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Distribution and age-specific plumage states of the long-tailed cuckoo (*Eudynamys taitensis*)

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Abstract Plumage states of the long-tailed cuckoo (*Eudynamys taitensis*) are reviewed and summarised from examination of museum study-skins. Besides the distinctive adult plumage (barred above, white background colour below) and immature plumage (spotted above, pale brown below), some birds (13% of those in the wintering grounds, plus 1 bird from New Zealand) show a "transitional" plumage presumed to be intermediate between the immature and adult condition. Also, some pale birds found in New Zealand may represent a hitherto-unrecognised juvenile plumage. A review of distribution records (museum specimens plus published sight-records) in both the summer and winter ranges of the cuckoo confirms a vast fan-shaped distribution extending 6,000 km north from New Zealand to the tropical Pacific, and 11,000 km from east to west in the tropics. Wake Island (19.3°N) in the north, Palau (134.5°E) in the west, Henderson Island (128.3°W) in the east and the Snares Islands (48.0°S) in the south are the extreme records in this range. Records of museum specimens reveal that almost all long-tailed cuckoos returning to New Zealand in October are in adult plumage. Autumn records show a gradual northward retreat of cuckoos within New Zealand, with a stronger-than-average bias in North Island records from March to May. There is no equivalent North Island bias for the spring influx in September and October. Museum specimens from eastern Polynesia exhibited an uneven sex ratio biased towards males (74%), whereas the sex ratio elsewhere was more even. Our study confirms the vast total range of the long-tailed cuckoo and provides age-specific details of the seasonal waxing and waning of the migratory patterns of the breeding population within New Zealand.

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INTRODUCTION

Long-tailed cuckoos (*Eudynamys taitensis*) weigh about 125 g and parasitise New Zealand's 3 small passerines in the genus *Mohoua* (Pachycephalidae). The cuckoos perform a spectacular overwater migration to winter in islands up to 6,000 km away in the tropical Pacific (Bogert 1937; Dorst 1962). Long-tailed cuckoos thus have an unusual fan-shaped total distribution, with a breeding range concentrated on the relatively small New Zealand archipelago and a vast wintering ground on islands to the north extending 11,000 km from west to east (Bogert 1937; Gill & Hauber 2012).

The Maori inhabitants of New Zealand were said to be unaware that the long-tailed cuckoo was a seasonal long-distance migrant, and some accounted for the spring appearance of the birds by the belief that they were the offspring of a kind of lizard, and for the winter disappearance by the notion that the birds buried or hid themselves in earth or mud, among stones or in tree holes (Yate

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1835; Best 1909). Polynesians of the tropical Pacific were perhaps more aware of this cuckoo's migration since its arrival from, or departure, out to sea might have been more evident from small islands than from the large land-mass and long coastline of New Zealand. Accordingly, there is a suggestion that the dispersal of human settlers from eastern Polynesia to New Zealand some 750 years ago may have followed the direction of long-tailed cuckoos departing on their southward journey (*e.g.*, Caughley 1989). This now seems less likely with new evidence that (at least a portion of) the long-tailed cuckoo wintering population undergoes an anti-clockwise loop migration, whereby birds return to New Zealand from and in the west (Gill & Hauber 2012).

The long-tailed cuckoo was seen in New Zealand in 1769 during Capt. James Cook's first voyage (Oliver 1955: 538), but it was not described and named (as *Cuculus taitensis*) until 1787, based on material from Tahiti and Huahine, French Polynesia, obtained in 1773 during Cook's second voyage (Lysaght 1959). The 'Tahitian cuckoo' species (as *Eudynamys*—or *Eudynamis*—*taitensis*) was given in the first systematic lists of New Zealand birds (G.R. Gray in Dieffenbach 1843; Gray 1844), showing that the Pacific and New Zealand birds were regarded as the same species taxonomically from an early date.

The European colonists in New Zealand noticed the annual appearance and disappearance of long-tailed cuckoos and soon put it down to migration (Hutton 1901; Fulton 1904). Dieffenbach (1843) stated that this cuckoo is migratory 'appearing near the coasts in the month of December' and there were reports that the cuckoo 'comes from the north to the neighbourhood of Port Nicholson [Wellington] in the month of October, and returns in April' (Gray 1844).

