.61	22.9-28.0	2
Hauraki Gulf Is	25.7	1.07	23.0-27.1	14	24.2	0.74	23.2-24.9	8
Tiritiri Matangi I.	26.1	0.53	25.1-27.2	40	24.3	0.43	23.6-25.2	23
North I.	26.0	1.19	23.6-27.5	8	22.6	0.81	21.7-23.2	3
Orongorongo	26.1	0.86	24-28	127	24.4	0.98	20-26	49
Western South I.	27.2	1.28	25.0-29.1	19	24.8	1.2	23.1-27.0	11
Punakaiki	26.8	0.84	25.8-28.0	14	25.7	0.87	24.5-27.5	13
Geraldine	26.4	1.05	23.3-28.5	31	24.8	1.34	19.7-27.3	23
Eastern South I.	26.5	1.53	24.2-28.8	12	24.8	0.82	24.0-25.8	4
Stewart I.	27.0	1.03	25.2-28.2	9	25.3	0.31	25.0-25.6	3
Auckland Is	26.9	1.37	24-29	16	25.9	1.2	25.0-27.7	6
Chatham Is	37.3	3.57	34-44	7	31.2	2.14	29-35	5

TABLE 5 — Length of mid-toe and claw of adults (mm)

	Adult ♂♂				Adult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Three Kings Is	21.8	1.61	19.6-23.5	4	21.0	2.82	19.0-23.0	2
Poor Knights Is	21.7	1.24	19.8-23.2	8	20.6	0.07	20.5-20.6	2
Hauraki Gulf Is	20.5	1.28	18.1-22.0	9	-	-	-	-
North I.	19.6	0.85	18.4-21.0	8	17.6	1.33	16.5-19.1	3
Orongorongo	20.8	1.19	17*24	147	19.9	1.18	17-23	61
Western South I.	20.9	1.31	18.6-23.2	17	19.5	0.69	18.2-20.7	10
Eastern South I.	21.3	0.63	19.9-22.0	8	19.5	0.92	18.4-20.0	3
Stewart I.	21.4	0.53	20.3-22.0	8	19.6	0.95	18.5-20.2	3
Auckland Is	23.3	1.25	21.1-25.0	14	21.2	1.34	19.8-22.7	4
Chatham Is	25.4	0.93	24.5-26.2	4	21.6	2.05	18-23	5

\* incorrectly measured

TABLE 6 — Wing length of adults (mm)

	Adult ♂♂				Adult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Three Kings Is	93.1	3.80	88.7-98.0	4	82	-	-	2
Poor Knights Is	87.7	2.40	81-94	251	77	2.10	72-83	142
Northland	85.3	2.52	83-88	3	80	4.69	75-85	5
Hauraki Gulf Is	87.8	2.56	83-92	14	77.5	1.19	75.8-79.3	8
Tiritiri Matangi I.	84.1	2.1	79.5-87.9	40	75.1	1.52	71.1-77.9	23
North I.	87.3	2.05	83-90	8	76.7	2.08	75-79	3
Orongorongo	86.1	2.43	80-92	200	76.4	2.33	66-81	94
Western South I.	92.1	2.25	88-97	19	80.6	2.84	75.0-84.5	11
Punakaiki	91.0	1.92	88-95	14	80.4	1.71	77-83	13
Geraldine	89.0	2.35	86-92	33	79.5	2.29	75-85	28
Eastern South I.	91.0	2.45	86-96	12	82	2.0	80-85	5
Stewart I.	94.4	1.59	92-97	9	83.5	3.5	79.5-86.0	3
Auckland Is	94.0	2.28	89-97	17	84.2	1.33	82-86	6
Chatham Is	106.4	3.7	102-112	7	92.8	1.79	92-96	5

\* probably incorrectly measured

TABLE 7 — Tail length of adults (mm)

	Adult ♂♂				Adult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Three Kings Is	84	2.58	81-87	4	71.5	0.7	71-72	2
Poor Knights Is	88.1	2.56	79-94	48	71.4	3.01	66-75	16
Northland	77.7	1.53	76-79	3	68.8	4.49	64-75	5
Hauraki Gulf Is	81.7	3.77	74-85	14	69.3	1.96	65.6-71.8	8
Tiritiri Matangi I.	81.5	2.97	76.7-87.6	38	68.4	1.94	65.1-71.7	23
North I.	84.1	3.56	77-87	8	70.0	3.61	67-74	3
Orongorongo	84.5	4.23	74-92	144	70.6	3.15	65-79	59
Western South I.	87.7	3.47	83-96	19	69.7	3.07	63-74	11
Punakaiki	91.8	3.62	89.5-96.0	3	73.9	4.42	66.4-80.0	8
Geraldine	88.0	3.08	83-94	8	73.5	1.98	71-76	6
Eastern South I.	85.3	4.32	78-92	12	70.6	2.3	67-73	5
Stewart I.	88.6	1.74	85-91	9	73.9	4.7	69.8-79.0	3
Auckland Is	88.2	3.95	83-94	15	74.4	2.41	71-77	5
Chatham Is	100.1	5.6	93-108	7	82.8	2.41	81-87	5

TABLE 8 — Weight in grams of adults

	Adult ♂♂				Adult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Poor Knights Is	36.2	3.37	25-47	86	26.8	2.52	22-35	46
Tiritiri Matangi I.	31.7	2.83	24.0-37.5	31	25.4	3.21	20.5-32.0	20
North I.	27.8	0.71	27.3-28.3	2	-	-	-	-
Orongorongo	30.7	2.42	21-38	202	23.6	2.16	20-32	94
Western South I.	33.8	2.35	30-37	9	25.5	3.54	23-28	2
Punakaiki	32.9	3.58	29.0-42.1	13	26.1	1.06	24.3-27.6	7
Geraldine	34.8	2.05	31-40	32	26.1	1.68	23-31	27
Eastern South I.	35.5	4.6	30.5-39.5	3	-	-	-	-
Auckland Is	35.5	0.00	-	3	30.5	2.12	29-32	2

TABLE 9 — Bill length of subadults (mm)

	Subadult ♂♂				Subadult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Poor Knights Is	15.0	1.13	14.2-15.7	2	13.8	-	-	1
Tiritiri Matangi I.	14.0	0.51	13.2-14.8	11	13.5	0.28	13.1-13.9	15
Mainland & Stewart I.	13.2	0.65	12.1-14.0	10	12.5	1.01	11.4-13.4	3
Geraldine	14.8	0.72	14.1-15.8	4	13.3	0.99	12.2-14.0	3
Chatham Is	14.2	1.15	13.1-15.4	3	-	-	-	-

TABLE 10 — Head &amp; bill length of subadults (mm)

	Subadult ♂♂				Subadult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Poor Knights Is	41.5	0.83	39.4-43.1	67	38.9	0.67	37.5-40.0	28
Tiritiri Matangi I.	40.9	0.65	39.8-42.3	18	38.2	0.48	37.1-39.0	21
Mainland & Stewart I.	40.2	0.92	39.4-41.2	3	37.9	1.20	36.7-39.1	3
Geraldine	40.3	0.54	39.8-41.2	5	37.4	0.95	36.4-38.3	3
Chatham Is	45.2	0.42	44.9-45.5	2	-	-	-	-

TABLE 11 — Tarsus length of subadults (mm)

	Subadult ♂♂				Subadult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Poor Knights Is	27.5	0.86	25.0-29.3	34	25.7	0.77	24.7-27.5	16
Tiritiri Matangi I.	25.9	0.55	24.8-27.2	21	24.1	0.48	23-25	25
Mainland & Stewart I.	25.9	1.33	22.6-27.3	9	25.1	0.83	24.2-25.8	3
Geraldine	26.9	1.08	25.6-28.1	7	24.5	0.46	24.0-25.3	6
Chatham Is	34.7	0.12	34.6-34.8	3	-	-	-	-

TABLE 12 — Wing length of subadults (mm)

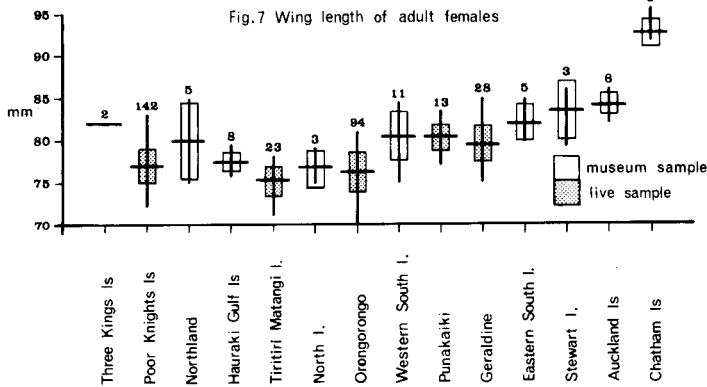
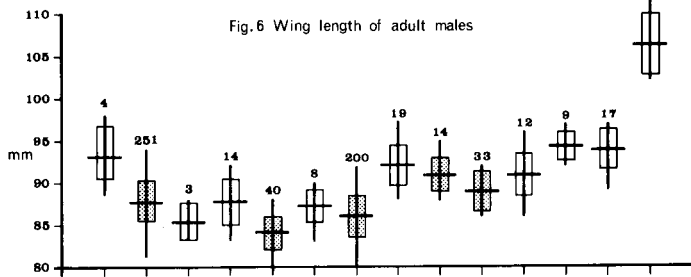
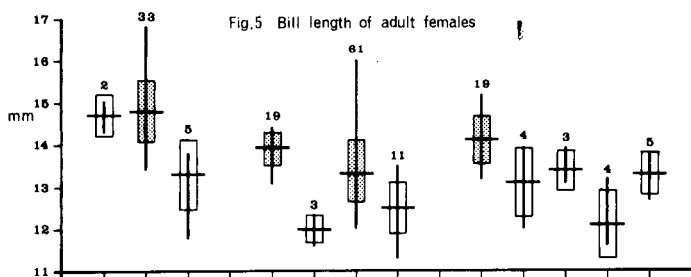
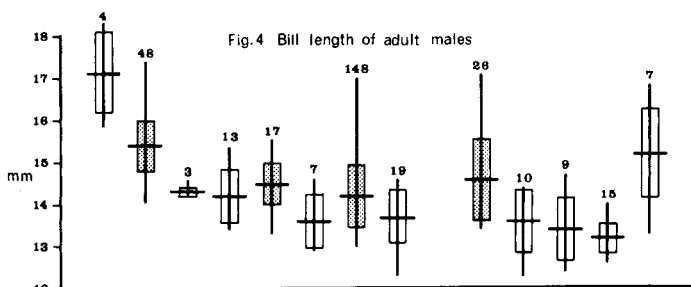
	Subadult ♂♂				Subadult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Poor Knights Is	84	2.28	78-90	167	74.3	2.03	70-78	67
Tiritiri Matangi I.	81.7	1.79	77.8-84.7	21	73.5	1.53	69.6-76.2	25
Mainland & Stewart I.	86.6	3.81	77-92	10	79.5	2.12	78-81	2
Geraldine	87.7	1.49	86-90	7	79.2	2.23	77-83	6
Chatham Is	105	3.0	102-108	3	-	-	-	-

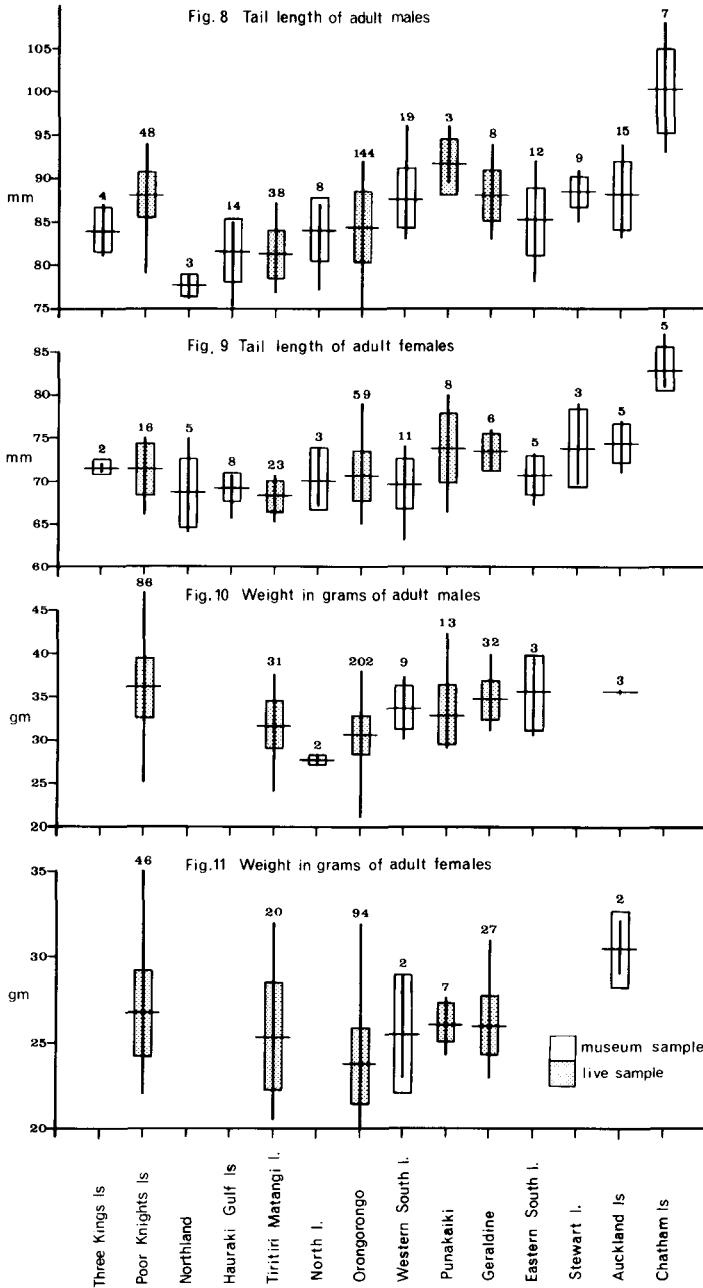
TABLE 13 — Tail length of subadults (mm)

	Subadult ♂♂				Subadult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Poor Knights Is	83.1	2.06	79-87	41	71.9	3.98	67-78	9
Tiritiri Matangi I.	78.2	2.22	73.1-83.7	21	66.3	2.04	62-70	25
Mainland & Stewart I.	78.5	8.23	62-90	10	70.0	0.00	-	2
Chatham Is	92	4.36	87-95	3	-	-	-	-

TABLE 14 — Weight in grams of subadults

	Subadult ♂♂				Subadult ♀♀			
	Mean	S.D.	Range	No.	Mean	S.D.	Range	No.
Poor Knights Is	33.9	2.15	30-38	44	25.0	2.11	18-28	45
Tiritiri Matangi I.	31.1	2.24	28.2-36.0	15	23.3	1.05	21.8-24.8	20
Geraldine	34.1	2.29	31.5-37.0	7	24.5	1.55	22.5-27.0	6





### Clinal variation

Morphometric data for bellbirds were grouped by locality to illustrate geographical trends in variation. These localities have been arranged in an approximate north-south sequence in Figures 4-11, with the island populations on the Three Kings, Poor Knights, and Chathams integrated.

A clinal pattern of continuous variation can be seen in the weights and measurements (except for bill plus head length and tarsus length) of adult males and females, and in subadult males and females from the mainland localities. Most measurements increase southwards. The exception is the bill, which becomes shorter. Morphometric characteristics of the populations on the nearshore Hauraki Gulf islands and on Tiritiri fall entirely within the range of variation of mainland populations, and the ranges and standard deviations of the means of these data coincide with those of other mainland populations (Fig. 4-11).

If mean values for measurements of mainland and nearshore island bellbirds are plotted against one another (bill length against wing length, for example, as in Fig. 14-15) they segregate along a line in general accordance with the latitude of the locality. The degree of spread varies, but is consistently highest in Geraldine birds, perhaps partly reflecting the bias resulting from measuring live birds. Differences between measurements of live birds and museum specimens can be inferred from Tables 2-14, and the segregation of measurements obtained from the two sources is particularly clear in Figures 12 and 13. Here the combined effect of *shorter* wing measurements and *longer* tail measurements in live-caught birds has caused the samples of both adult males and females to lie along a different regression line than the samples of museum specimens.

From the values for island populations plotted on Fig. 14-15, it can be seen that the Stewart and Auckland Is measurements lie further along the same line of latitudinal variation than do the mainland and nearshore island samples. For example, when the mean dimensions of Auckland Is bellbirds are compared with those of birds from the eastern South Island (Table 15), only one significant difference emerges at the 5% level, that of tail length of females. This is in sharp contrast to the situation with the Chathams, Three Kings and Poor Knights birds: the mean values for these populations lie well to the side of the latitudinal gradient formed by the mainland, nearshore island, Stewart and Auckland Is birds, and it is apparent that factors other than latitude must determine the mean dimensions of birds on the Chathams, Three Kings and Poor Knights.

However, if wing and tail length (which both increase with latitude) are plotted against each other (rather than against a measurement such as bill length that decreases with increasing latitude), the Three Kings and Poor Knights populations are not separated, but lie within the range of values and along the same line as do the measurements from the main cline (Fig. 12-13). We believe that this shows that two different modes of geographical variation exist within the bellbird populations scattered through the New Zealand archipelago.

The first mode, already discussed, is increasing size with latitude (Bergmann's rule), which primarily affects weight (Fig. 10-11). That many South I. Bird species and subspecies are larger than their close relatives in

the North I. is well known (Bull & Whitaker 1975). Although the pattern shown in Figures 10 and 11 tempts one to speculate that the gradient is steeper with females than with males, the sample (only two birds) from the only southern locality from which we have weight data (Auckland Is) is too small to allow a definite statement. If wing or tail length is plotted against weight (Fig. 16), the points rise along a line roughly in latitudinal order. We therefore conclude that the latitudinal increase in wing and tail length shown by the centrally grouped localities in the tables (Northland south to the Auckland Is) simply reflects the advantage of increased weight in colder latitudes.

Bill length also declines markedly with increasing latitude (Fig. 4-5). This is particularly noticeable for adult males, in which mean bill length decreases continuously (Table 2) through the centrally grouped localities in the tables and, at the extremes of the cline, the standard deviation of the mean Auckland Is bill length does not overlap those for the three northernmost populations (Fig. 4).

Mid-toe and claw length increases southward (Table 5). This could be a function of increasing weight, for toe length is also markedly greater in the heavier island populations (Poor Knights, Three Kings, and Chatham).

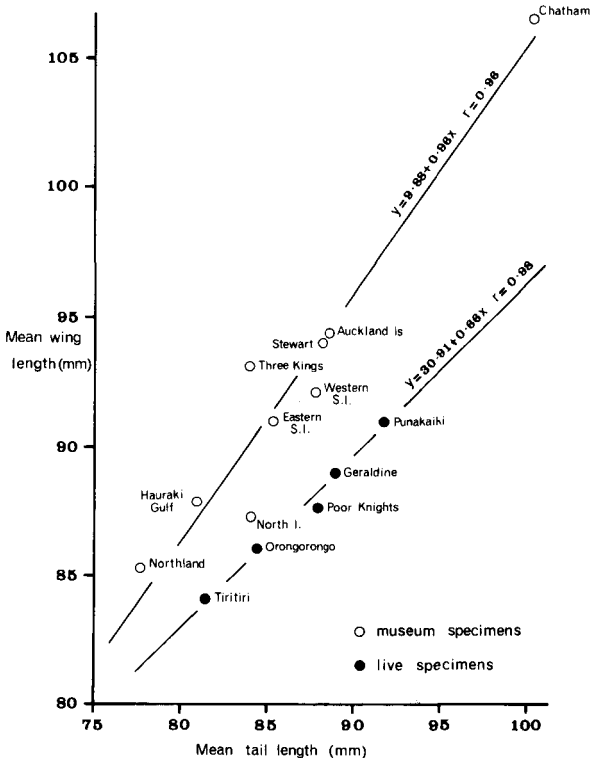


FIGURE 12 — Wing length plotted against tail length of adult male bellbirds



Conversely, the constancy of tarsal length with latitude (Table 4) contrasts with its increase on islands. We therefore conclude that clinal variation in toe length of bellbirds, as with bill length, is independent of other characters, as in Australian honeyeaters of the genus *Meliphreptus* (Keast 1968).

**Variation in island populations**

The second trend of geographical variation in the morphometric data is insular. Because this is overlain on a latitudinal cline, the island effects are more difficult to separate. However, island bellbirds are much heavier than mainland birds from similar latitudes. This trend is less marked with Tiritiri birds (Fig. 10-11), but only a small sample of two weights of adult males from the northern North Island mainland is available for comparison. The difference is greater with Poor Knights birds, and the mean weights are well above the comparably sized Orongorongo sample. Judging by their other dimensions, the large Chatham and Three Kings bellbirds would be far heavier than any from the mainland.

