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INTRASPECIFIC VARIATION IN THE NEW ZEALAND BELLBIRD Anthornis melanura

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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 midtoe 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 ($P \le 0.001$).

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., Ereb. Terr.*, Birds, pt. 4, p1.2). 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. VARIATION IN BELLBIRDS

	Adults (both sexes)									Subadults (both sexes)							
Moult Category	Jan	Feb- Mar	May	Sept	early Oct	late Oct	Nov	Dec		Jan	Feb- Mar	May	Sept	early Oct	late Oct	Nov	Dec
1	-	98	-	-	-	-	-	-	Į	-	1	-	-	-	-	-	-
2] -	-	85	-	-	4	-	-	1	-	-	-	-	-	-	-	-
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	ſ	-	18	5	-	3	38	79	79
(a & b)	28									-		-			1	3	21
n	136	397	137	184	49	193	70	29	ļ	90	156	62	48	31	72	40	19

TABLE 1 - Seasonal	variation in the p	percentages of	adult and	subadult	bellbirds
in differen	t moult categorie	es on the Poor	Knights Is		

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 (Prosthemadera 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 fingerlike 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 knownaged 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 later breeding mentioned by Travers (1873).

Three Kings Islands

Aff 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

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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,

		Adult da				Adult oo				
	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		

TAE	BLE	2	—	Bill	length	of	adults	(mm))
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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.).

		Adult dd				Adult çç				
	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 3 — Head & bill length of adults (mm)

TABLE 4 — Tarsus length of adults (mm)

		A	dult 🛷 🔄		í	A	dult oo	
	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
North]and	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

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

	Adult adult adult Mean S.D. Range 21.8 1.61 19.6-23 21.7 1.24 19.8-23 20.5 1.28 18.1-22 19.6 0.85 18.4-21 20.8 1.19 17*24 20.9 1.31 18.6-23 21.3 0.63 19.9-22 21.4 0.53 20.3-22			Adult go				
Mean	S.D.	Range	No.	Mean	S.D.	Range	_No.	
21.8	1.61	19.6-23.5	4	21.0	2.82	19.0-23.0	2	
21.7	1.24	19.8-23.2	8	20.6	0.07	20.5-20.6	2	
20.5	1.28	18.1-22.0	9	- 1	-	-	-	
19.6	0.85	18.4-21.0	8	17.6	1.33	16.5-19.1	3	
20.8	1.19	17*24	147	19.9	1.18	17-23	61	
20.9	1.31	18.6-23.2	17	19.5	0.69	18.2-20.7	10	
21.3	0.63	19.9-22.0	8	19.5	0.92	18.4-20.0	3	
21.4	0.53	20.3-22.0	8	19.6	0.95	18.5-20.2	3	
23.3	1.25	21.1-25.0	14	21.2	1.34	19.8-22.7	4	
25.4	0.93	24.5-26.2	4	21.6	2.05	18-23	5	
	Mean 21.8 21.7 20.5 19.6 20.8 20.9 21.3 21.4 23.3 25.4	A Mean S.D. 21.8 1.61 21.7 1.24 20.5 1.28 19.6 0.85 20.8 1.19 20.9 1.31 21.3 0.63 21.4 0.53 23.3 1.25 25.4 0.93	Adult ad Mean S.D. Range 21.8 1.61 19.6-23.5 21.7 1.24 19.8-23.2 20.5 1.28 18.1-22.0 19.6 0.85 18.4-21.0 20.8 1.19 17*24 20.9 1.31 18.6-23.2 21.3 0.63 19.9-22.0 21.4 0.53 20.3-22.0 23.3 1.25 21.1-25.0 25.4 0.93 24.5-26.2	Adult ad Mean S.D. Range No. 21.8 1.61 19.6-23.5 4 21.7 1.24 19.8-23.2 8 20.5 1.28 18.1-22.0 9 19.6 0.85 18.4-21.0 8 20.8 1.19 17*24 147 20.9 1.31 18.6-23.2 17 21.3 0.63 19.9-22.0 8 21.4 0.53 20.3-22.0 8 23.3 1.25 21.1-25.0 14 25.4 0.93 24.5-26.2 4	Adult ad Range No. Mean 21.8 1.61 19.6-23.5 4 21.0 21.7 1.24 19.8-23.2 8 20.6 20.5 1.28 18.1-22.0 9 - 19.6 0.85 18.4-21.0 8 17.6 20.9 1.31 18.6-23.2 147 19.9 20.9 1.31 18.6-23.2 17 19.5 21.3 0.63 19.9-22.0 8 19.5 21.4 0.53 20.3-22.0 8 19.6 23.3 1.25 21.1-25.0 14 21.2 25.4 0.93 24.5-26.2 4 21.6	Adult $\sigma\sigma$ AMeanS.D.RangeNo.MeanS.D.21.81.6119.6-23.5421.02.8221.71.2419.8-23.2820.60.0720.51.2818.1-22.0919.60.8518.4-21.0817.61.3320.81.1917*2414719.91.1820.91.3118.6-23.21719.50.6921.30.6319.9-22.0819.50.9221.40.5320.3-22.0819.60.9523.31.2521.1-25.01421.21.3425.40.9324.5-26.2421.62.05	Adult $\sigma\sigma$ Adult gq MeanS.D.RangeNo.MeanS.D.Range21.81.6119.6-23.5421.02.8219.0-23.021.71.2419.8-23.2820.60.0720.5-20.620.51.2818.1-22.0919.60.8518.4-21.0817.61.3316.5-19.120.81.1917*2414719.91.1817-2320.91.3118.6-23.21719.50.6918.2-20.721.30.6319.9-22.0819.50.9218.4-20.021.40.5320.3-22.0819.60.9518.5-20.223.31.2521.1-25.01421.21.3419.8-22.725.40.9324.5-26.2421.62.0518-23	