Long-tailed cuckoos were sometimes recorded on Pacific islands during the breeding season, and so they were considered by some as year-round residents of Polynesia (Dorst 1962). Separate species or subspecies from Fiji (*Eudynamys cuneicauda* Peale, 1848), Otago in New Zealand's South I (*Urodynamis taitensis pheletes* Wetmore, 1917) and Norfolk I (*Urodynamis taitensis belli* Mathews, 1918) were described without commentary on implications for migratory patterns. The long trans-Pacific migration over water was itself questioned: Wallace (1876: 452) found the distances from New Zealand to Pacific island localities extremely improbable and felt it was premature in so sparsely settled a country to rule out a purely internal New Zealand migration.

After the systematic collecting of birds on islands across the south Pacific by the Whitney South Sea Expedition (1921–1933) of the American Museum of Natural History, all long-tailed cuckoos from New Zealand and the tropical Pacific could be confidently regarded as conspecific. Bogert (1937) used museum specimens to confirm this cuckoo's spectacular migration, documenting the full extent of the bird's range in the Pacific and the general timing of its migration.

Far too few long-tailed cuckoos have been banded for recoveries to have aided an understanding of the bird's distribution and migration, and studies with satellite transmitters are only now being attempted in this species. We recently followed Bogert's approach of examining migratory patterns indirectly (Gill & Hauber 2012) and assembled updated records of museum specimens and published sight-records to establish the presence of the cuckoo at all times (months) and places (latitude, longitude) over the course of its annual cycle of breeding and migration. Gill & Hauber (2012) provide a large-scale analysis of the bird's annual distribution, including the timing and direction of the migratory behaviour of long-tailed cuckoos between New Zealand and the western south Pacific wintering grounds. Here, we present complementary results by reviewing the literature on the distribution of the cuckoo throughout its breeding and wintering ranges, summarising plumages of the cuckoo based on examination of museum skins, analysing the seasonal distribution of cuckoos within New Zealand, and considering the sex ratio of museum specimens.

METHODS

We compiled a database of 1120 geographic records of long-tailed cuckoos, nearly all with the month and year of collection or observation. Most records were between 1873 and 2011, with another 5 records from before 1873. A total of 66% were sight-records compiled from the literature, and these seldom gave the age of cuckoos based on plumage traits. Most New Zealand sight-records (North I, n = 410; South I, n = 160) were obtained from the Classified Summarised Notes section of *Notornis* (1943–2006). Pacific island sight-records (n = 170) were obtained mostly from books and periodical articles on the local ornithology of the various island groups.

The remaining 34% of records were based on museum study-skins (nearly all examined by BJG): 180 cuckoo specimens collected in New Zealand and 200 collected in Pacific islands (see Gill & Hauber 2012 for further details). The following museum acronyms are used (Sabaj Pérez 2010): AIM (Auckland), AMNH (New York), MVZ (Berkeley, California), NMNZ (Wellington), and NMV (Melbourne). The age of museum cuckoos was assigned by BJG from the known plumage dimorphism between adults and immatures (Heather & Robertson 1996). There is no reported sexual dimorphism in plumage and none was noted by us; the sex of specimens was taken from museum labels. Localities of collecting or observation were