As weight increases in bellbirds, so do wing and tail lengths (see previous section). The clinal increase in weight occurs at about the same rate as does wing length (Fig. 16), except on the Poor Knights, where adult males are

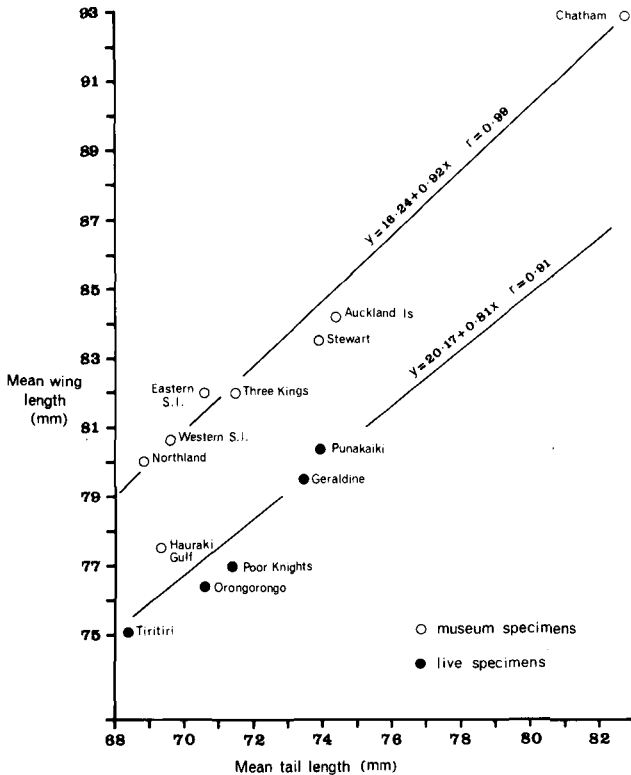


FIGURE 13 — Wing length plotted against tail length of adult female bellbirds

far heavier proportional to their wing and tail lengths. Compared with Tiritiri birds, the mean weight of Poor Knights adult males is 14% higher, the wing 4% longer, and the tail 8% longer. As noted earlier, the equivalent figures are lower for females (6%, 2.5% and 4%, respectively) and for subadults (9%, 3% and 6%, respectively, for subadult males).

The tarsus, which does not show variation with latitude is, however, longer on the Three Kings, Poor Knights and Chathams, but not on nearshore islands in the Hauraki Gulf, on Tiritiri, or on the Auckland Is (Table 4). The proportional difference, compared with mainland populations, is highest on the more isolated islands (Three Kings, Chathams), and the tarsi of males from the Chathams are a massive 41% longer than those of mainland males from a similar latitude. Again, the degree of difference is much more in males than in females.

It is difficult to see why bills should be longer on offshore islands, especially on those where the larger Tui was also present (Three Kings and Chathams). Although Tui are no longer found on Three Kings (Turbott & Buddle 1948), they have been on the Chathams long enough to differentiate into a well-defined subspecies (Oliver 1955). According to Craig *et al.* (1981b)

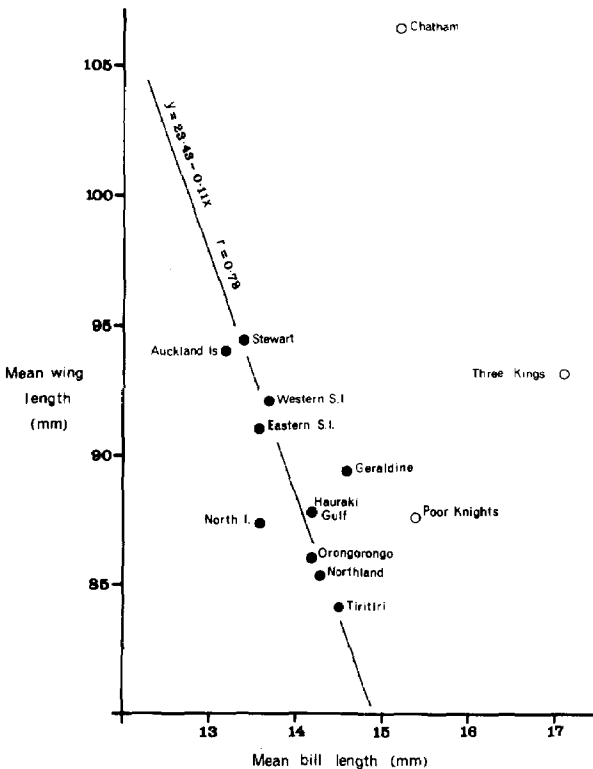


FIGURE 14 — Bill length plotted against wing length of adult male bellbirds. Three Kings, Poor Knights and Chathams (open circles) omitted from regression

New Zealand honeyeaters compete strongly for food. The difference in bill length between mainland and isolated island populations is considerable, but it is less marked on the Poor Knights and Chathams than on the Three Kings, where bills of adult males exceed those of Northland birds by 20%. Environmental differences between the Three Kings and Poor Knights seem inadequate to explain why male Three Kings bellbirds should have much longer bills than Poor Knights birds, when bills of females from the two localities are almost identical (Table 2). So perhaps the longer bill of Three Kings males is the result of greater isolation and/or lower gene flow from mainland populations.

On the Chatham Is, bills of adult males are 12% longer than those of mainland males from a similar latitude, but female bill length is well within the range of variability of mainland birds (Table 2). Hence the longer bill of the Chathams male may be the result of specific factors causing increased sexual dimorphism on islands, rather than a general tendency for island birds to have longer bills, as in some Australian species (Keast 1968). If bill length was governed by an equilibrium between opposing latitudinal and insular

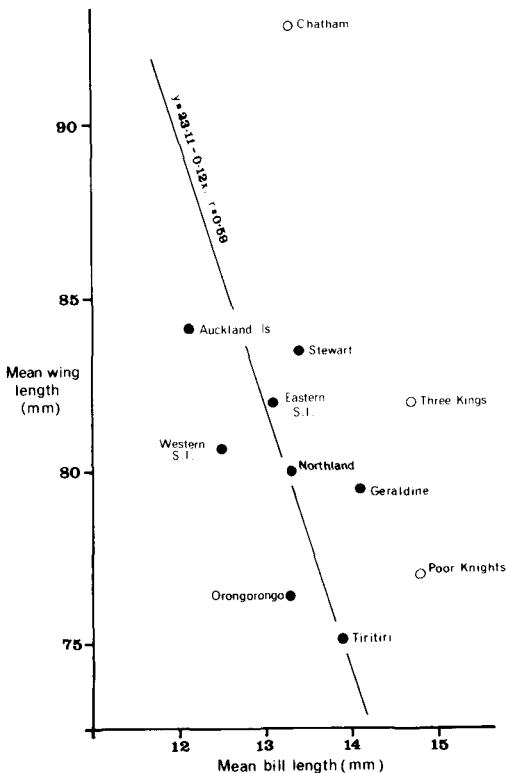


FIGURE 15 — Bill length plotted against wing length of adult female bellbirds. Three Kings, Poor Knights and Chathams (open circles) omitted from regression

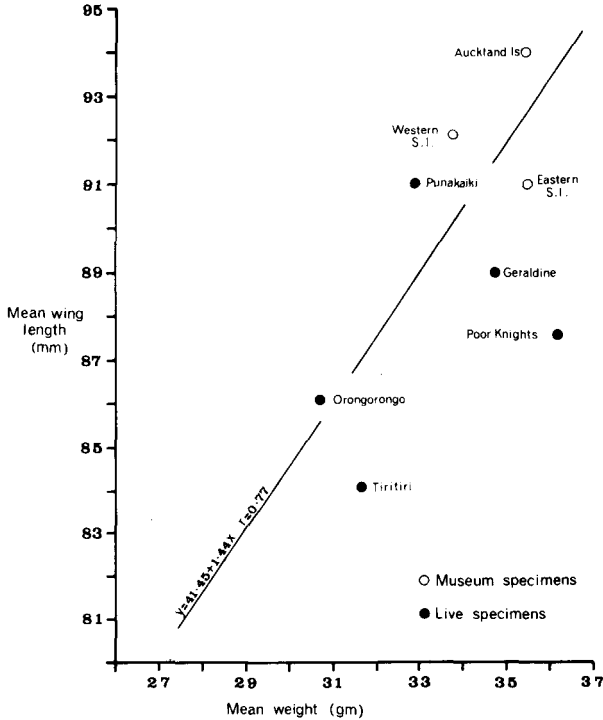


FIGURE 16 — Wing length plotted against weight of adult male bellbirds. Poor Knights omitted from regression

effects (adult male bill lengths are shorter on the Chathams than on the Poor Knights, Table 2), one would also expect the bills of females to be 12% longer than on the mainland, but this is not so.

Finally, bellbirds are larger in all dimensions on isolated islands. The exception is the Auckland Is, where the morphometrics of the population suggest a recent origin from southern New Zealand, and that isolation has not yet played a part in shaping its characters.

Evolutionary trends among island birds in New Zealand were listed by Bull & Whitaker (1975):

- (a) large size and, possibly partly as a result,
- (b) flightlessness. Some authors (e.g. Olson 1973, Feduccia 1980) have suggested that there must be other aspects to flightlessness on islands such as developmental predisposition and energetic advantages.
- (c) melanism, or duller plumage colouration.
- (d) larger eggs and a smaller clutch size (Lack 1974) as a result of higher survival of chicks and/or longevity of adults (Niethammer 1970).

Chatham Is bellbirds exhibited characteristics (a), (c) and (d); while (a), at least, is true for Three Kings bellbirds; and (d) is true for Poor Knights Is bellbirds, which also show a tendency towards (a).

## CAUSES OF CLINAL AND INSULAR VARIATION

Patterns of clinal and insular variation can be caused by partial sympatry with competing species (Mayr 1963, Keast 1968). Because bellbirds eat a wide range of foods, ranging from nectar and fruit to honeydew and insects (Craig *et al.* 1981a; Gaze & Clout 1983; Taylor, *in* Godley 1985; Sagar 1986 and *in prep.*), nearly all forest passerines are potential competitors. However, we shall limit our discussion to the other New Zealand honeyeaters (Stitchbird and Tui).

Tui occur throughout the bellbird's range in New Zealand and on the offshore islands, except for the Three Kings and Poor Knights. Stitchbirds, which are much closer in size to bellbirds (Craig *et al.* 1981b), are today confined to Hen and Cuvier Is (recently introduced) and to Little Barrier I. in the Hauraki Gulf. Before 1870 Stitchbirds were abundant throughout the North I. and on some offliers, but a mysterious agent (perhaps disease, Oliver 1955) caused their rapid disappearance (Angehr 1986).

Except on the Three Kings and Poor Knights, there is no obvious relationship between variation in the bellbird and the presence or absence of competitors. Similarities between most island populations (Hauraki Gulf islands, Tiritiri, Auckland Is) and mainland bellbirds support this view. Other environmental factors must be responsible for clinal variation.

Canary Is Chaffinches (*Fringilla coelebs*) do not differ from mainland Chaffinches in colour and dimensions according to whether the closely related earlier invader, the Blue Chaffinch (*Fringilla teydea*) is present, but rather in response to the milder and more humid climate of the islands compared with Africa, and the more generalised diet of insular *coelebs* (Grant 1979b). Indirect evidence suggests that *F. teydea* also remained generalised in the absence of selection forces driving it towards specialisation, before the arrival of "modern" *coelebs*. Grant (1979b) concluded that the present differences between *F. coelebs* and *F. teydea* throughout the islands arose partly through subsequent character displacement.

There is a parallel situation on the Chatham Is where, instead of diverging in size from the large endemic subspecies of Tui still occurring there, the extinct bellbird resembled the Tui more closely than on the mainland. The degree of difference between *A. m. melanocephala* and *A. m. melanura* is greater than between *Prothemadera n. chathamensis* and *P. n. novaeseelandiae*, suggesting that the Tui was the more recent arrival on the Chathams.

Like the bellbirds on the Chathams, the most isolated populations of Chaffinches on the Atlantic islands are the most differentiated. Grant (1979b) suggested that isolation has a direct effect on variation in island birds, through reduction in gene flow from the mainland. We believe, however, that the Three Kings and Chatham Is bellbirds have been isolated from mainland populations for a long time, perhaps since the islands were first colonised.

The trend towards longer wings and tails with increasing latitude and body weight in mainland and Auckland Is bellbirds (Tables 6 and 7; Fig. 12, 13 and 16) is similar to that described by Power (1970) for Red-winged Blackbirds (*Agelaius phoeniceus*). However, only part of this kind of continuous variation has a genetic basis, the rest being environmentally

induced, as elegantly demonstrated by James (1983) in an experimental study on the same species.

With insular variation, on the other hand, changes in plumage and dimensions (though possibly not clutch size, time and frequency of breeding, and time of moult) must represent genetic changes in response to different selection pressures on depauperate islands. James' (1983) findings will apply on offshore islands only if morphometric variation fits the clinal trend (e.g. Hauraki Gulf islands, Auckland Is), but not when the trend is reversed (e.g. Three Kings, Poor Knights). Nor can environments differentially influence the development of the sexes and lead to a pattern of increased sexual dimorphism on islands, as in bellbirds. Selection for increased sexual dimorphism on islands reduces competition between pairs, allowing for smaller breeding territories and reduced energy costs (Selander 1966, Rothstein 1973, Grant 1979b, Ebenman & Nilsson 1982).

### Expansion of niche width on islands

Exceptionally high densities of bellbirds in all forest habitats on the Three Kings (16 birds  $\text{ha}^{-1}$ , Turbott & Bull 1954) and Poor Knights reflect a wider niche for bellbirds on these islands than on the mainland (cf. Rothstein 1973). Poor Knights bellbirds are at least 30 times as abundant as any other resident land bird. Their overall density on Aorangi, Poor Knights Is (Sagar 1985, 1986 and in prep.), is 71 birds  $\text{ha}^{-1}$ , nearly three times the total density of all resident land birds at the site of maximum recorded density on the mainland, and 26 times the *maximum* density of bellbirds on the mainland (14 South I. sites; Kikkawa 1960a, 1966). Compared with *mean* densities of mainland bellbirds today, these island figures are even more astonishing – Three Kings bellbirds are 12 times and Poor Knights bellbirds 54 times as abundant as those in average South Island sites (Turbott & Bull 1954; Kikkawa 1960a, 1966).

Wider niches result from a lack of potential competitors (Rothstein 1973). On the Three Kings 58% of all birds censused were bellbirds (Turbott & Bull 1954), and only three other species exceeded 5% of the total in number. On the Poor Knights much the same situation prevails (Sagar 1986). In contrast, Hen I. (Turbott 1940) and Little Barrier I. (Kikkawa 1964) in the Hauraki Gulf and Kapiti I. off the Wellington coast (Kikkawa 1960b) have more than eight forest species abundant enough to be considered as potential competitors of bellbirds. Nevertheless, on Little Barrier I., where Tui and Stitchbirds also occur, Angehr (1986) was struck by the great difference in diet, foraging pattern, and habitat use between male and female bellbirds. He thought this was why bellbirds were more common and widespread on Little Barrier I. than the other two honeyeaters (Kikkawa 1964, Gravatt 1971). We also believe it to be the reason for the great abundance of bellbirds on many offshore islands, especially those which cannot support Tui or Stitchbirds (Three Kings, Poor Knights, Tiritiri).

Intraspecific competition must be greatly intensified on islands where bellbirds are abundant and competitors rare. Bellbirds are very aggressive, in defence of both territory and food resources (pers. obs.; Flack 1976; Craig 1984a), and this characteristic has helped to discourage other species, such as the ubiquitous Silvereye (*Zosterops lateralis*), from colonising the Poor Knights. Segregation of sexes and age classes into niches left vacant by the exclusion or lack of other species can be expected.

The niche is widened both by the increased range of resources available to the individual in the absence of interspecific competition (the within-phenotype component of Roughgarden, 1974) and by the way different groups in the population (e.g. males, females, and immatures) diverge to specialise on different foods (cf. Sagar 1986 and in prep.). These extremes are then selected for, rather than against (Ebenman & Nilsson 1982), and the niche is further widened (between-phenotype component). Rothstein (1973) was sure that wider niches led to increased sexual dimorphism, basing his argument on the findings of Selander (1966) and on his own re-analysis of data from Pitelka (1951). Existing sexual differences serve as preadaptations towards the exploitation of a wider niche. When the sexes are using different parts of the niche, each pair can use within its territory the total niche width of the species, because the two individuals represent the extremes (Rothstein 1973). This reduces intraspecific competition and allows territories to be smaller and more tightly packed on islands (Stamps & Buechner 1985).

Perhaps selective pressures which favour territory establishment and maintenance are stronger in a dense island population than on the mainland. On Heron I., Queensland, Kikkawa *et al.* (1975) studied an isolated endemic population of Silvereyes (*Zosterops lateralis chlorocephala*) which varied greatly in density according to rainfall. A bird's breeding, particularly a first-year bird's, depended on its position in the hierarchy when the population was high. Although increased weight and bill and tarsus length had been expected in the dominant classes, no correlation was found between dominance and body size in Heron I. Silvereyes by Kikkawa (1980). Perhaps because males were not distinguished from females in Kikkawa's study and because large size is usually of greater importance for males, the expected trend (Kikkawa *et al.* 1975) was not clearly shown. When males are responsible for establishing breeding territories, as in bellbirds, competitive pressures in dense island populations can be expected to result in larger adult males. This would explain why, in island populations of New Zealand bellbirds, age and sexual segregation of morphometric characters consists largely of an increase in the size of adult males (especially bill, tarsus and weight).

Ebenmann (1986) found a different situation in southern Swedish populations of the Great Tit (*Parus major*). Here sexual dimorphism increased where potential competitors were fewer, but the greater dimorphism occurred largely as a result of reduced bill and tarsus lengths in females, rather than because of larger males. Thus Ebenmann ascribed sexual differences in these tits wholly to differences in niche utilisation, rather than to sexual selection. In high-density populations of bellbirds on islands, sexual differences in foraging (Sagar in prep.) suggest that, together with the findings of Kikkawa *et al.* (1975) and others on dominance relationships, both selective forces operate together, in parallel.

### **Changes in size and colour**

Island birds adapt to their broader niches in response to changed feeding conditions and social climate. Food probably limits most avian populations and should be the most critical aspect of avian niches. The bill and, to a lesser extent, the tarsus are intimately related to food and feeding and changes in their size are of greater ecological significance in determining niche dimensions than other features (Keast 1968, Rothstein 1973).

Grant (1965b) discovered that the bill and tarsus lengths of island birds change much more than wing and tail lengths. He described how, on the Tres Marias Is, off the Pacific coast of Mexico, 19 species (many of them represented by island subspecies) showed allometric growth in bill and tarsus apparently related to differences in feeding and foraging. Dietary differences were found between island and mainland populations which in each case paralleled differences in the bill. Kear's (1962) finding that, when finches have larger bills, they are more efficient in dealing with a wide range of food sizes was supported in the Tres Marias study. Kear showed that the feeding rate of birds with bills of different sizes was much the same for small food items, but that birds with small bills were not capable of dealing with larger items.

In Australian *Melithreptus* honeyeaters, Keast (1968) showed that geographical variation in bill, tarsus and toe length was correlated with specific changes in feeding patterns. On Kangaroo I. and Tasmania, which have impoverished faunas, especially of honeyeaters, niche width was greatly expanded. There was no evidence that changes in bill and tarsus were related to differences in the availability or type of food on islands. The much longer bills of *Melithreptus validirostris* and *M. brevirostris magnirostris* were associated solely with increased ecological versatility.

A long tarsus is advantageous to birds using firm perches. After reviewing foraging differences between eight groups of closely related species or forms which had different tarsal lengths, on either the mainland or on islands, Grant (1965b, 1966) showed that most species which make greater use of rigid perches (thicker twigs, lower parts of a tree, and the ground) had disproportionately long tarsi (tarsometatarsi), though not necessarily larger bodies, femora, or tibiotarsi. A similar allometric extension of tarsal length was noted in Three Kings, Poor Knights, and Chatham Is bellbirds, without a comparable increase in wing length, body weight, or toe length.

Fleming (1950) provided a tarsus/wing length scatter diagram which illustrated a progressive increase in the relative length of tarsus from continental to insular races of east Australian, Polynesian and New Zealand tits (*Petroica multicolor* superspecies). Increases occurred with higher latitude and greater isolation. Maximum development of the tarsus in this enormous region was reached on the Chathams. There was also evidence of allometric growth along a geological timescale, for the endemic New Zealand subgenus *Miro* had the relatively longest tarsus of any "flycatcher".