* incorrectly measured

	Adult_do				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	
	* prol	bably in	ncorrectly me	easured					

TABLE 6 — Wing length of adults (mm)

TABLE 7 — Tail length of adults (mm)

	Adult aa				Adult oo				
	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	
North?and	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 do				Adult 99				
	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	- 1	-	-	-		
Auckland Is	35.5	0.00	-	3	30.5	2.12	29-32	2		

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	Subadult ਰੁਰ				Subadult 99				
	Mean	S.D.	Range	No.	Mean	<u>S.D.</u>	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 9 — Bill length of subadults (mm)

TABLE 10 - Head & bill length of subadults (mm)

		Subadult do				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	- 1	-	-	-		

TABLE 11 — Tarsus length of subadults (mm)

	Subadult dd			Subadult 99				
	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 dd			Subadult çç				
	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 do			Subadult 99				
	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	- 1	-	-	-

TABLE 14 - Weight in grams of subadults

	Subadult dd				Subadult 99			
	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

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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 Chathams).



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 *Melithreptus* (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 Prosthemadera 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 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 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 withinphenotype 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 Marías, 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 Marías Is. Allometric change in dimensions has enabled only a few Tres Marías birds to become more dense than mainland populations of the same species (Grant 1965b). The number of bird species is higher on the Tres Marías 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 Marías, 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 Museum 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 museum 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-Zelande".

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 Zelande 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(elande) (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, 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 metallisés, 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 Anthomis 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).

	Bill	Wing	Tail	Tarsus				
adult males	1.6 n.s.	0.89 n.s.	1.80 n.s.	0.69 n.s.				
	(23)	(27)	(25)	(26)				
adult females	1.73 n.s.	2.10 n.s.	2.55 *	1.85 n.s.				
	(6)	(9)	(8)	(8)				
	n.s. = not significant, P> 0.05							
	<pre>* = significant, P< 0.05</pre>							

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).

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.auriocula 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 vardstick 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. Nonmorphometric 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 vellowish 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 Ngatitoki 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: NMNZNo. 22065, ad. female, 50 ma.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. Lores 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: Buffy 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 bil 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 measurments 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 ^{dd}	5.73 ***	9.59 ***	10.87 ***	10.24 ***	7.20 ***		
	(63)	(289)	(84)	(153)	(115)		
Tiritiri: ad 🕫	5.38 ***	5.24 ***	3.47 ***	7.82 ***	1.88 n.s.		
	(50)	(163)	(37)	(94)	(64)		
Orongorongo: ad dd	10.62 ***	6.37 ***	7.09 ***	10.79 ***	13.60 ***		
	(194)	(449)	(190)	(240)	(286)		
Orongorongo: ad ହହ	8.60 ***	2.01 *	0.85 n.s.	5.92 ***	7.38 ***		
	(92)	(234)	(73)	(120)	(138)		
	n.s. = not significant, P> 0.05						
	* = sig	nificant, P<	0.05				
	*** = hia	hlv signific	ant. 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 ($\overline{CD} = \overline{0.8}$). 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 (Sparrman, 1786)

- a. A.melanura obscura Falla, 1948 Three Kings Bellbird Three Kings Is
- b. A.melanura oneho n.subsp. Poor Knights Is
- c. A.melanura melanura (Sparrman, 1786) 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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