How much of this variation is related to body size? Are island birds larger (i.e. heavier and longer-winged) than their mainland relatives? Patterns seem quite variable in different taxonomic groups for, on the Canary Is, adult tits are smaller on Tenerife than in Algerian populations (Grant 1979a), but Chaffinches are much heavier (up to 20% more on La Palma – Grant 1979b). In the Canary Is, Chaffinch wing length decreases as body weight increases (Grant 1979b). Data on the weights of island birds comparable with those of their mainland relatives are scarce, and usually longer wings are taken to mean larger size and weight. This may partly account for the following contradictory results. Island birds were found to be larger in Australian honeyeaters (Keast 1968), Heron I. Silvereyes (Kikkawa *et al.*



1975), New Zealand tits (Fleming 1950), and in the Gulf of Guinea (Amadon 1953), but not on the Cape Verde Is (Bourne 1955), Tres Mariás, and other islands (Grant 1965b).

There is evidence that insular specialisation of bellbirds on the Three Kings, Poor Knights, and Chathams is more advanced than for birds on the Tres Mariás Is. Allometric change in dimensions has enabled only a few Tres Mariás birds to become more dense than mainland populations of the same species (Grant 1965b). The number of bird species is higher on the Tres Mariás and the avian communities have not been simplified as much as on the New Zealand islands. Sexual dimorphism does not yet seem to be a measurable factor in insular population variation on the Tres Mariás, either. Grant (1965a) found no increase in plumage dichromatism, or (1971) of sexual dimorphism in mean tarsus length. Again, the number of potential competitors may have restricted morphological divergence.

### Summary

Intraspecific variation in colour and size of passerine birds on islands has been documented in New Zealand (e.g. Fleming 1950) and elsewhere (Grant 1965a – colours; Grant 1965b, 1966, 1979a,b – dimensions). An important reason for island populations having duller plumage may be to reduce intraspecific aggression (cf. Ewald & Rohwer 1980, Stamps & Buechner 1985). Most changes in dimensions are associated with expanded niches on islands (Grant 1965b, 1979a; Keast 1968; Diamond & Marshall 1977) rather than with environmental variation (e.g. Snow 1954, 1955). Widespread allometric changes in characters used in feeding (bill, tarsus) rather than in body size (Grant 1965b, 1966, 1979a,b; Keast 1968) support this.

On reviewing morphometric variation in bellbirds, the clinal component is thus seen to be environmentally induced and probably only partly genetic. In contrast, insular variation disrupts clinal trends, leading to major differences in body proportion which clearly have a genetic basis, reinforced by isolation.

## TAXONOMIC SIGNIFICANCE OF BELLBIRD VARIATION

### Criteria used for subspecific recognition

Taxonomists agree that there is little purpose in delineating taxa when geographical variation is smoothly clinal, as it is with bellbirds from the New Zealand mainland, nearshore islands and the Auckland Is. However, modern opinion remains firmly in favour of the usefulness of subspecific recognition under certain conditions. For example, Monroe (1982) and Fjeldsa (1985) thought that, although subspecific names should not be used for populations differing only through clines reflecting primary integration, they should be used for allopatric populations showing clear characters that are nearly totally distinct. Mayr (1982) considered that the subspecies concept is most useful in island regions, and O'Neill (1982) differed from other authors (e.g. Mayr 1963) in thinking it helpful to use subspecific names for evolutionary units which are on the way towards reproductive isolation. Until recently, many systematists believed that subspecies took tens of thousands of years to

acquire unique characters (e.g. Barrowclough 1982). There is now good evidence (e.g. Johnston & Selander 1964, Niethammer 1971, Lack 1974, Fjeldsa 1985) to show that well-marked geographic races of passerine birds can differentiate in less than 60 years.

Nearly all taxonomists now see an advantage in defining a subspecies in terms of a whole suite of characters, including biochemical, behavioural, and ecological traits (Mayr, Johnson, O'Neill, Phillips, *et al.* in Wiens 1982). We have used this approach as far as possible, relying on museum specimens to reconstruct the breeding and moult cycle of Three Kings, Auckland Is, and the extinct Northland and Chatham Is bellbirds. In the following sections we summarise information on morphometrics, plumage colouration, clutch size and breeding frequency, breeding season, moult pattern and timing, and song for named bellbird subspecies and use it to assess the validity of these taxa. Some characters are more variable than others – for example, local song dialects are well known in New Zealand birds, such as kiwis (*Apteryx* spp. – Roderick, unpubl.) and Saddlebacks (*Philesturnus* – Jenkins 1975) and have been described in bellbirds (Marples 1944). Morphometrics and plumage colouration were usually less variable than other traits within each population.

In conclusion, we consider that it is best to propose names for distinct and identifiable bellbird populations which show disjunct, rather than clinal variation. In New Zealand bellbirds disjunct distributions of characters are always caused by insular effects.

### **The extinct bellbird of Northland: *Philedon dumerilii* Lesson & Garnot, 1828**

The appearance and morphometrics of Northland bellbirds, which became extinct before 1870, are of interest because these birds may have been genetically different from those which survived whatever affliction greatly reduced mainland bellbird numbers last century. It was thought that, if such genetic differences were expressed in plumage or in morphometrics, this extinct population might have resembled the birds at present on the Poor Knights Islands.

We therefore searched collections for bellbirds taken in Northland before 1860. Eight specimens were found which certainly came from Northland: five from the Bay of Islands and three from the Waitemata Harbour. Four of those collected in the Bay of Islands were shot by R. P. Lesson in April 1824 and are syntypes (Benson, *in press*) of *Philedon dumerilii* Lesson and Garnot. Two of these are figured in plate 21 (Fig. 1-2) of the *Atlas* of plates from Lesson and Garnot's account of the zoology of the voyage of *La Coquille*. The *Atlas* was published in 1828, two years before the full description of *Philedon dumerilii* (1830, livr. 14, pp.644-645).

The birds in the plate are said to be an adult (Fig. 1) and young (Fig. 2) but are an adult male and adult female. The iridescence on the head of the figured male is bright blue, similar to that of the Poor Knights adult male. It therefore became a priority to examine the specimens on which this plate was based.

In the Laboratoire d'Ornithologie at the Muséum National d'Histoire Naturelle (MNHN) in Paris there is a MS "Catalogue 1823 à 1829" (No. 107). This contains two lists of birds and mammals entitled, "Catalogue des animaux données au muséum d'histoire naturelle par MM Garnot et Lesson . . . à bord de la corvette la coquille, commandée par le Capitaine Duperrey Voy. aut. du monde avril 1829". The first is of 139 birds dated April 1829. The second is of 254 birds dated August 1829, and it includes the following entry:

"63. Phi verderin 4 N.Ze 1 in gallerie".

There are no entries in either of the two lists or in the main catalogues to suggest that Lesson brought back any more specimens, and the MNHN collection has no others collected by Lesson. Thus there is some evidence that Lesson brought back five specimens of bellbirds from the Bay of Islands (*La Coquille* did not call at other parts of New Zealand on this voyage). The final sentence in their description (*Voy. La Coquille*, Zool., 1830, livr. 14, p.645) reads "Nous en tuâmes plusieurs individus sur les bords de la baie des Iles à la Nouvelle-Zélande".

Of these five specimens, that in the gallery (if it still exists and is identifiable) would be faded and useless for study and is inaccessible at present anyway. But the MNHN collection has two bellbirds, previously mounted but now relaxed to form study skins, clearly labelled as types of *Philedon dumerilii*. These bore labels on their bases inscribed:

"Nouvelle Zélande La Coquille Lesson et Garnot . . . Type".

New Catalogue No. 544 and 545, Old Catalogue No. 10131 and 10132.

The first is an adult male, the second an adult female.

In addition to these two specimens in Paris, there are also two skins at the University Museum of Zoology, Cambridge, England (UMZC). These are: "27/Mel/3/a/6 and 7, baie des Iles, N(ouvelle) Z(élande) (No. 6 only) Voyage of the Coquille (No. 7 only)" ex Swainson Collection.

Research at UMZC by Benson and Bartle (summarised by Benson, in press) has clarified the identity and source of these specimens. Both were acquired by Swainson from his friend Lesson, possibly during Swainson's visit to Paris in 1828 (Stresemann 1975) and were, in turn, purchased by Newton (Professor of Zoology at Cambridge) before Swainson left for New Zealand in 1840. They bear early pre-Swainson labels identical with each other in appearance and handwriting, but dissimilar to other Lesson specimens from the voyage of *La Coquille* (Benson, in press). Like the Paris specimens, they consist of an adult male (27/Mel/3/a/6) and an adult female (27/Mel/3/a/7), as shown by plumage and measurements.

It is probable that Lesson had both pairs available for his account of the zoology of the voyage of *La Coquille*, hence their current status as syntypes (Benson, in press). Although we believe it slightly more probable that the *Atlas* plate (1828) was based on the Paris specimens because they were mounted, resolution of this point is not central to our problem, as the pairs are very similar in plumage and measurements.

Close examination of these four freshly moulted birds has shown the blue colouration of the head of the figured male in the *Atlas* to be an error,

probably by those who hand coloured the plates. The iridescence on the heads of Lesson's two males is violet, and this is also confirmed in the description (Lesson in Lesson and Garnot 1830, livr. 14, p.644), "Des reflets d'un pourpre brillant et comme métallisés, colorant le dessus de la tête jusqu'à l'occiput, les joues et la gorge". Benson (in press) has also pointed out other errors in these particular plates.

Not only are the four syntypes of *Philedon dumerilii* identical with other mainland bellbirds in plumage colouration, but their measurements are in accordance with the mainland cline (see Fig. 4-9) and are different from those of Poor Knights birds. Measurements of these syntypes were included in the values for extinct Northland birds given in Tables 2-7, and these may be contrasted with the measurements of Poor Knights bellbirds in the same tables.

**Current status:** Following the publication of the *Atlas* (1828, *Voy. La Coquille*, Zool., 1, atlas livr. 6, p1.21 Fig. 1-2), Lesson referred to *Philedon dumerilii* briefly in the general zoological account of the voyage (1829, livr. 9, p.416 and footnote) and provided a detailed description (1830, livr. 14, pp. 644-645). In the 1829 footnote he drew attention to the description and figure of *Certhia sannio* Gmelin, 1788 contained in Blumenbach (1803, tome 1, p.209, p1.14), but thought both description and figure of *Certhia sannio* to be imperfect and unhelpful for resolving the identity of his *Philedon*. We now know *Certhia sannio* Gmelin, 1788 to be a synonym of *Anthornis melanura* (Sparrman, 1786).

By 1830, Lesson (*Voy. La Coquille*, livr. 14, p.644) was sure that the birds which had been described as *Philedon dumerilii* were the same as described and figured by Sparrman (1786) as *Certhia melanura* and by Blumenbach (1803) as *Certhia sannio*. Lesson thought that Sparrman's description was short and incomplete, and provided a satisfactory one of both adult male and adult female (the first good description of the bellbird), under the heading *Philedon dumerilii*. He also noted Sparrman's error in giving the Cape of Good Hope as the type locality of *Certhia melanura*.

We believe that this unambiguous statement on the identity of *C. melanura* means that Lesson had already accepted that *P. dumerilii* was a synonym of *C. melanura* as early as 1830. Certainly *P. dumerilii* was treated as a synonym of *A. melanura* in subsequent years (e.g. Gadow 1884), except by Mathews (e.g. Mathews & Iredale 1913).

We were, therefore, surprised to find that Salomonsen (1967) had resurrected Lesson & Garnot's name as *Anthornis melanura dumerilii* and used it for all North Island bellbirds as well as those from the Hauraki Gulf islands (including the Poor Knights!). Salomonsen gave no characters for separating *A. m. dumerilii*, and inspection of our Tables 2-14 and Fig. 3-13 shows that this taxon cannot be recognised on morphometric criteria. The moult categories for Northland bellbirds collected in August-November, February, and April also suggest that the Northland birds moulted much later than the Three Kings or Poor Knights birds and in synchrony with mainland bellbirds elsewhere. Nor are there any constant plumage differences (see previous section).

We therefore confirm *A.m.dumerilii* (Lesson and Garnot, 1828) as a synonym of *A.melanura melanura* (Sparrman, 1786).

### Current status of *Anthornis incoronata* Bangs, 1911

In describing their morphometrics and moult cycle, we have shown that Auckland Is bellbirds differ slightly from mainland birds in having shorter bill and longer wing, tail, and toe measurements, but the standard deviations of the means overlap by much more than 25%. Although Gray (1845) and Bangs (1911) considered the larger size of Auckland Is birds to be noteworthy, our figures show that their measurements merely lie further along the same gradient of latitudinal variation shown by the mainland samples.

No insular variation can be seen in the morphometrics and moult cycle. The bill tends to be shorter than in mainland birds, unlike the bellbirds of other outlying islands. Compared with the nominate mainland subspecies, variation in all morphometric characters is smoothly clinal. Proportional difference in size between sexes is the same as on the mainland. Timing of moult and absence of an immature plumage stage appear to be the same as for mainland populations.

Although Bangs' diagnosis of *A.incoronata* referred only to size and to head colour, the overall chroma of the plumage is more vivid. We have shown how this clinal increase in plumage colour intensity is the result of increasing melanism southwards. The trend was first noted by Reischek (1887), who described the birds which he procured in Dusky Sound (such as AMNH No. 697239) as being "consistently larger, darker, and softer in plumage than those of the North Island". Softer body plumage in cooler climates is caused by larger contour feathers with more elongate barbs (Moreau 1957), and this is also a feature of isolated island populations of bellbirds.

Bangs said that the iridescence on the heads of his two Auckland Is males was limited to their foreheads and ear coverts, and considered that to be a feature distinguishing them from *A.melanura* and *A.melanocephala*. This may have been the result of wear, for eight adult males in fresh plumage (collected on the Auckland Is between April and September) have extensive Manganese Violet (Ridgway) iridescence on the forehead, crown, ear coverts and throat, whereas another three (collected between November and March) show some reduction in extent and brilliance of the iridescence. Thus, as far as morphometric, moult and plumage characters are concerned, Bangs' claim of specific status for Auckland Is bellbirds can be dismissed. Falla (1948) erred in thinking that "the Auckland Island subspecies is distinguished by very slight and secondary colour tone differences in the metallic feathering". As noted by Bangs, the hue and intensity of the iridescent head colour are very different in Chatham Is birds, but the head colour of mainland and Auckland Is birds is identical.

As Auckland Is bellbirds cannot be distinguished from southern mainland specimens by measurements, head colour, overall plumage colouration or other features, we leave *A.incoronata* Bangs, 1911 in synonymy with *A.m.melanura* (Sparrman, 1786).

TABLE 15 — Student's t-values obtained by comparing measurements of bellbirds from the Auckland Is with those from the eastern South I. (n-2 in parentheses after each t-value).

	Bill	Wing	Tail	Tarsus
adult males	1.6 n.s. (23)	0.89 n.s. (27)	1.80 n.s. (25)	0.69 n.s. (26)
adult females	1.73 n.s. (6)	2.10 n.s. (9)	2.55 * (8)	1.85 n.s. (8)

n.s. = not significant,  $P > 0.05$

\* = significant,  $P < 0.05$

### Current status of *Anthornis melanocephala* G. R. Gray, 1843

Chatham Is bellbirds differ greatly from mainland bellbirds in size. Adult and immature males are at least 10% larger in every dimension than mainland birds from a similar latitude (Tables 2-13). We have shown that insular processes particularly affect sexual dimorphism in size, and this dimorphism is greatest on the Chatham Is. Thus the females differ from mainland bellbirds less than males do, and all female measurements except wing, tarsus, and head plus bill length overlap those of mainland birds (Tables 2-7).

Chatham Is bellbirds also differ in plumage colouration. Although Gray (1843, 1845) failed to mention or figure iridescence on the head of the holotype (BM No. 1842.9.29.26), a male collected in the winter of 1840 (Dieffenbach 1841), a recent re-examination of this specimen revealed that the black head feathers show a definite bluish iridescence (P. R. Colston, pers. comm.). However, the Pyrite Yellow (Ridgway) edges to the rectrices, described by Gray (1843), are an immature feature in Chatham Is males, as Gray later implied (1845). Furthermore, the brownish immature tail feathers are being replaced (asymmetrically) by glossy black rectrices (T2-4) and the brownish secondaries by glossy black feathers (P. R. Colston, pers. comm.). Iridescence on the head of this specimen shows that it had undergone a post-juvenile moult, and yet the brown rectrices with yellowish edges, together with the relative dullness of the iridescence on the head, indicate that this bird must be moulting from post-juvenile immature body plumage into the adult stage.

Buller (1873) had recognised that Gray's type of *A. melanocephala* was not mature, and he provided a detailed and accurate description of the adult male, presumably based on Travers' specimens collected on Pitt I. in 1871-72 (NMNZ No. 5018 and 5019). Buller (1873) was also able to place *A. auriculata* Buller, 1865, into synonymy under *A. melanocephala* G. R. Gray, 1843, after having examined the type specimen of *A. melanocephala* and appreciating the imprecision of Gray's original description (1843) and, particularly, his later account (1845).

The iridescence on the head of the adult male Chatham Is bellbird has a different hue from that of other New Zealand bellbirds, being only slightly lighter than Cyanine Blue (Ridgway). This wears to a dull bluish black and corresponds with the high degree of melanisation of the plumage. The head colour of Chatham Is males is somewhat more intense and of a different hue

from that of Poor Knights birds, and the hue and chroma are entirely different from the Manganese Violet (Ridgway) of mainland bellbirds. Iridescence on the head of Chatham Is females is almost identical in hue to that of Poor Knights and mainland females but tends to have a slightly more intense chroma in freshly moulted specimens. Adult males and females from the Chatham Is have longer and more conspicuous rictal bristles, again perhaps because of increased melanisation. However, the elongate rictal bristles and disproportionately long tarsi suggest that *A. melanocephala* may have had different foraging habits from *A. melanura*. The rest of the plumage is similar in colour to birds from southern and western localities but adult males show higher colour values of Citrine and Warbler Green than do mainland birds, particularly on the flanks, which can be Lemon Chrome (Ridgway) in places.

Buller (1865) was the first to note that the bright yellow iris of adult and immature male Chatham Is birds was completely different from the iris colour of other New Zealand bellbirds. Females also had yellow eyes, for on the label of NMNZ No. 5017 Travers described the iris colour as "golden yellow". It is noteworthy that immature birds also had yellow irises (the type of *A. auriocula* Buller, 1865; and NMNZ No. 2461), and thus iris colour may not have changed with age, unlike *A. melanura*.

There appears to have been an immature plumage phase on the Chatham Is but we do have firm evidence on the timing of moult in adults or in juveniles. Clutch size on the Chatham Is was smaller than on the mainland, the eggs were larger and more pigmented (Potts 1884), and the nest was constructed differently (Buller 1876). The breeding season was shorter and probably earlier than on the mainland. Although the song was said to differ from those on the mainland (Travers 1873), this character has no taxonomic significance for bellbirds.

In view of these marked and consistent differences in measurements, iris colour, plumage and breeding, we recognise *A. melanocephala* G. R. Gray, 1843, as a strong subspecies of *A. melanura* (Sparrman, 1786). If the taxon was not extinct and if experiments could be carried out on interbreeding with the mainland form, a case might be made for full specific status for *A. melanura melanocephala*. However, because of the overall similarity between these taxa, we favour subspecific status.

#### **Current status of *A. melanura obscura* Falla, 1948**

Falla (1948) clearly described the definitive characters of Three Kings and mainland bellbirds, even though he tended to exaggerate the plumage differences. His conclusion that *A. melanura obscura* was the most distinct insular bellbird population is correct only if *A. m. melanocephala* is not considered. Unfortunately, little more is known of *A. m. obscura* today than in 1948, despite its tremendous abundance on the Three Kings Is (Turbott & Buddle 1948; Bartle, pers. obs. 1975).

Three Kings bellbirds have marked differences in measurements from mainland bellbirds. The bill is longer than in other bellbirds (Table 2) and the wing, tail, tarsus, and mid-toe are longer in both sexes than in northern mainland and nearshore island birds (Tables 4-7). The taxonomic status of *A. melanura obscura* has been assessed primarily by comparison with

*A.m.melanura*, and the morphometrics of Poor Knights birds are not discussed in this section. On the Three Kings, males are proportionately larger than females, when compared with mainland birds. If mean bill length is plotted against mean wing length the small samples from the Three Kings lie as far aside from the regression (Fig. 14-15) of the mainland and nearshore island samples as do those of the Chatham Is birds.

Wing, tail, and toe length usually increase southward, and thus the reversal of this trend in the Three Kings birds supports their status as a separate taxon. Although bill length increases northward, bills of males and females on the Three Kings are much longer than would be expected from the bills of Northland birds. The tarsus, which does not vary latitudinally, is somewhat longer in Three Kings birds than in mainland populations.

Mayr (1969) proposed a statistic which he called the Coefficient of Difference (CD) as a yardstick in assessing the degree of overlap in measurements from conspecific populations. This statistic is based on the observation that the less overlap there is between two population parameters, the larger is the difference between the means when divided by the standard deviations. The conventional level of subspecific difference, based on the so-called 75% rule (Amadon 1949), results in a minimum CD level of 0.675, but most authors now recognise subspecies on the basis of a CD of 1.28 or more (Mayr 1969). Of the CDs calculated for the Three Kings and Hauraki Gulf island bellbirds, only the CD of bill length in males (1.74) lay above the threshold of 1.28; the other CDs (except for tail length of males) were above 0.83. Hence the non-overlap in these measurements was above 80%. Mayr's CD seems to have been intended for use where subspecies could be separated only by single characters rather than by a suite, as here. Non-morphometric characters which distinguish bellbird subspecies are sometimes wholly non-overlapping. The most outstanding of these is plumage colouration.

The iridescent head colour of adult male Three Kings bellbirds is identical in hue to that of mainland birds but has a lower colour value, being close to Ridgway's Deep Heliotrope Gray, an admixture of grey on violet. Adult males are basically Olive Green above and Warbler Green below, and there is no trace of yellow on the belly of the holotype (AIM No. Av. 15.22). However, another adult male (AIM No. Av. 15.29) has Olive Yellow flanks, of the same hue as mainland specimens but with a higher chroma. On the underparts of the holotype the plumage lightens from Citrine to Ridgway's Sulphine Yellow towards the tail. This is still an olive hue, but on AIM No. Av. 15.29 the Citrine feathers of the breast give way to some Lemon Yellow (Ridgway) on the abdomen. However, despite the presence of some yellow on the bellies of Three Kings adult males, the extent of Marguerite Yellow (described by Falla as "white tinged with cream") is much greater than on mainland specimens, extending from the lower abdomen through the cloacal area and undertail-coverts.

The plumage of adult Three Kings females is duller than that of mainland females, but the two specimens are both badly faded. Falla's description of their plumage as "more greenish grey and much less olive brown" than in *A.m.melanura* is reasonable and is to be expected from the reduced melanism of Three Kings males.



Falla stated that the larger size and more striking colour contrast of Three Kings birds are readily apparent in the field. This has not been our experience, and we doubt that the greater mean wing length of 4.5 mm could be detected, especially since the tail is no longer than on the Poor Knights (Table 7). The mantle is certainly not "almost black", as stated by Turbott & Buddle (1948), nor are the flight feathers "deeper black" than on mainland specimens (Falla 1948), for the degree of melanisation is less rather than more on the Three Kings. Falla also erred in thinking a reduced amount of yellowish Olive Green on the outer webs of the secondaries to be diagnostic, for this feature varies individually in both Three Kings and mainland birds.

All available specimens suggest that adult moult on the Three Kings Is is compressed into December and January. This is very similar to the moult of Poor Knights bellbirds and it is significant that the breeding season is also early, with fledging completed by early December on the Three Kings (Turbott & Buddle 1948), apparently 2-4 weeks earlier than on the Poor Knights, and very much earlier than on Tiritiri. Pressure to moult early on the Three Kings Is may arise partly in response to the high late-summer (January-March) deficit in water balance (extrapolated data from Cape Reinga, average of 1942-1970; NZ Met. Serv. 1973). As we have suggested, reduced melanism appears to be correlated with dryness, and therefore the reduced melanism of Three Kings bellbirds (unlike the other island races) may partly result from adult moult overlapping with the drought period.

In view of the differences in size, plumage colouration, and time of breeding and adult moult, we recognise *A. melanura obscura* Falla, 1948, as a subspecies of *A. melanura* (Sparrman, 1786).

#### ***Anthornis melanura oneho* n. subsp.**

**ETYMOLOGY:** The name *oneho* is a nominative singular in apposition derived from the name of a hill (216 m) on Aorangi I., Poor Knights group. This geographical feature was named after Oneho, wife of Tatua, last chief of the Ngaitoki hapu (Fraser 1925), most of whom were massacred in December 1823.

**HOLOTYPE:** NMNZ No. 22064, ad. male, 50 m a.s.l. Aorangi Island, Poor Knights Islands, 6 March 1980, coll. J. A. Bartle. Bill 15.2, tarsus 27.4, toe 21.9, wing 91, tail 89, bill plus head 43.5, weight 43 g.

**PARATYPES:** NMNZ No. 22065, ad. female, 50 m a.s.l. Aorangi Island, Poor Knights Islands, 5 March 1980, coll. J. A. Bartle.

NMNZ No. 22061, imm. male, 50 m a.s.l. Aorangi Island, Poor Knights Islands, 23 February 1980, coll. J. A. Bartle.

AIM No. Av. 15.31, ad. male, Tawhiti Rahi Island, Poor Knights Islands, 23 January 1943, coll. G. A. Buddle.

**ADULT MALE:** Iridescence on forehead, crown, and ear coverts Hyacinth Blue (Ridgway), with less well-marked iridescence extending on to the nape, chin, and throat. Loes and flight feathers Jet Black, but with Yellowish Olive-Green colouration of the outer webs of the secondaries and inner primaries. Contour feathers vary subtly in hue from Citrine to Warbler Green (Ridgway), and in shade and chroma from Yellowish Olive-Green on the flanks and rump to Olive-Green on the back. Paler on sides of breast, belly, and undertail-coverts, the Citrine hue lightening in tint to Primrose Yellow (Ridgway) and even Marguerite Yellow (Ridgway). The basal halves of all contour feathers and the proximal webs of the greater wing coverts are Blackish Neutral Gray. Bill and claws Blackish Neutral Gray, tarsi and toes Deep Green-Blue Gray (Ridgway), soles yellowish. Iris bright red. Weights and measurements of live birds are in Tables 2-8.

**ADULT FEMALE:** Iridescence on forehead and crown intense Niagara Green (Ridgway), extending lightly on to the nape and ear coverts. Lores Jet Black, cheek stripe Pale Olive-Buff (Ridgway). Upperparts distinctly darker than underparts: Buff Olive (Ridgway) on back, gradually changing to Yellowish Olive (Ridgway) on rump. Compared with the male, these colours are different shades of the same hues. The underparts are, however, browner than in the male. The chin, throat and breast are mostly Isabella (Ridgway), paler on belly (Primrose Yellow, Ridgway) and undertail-coverts (Marguerite Yellow, Ridgway). The bases of all contour feathers and the inner webs of the greater wing coverts are Blackish Neutral Gray. The flight feathers are Dark Olive (Ridgway), noticeably browner than with males, but the outer webs of the inner primaries, secondaries, and greater coverts are Olive-Yellow. Unlike the male, the edges of the outer webs of the rectrices are also Olive-Yellow. Weights and measurements of live birds are in Tables 2-8.

**SUBADULT PLUMAGES:** Juvenile and immature plumages of Poor Knights bellbirds were briefly described in the section on moult. The distinctive plumage of the immature male is described in full below, as this plumage is not known on the mainland. The colouration of immature females bears the same general relationship to adult females as does that of immature males to adult males.

**IMMATURE MALE:** Hyacinth Blue iridescence on forehead, crown and ear coverts not as extensive or well-developed as in adults, being largely confined to the feather tips and intermingled with non-iridescent Dark Greenish Olive (Ridgway) feathers. Nape, back, and rump Warbler Green (Ridgway), this colour also extending over the breast and flanks. Chin and throat feathers tipped with Deep Olive-Buff (Ridgway). The belly is an indeterminate pale olive and the terminal (exposed) parts of the undertail-coverts are Marguerite Yellow (Ridgway). Primrose Yellow (Ridgway) pectoral plumes, not present in the juvenile, have now appeared. The flight feathers are Blackish Green-Gray (Ridgway), not quite as dark as in adults, with the edges of the outer webs of the inner primaries, secondaries, and greater coverts Warbler Green (Ridgway). The lores and bill are Blackish Neutral Gray, and the tarsi and toes Glaucous. The yellow cheek stripe of juveniles has disappeared, but the iris is still brown. Weights and measurements of live subadults are in Tables 9-14.

The Poor Knights Bellbird (*A.m.oneho*) is only weakly differentiated from the mainland form by plumage and morphometric characters. However, substantial behavioural differences between Poor Knights bellbirds and all other populations (including the extinct Chatham Is subspecies) lead us to believe that when all factors are taken together it will be useful to accord taxonomic recognition to this isolated population. All available information shows that the bellbirds of other islands in the Hauraki Gulf area (Hen and Chicken Is, Little Barrier I., Cuvier I., Tiritiri Matangi I. and Motuihe I.) have no important differences from mainland birds in plumage, morphometrics, breeding season, clutch size, and timing and pattern of moult. However, the Poor Knights Bellbird differs in all the following characters.

(a) **Plumage:** The only consistent and non-overlapping difference is the iridescent head colour of adult males – Hyacinth Blue on the Poor Knights, a very different shade and hue from the Manganese Violet (Ridgway) of all adult males on the mainland, the Three Kings, Hauraki Gulf, Tiritiri, Stewart and Auckland Is. The only other New Zealand bellbirds with iridescent blue rather than violet heads are those of the well-defined Chatham Is race. Here, however, the blue is of a different hue from that of the Poor Knights birds, although of similar intensity. The blue heads of these isolated island populations are caused by the shape and density of melanin granules in the barbules, probably part of the tendency toward increased melanism on islands.

(b) **Morphometrics:** To reduce the biases caused by clinal variation and by shrinkage of museum specimens, we compared Poor Knights bellbirds with the fairly large sample of live-caught birds from Tiritiri Matangi I., assuming them to be typical of the extinct Northland birds at the latitude of the Poor Knights Is. Mean weights and measurements of Poor Knights bellbirds are higher than on Tiritiri (Tables 2-14). When adult values are compared by Student's t-test (Table 16), all except female weight are found to differ significantly ( $P < 0.001$ ). There is, however, some overlap, showing that individuals cannot always be identified by morphometric characters alone.

TABLE 16 — Student's t-values obtained by comparing weights and measurements of live-caught bellbirds from the Poor Knights Is with those from Tiritiri Matangi I. and Orongorongo (n-2 in parentheses after each t-value)

	Bill	Wing	Tail	Tarsus	Weight
Tiritiri: ad ♂♂	5.73 *** (63)	9.59 *** (289)	10.87 *** (84)	10.24 *** (153)	7.20 *** (115)
Tiritiri: ad ♀♀	5.38 *** (50)	5.24 *** (163)	3.47 *** (37)	7.82 *** (94)	1.88 n.s. (64)
Orongorongo: ad ♂♂	10.62 *** (194)	6.37 *** (449)	7.09 *** (190)	10.79 *** (240)	13.60 *** (286)
Orongorongo: ad ♀♀	8.60 *** (92)	2.01 * (234)	0.85 n.s. (73)	5.92 *** (120)	7.38 *** (138)

n.s. = not significant,  $P > 0.05$

\* = significant,  $P < 0.05$

\*\*\* = highly significant,  $P < 0.001$

For individual birds from unknown localities a better approach is to take unrelated pairs of characters, such as bill length and wing or tail length, and plot them against each other so that the relative proportions can be defined, and insular effects segregated from clinal variation. For bill against wing length, the values of the correlation coefficients ( $r = 0.59-0.79$ ) of the mainland bellbirds (including Tiritiri) indicate a similarity in relative proportions. In contrast, paired characters of the three island subspecies of bellbird recognised here lie well outside the range of clinal variation (Fig. 14-15). However, there has not yet been any increase in sexual dimorphism in Poor Knights bellbirds and, although larger, males from the Poor Knights are more similar in relative proportions to mainland birds than those from the Three Kings and Chathams (e.g. Fig. 14).

Wings and tails are shortest on Tiritiri and in Northland (Fig. 12-13) and not, as one might expect, on isolated islands. This trend is probably because wing length and weight are correlated (Fig. 16,  $r = 0.77$ ). However, the mean value for Poor Knights birds lies twice as far from the regression of mainland and nearshore island populations such as Tiritiri (Fig. 16), representing a reduction in *relative* wing length on the Poor Knights.

From a taxonomic viewpoint the increases in mean wing, tail and tarsus lengths on the Poor Knights are of greater interest than the increase in bill length. Whereas greater bill length may be expected as part of the clinal

increase northward and on islands, tarsus length does not vary clinally, and the trend of wing and tail lengths on the Poor Knights is in reversal of the latitudinal cline.

Coefficients of Difference (CDs) were calculated between Poor Knights and Tiritiri birds. Measurements of bill, tarsus, wing and tail differed among adult males and females by CDs of 0.78-1.19, except for female tail length (0.61). Thus the percentage of non-overlap ranged from around 79 to 89 in all but one dimension. These values are less than the 90% recommended by Mayr (1969) for subspecies recognition, but more than the figure of 75% put forward by Amadon (1949). Coefficients of Difference between *oneho* and *obscura* were also calculated, but only for adult males because too few Three Kings females were available. CDs for bill and wing were 0.87 and 1.03, reflecting the larger size of Three Kings males. The tarsus and toe were of similar length, although larger than in *A.m.melanura*, and the tail of *obscura* was much shorter (CD = 0.8). Such inconsistencies in the trend of CDs reflect important differences in the relative proportions of Three Kings and Poor Knights bellbirds and thus a probable lack of uniformity in selective forces despite the apparent similarity in environment of the two island groups.

**Summary:** Mean dimensions of *oneho* are significantly greater than those of neighbouring populations of *A.m.melanura*, but there is some overlap. Individuals and samples from the mainland or other northern islands can most easily be distinguished by considering all their measurements together or by plotting bill length against another dimension to compare differences in relative proportion.

(c) **Breeding season:** The breeding season of Poor Knights bellbirds is early and compressed. Laying of Poor Knights bellbirds is at its peak in October-November, whereas we estimate the peak in *A.m.melanura* to be during December and January, irrespective of latitude.

(d) **Clutch size and number:** Reliable data for *A.m.melanura* were available from Tiritiri (J. L. Craig and M. E. Douglas, pers.comm.) and localities on the mainland. Clutches of *A.m.melanura* vary from 3 to 5 eggs, with a mean of 3.6 ( $n = 11$ ) on Tiritiri. On the Poor Knights clutch size varies from 2 to 4 (mean 2.9,  $n = 37$ ), and only single clutches are laid. There are few observations on the frequency of double-clutching in *A.m.melanura*, but apparently it is usual. However, these differences in clutch size and number are more probably related to population density (Sagar 1985, 1986) and so are not reliable evidence for subspecific status. A recent review (Stamps & Buechner 1985) showed that reduced size and frequency of clutches are widespread among high-density island populations of vertebrates,

(e) **Time and pattern of moult:** Adults on the Poor Knights moult in December and January (Table 1), whereas in other bellbird populations (except for *obscura*), adult moult extends through February, March and April. As on the Three Kings, the dryness of late summer is probably a factor in the tight synchrony and early timing of the moult. However, Poor Knights juveniles replace their body plumage during February and March, in contrast to mainland juveniles, which may moult their body feathers as early as January. Until more mainland bellbirds banded as fledglings are recaptured

we cannot test our hypothesis that juveniles complete their moult at a younger age in *A. m. melanura*.

In *A. m. melanura*, juveniles moult directly into adult body plumage but, on the Poor Knights, juveniles moult into a distinct immature body plumage, an important characteristic of *oneho*.

(f) **Origin:** Of the bellbird taxa recommended for recognition, *oneho* is the least different from the nominate race. This could reflect recent isolation, but the Poor Knights Is were cut off from the mainland even during the lowered sea levels of the Pleistocene (Hayward 1986) and probably remained forested. Nor does it seem credible, on the basis of insular trends in variation, that *A. m. melanura* was derived from *oneho* or *obscura*, *oneho* from *obscura*, or *obscura* from *oneho*. Male bellbirds readily cross gaps of open sea between nearshore islands and the mainland (Craig & Douglas 1984; pers. obs.). Thus, despite models (e.g. Endler 1973) which show that differentiation will occur even with a significant amount of genetic interchange, perhaps the Poor Knights bellbirds have changed more rapidly since *A. m. melanura* died out in Northland.

#### Proposed subspecific arrangement

The taxa are, in order of latitude, following the Checklist Committee, OSNZ (1953, 1970, 1980):

#### *Anthornis melanura* (Sparman, 1786)

- a. *A. melanura obscura* Falla, 1948 **Three Kings Bellbird**  
Three Kings Is
- b. *A. melanura oneho* n. subsp. **Poor Knights Bellbird**  
Poor Knights Is
- c. *A. melanura melanura* (Sparman, 1786) **Bellbird**  
Restricted synonymy: *Philedon dumerilii* Lesson and Garnot, 1828  
*Anthornis incoronata* Bangs, 1911  
Hen and Chickens Is, Little Barrier I. and other forested islands in the Hauraki Gulf and Bay of Plenty except for Great Barrier I.; North, South and Stewart Is and nearshore islands; Auckland Is.
- d. *A. melanura melanocephala* G. R. Gray, 1843 **Chatham Island Bellbird**  
Chatham Is. Extinct since 1906.

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## SHORT NOTE

### Skuas mobbing Black-backed Gulls

On 24 January 1987 at Henderson Bay in the Far North, while beach patrolling in overcast, blustery conditions, we noticed a group of birds swirling in the air. The group of birds consisted of 23 juvenile and four adult Black-backed Gulls (*Larus dominicanus*) and 18 birds, which we later identified as skuas (*Stercorarius* sp.). The skuas were mobbing and chasing the gulls. Occasionally some of the gulls briefly chased a skua but stopped when chased by another skua. During the encounter a few of the skuas landed on the beach briefly, but most remained airborne. Several skuas also harried and chased a pair of Variable Oystercatchers (*Haematopus unicolor*) which were on the beach. After 15 minutes the gulls dispersed, and the skuas flew out to sea. The skuas were identified by the differences in flight, behaviour, and plumage, with juvenile Black-backed Gulls to compare with. The wings were more slender, and angled. The skuas were overall darker birds than the juvenile Black-backed Gulls. The skuas had a dark stripe above the eye. Observations were made in good light about 20 metres from the birds.

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# ABUNDANCE OF YELLOWHEADS IN THE HAWDON RIVER VALLEY, ARTHUR'S PASS NATIONAL PARK, IN 1983 AND 1984

By A. F. READ and C. F. J. O'DONNELL

## ABSTRACT

Yellowheads (*Mohoua ochrocephala*) have disappeared from many parts of the South Island. The northernmost self-sustaining populations now occur in Arthur's Pass National Park, where we surveyed Yellowheads in the Hawdon River Valley during their breeding in 1983 and 1984. Survey techniques were developed for assessing Yellowhead numbers at low densities. In 1983, 11 breeding pairs were found in 500 ha of forest, and in 1984, 21 breeding pairs were found in 2900 ha. About 70% of the birds occurred as breeding pairs, and the rest were itinerant non-breeders and helpers at nests. Yellowheads were spread throughout the valley but were more common at low altitudes. Breeding pairs preferred red beech (*Nothofagus fusca*) forests. There is some evidence that the nationwide decline of the species is continuing in the Hawdon River Valley.

## INTRODUCTION

Yellowheads (*Mohoua ochrocephala* Gmelin 1789) were once widespread in most forests of the South Island and Stewart Island. However, they disappeared from some forests before the turn of the century and by the 1920s had all but disappeared from Marlborough, much of the Nelson district, the podocarp forests of Westland and all of Stewart Island (Gaze 1985). In the remaining parts of Westland the decline has continued through the 1960s and Yellowheads are now absent from almost all Westland forests (O'Donnell & Dilks 1986). There is now concern over the conservation status of the species, and the New Zealand Wildlife Service considers it threatened (B. D. Bell, pers. comm.). Today the species remains in Fiordland and Mount Aspiring National Parks and parts of Otago and Southland. The northernmost sustained population apparently occurs in Arthur's Pass National Park (Gaze 1985).

There are indications that, until recently, Yellowheads were more widespread in Arthur's Pass National Park than they are now. As far as we are aware, sightings west of the main divide in the late 1960s and early 1970s (C. Burrows, pers. comm.) and around Arthur's Pass township in the mid-1970s (OSNZ Bird Mapping Scheme) have not been repeated. Yellowheads are now widespread in only five valleys in the park – the Poulter and Hawdon Rivers and the East Hawdon, Andrews and Sudden Streams. Sightings elsewhere are now rare and are usually of single birds, for example, Binser Saddle in 1983 (A. Wilson, pers. comm.) and Mt O'Malley in 1984 (New Zealand Forest Service, pers. comm.).

In 1983 we began a study of the number and distribution of Yellowheads in the Hawdon River Valley to provide a baseline for measuring future population trends in the area and also for comparison with Yellowhead numbers elsewhere.

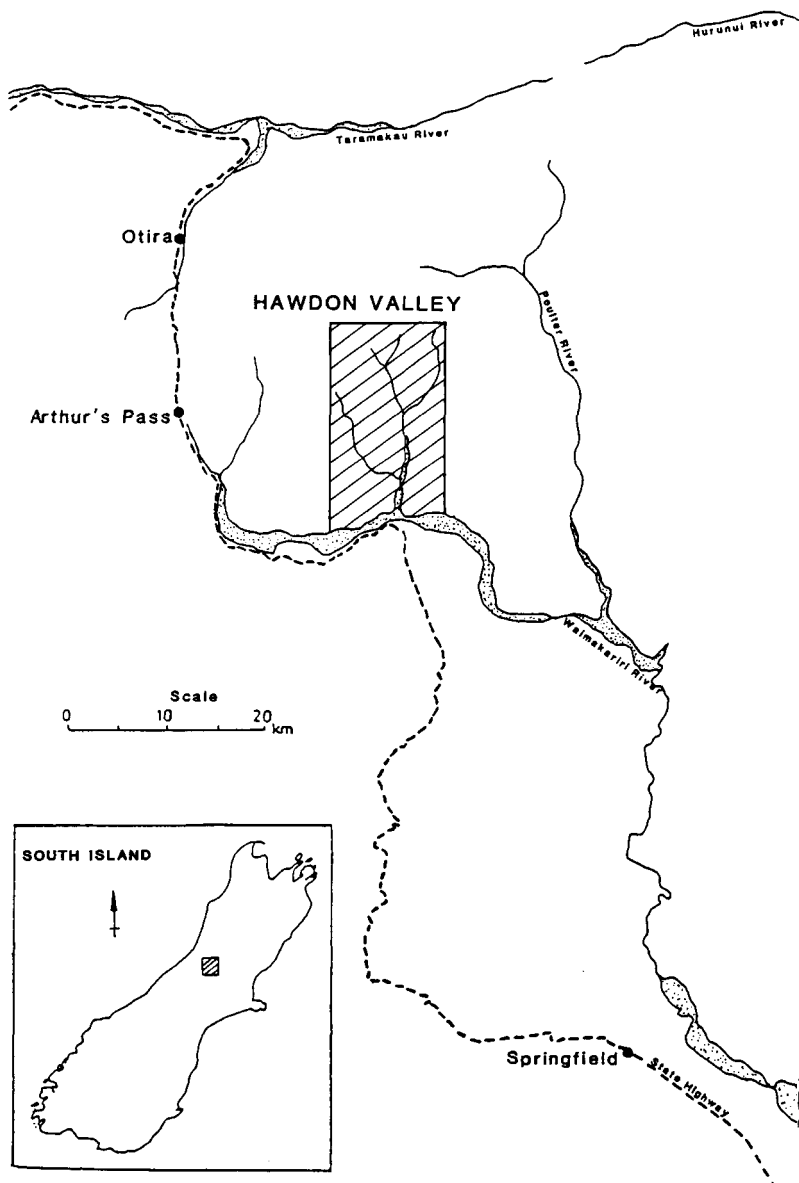


FIGURE 1 — Location of Hawdon Valley

## STUDY AREA

The Hawdon River (42°58' S, 171°45' E) is a tributary of the Waimakariri River, which flows eastwards from the main divide (Figure 1). The Hawdon River Valley is of glacial origin, with steep slopes and fluvio-glacial terraces along the valley floor. The river drains from peaks 1800 m a.s.l. and is steep and gorged in its upper reaches. Below the junction with the East Hawdon Stream it becomes braided and meanders across a wide flood plain to its confluence with the Waimakariri at 600 m a.s.l. (Figure 2).

The slopes and lower terraces are covered by montane beech (*Nothofagus*) forest, which rises to a sharp timberline at 1200-1300 m a.s.l. Mountain beech (*Nothofagus solandri* var. *cliffortioides*) is the dominant tree species, but there are stands of red beech (*N. fusca*) at the toe of the slopes to about 750 m a.s.l. and small stands of silver beech (*N. menziesii*) north of the confluence with the East Hawdon Stream. A more detailed description of the history, landforms, vegetation and fauna of the area is given by Read (1984).

## METHODS

Two surveys of Yellowhead distribution were undertaken: (i) late November and early December 1983 (12 person-days) and (ii) late November 1984 (20 person-days). As the Yellowheads are breeding, this is the ideal time for distribution surveys because the birds are most conspicuous (Read 1984) and stay in the area around their nests (Read 1987). In 1983 about 500 ha of forest were surveyed up to 1000 m a.s.l. (Figure 2). The survey was extended in 1984 to cover about 2900 ha of forest up to the bushline over the whole valley and the East Hawdon Stream (Figure 3).

In 1983 Yellowhead distribution was mapped by teams of observers following traverses 300-400 m apart along the contours of the hills. The Yellowheads were very vocal and calls could be heard over 200 m away in good conditions. Tape recordings of Yellowheads from Eglinton Valley, Fiordland National Park, were played in an attempt to elicit a vocal response from the birds. The tape was played for 1-2 minutes every 200 m, followed by 1-2 minutes of silence and a repeat playing. If nothing was heard the observer moved on another 200 m with frequent listening pauses. If a Yellowhead was heard, the tape was immediately stopped, the bird(s) located and followed, and the number and sex of the birds, the altitude and a vegetation description were recorded. To distinguish breeding Yellowheads near a nest from itinerant non-breeders (Read 1987), we assumed that a female together with a male in bright yellow plumage represented a breeding pair. All transects were repeated, and birds encountered twice at the same location were also taken to indicate a home range and a breeding pair.

Based on the experience of the 1983 survey, two methods were applied in 1984. Using similar traverses, but without playing tape recordings, one team searched the area surveyed in 1983. At least two visits were made to each area where Yellowheads were located in 1984 to see whether the birds were a breeding pair. The second method was the intensive bird distribution mapping developed by O'Donnell & Dilks (1986). Observers walked through

each 1000-yard grid square (NZMS 1 S59 Otira) in the study area, and all Yellowheads seen and heard were counted and their positions and a vegetation description recorded. Transects traversed each grid square along the most practical route, for example, up ridges and across terraces. The observers walked slowly along each transect, pausing to record birds for 2-3 minutes about every 100 m. On average, 52 minutes (SD 23; range 16-100) were spent in each 1000-yard square. A female together with a male was regarded as a breeding pair. A second visit was not made to localities where Yellowheads were found by the mapping method.

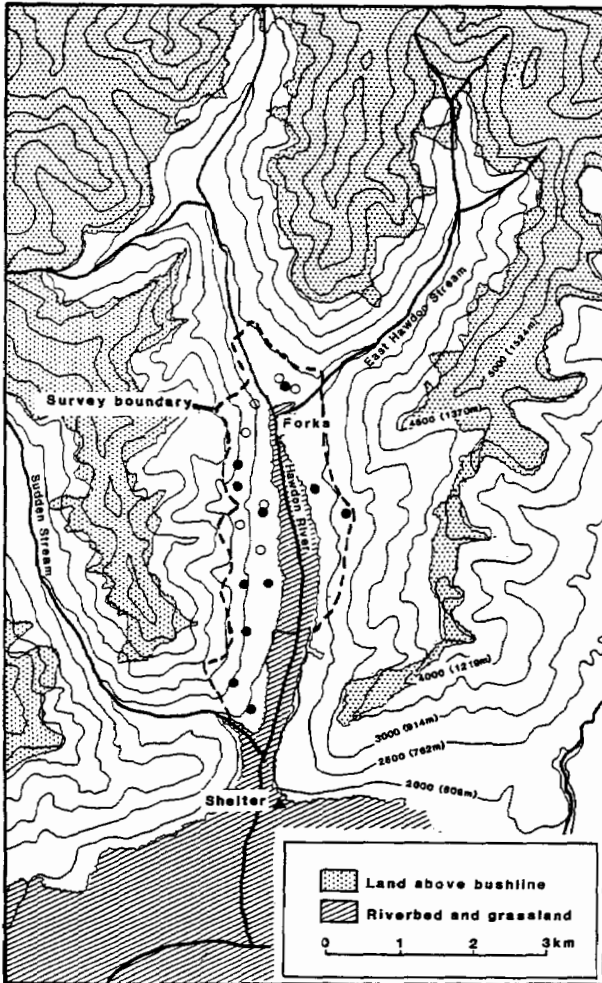


FIGURE 2 — Yellowhead distribution in the Hawdon Valley, November 1983 (● pair, ○ single bird)

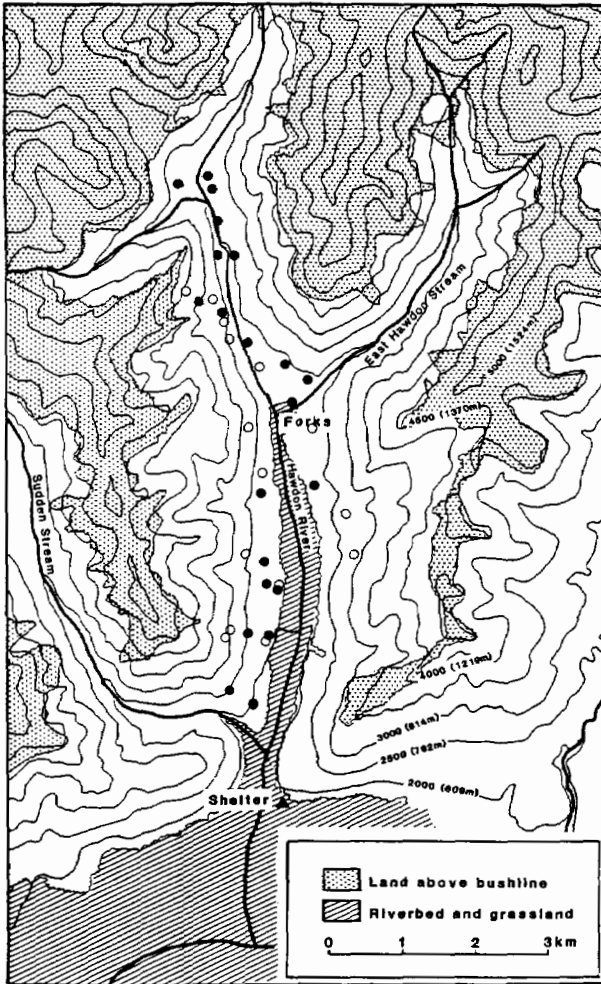


FIGURE 3 — Yellowhead distribution in the Hawdon Valley, November 1984 (● pair, ○ single bird). Survey boundary = bushline

## RESULTS

Totals of 31 and 35 Yellowheads were found in the lower section of the valley in 1983 and 1984 respectively (Table 1; Figures 2 and 3). About 70% of the birds occurred as breeding pairs, and the rest were itinerant non-breeders or helpers associated with the pairs. A flock of 4-6 birds seen on 23 November 1983 was the latest a flock was seen in either year. The density of breeding pairs found in the lower section of the valley was one pair per 45.5 ha in

1983 and one pair per 41.7 ha in 1984. In 1984, 59 were found in the whole valley (Table 1, Figure 3). The approximate average distance between breeding pairs was 650 m, the closest being 300 m apart. Read (1987) found that adults ranged up to 150 m from the nest during breeding. He did not see any adjacent pairs interact, and so the home ranges of these pairs were probably not contiguous.

Yellowheads were concentrated at lower altitudes in the valley, on terraces and the toes of slopes (Table 2, Figures 2 and 3). The highest breeding pairs were at about 900 m a.s.l., but most were at between 600 and 800 m a.s.l. Single birds were found up to 1200 m a.s.l. Breeding pairs were most often found in forests with predominantly red beech canopies (Table 3). Itinerant non-breeders were distributed more evenly between red and mountain beech forests.

During the 1983 survey, 60% of the Yellowheads were detected by their response to the tapes. The proportion of itinerant non-breeders and pairs responding to the recordings was the same. We cannot tell, however, whether the use of tapes increased the chances of finding Yellowheads.

## DISCUSSION

Our estimates of the number of Yellowheads in the valley are not likely to be exact because itinerant non-breeders, which are not individually recognisable, could have been missed or counted twice. To be valid, comparisons of our results with those from other areas or with future surveys in the Hawdon Valley should be based only on breeding pairs. Breeding pairs may, however, be harder to count when they are at much greater densities and their home ranges are close together.

Our survey results probably give a reliable estimate of the density of breeding pairs, and not just a relative index. There was no evidence that we had missed any breeding pairs after the first transect through or near their home ranges: at no stage was a breeding bird detected after we had moved through a home range, nor were additional pairs found after the first survey of an area. Furthermore, the pairs were so far apart that we were not likely to underestimate the number of home ranges, which can occur when home ranges are contiguous, making individual pairs hard to distinguish (Dawson 1981).

The density of Yellowheads in the Hawdon Valley is very low for a forest passerine. Although directly comparable data are lacking, several sources suggest that Yellowhead numbers can be much greater. In his three Fiordland study areas which contained Yellowheads, Kikkawa (1966) found an average density of one pair per 3.7 ha, a density 12 times greater than that found in the Hawdon Valley. In the 1983 breeding season in the Caples Valley, Wakatipu State Forest, breeding pairs could be heard from adjacent nest sites (G. Elliott, pers. comm.). In the Eglinton Valley, Fiordland National Park, during breeding in 1984, G. Elliott (pers. comm.) recorded one family group per 2.85 ha. Buckingham (New Zealand Forest Service, Unpubl. Report, Invercargill, 1982) found that in the Catlins State Forest during



TABLE 1 — Yellowheads seen in the Hawdon Valley during the 1983 and 1984 surveys

	Forks to Shelter 1983		Forks to Shelter 1984		Whole Valley 1984	
	No. birds	%	No. birds	%	No. birds	%
Pairs	22	71.0	24	68.6	42*	71.2
Birds associated with pairs	3	9.7	2	5.7	2	3.4
Itinerant non-breeders	6	19.4	9	25.7	15	25.4
<b>Total</b>	<b>31</b>		<b>35</b>		<b>59</b>	

TABLE 2 — Altitude of Yellowheads seen in the Hawdon River Valley during the 1983 and 1984 surveys

	Altitude (m a.s.l.)				
	600-700	701-800	801-900	901-1000	>1000
<b>1983</b>					
Breeding pairs n=11	5	5	1	0	-
Itinerant non-breeders n=6	1	3	2	0	-
<b>1984</b>					
Breeding pairs n=21	6	9	5	1	0
Itinerant non-breeders n=15	2	5	4	1	3

TABLE 3 — Dominant canopy species of forest in which Yellowheads were seen in the Hawdon River Valley during the 1983 and 1984 surveys

	Dominant Canopy Species			
	Red Beech	Mountain Beech	Mixed Red and Mountain Beech	Silver Beech
<b>1983</b>				
Breeding pairs n=11	7	2	2	-
Itinerant non-breeders n=6	3	3	0	-
<b>1984</b>				
Breeding pairs n=21	12	7	1	1
Itinerant non-breeders n=15	4	7	4	0

1981-82 Yellowheads were not evenly distributed through the forest, but were concentrated in beech forest gullies. In these areas pairs were 50-200 m apart, much closer than any of the Hawdon Valley pairs. Guthrie-Smith (1936) believed that Yellowhead pairs in what is now Abel Tasman National Park occupied a range of 8-10 acres (3.2-4.0 ha). By following birds in the Hawdon Valley in 1983, AR estimated that a nesting pair ranged over a maximum area of 7 ha (Read 1987). Thus, a large area between pairs was apparently unused by Yellowheads until their young were fledged and their nests abandoned.

Read (in prep.) sampled the vegetation of an area in the Hawdon River Valley similar to that surveyed here (but with different boundaries) to determine the composition of the forests. Using these figures as an approximate indication of forest availability, and relating them to Yellowhead distribution and abundance, it seems that Yellowhead pairs preferred forests with canopies dominated by red beech: 59-64% of pairs were found in such forests, whereas red beech dominated only 18% of the forested area. Mountain beech dominated 73% of the forested area, and mixed red and mountain beech canopies dominated the rest. Red beech forests are believed to occupy more fertile sites with a more equable climate. The trees are taller, on average older, with larger stem diameters and greater canopy spreads than mountain beech trees at the same altitude (Burrows 1977). As a result, arboreal invertebrates may be more numerous in red beech forests. If so, this may be why we found more Yellowheads (which are almost entirely insectivorous) in these forests. A more detailed habitat-use analysis demonstrated similar preferences in the Hawdon Valley after the breeding season (Read, in prep.).

The low number of Yellowheads in the Hawdon Valley, compared with that found in other areas, suggests that the national decline could be continuing in Arthur's Pass National Park, particularly given that their range is contracting to the north, west and east of the park (Gaze 1985, O'Donnell & Dilks 1986). However, the distribution of pairs and the number of Yellowheads in the lower section of the valley were similar in 1983 and 1984 (Figures 2 and 3). Two additional pairs were present on the terraces at the East Hawdon Stream junction in 1984, but two pairs were not found on the adjacent western valley slopes. The location of itinerant birds was different, but these are likely to be more mobile than pairs. So, at least between 1983 and 1984, there was no local decline. Nevertheless, because large areas of forest in the Hawdon River Valley were unoccupied by breeding pairs, there were apparently fewer Yellowheads than the forests could support, even though the carrying capacity does not seem low for birds overall (see bird counts by Read 1984). Only by monitoring the birds over the next few years can we tell whether the low number of Yellowheads in the Hawdon River Valley is part of a continuing decline of the species nationally.

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## SHORT NOTE

## Cattle Egrets in Fiordland National Park 1973 - 1987

Various observers have seen Cattle Egrets (*Bubulcus ibis coromandus*) in Fiordland National Park, some near landfalls. These Cattle Egret records supplement those published by Heather (1978, 1982, 1986). I am very grateful to the following for their information: I. G. Adam, K. F. Bradley, N. M. Drysdale, W. Ellis, M. A. Gunn, R. D. Kerr, J. Landreth, J. S. Ombler, B. W. Paddon, R. J. Peacock, A. J. Pearce, B. Roderick, G. A. T. Taylor, B. W. Thomas, I. D. Thorne, J. G. Trotter, K. Wells, A. Wright.

**1973:** Preservation Inlet, Puysegur Point lighthouse farm, P. Daniels, lighthouse keeper, saw 1 feeding near cows during the last week of April and the first week of May (Wright, A., 1973. Preservation Inlet: July 1973. Unpubl. report. NZ Wildlife Service; Heather 1982 : 254).

**1974 - 1976:** No records.

**1977:** Lower Hollyford Valley, Hollyford Camp, 2 feeding with horses in May (WE, MAG).

**1978:** No records.

**1979:** Lower Hollyford Valley, Hollyford Camp, 13 stayed a few days in May (MAG).

**1980:** Preservation Inlet, Puysegur Point lighthouse farm, 1 sheltered under a cow when attacked by a New Zealand Falcon (*Falco novaeseelandiae*) on 16/4 (RJP; Heather 1982 : 254). Lake Te Anau, near Te Anau Wildlife Centre, seen in lake shallows adjacent to shore roost : 3 on 28/4, 3 on 29/4, 13 on 1/5, 7 on 6/5, 2 on 8/5, 7 on 9/5, 7 on 11/5, 7 on 15/5, 1 on 19/5, 1 on 24/5 (pers. obs.).

**1981 - 1982:** No records.

**1983:** Eglinton Valley, Lake Lochie, 1 near shore on 5/5 (JGT).

**1984:** Milford Sound, 16 first seen on tidal flats on 6/4, on 11 - 20/4 feeding at end of airstrip by day and roosting overnight in beech tree behind Milford Hotel (RDK: Heather 1986 : 187). Chalky Inlet, Reef Point, 2 "egrets" perching in shore manuka one day during 16 - 28/4. The day after the sighting remains of a predated bird (bill and feathers) were found at the same spot (JL). The bill was identified as Cattle Egret at National Museum (N. Hyde, pers. comm.). Doubtful Sound, Deep Cove, flock of 9 flying 30 m above the sea towards head of cove on 5/5, not seen again (KFB, JSO). Hollyford Valley, Martins Bay, 1 feeding on riverbank and grass by his house for 10 days in early August (NMD).

**1985:** Clinton Valley, Glade House, 3 perching in beech trees and fluttering about clearing on 9/5 (IGA).

**1986:** Doubtful Sound, Deep Cove, 1 near Deep Cove Hostel on 20 - 23/3 (IDT); Deep Cove tailrace embankment, B. W. Paddon, a Fiordland Travel bus driver, saw a New Zealand Falcon dragging a Cattle Egret on the road on 7/4. The falcon hopped on one foot while its other foot held the egret by the neck. The Cattle Egret was "rescued" and taken to Te Anau Wildlife Centre where its only injury was a bunch of feathers missing from the nape (BWP). Deep Cove, 5 seen about 0900 hours on 16/4 (IDT). George Sound, Whitewater River estuary, 1 on 6/4 which backed up under a log to avoid a New Zealand Falcon attack on 7/4 (BR, KW). Milford Sound, 7 on mudflats with a White Heron (*Egretta alba*) on 6/4 (RDK); 3 feeding near a White Heron on 19/4 (pers. obs.); 1 on 2/5 (JGT). Upper Hollyford Valley, near Monkey Creek, A. J. Pearce and M. W. D. staff saw a large New Zealand Falcon (obviously a female) standing beside a Cattle Egret it had killed on 8/4. The falcon, which appeared gorged after eating all of the egret's neck, was not able to fly away (AJP). Breaksea Sound, second outermost Gilbert Island, 1 on north-east shoreline rocks at 1510 hours on 11/4 (first Fiordland island record) (GAT, BWT). Lower Hollyford Valley, Hidden Falls, 1 on flat on 20/4 (RDK); Hollyford Camp, 6 on grassy flat behind camp on 26/4 (RDK).

**1987:** Hollyford Valley, Martins Bay, 13 on 10/4 (NMD). Milford Sound, 1 near airstrip on 22 - 29/4 (RJP, AJP).

**Discussion:** Combining the likely highest Cattle Egret numbers for each locality annual totals are 1973 (1), 1977 (2), 1979 (13), 1980 (14), 1983 (1), 1984 (28), 1985 (3), 1986 (24), 1987 (14). Localities with the highest Cattle Egret numbers in 1973 - 87 are Hollyford Valley 37, Milford Sound 24, Deep Cove 16.

Cattle Egrets have arrived in ones, twos, or small groups between 20 March and 5 May throughout the 257 km span of coast between Long Reef and Puysegur Point. Some birds have probably dispersed 98 km south from Martins Bay to the nearest pasture with enclosed stock at Te Anau Downs Station where Cattle Egret numbers in 1986 were 2 on 19/4, 22 on 3/5, 8 on 17/5 (pers. obs.).

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# THE SOCIAL STRUCTURE OF THE WEKA (*Gallirallus australis*) AT DOUBLE COVE, MARLBOROUGH SOUNDS

By ANTHONY J. BEAUCHAMP

## ABSTRACT

The study group comprised territorial pairs and non-territorial adults and subadults. Pairs were maintained all the year and occupied minimum areas of between 2.6 and 15.8 ha. Most non-territorials were younger than 18 months. All wekas that obtained territorial positions in the study period were under 2 years old. Most pairs bred successfully at least once per year and one bred successfully three times in the same year, raising nine young. Recruitment exceeded losses in the territorial group. In the 1985 season, 37.5% of the territorial birds were lost through death or displacement.

## INTRODUCTION

The territorial status of mainland wekas has been reported as temporary in some parts of Fiordland (Harper 1946) and permanent in other regions of New Zealand (Blackburn 1955).

Of the three recent weka studies (Coleman *et al.* 1983, Brothers & Skira 1984, Beauchamp 1987), only that of Coleman *et al.* was on the main islands of New Zealand and then as a sideline to possum research. Coleman *et al.* (1983) gave information on population dispersion and changes in numbers, but provided only limited information on the breeding performance and the social structure of their study birds.

The purpose of this study was to investigate the composition of a mainland weka population and the factors influencing changes to it.

The study area at Double Cove, 6 km north of Picton on the west side of Queen Charlotte Sound, comprised 66 ha of regenerating manuka (*Leptospermum scoparium*), kanuka (*L. ericoides*) and early seral broadleaf forest. Much of the area is private land but some is the Rocks Scenic Reserve administered by the Marlborough Sounds Maritime Park Board (Walls 1984). In the study area are 30 holiday homes, none of which were permanently occupied.

The wekas there were derived from birds that arrived in the late 1960s, when the hillsides were covered with bracken (*Pteridium esculentum*) (D. Travers and D. & V. Burton, pers. comm.). Wekas could have come from both the north-east and south-west. Anecdotal accounts suggest that weka density was higher in the 1970s than during the study period (R. O'Neill and D. Travers, pers. comm.) and that weka density is highly variable.

## METHODS

I visited the study area in April, October, November 1984, February and April 1985, and January 1986 for 4, 5, 6, 6, 1 and 9 days respectively. All the area was searched for wekas throughout the daylight period.

Wekas were caught in cage traps and with hand-held snares. Adults were banded with numbered stainless steel colour bands. Subadults (wekas less than 12 months old) and dependent young were banded with numbered bands, and subadults were subsequently colour banded if they stayed in the study area for longer than 2 months after independence.

When a bird was first captured I analysed its plumage and state of moult. To aid in sexing I took two bill and four leg measurements, maximum tail length, compressed wing length, and weight (Beauchamp 1987). I aged each bird by its eye and leg colour and by the state of its wing spur and plumage as being in its first or second year, between its third and sixth year, or more than six years (Beauchamp 1987). When birds were recaptured I noted their state of moult, weight and breeding status.

During each visit I recaptured as many territorial wekas as possible and asked house owners about the breeding performance of the pairs they saw regularly.

All statistical tests are Wilcoxon-t normality approximation tests.

## RESULTS

### Composition and distribution of the study group

The Double Cove wekas comprised both resident territorial pairs and non-territorial adults and subadults. Figure 1 gives the distribution of territorial pairs in November 1984 and January 1986. The territories did not overlap and some apparently lacked common boundaries. The actual size of many was hard to gauge because of the timid nature of the birds, the limited period of diurnal activity, and the dense vegetation. The mean known size was 4.8 ha (range 2.6-15.8 ha). The changes evident in some boundaries were associated with changes in pair composition or the death of both members of a pair.

The wekas maintained their territories by spacing calls and fighting. Territorial boom calls were generally associated with pair greeting and fighting. Birds gave few calls while foraging.

Table 1 gives the composition of the population throughout the study period. The numbers of territorial and non-territorial birds remained almost constant throughout the year, but the number of subadults was more variable. In April 1984, I saw only two non-territorials in four days. However, in a 24 hour visit in April 1985 I saw six in only a partial reconnaissance of the area. In 1984, I considered two territorial birds, one of each sex, to be 6-10 years old and three to be 2 years old or less. The rest were between 3 and 6 years. By January 1986 all 17 territorial birds were considered to be 6 years old or less, seven (41%) of them being under 2 years old.

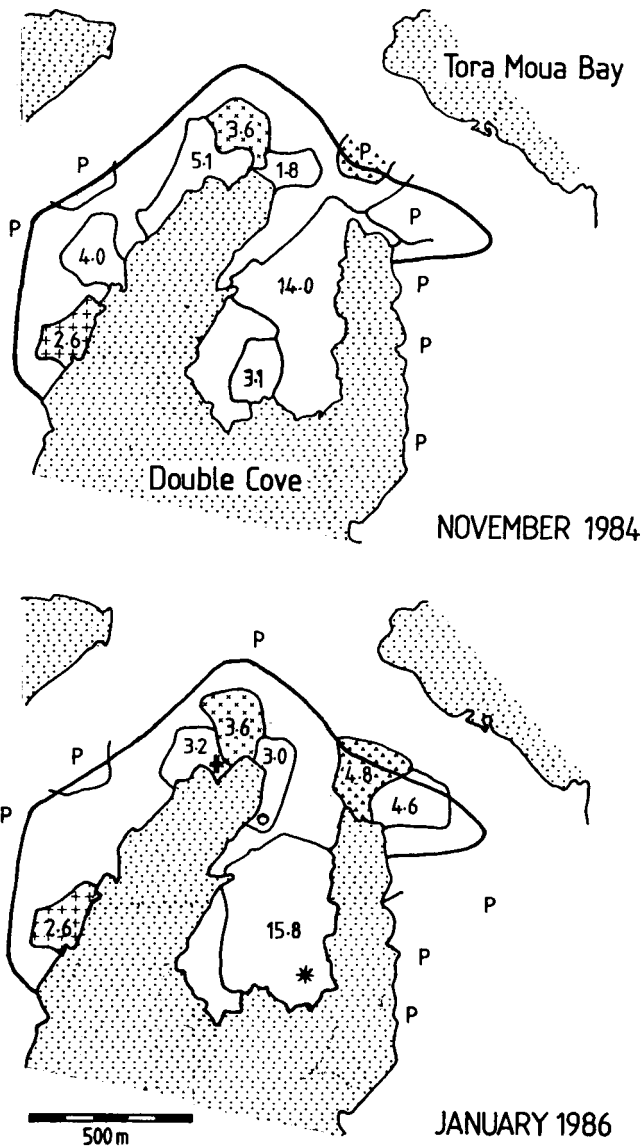


FIGURE 1 — Weka territories in Double Cove, Marlborough Sounds, in November 1984 and January 1986. Numbers indicate planar estimates of territory size in hectares. The solid line is the boundary of the 66 ha area that was carefully searched each visit. The same pair is shown by the same shading pattern in each diagram. o = a new pair, \* = a new female, # = a new male, P = an unbanded pair, as indicated by calling. The dotted areas are salt water.

The longest-known periods of non-territorial residency were 18 and 14 months for two females and 14 months for a male. All non-territorial wekas ranged widely. One female was seen throughout the study area and others probably ranged over more than 70 ha.

TABLE 1 - Study group structure

	Apr 1985	Oct-Nov 1984	Feb 1985	Jan 1986
Territorial wekas	14*	18	20	17
Non-territorials	1	1	2	2
Subadults	1	11	3	8
Dependent young	3	15	2	4

\* = Minimum estimate as not all birds were banded

### Breeding performance and movement of young

Table 2 summarises the breeding performance of eight pairs. The main period of breeding was late August to October, although successful breeding occurred during most of the year, including the period of moult. One pair raised nine chicks to independence in a calendar year, but most pairs showed no signs of courtship outside the main breeding period.

TABLE 2 — Times when successful breeding and breeding attempts occurred and territorial wekas died or were displaced

PAIR	1984												1985												1986											
	M	A	M	J	J	A	S	O	N	D	D	J	F	M	A	M	J	J	A	S	O	N	D	D	J	F										
1	.....2Y.....PL																																			
2	.....3Y.....2Y.ML...3Y.																																			
3	.....2Y.....1Y.....																																			
4	3Y.....3Y..3Y.....FL.COURT.....																																			
5	.....1Y....PL																																			
6	.....1Y.....PL																																			
7	.....2Y.....1Y																																			
8	.....COURT.....COURT																																			

1Y = one young, 2Y = two young, 3Y = three young,  
 PL = pair lost, FL = female lost, ML = male lost,  
 COURT = courtship

Parental care (six pairs) lasted 60-80 days and young remained near their parental territory for up to 2 months. Most had dispersed from these areas by 4 months after independence, and in summer young birds were passing constantly through the study area.

During the 22 months, the study group raised 23 chicks, only two of which were still present more than a year after fledging. However, no locally raised bird obtained a territorial position within the study area. The only known bird raised in the study area that established a territory was a female



that moved to Portage, 5 km from the study area, within 4 months of moving from its parents' territory.

### Age of territorial establishment and first breeding

During the study five wekas, all between 10 and 18 months old, obtained territorial positions within the study area. Two of the females paired with older males, and one of them bred successfully at the age of 18 months, 3 months after territorial establishment. A 12-month-old male established with an older female and bred within a month, and the other two wekas established as a new pair (see Figure 1).

### Population losses

During the 12 months February 1985 to January 1986, 37.5% of the territorial wekas were lost through death or displacement. Each sex was equally represented, and two pairs disappeared (see Figure 1). Two birds lost from different pairs were 6 or more years old and all the others were older than 3 years. Only one dead weka was recovered and she had a leg injury similar to those associated with gin traps. Another female was apparently displaced by a newly established neighbouring pair of subadults after the loss of her partner, and one male was displaced by a non-territorial subadult. All the other territorial wekas that disappeared probably died.

During the study period one non-territorial banded weka was recovered after being shot, 4.5 km from the study area at Lochmara Bay. The deaths of other non-territorial subadult wekas were probably associated with poor condition, due to frequent attacks and disturbance by other wekas. Subadults in poor physical condition (low weight for size) were seen moving throughout the study area in January 1985 and February 1986.

### Weights

Figure 2 shows the known weight cycle of the population. The observed pattern of peak weights in autumn and winter, and lower weights associated with breeding, are typical of wekas elsewhere (Carroll 1963, Coleman *et al.* 1983, Beauchamp 1987). Most losses were associated with winter, but there was no indication that deaths were associated with a food shortage.

Two territorial wekas disappeared at the end of the breeding season, when wekas would be more easily displaced by heavier non-territorial birds (Beauchamp 1987).

## DISCUSSION

In this study I found a population structure similar to that on Kapiti Island (Beauchamp 1987) and a pattern that I interpret, from the individual longevity and range information presented by Coleman *et al.* (1983), to be similar to that at Lake Haupiri, Westland. There was no indication of pair bonds dissolving after the breeding season, as suggested by Harper (1946) for Fiordland.

**Distribution:** The results of this study, although based on less than 2 years' information, indicate a series of demographic differences between wekas on the mainland and those on some offshore islands. Some of these differences are habitat related but they also reflect the different influences working on the birds.

The Double Cove birds occupied an earlier successional stage of smaller-leaved forest, on a drier shallower soil, than the Kapiti Island birds.

In Double Cove not all territorial pairs had boundaries in common with other pairs, and birds were found up to 200 metres into a neighbouring territory. Territorial wekas seldom gave the territorial boom call while foraging, indicating a low level of direct territorial conflict or of interaction with non-territorial wekas.

In contrast, wekas on Kapiti Island held territories that were significantly smaller ( $p < 0.0001$ ), averaging 1.96 ha; territorial conflicts were higher, averaging one every 3 hours; and booming occurred on average once an hour (Beauchamp 1987). Population density averaged 0.8 weka per hectare as opposed to 0.3 weka per hectare in Double Cove, and non-territorials were a much higher proportion of the population throughout most of the 5 years of the Kapiti study. This led on Kapiti to territorial wekas intruding more often into neighbouring territories, though the average distance of incursion was only about 10 metres.

The principal-use areas of non-territorials on Kapiti overlapped more territories than at Double Cove and, because of the higher density of birds, conflicts were more frequent.

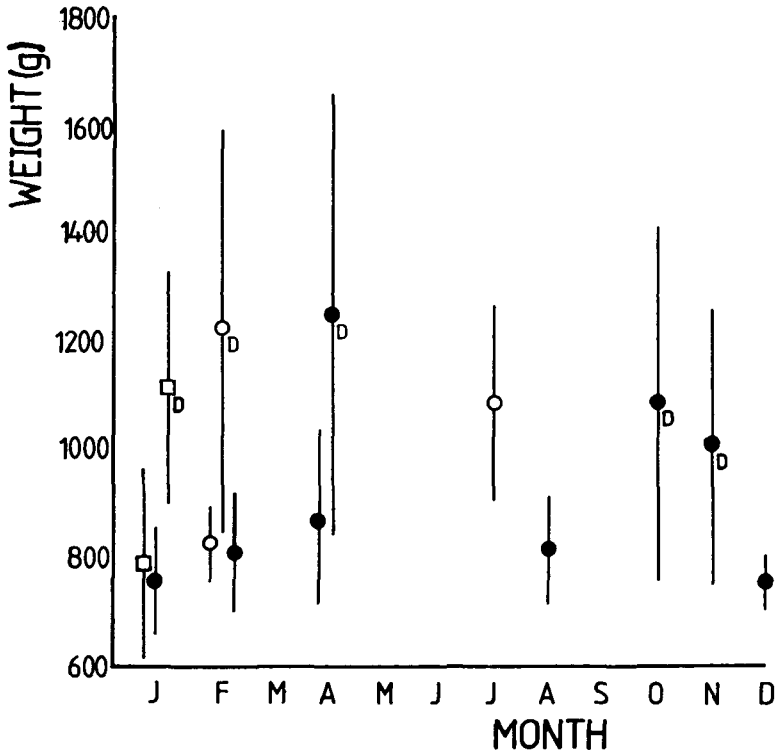


FIGURE 2 — Weights + 95% confidence limits of Double Cove (D) and Kapiti Island male wekas. o = weights in 1984, ● = weights in 1985, □ = weights in 1986.

**Foods and breeding frequency:** Major differences between the Kapiti Island and Double Cove populations were associated with food supply, the overall level of population condition (as expressed by weight for size), and the time taken by wekas to regain condition after breeding. These differences led to differences in the rate of breeding, the number of young raised per clutch and the timing of renesting attempts.

The Double Cove wekas had extensive and almost year-round supplies of fruit, especially fivefinger (*Pseudopanax arboreum*) and karamu (*Coprosma lucida*), which give a high energy yield per unit time of collection (Williams 1982), and so the birds could recover their weight quickly after breeding. Kapiti wekas relied more on invertebrates, which usually give less energy per unit time of collection and so their recovery time was longer (Beauchamp 1987).

Both groups of weka had similar duration of parental care. On Kapiti, however, the minimum time taken to recover breeding condition was 2 months. Food levels were inadequate for year-round breeding and weka pairs did not maintain courtship throughout the year (Beauchamp 1987). At Double Cove, recovery times were less than 1 month and food levels and year-round courtship permitted multiple breeding attempts. As a result, the number of young raised per pair at Double Cove (2.8, averaged over 2 years) was significantly higher ( $p < 0.001$ ) than on Kapiti (0.3, average over 6 years).

**Survival and mortality:** In both places productivity exceeded losses of territorial birds, and the life expectancy of non-territorial birds that did not obtain a territorial position was much lower than that of the territorial birds (Beauchamp 1987).

The higher breeding rate and survival of young at Double Cove were associated with a higher turnover in the population and a lower age of territorial establishment. The higher level of turnover in the Sounds was also indicated by the proportionately lower numbers and ages of the resident non-territorial birds. On Kapiti, the average annual adult turnover rate over 10 years was 14%. The highest annual adult death and displacement rate recorded was 27%, much lower than the 37.5% recorded at Double Cove in 1985.

**Recruitment into territories:** In both populations the path to recruitment into the territorial group varied. On Kapiti, most subadults became part of the non-territorial group, from which most territorial recruitment occurred (Beauchamp 1987). Non-territorial adults and subadults made up about 30% of the population. Few subadults (<5%) entered the territorial group directly. The ages of the birds recruited into the territorial group depended on the success of the subadults in entering the non-territorial group, the rate and level of loss from the non-territorial and territorial populations, and the age classes represented in each group of the population (Beauchamp 1987). Most birds were at least 2 years old before they obtained a territorial position, and males tended to establish younger than females.

At Double Cove, however, all wekas that established territorial positions were less than 18 months old. The non-territorial component varied between

6% and 12% of the permanent population and there were many spaces where wekas could establish. The rate of territorial recruitment depended more on the ability of subadults to enter the territorial group.

In both places, recruitment into the territorial group varied from year to year. On Kapiti, this variation was due to uneven breeding, uneven entry into the non-territorial group, and uneven survival; whereas in Double Cove, it depended more on uneven annual breeding success.

If the long-term longevity trend in the Sounds is similar to the trend observed in the two years studied, the mean longevity of a territorial bird could be as low as 4 years. This is much lower than the 6.5 years on Kapiti and a short life span for the size of the bird (Ricklefs 1973). It is also likely that the life span of the territorial wekas in the Marlborough Sounds is more variable than on Kapiti because the Sounds wekas depend much more on fruit, which can differ markedly in quantity between seasons.

It is conceivable that the oldest wekas at the start of the study were survivors of population crashes associated with unfavourable dry conditions which had greatly reduced fruit and invertebrate foods. Such high annual variability appears to be a feature of this population (D. Burton, pers. comm.) and the populations in the North Island (Guthrie-Smith 1926).

The long-term survival and density of the weka in the Double Cove region of the Marlborough Sounds is likely to depend on the habitats that result from forest succession. Terminal forests in the Marlborough Sounds have lower densities of wekas than the earlier-succession broadleaf forests. Pure beech forests lack wekas probably because they have few fruit-bearing plants and a poorer supply of litter invertebrates.

Current succession in Double Cove and the surrounding areas is moving towards a broadleaf and pine (*Pinus radiata*) forest. Beech is now restricted to the coastal margin and will only slowly spread back up the hillsides. It appears that pine forest is as unsuitable as beech forest for wekas, and ultimately the suitability of this area will be governed by the continuing availability of the fruits of fivefinger, karamu, mingimingi (*Cyathodes fasciculata*) and mahoe (*Melicytus ramiflorus*) and by the composition and density of invertebrates. Both the forest composition and the litter quality will depend on the density of the pine cover and how possums affect the native component of the forest (Fitzgerald 1978, Coleman *et al.* 1985). Any reduction in the broadleaf component is likely to lead to a permanent reduction in weka numbers.

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## SHORT NOTE

## A beach-wrecked White-naped Petrel

On 27 January 1986 at Karikari Bay, Northland, with Geoff Arnold and Julie Macefield, I found the remains of a large grey and white gadfly petrel which I subsequently identified as a White-naped Petrel (*Pterodroma cervicalis*). The bird was incomplete, with one wing largely missing and the other damaged. Some tail feathers and part of the forehead and facial plumage were also missing. The bird had begun to dry and there was probably some shrinkage of soft parts.

**Description:** Upper wing and crown predominantly dark grey to black. Mantle, back and scapular feathers white at the base, distally frosty-grey, with a few of the scapulars narrowly tipped with white. There was a partial collar of grey-tipped feathers. Remaining (outer) rectrices were white, some tipped and flecked with grey. Nape and underparts white. Primaries had black shafts, black outer webs and grey and off-white inner webs. The bill was dull black. The feet were largely white to pale flesh with the distal parts of the toes and webs grey-black.

**Measurements (mm)**

Body: Length	c. 420	Foot: Tarsus	40
Wingspan	c. 990	Mid-toe and claw	53
Wing	305	Bill: Length	36
Tail (incomplete)	123	Depth	16
		Width	17

The White-naped Petrel closely resembles the Juan Fernandez Petrel (*P. externa*). Until recently the two were considered races of the same species but are now believed to be distinct (Imber 1985). Specific identification of incomplete specimens may be difficult, but *P. cervicalis* is usually slightly smaller in all dimensions. Falla (1976) gave a comprehensive list of features by which the two can be distinguished (but note the error in the culmen mean for *externa*).

**Discussion:** The White-naped Petrel is known to breed only on Macauley Island in the Kermadec Group. Eggs hatch in late February and this bird was therefore at least 11 months old. The white-tipped scapulars, however, suggest an immature bird (Oliver 1955). Birds winter in the north-west Pacific Ocean (Tanaka & Inaba 1981) and only rarely straggle to the New Zealand mainland. This record is the third, the others being of a bird near Rotorua in April 1968 (Kinsky 1971) and a juvenile found north of Gisborne in 1977 (Blackburn 1977).

The beach patrol on 27 January 1986 also yielded a White-capped Noddy (*Anous minutus*). Other patrols in the Far North at the same time yielded other tropical seabirds – two White-tailed Tropicbirds (*Phaethon lepturus*) and a Sooty Tern (*Sterna fuscata*) (L. Howell, pers. comm.). The weather pattern in January seems to account for their presence near northern New Zealand. From 15 to 25 January a blocked anticyclone lay to the east of New Zealand. In the Far North, the associated north-easterly winds varied between 10 and 20 knots throughout this period, rising to 50-55 knots on 25 January. This was unusually protracted for such a weather pattern; in the Auckland region winds were from the north-east for 73% of the time during January, the highest figure ever recorded for that month (January average = 30%).

This record has been accepted by the Rare Birds Committee of OSNZ and the bird has been deposited in the Auckland Institute and Museum collection (B 1340). I am grateful to Jim Hessel, Chief Meteorologist, Auckland Weather Centre, for weather information, to Brian Gill, Auckland Institute and Museum, for access to specimens and to Mike Imber for improvements to this note.

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# CHANGES IN GULL NUMBERS OVER 25 YEARS AND NOTES ON OTHER BIRDS OF THE OTAKI-OHAU COAST

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## ABSTRACT

The number of Black-backed Gulls (*Larus dominicanus*) between the Otaki and Ohau Rivers, on the southwest coast of the North Island, has more than doubled in the last 25 years. There was a significantly larger proportion of subadults in 1961 than now, indicating that the population may have been in a growth phase in the early 1960s. The number of Red-billed Gulls (*L. novaehollandiae*) was about one-third of the 1961 level; this coincides with a sharp fall in the number of Red-billed Gulls nesting on nearby Kapiti Island. Numbers of other coastal birds were recorded and are discussed.

## INTRODUCTION

In March 1961, the late Dr. K. Wodzicki made 11 traverses along the coast between the Otaki and Ohau River estuaries to count Black-backed Gulls and Red-billed Gulls. In his paper, Wodzicki (1962) gave the mean number of each gull species per mile for sections of the coast. In addition, he noted the proportion of adult and subadult Black-backed Gulls.

This paper describes counts of birds (excluding passerines) along the same stretch of coastline as that traversed by Dr Wodzicki, in the same month 25 years later, to determine whether gull numbers and proportions of adult and subadult had changed since 1961.

## METHODS

We repeated the methods used by Dr Wodzicki as closely as possible by doing the counts throughout March, and by randomly including a variety of states of tide, weather conditions and times of day. The coastline between the Otaki and Ohau Rivers was divided into the same five beach sections and five estuaries that Wodzicki (1962) had used (Figure 1). Members of the Wellington Branch of the Ornithological Society of New Zealand, walking steadily along the beach alone or in pairs, recorded the numbers of birds seen between the foredune and the outermost breakers, or in the tidal part near the mouth of the estuaries. The observers were asked to record numbers of birds for a variable number of sections but were not required to walk the entire distance between the two main rivers as Dr Wodzicki had done. They recorded the numbers of adult and subadult Black-backed Gulls and numbers of other coastal birds, and were given an option of describing the activities of the gulls.

The ten coastal segments (five estuaries and five beach sections), their reference codes, the linear distance of the coast (in km), and the number of counts are given in Table 1.

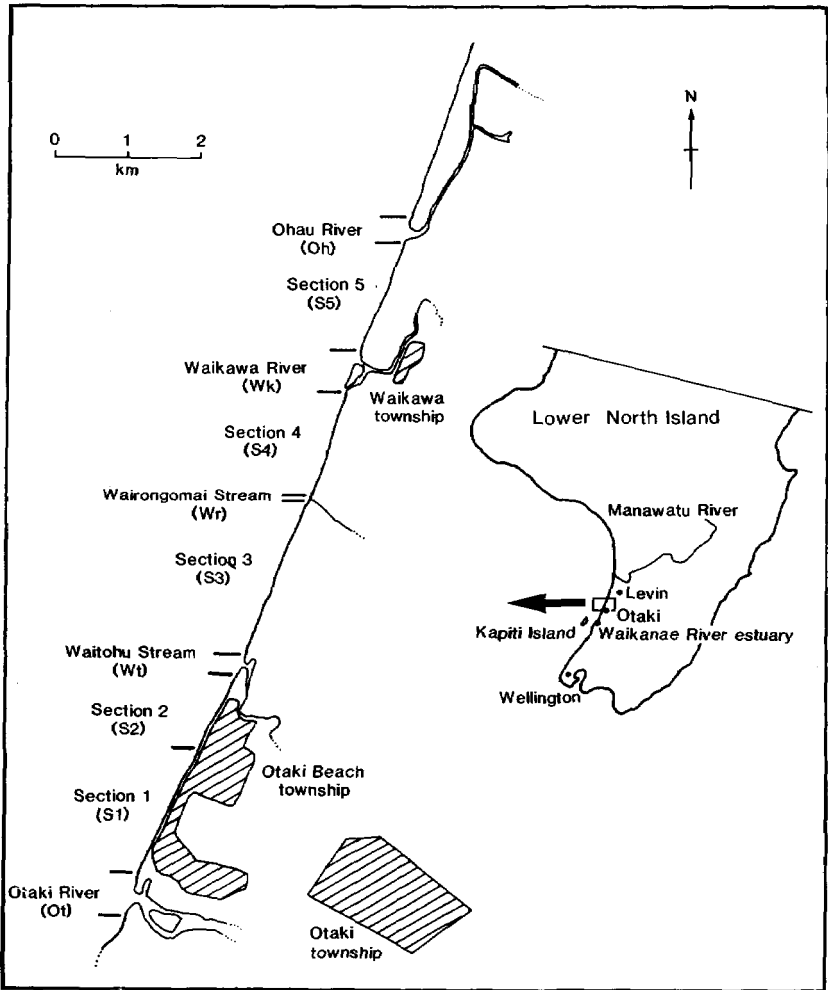


FIGURE 1 — The Otaki-Ohau coast, showing the positions of the five estuaries and five beach sections, and an inset of the lower North Island showing the positions of places mentioned in the text.

The point at which the Ohau River entered the sea in 1986 was apparently 0.9 km further south than in 1961 and so the total length of coastline between the two rivers was 10.2 km in 1986, compared with 11.1 km in 1961. This meant that total counts could not be compared, but counts per kilometre were still valid.

Full details of the counts have been deposited on file at both the Conservation Sciences Centre, Department of Conservation, and Ecology Division, DSIR. Despite careful searches, we could not locate Dr Wodzicki's



raw data which, in his paper, he said he had deposited at Ecology Division, DSIR. Without them we have been unable to perform statistical tests on many of the comparisons between 1961 and 1986. We were surprised that Black-billed Gulls (*L. bulleri*) were not mentioned by Wodzicki (1962), since they would almost certainly have been present.

### BLACK-BACKED GULL (*Larus dominicanus*)

#### Counts

In 1986, there were on average 44 Black-backed Gulls per kilometre for the entire study coastline (Table 1). This was 2.4 times the rate of 18 per kilometre (29 per mile) found in 1961. We found a significantly greater density of Black-backed Gulls at estuaries (92 per kilometre) than on beaches (27 per kilometre), but because Wodzicki combined some adjacent beach and estuary sections, we cannot make a complete historical comparison. He did, however, give mean counts for Otaki and Waitohu estuaries separately. At Otaki River estuary we found on average 162 birds per count compared with 69 in 1961, but at Waitohu Stream there were only 6 per count compared with 31 in 1961. On the beach between these two estuaries (i.e. S1 and S2) we found 121 Black-backed Gulls per count, where Wodzicki had found only 61. Wodzicki recorded few Black-backed Gulls north of Waitohu Stream (mean of 45 per count or 5 per kilometre), whereas in 1986 we found a mean of 145 per count or 23 per kilometre. The indication is that the number of Black-backed Gulls has increased and that the increase has been distributed fairly evenly between the estuaries and the beach. The increase has been greater in the northern part of the area near Waikawa and Ohau than in the Otaki area.

This widespread gull has an extremely varied diet. On land, it eats refuse from rubbish dumps, offal, carrion, worms, crustaceans, insects, frogs, small reptiles and mammals, young birds and eggs. At sea, or in shallow water, it takes echinoderms, krill, molluscs and fish (Fordham 1985). A few pairs nest just north of the Ohau River estuary, but the nearest large colony is on Kapiti Island (16 km from Otaki Beach), where several hundred pairs nest. Fordham (1968) showed that many of these Kapiti birds move to the Wellington West coast to forage. Wilkinson & Wilkinson (1952) noted that Black-backed Gull nests on Kapiti Island in 1924-1942 were well separated from one another around the coastline and made no mention of a colony on the island. Stidolph (1948) counted 129 nests at the north end of Kapiti Island in November 1941 and 120 nests in 1942. Fordham (1967) noted a marked increase to 589 occupied nests on 23 November 1963. On 23 November 1986, we counted 275 Black-backed Gull nests in about half of the colony that now extends continuously along about 1 km of the northern coast of Kapiti, near Lake Okupe, and we estimated that 500-600 nests were occupied in the whole colony. In addition, we recorded 31 nests at Rangatira Point, where none existed in 1963 (Fordham 1967) and only two were seen in 1941. This shows that the number of gulls on the island has increased greatly in the last 45 years, particularly between 1942 and 1963. Wodzicki *et al.* (1978), however, found no increase in the number of Black-backed Gulls at Waikanae estuary between 1941-1943 and 1971-1974.

TABLE 1 — The number of adult and subadult gulls, and the density (number per kilometre), including those of unknown age, of three species of gulls between the Otaki and Ohau River estuaries in March 1986

Species	Estuaries and beach sections											Totals for			
	Ot*	S1	S2	S3	S4	S5	Wt	Wr	S4	Wk	S5	Oh	Total	Estuaries	Beaches
Distance (km)	0.7	1.9	1.1	0.3	2.2	0.1	1.4	0.6	1.5	0.4	10.2	2.1	8.1		
No. counts	3	3	7	9	10	10	12	8	12	6					
<b>Black-backed Gull</b>															
Adult	424	215	218	44	314	33	218	107	161	214	1948	822	1126		
Subadult	63	41	33	9	62	9	121	56	40	65	499	202	297		
Density	232	45	33	22	18	43	20	34	11	116	44	93	27		
<b>Red-billed Gull</b>															
Adult	18	35	24	18	27	0	2	12	3	0	139	48	91		
Subadult	1	13	9	0	6	0	0	4	14	0	47	5	42		
Density	9	8	4	7	2	0	0	3	1	0	4	4	3		
<b>Black-billed Gull</b>															
Adult	0	3	3	1	0	0	0	0	0	0	7	1	6		
Subadult	0	0	0	59	10	2	5	132	7	49	264	242	22		
Density	0	1	0	22	1	2	0	28	0	21	3	12	1		

\* Ot = Otaki River, Wt = Waitohu Stream, Wr = Wairongomai Stream, Wk = Waikanae River, Oh = Ohau River, S1 ... S5 = Sections 1 to 5

We suspect that the marked increase in the number of Black-backed Gulls between Otaki and Ohau in the last 25 years is a result of more food becoming available from refuse dumps and general rubbish, such as remains of fish gutted on the beach. This increase has been greatest in the northern part of the beach study area, around Waikawa Beach township, where the human population has grown most.

### Age ratio

In 1986, 2447 Black-backed Gulls were seen, of which 499 (20.4%) were in subadult plumage (Table 1). This is a significantly smaller proportion of subadults than the 262 (23.9%) of 1549 gulls counted by Wodzicki in 1961 ( $X^2 = 5.47$ ,  $p < 0.05$ ). The proportions of adults to subadults at both estuaries and beaches were almost identical for each set of counts. The subadult category includes all birds up to four years old (Kinsky 1963), and the difference in age ratio between the two counts may reflect one or two exceptionally good or poor breeding seasons before the surveys. Fordham (1968), working at Wellington Harbour (60 km south of our study area), found a higher proportion of yearlings in 1961 than in the two subsequent years, indicating that the 1960-61 breeding season may have been very successful. Moreover, a growing population would be expected to have a higher proportion of subadult birds. Fordham (1967) showed that the Black-backed Gull population in the Wellington area had grown very quickly in the years leading up to 1965. The population that Wodzicki recorded may have been in a growing phase in 1961, which has now levelled off. Preliminary results from monthly counts of Black-backed Gulls in Wellington Harbour in 1986-1987 show that there has been no marked increase since 1975-1977 (HAR, unpubl.). Further checks on the ratios of adult to subadult birds are needed.

TABLE 2 — Activity recorded for different age classes of Black-backed Gull: number of observations (percentage)

	Adult		Subadult	
Fly	183	(16%)	84	(28%)
Rest	676	(61%)	147	(49%)
Forage	195	(17%)	48	(16%)
Comfort	33	(3%)	12	(4%)
Swim	23	(2%)	7	(2%)
	<hr/>		<hr/>	
	1110		298	

$$X^2_4 = 23.54, p < 0.001$$

### Activity

The activity of Black-backed Gulls was recorded by description and then grouped into broad behavioural categories: fly, rest (including sitting, standing and roosting), forage (feeding, walking, dropping shells), comfort (preening, bathing and drinking), and swim. These are summarised in Table 2 for adults and subadults separately. There was a clear difference between the age classes, with adults spending more time resting and subadults spending more time flying. The age classes spent a similar proportion of time foraging. There was a significant difference between the age classes in the number of birds displaying different activities ( $X^2 = 23.54$ ,  $p < 0.001$ ). This may indicate that adults have a greater overall feeding success, and also perhaps a greater dominance, which would combine to give them more time to rest.

### RED-BILLED GULL (*Larus novaehollandiae*)

#### Counts

In March 1986, 186 Red-billed Gulls were seen, giving a rate of 3.5 per kilometre compared with 10.6 per kilometre in 1961. This suggests a three-fold decrease in the last 25 years. By contrast, numbers did not change significantly between 1941-1943 and 1971-1974 at Waikanae estuary (Wodzicki *et al.* 1978) nor in the last 20 years in the large Kaikoura Peninsula colony that contributes substantially to the southern North Island population (J.A. Mills, pers. comm.). The nearest colony to this stretch of coast is on the northeastern corner of Kapiti Island. In 1942, Stidolph (1948) found 80 nests on a rock at Te Rere and six nests at the northern end of the island. There must have been a spectacular population increase because by 1960-61 there were 73 breeding pairs at the north of the island, below Tokohaki Trig, and another 400 breeding pairs at Rangitira Point, on the east coast. In 1961-62, 300 pairs nested below Tokohaki Trig, 500 pairs at Rangitira Point, and 8 pairs on a raised beach east of Tiwhapau Trig. This last site was the main colony (550 pairs) in 1963-64 (Gurr & Kinsky 1965). On 23 November 1986 we counted no nests at Rangitira Point and only 74 breeding pairs at the raised beach site east of Tiwhapau Trig in Waiorua Bay. The marked decline of this nearby breeding population on Kapiti Island probably explains the drop in the number of Red-billed Gulls on the Ohau-Otaki coast. Another contributing factor could be the timing of the northward movement of birds from the big breeding colonies at Kaikoura and Nelson Haven. This movement leads to a sudden increase in Red-billed Gulls in Wellington Harbour in March (HAR, unpubl.), and this influx may continue up these western beaches. This is supported by sightings of several colour-banded birds at Otaki that came from the Kaikoura Peninsula (pers. obs.).

The Red-billed Gull is common along the New Zealand coast and occasionally inland. It eats a wide variety of foods. During the breeding season, its main food is planktonic crustaceans found offshore. Outside the breeding season, some birds continue to feed at sea, some forage along the shore for marine invertebrates, and others eat refuse at sewage outfalls, rubbish dumps, parks and fishing ports (Mills 1985).

The density figures for Red-billed Gulls for each estuary and beach section (Table 1) show that most were found south of Waitohu Stream estuary. In contrast to Black-backed Gulls, the densities of Red-billed Gulls were similar for the estuaries (4.0 per kilometre) and the beaches (3.4 per kilometre). There were too few observations of activities to analyse, but all of the birds seen feeding (15/121) were on beaches, generally at the water's edge.

#### Age ratios

Overall, 25% of the Red-billed Gulls were in subadult plumage, but this proportion varied significantly ( $X^2 = 51.7$ ,  $p < 0.001$ ) between estuaries (9%) and beaches (32%). Unfortunately, Wodzicki (1962) gave no comparative figures for the 1961 counts.

### BLACK-BILLED GULL (*L. bulleri*)

#### Counts

In total, 271 Black-billed Gulls were recorded, at a density of 3.4 per kilometre. Although this density is very similar to that of Red-billed Gulls, the two used the area quite differently. For example, no Black-billed Gulls were seen at the Otaki estuary, where the Red-billed Gulls tended to congregate. However, the Black-billed Gulls were concentrated at the other small estuaries, with very few along the beaches. There were 12.2 Black-billed Gulls per kilometre at the estuaries compared with 0.4 per kilometre on the beaches.

#### Age ratios

Almost 97% of the Black-billed Gulls were subadults. This suggests that, like many migratory species, at least the one-year-old birds do not move from their wintering ground to the breeding colonies in spring. March is probably too early for many of the adults from South Island colonies to have reached the southwest of the North Island. A few Black-billed Gulls nest in the North Island, with the closest colonies being on the upper Manawatu River, in coastal Hawke's Bay and at Lake Rotorua. Preliminary results of colour-banding at the Lake Rotorua colony indicated that these birds stay near the breeding colony or move north or east to nearby coasts (J. Innes, pers. comm.).

All but one of the 243 Black-billed Gulls seen at estuaries were subadults, compared with 79% of the birds seen along the beach. These numbers are very significantly different ( $X^2 = 35.2$ ,  $p < 0.001$ ), but the reason is not clear.

### COUNTS OF OTHER COASTAL BIRDS

We kept records of other coastal birds during our survey in the various segments (Table 3).

#### AUSTRALASIAN GANNET (*Sula bassana*)

Three gannets were seen during the survey, all in flight. At other times of the year, gannets are occasionally seen along the Wellington West coast and in Wellington Harbour. The nearest colonies are at Waimaru Bay in Pelorus Sound and at Farewell Spit (Wodzicki *et al.* 1984).

TABLE 3 — The density (number per kilometre) of coastal birds other than gulls between the Otaki and Ohau River estuaries in March 1986

Species	Estuaries and beach sections										Totals for		
	Ot*	S1	S2	Wt	S3	Wr	S4	Wk	S5	Oh	Total	Estuaries	Beaches
Distance (km)	0.7	1.9	1.1	0.3	2.2	0.1	1.4	0.6	1.5	0.4	10.2	2.1	8.1
No. counts	3	3	7	9	16	10	12	8	12	6			
Gannet	-	0.4	-	-	<0.1	-	-	-	-	-	0.1	-	0.1
Black Shag	3.9	-	0.1	-	0.4	-	0.2	0.4	2.0	48.3	2.5	8.6	0.4
Little Shag	10.4	0.7	0.3	-	-	-	-	-	-	-	0.7	2.8	<0.1
Spotted Shag	-	0.2	-	-	-	-	-	-	-	-	<0.1	-	<0.1
White-faced Heron	1.9	-	-	-	-	-	-	-	0.1	-	0.1	0.5	<0.1
Black Swan	-	0.4	-	-	-	-	-	-	-	-	<0.1	-	<0.1
Paradise Sheilduck	1.4	-	-	0.7	-	-	-	-	-	-	0.1	0.5	-
Variable Oystercatcher	-	-	-	-	0.5	8.0	0.2	1.0	0.6	5.0	0.6	1.5	0.3
Spur-winged Plover	12.4	-	-	-	-	8.0	-	1.0	1.2	4.5	1.3	4.8	0.2
Banded Dotterel	1.4	-	-	-	-	-	-	0.1	-	-	0.1	0.4	-
Black-fronted Dotterel	1.9	-	-	-	-	-	-	-	-	-	0.1	0.5	-
Godwit	-	-	-	-	-	-	-	-	0.1	-	<0.1	-	<0.1
Pied Stilt	34.3	0.5	-	1.0	-	-	0.2	6.2	1.6	9.3	3.7	13.4	0.4
Pomarine Skua	-	0.4	-	-	<0.1	-	0.4	-	-	-	0.1	-	0.2
Arctic Skua	-	-	-	-	-	-	0.2	0.1	-	-	<0.1	<0.1	<0.1
Skua spp.	-	-	-	-	<0.1	-	-	0.1	-	-	<0.1	<0.1	<0.1
Black-fronted Tern	-	-	-	-	-	-	-	-	0.1	-	<0.1	-	<0.1
Caspian Tern	16.1	0.2	0.1	0.3	<0.1	-	0.2	2.6	0.5	21.5	2.4	8.8	0.2
White-fronted Tern	292.0	45.3	1.5	57.7	7.2	-	25.9	94.8	-	165.5	54.6	151.1	21.6

\* Abbreviations as in Table 1 and Figure 1.

**BLACK SHAG** (*Phalacrocorax carbo*)

This shag is regularly seen along the coastline. As well as feeding just offshore, particularly at rivermouths, it forages up the major rivers in the region (Wodzicki *et al.* 1978). A small colony is in karaka trees near the Te Mimi Stream on the eastern coast of Kapiti Island (P. Daniel, pers. comm.) and at coastal lakes near Waitarere (17 km north of Waikawa). Three other breeding colonies known in the Wellington region are at Lake Kohangatera, at Wainuiomata Dam and in the Hutt River gorge downstream from the Pakuratahi Forks (Parrish 1984).

During the counts, Black Shags were seen mainly at estuaries, particularly at the Ohau River estuary (Table 3). The few shags between the river estuaries were either flying or feeding just offshore. Those at the Otaki and Ohau River estuaries were all roosting. The roosting Black Shags concentrate on the northern side of the Ohau estuary, probably because the spit is relatively inaccessible to people and dogs. The Black Shag takes much more effort and space to get airborne than other birds on this coast and so it seems to need roost sites free of frequent disturbance.

**LITTLE SHAG** (*Phalacrocorax melanoleucos brevirostris*)

The 28 Little Shags seen during the counts were mostly at the Otaki River estuary (Table 3), usually roosting. They feed along rocky coastlines, in bays, estuaries, ponds, rivers and streams, and largely avoid coastal waters over sandy substrates. This is presumably why they were not seen foraging or flying just offshore from the beaches.

**SPOTTED SHAG** (*Stictocarbo punctatus*)

Just one Spotted Shag was seen, on the beach of Section 1. The species is a frequent visitor to the Waikanae River estuary from April to September (Wodzicki *et al.* 1978) and an occasional visitor to Kapiti Island (Wilkinson & Wilkinson 1952). The nearest breeding colony is on Somes Island, in Wellington Harbour, where a few pairs have nested since 1973 (Stephenson 1977).

**WHITE-FACED HERON** (*Ardea novaehollandiae*)

White-faced Herons were seen mainly at the Otaki River estuary (Table 3). They feed in a variety of habitats, particularly along the edges of rivers and estuaries, but sometimes forage along the high-tide line of the beaches in the study area. They probably nest in trees on farmland adjacent to the beaches and estuaries between Otaki and Ohau.

**BLACK SWAN** (*Cygnus atratus*)

Two Black Swans were seen in flight over Section 1 during the counts. Black Swans are occasionally recorded on the upper reaches of the Ohau River estuary and on the Otaki River estuary (pers. obs.). Black Swans nest at Okupe Lagoon on Kapiti Island (P. Daniel, pers. comm.) and at lakes in coastal Horowhenua.

**PARADISE SHELDUCK** (*Tadorna variegata*)

All of the Paradise Shelducks were seen at estuaries (Table 3). From our observations during regular visits to this coastline, and those of Wodzicki *et al.* (1978), the Paradise Shelduck seems to be an uncommon but regular

visitor to the estuaries between Waikanae and Ohau. Several shelducks inhabit nearby Kapiti Island, each year raising broods on Okupe Lagoon, and they probably breed at the coastal lakes in Horowhenua.

#### VARIABLE OYSTERCATCHER (*Haematopus unicolor*)

Variable Oystercatchers are common residents of the coastline. During the counts they were present at the three northern estuaries and the adjacent sections of beach (Table 3). Perhaps they were absent from the Otaki River estuary and Section 1 because of the stony substrate; the other estuaries and sections have sandy substrates. Wairongomai Stream estuary had an unusually high density because two observers saw a family group there, consisting of two adults and two juveniles. We have found nests at the Waikawa River estuary, and up to eight pairs regularly nest on the spit between the Ohau River and the coast, where the river flows parallel to the sea (Figure 1).

Variable Oystercatchers are often seen probing in the sand for prey on the out-going tide along the beaches and about the estuaries. They are also sometimes seen foraging among the wrack at the high-tide line. Feeding birds often leave numerous probe-holes about decaying seaweed where they have searched for sandhoppers (*Talorchestia* spp.).

#### SPUR-WINGED PLOVER (*Vanellus miles*)

Although Spur-winged Plovers first bred in the North Island as recently as 1973 (Barlow 1985), this species is now rapidly colonising suitable habitat in the region. Though few birds were counted, they were often seen as a flock. The largest flock consisted of 22 birds at the Otaki River estuary, and others contained 13, 11, 8 and 7 birds. Nearly all Spur-winged Plovers were seen at estuaries (Table 3). We suspect that this species occasionally visits the coastline for some social display purpose, because we did not see them feeding at all. They did not allow close approach, flying inland as a group when disturbed.

#### BANDED DOTTEREL (*Charadrius bicinctus*)

Three Banded Dotterels were seen at the Otaki River estuary and one at the Waikawa Stream estuary (Table 3). Although numbers are always low, the species is seen frequently at estuaries of the region in the non-breeding season, particularly from February to June (Wodzicki *et al.* 1978). On 31 March, 41 were seen higher up the tidal part of the Ohau estuary than our counting area at the river mouth.

#### BLACK-FRONTED DOTTEREL (*Charadrius melanops*)

Four Black-fronted Dotterels were seen once at the Otaki River estuary. This recent immigrant to New Zealand was not seen at the Waikanae River estuary before 1975 (Wodzicki *et al.* 1978). Since 1980, single birds or small flocks have been seen at several estuaries along the Wellington and Horowhenua coasts, particularly in the non-breeding season. The Black-fronted Dotterel forages along the water's edge of backwaters and at river margins over muddy substrates at the estuaries.



**GODWIT** (*Limosa* sp.)

A godwit was seen on Section 5. Bar-tailed Godwits occur regularly at the Ohau River estuary but higher up the estuary than we went during the counts (pers. obs.) and at the Waikanae River estuary (Wodzicki *et al.* 1978). The main site for the species in the vicinity is the Manawatu River estuary, 20 km to the north, where about 350 spend the summer and 30 overwinter (pers. obs.).

**PIED STILT** (*Himantopus himantopus*)

Pied Stilts were recorded at most estuaries and beaches during the counts, but the density of stilts was much greater at estuaries (13.4 birds per kilometre) than on beaches (0.4). The birds at estuaries were foraging on wet sandflats and along the margins of deep channels or were roosting. Those along the beaches foraged in the shallow waves or among the wrack at the high-tide line.

**POMARINE SKUA** (*Stercorarius pomarinus*)

In total, 10 Pomarine Skuas were seen. All were in flight along beaches, and seven were counted on 2 March 1986 along Section 4 (Table 3). Although Falla *et al.* (1979) stated that the Arctic Skua is the most numerous of the *Stercorarius* species off New Zealand coasts each summer, these seven were seen, together with an Arctic Skua, harassing a large flock of White-fronted Terns. The following morning HAR saw a group of five Pomarine Skuas and two Arctic Skuas working a flock of White-fronted Terns.

**ARCTIC SKUA** (*Stercorarius parasiticus*)

Two Arctic Skuas were identified and two skuas (*Stercorarius* spp.) were seen but not identified as to species.

**BLACK-FRONTED TERN** (*Sterna albostrata*)

One Black-fronted Tern was seen during the counts, flying along Section 5. A few birds are frequently seen along the south-western Wellington coastline in the non-breeding season, but occasionally large flocks visit Waikanae estuary, e.g. 110 on 22 May 1985 (Tennyson 1986). Black-fronted Terns first appear in February (Wodzicki *et al.* 1978).

**CASPIAN TERN** (*Hydroprogne caspia*)

The Caspian Tern was seen at most estuaries and along all beaches, but mostly at estuaries (Table 3). All terns along beaches were flying, while most at estuaries were roosting. We watched birds diving for prey in the sea and in the estuaries.

**WHITE-FRONTED TERN** (*Sterna striata*)

This was the most common species seen during the counts, with a mean of 55 per kilometre compared with 44 Black-backed Gulls per kilometre. They were recorded at most estuaries and beaches, but over seven times more densely at estuaries (Table 3). The terns at estuaries were mainly roosting, whereas those along beaches were flying, either foraging along the outer breakers or moving between their offshore feeding grounds and the roosting sites.

The presence of large flocks of White-fronted Terns along the coastline was probably the main reason for the frequent sightings of skuas. The White-fronted Tern does not breed within the survey area, but a small colony is at Pipinui Point (Stephenson 1977) and small colonies are on rock stacks about Mana Island (R.O. Cossee, pers. comm.) and Kapiti Island (P. Daniel, pers. comm.).

### CONCLUSION

We found significant changes in the number and age structure of gulls on this coast since Dr Wodzicki did his counts 25 years ago. As human activity continues to increase here, further changes are inevitable. We hope that the gull counts will be repeated in the future and that counts of other coastal species will also be made to allow further comparisons.

### ACKNOWLEDGEMENTS

Dr Kazimierz Wodzicki, former Director of Ecology Division, DSIR, and more recently Honorary Lecturer of Zoology, Victoria University of Wellington, who died on 15 June 1987, aged 87, did considerable work on the birds of the south-west coast of the North Island, notably at Waikanae estuary. His counts were the basis of this historical comparison.

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## OBITUARY

**Count Kazimierz Antoni Z Granowa Wodzicki**

OBE, PhD, DSc, FRSNZ

1900-1987



Dr Wodzicki (left) and the late Keith Hindwood birdwatching near Sydney, c. 1941

Dr Wodzicki, known as Kazio to his many friends throughout New Zealand and overseas, died peacefully at his home in Wellington on 15 June 1987. He was 87.

Born and educated in Poland, Dr Wodzicki came to New Zealand in 1941 to serve as Consul-General for the exiled Polish Government in London. He and his family had miraculously escaped to Britain when the Germans invaded Poland, where he had been Professor of Anatomy and Histology at the University College of Agriculture in Warsaw. Before leaving Poland

he had published 39 research papers on topics ranging from the anatomy and reproductive physiology of poultry to the neolithic and medieval goats of Poland, but his main interest was in birds, particularly the ecology and migration of storks.

Despite the busy and stressful life of a war-time diplomat, Dr Wodzicki found time to pursue his ornithological interests in New Zealand. He is listed as a member of the Ornithological Society in the Annual Report for 1940-41, and, on 21 September 1941, in company with C.A. Fleming and the late A.A. Kirk, he made the first of his many visits to the Waikanae River estuary near Wellington. He was a frequent contributor to *N.Z. Bird Notes* (later *Notornis*) from 1942 onwards. (Although he held the title of Count, he preferred in New Zealand to use his academic title of Doctor.)

At the end of the war, when Poland fell under the Russian sphere of influence, Dr Wodzicki could no longer represent his country as a diplomat, and he did not wish to return there. The New Zealand Government found work for him in DSIR investigating the problems caused by the various introduced mammals that inhabited New Zealand's farmlands, forests and mountain lands. This work, published in 1950 as DSIR Bulletin No. 98 *Introduced Mammals of New Zealand - An Ecological and Economic Survey*, led to the establishment of the Animal Ecology Section of DSIR (now Ecology Division, DSIR) and Dr Wodzicki became its first Director.

Although the Section was primarily concerned with mammals, Dr Wodzicki catered for his ornithological interests by working extra hours and he encouraged his staff to do likewise; thus, work on gannets, rooks and ornithological surveys continued along with research on various aspects of the rabbit problem. His retirement from DSIR in 1965 represented little more than a comma in his life of research. He soon turned his attention to the problem of how to control rat damage of coconuts in the Tokelau Islands and later in Niue. True to his character, and despite the demands of the rodent work, he found time to be interested in, and to publish on rodent parasites, land crabs, fruit bats and birds. Back in New Zealand he worked on his material in the Zoology Department of Victoria University, where he was an Honorary Lecturer, and at the National Museum, where he was an Honorary Research Associate. At the time of his death he had no less than 138 scientific publications to his credit. A list of these is held in the library of Ecology Division, DSIR.

Among his many ornithological contributions (often published jointly with colleagues), the studies of bird life at Waikanae Estuary and of the gannets at Cape Kidnappers were especially significant because they were continued over many years, thus allowing the detection of important changes. The Waikanae Estuary surveys, first published in 1946 and with the help of Max Falconer repeated in 1978, recorded in detail the changes that occurred in the birdlife as new houses encroached on the nearby sandhills and as the estuary and its adjacent beaches were subjected to greatly increased human use. The work on gannets was even more productive. In 1946-47, with Dr C.A. Fleming, Dr Wodzicki censused the gannet population of New Zealand by counting occupied nests shown on aerial photographs and

checking the results by ground visits to some of the gannetries. This was the first full census of any New Zealand seabird. Another first in gannet research came from Dr Wodzicki's banding operations, which revealed the previously quite unsuspected fact that young New Zealand gannets disperse to Australian seas within a few days of leaving their natal colonies. Yet another surprise came when, in 1969-70 and again in 1980-81, Dr Wodzicki and his co-workers repeated the gannet census and found that the population had been increasing at the rate of 2.3% per year since 1946-47. Apart from his own personal research, Dr Wodzicki had an important influence on New Zealand ornithology by encouraging and supporting the work of other people, particularly the members of his staff in Ecology Division and, later, the graduate students he helped supervise at Victoria University.

While it seems appropriate for this journal to emphasise Dr Wodzicki's ornithological achievements, it must not be forgotten that he made equally important contributions in other branches of zoology. These, together with his ornithological work, were recognised when he was elected a Fellow of the Royal Society of New Zealand in 1962, awarded an Honorary DSc by Victoria University in 1980, and made an Honorary Life Member of the New Zealand Ecological Society in 1984.

But science was not his only activity. As Polish Consul-General he assisted his late wife, the Countess Maria Wodzicka, in persuading the New Zealand Government to accept a large number of Polish war refugees, mostly children, and to set up a special camp near Pahiatua to provide for their needs. The Wodzickis continued their interest in these children as they grew up and had families of their own. In this way, and by his personal interest in the New Zealand way of life, Dr Wodzicki did much to foster the understanding and respect the two cultures now have for each other. Dr Wodzicki's services to New Zealand, both cultural and scientific, were recognized publicly in 1976 when he was awarded the OBE. Sadly, his gracious and talented wife, who had contributed so much to the Polish community in New Zealand, had died before this honour was bestowed.

Dr Wodzicki's achievements did not come easily. Born into an aristocratic land-owning family and accustomed to the help of servants, he was perhaps ill-equipped to survive with modest means in the New Zealand do-it-yourself society. Yet survive he did despite having to cope with a lengthy illness in 1956. He not only learnt to look after himself in the field in New Zealand and on remote Pacific islands but also became quite an accomplished cook in his own kitchen. His dignity, impeccable manners and personal charm enabled him to make friends with people from all walks of life. He applied some of the skills acquired as a diplomat to help him survive in the New Zealand Public Service, where he showed an astonishing capacity to circumvent obstructions and get funding for his research.

Dr Wodzicki was a faithful attender at meetings of the Wellington Branch of OSNZ and rarely did a speaker escape without a question from Dr Wodzicki, or more often several questions delivered all at once. He was always ready to compliment good work but equally ready to voice constructive criticism of work he considered shoddy. Although he will be

missed by his many friends, we can rejoice in his long life of achievement, most of it preserved in print for future generations, and in the privilege many of us have had in enjoying Kazio's friendship and his company on bird-watching outings.

The Society extends its sympathy to Dr Wodzicki's daughter, Professor Manika Cockrem of Bogor, Indonesia; to his son Professor Jontek Wodzicki of Washington State University, Bellington, U.S.A.; and to his seven grandchildren.

P. C. Bull



## NOTICE

The Deutsche Ornithologen-Gesellschaft will hold its 100th annual meeting as the "International 100th Annual Meeting" September 24 to October 1, 1988 at the Museum Alexander Koenig in Bonn, West Germany. The two key themes will be Zoogeography & Systematics and Behavioral Ecology. All interested in participating should contact:

**Dr K. -L. Schuchmann,  
Museum Alexander Koenig,  
Adenauerallee 150-164,  
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Federal Republic of Germany.**

## LETTERS

### SUBFOSSIL SNIPE

It was with considerable interest that I read about the subfossil distribution of *Coenocorypha* in the North and South Islands (Miskelly 1987), but it was with some consternation that I saw subspecific status being applied to the bird represented by these bones. Firstly, no osteological comparison is presented to show that South Island snipe are the same as those that were on islands around Stewart Island, or are indeed different to those from the North Island. The proposed scheme is consistent with taxonomic trends in other avian taxa in New Zealand but is it really warranted? The majority of avian subspecies in New Zealand are indistinguishable osteologically, e.g. tits, fantails, bellbirds, and their status is only maintained to distinguish differences in plumage and/or behaviour. Neither of these characters are available for description in subfossil material. If there is variation, it may be clinal, it may separate Northland birds from the rest, but at present variation is not demonstrated; therefore I suggest that subfossil snipe in New Zealand be called *Coenocorypha aucklandica*. After all, does this obscure information?

#### REFERENCE

MISKELLY, C.M., 1987. The identity of the hakawai. *Notornis* 24: 95-116.

T.H. WORTHY, *National Museum of Wellington, Private Bag, Wellington*



I accept Mr Worthy's criticism of giving subspecific status to bones in the absence of known differences in plumage and/or behaviour. However, subspecific names have been proposed for skins of New Zealand Snipe collected at either end of a geographic range within which subfossil snipe bones have been found (Oliver 1955). To lump all subfossil bones from the North and South Islands into one taxon does obscure information, as this scheme ignores any heuristic hypotheses on the historical distributions of two demonstrably distinct forms. For example, the scheme proposed by Worthy would leave *C. a. barrierensis* as a form endemic to Little Barrier Island. As no other avian subspecies are currently recognised as having evolved in isolation on any island thought to have been connected to the North Island during the last glaciation, a more parsimonious hypothesis is to consider Little Barrier I. as the final refuge of a formerly widespread North Island form (as has occurred more recently with the Stitchbird (*Notiomystis cincta*)).

My proposed distribution of snipe subspecies on the New Zealand mainland was admittedly premature. I raised the issue to point out the availability of the names *iredalei* and *barrierensis* (the latter consistently overlooked by New Zealand ornithologists, e.g. Kinsky 1970, 1980), and in the hope of preventing any attempts to erect new subspecific names for mainland snipe (see Medway 1971, Millener 1981: 417). Since submitting the "Hakawai" manuscript I have measured all available *Coenocorypha* bones in New Zealand institutions and have obtained X-rays of the unique holotype of *C. a. barrierensis*. A revised classification of the genus is in preparation.

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