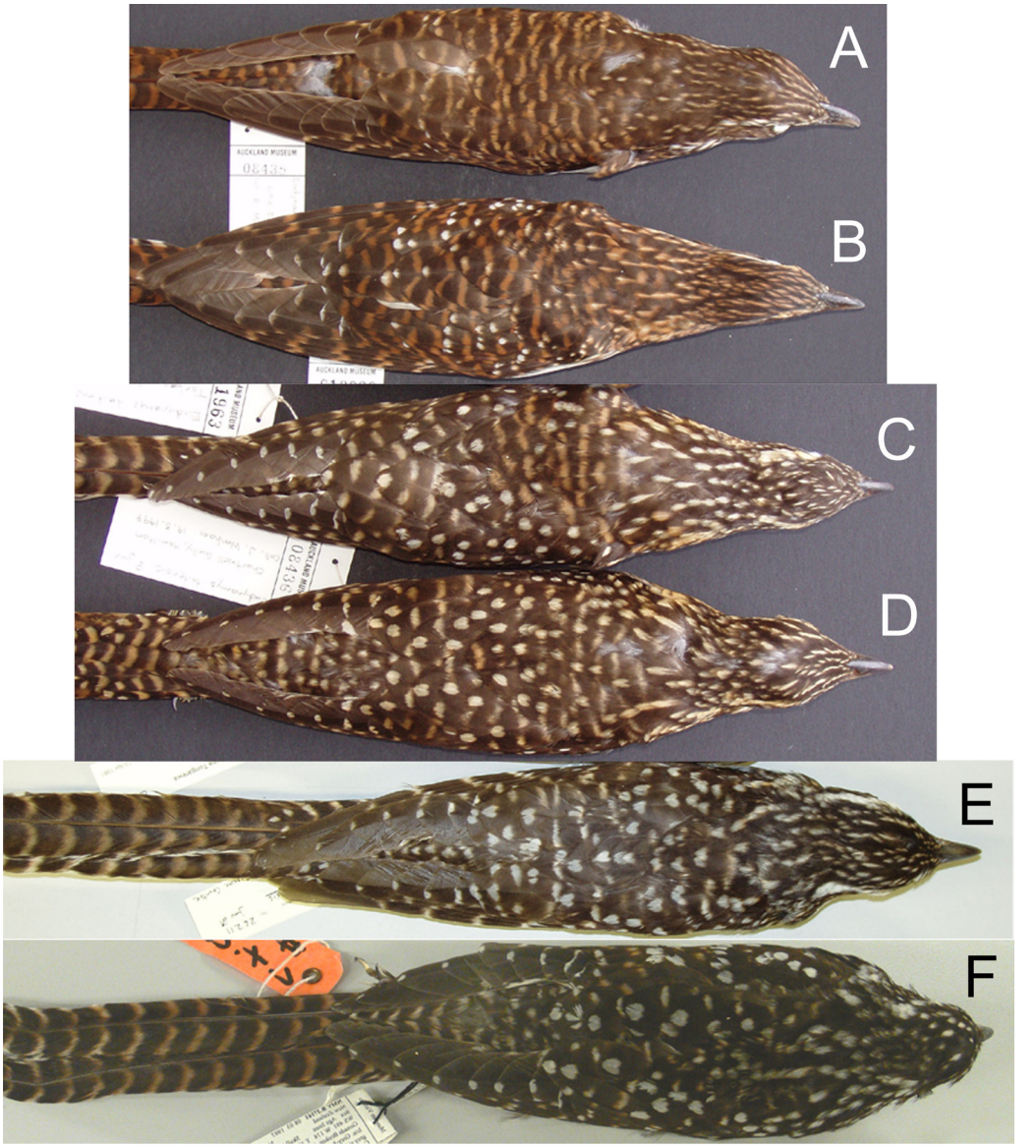

Fig. 1. Study-skins of long-tailed cuckoos (dorsal) illustrating different age/moult classes. A, typical unspotted adult (AIM LB8435). B, variant adult with white spots (AIM LB13320). C, transitional with mixed plumage (AIM LB11963). D, immature (AIM LB8436). E, possible juvenile (NMNZ 26211). F, possible juvenile (NMV B27161; photo W. Longmore).

converted to latitude and longitude so they could be plotted. To graph locations on a map, latitudes south of the equator were made negative and longitudes were modified to continue east beyond 180° (*e.g.*, 170°W was plotted as 190°).

Weights of museum specimens were as noted in museum records. BJG took 3 size measurements: wing length (Wing L, flattened but unstraightened chord), tail length (Tail L, ventrally base to tip), and bill length (Bill L, anterior edge of nostril to tip). The wing and bill lengths of adults and immatures were taken from dry museum skins, but tail length was taken from defrosted birds at AIM during post-mortem examination. For the 5 putative juvenile cuckoos (Table 2) measurements were of necessity a mixture—some were taken on dried specimens while others were recorded only while the bird was fresh. In dried specimens there is a small degree of shrinkage (Winker 1993); therefore measurements are used here merely to give an indication of trend

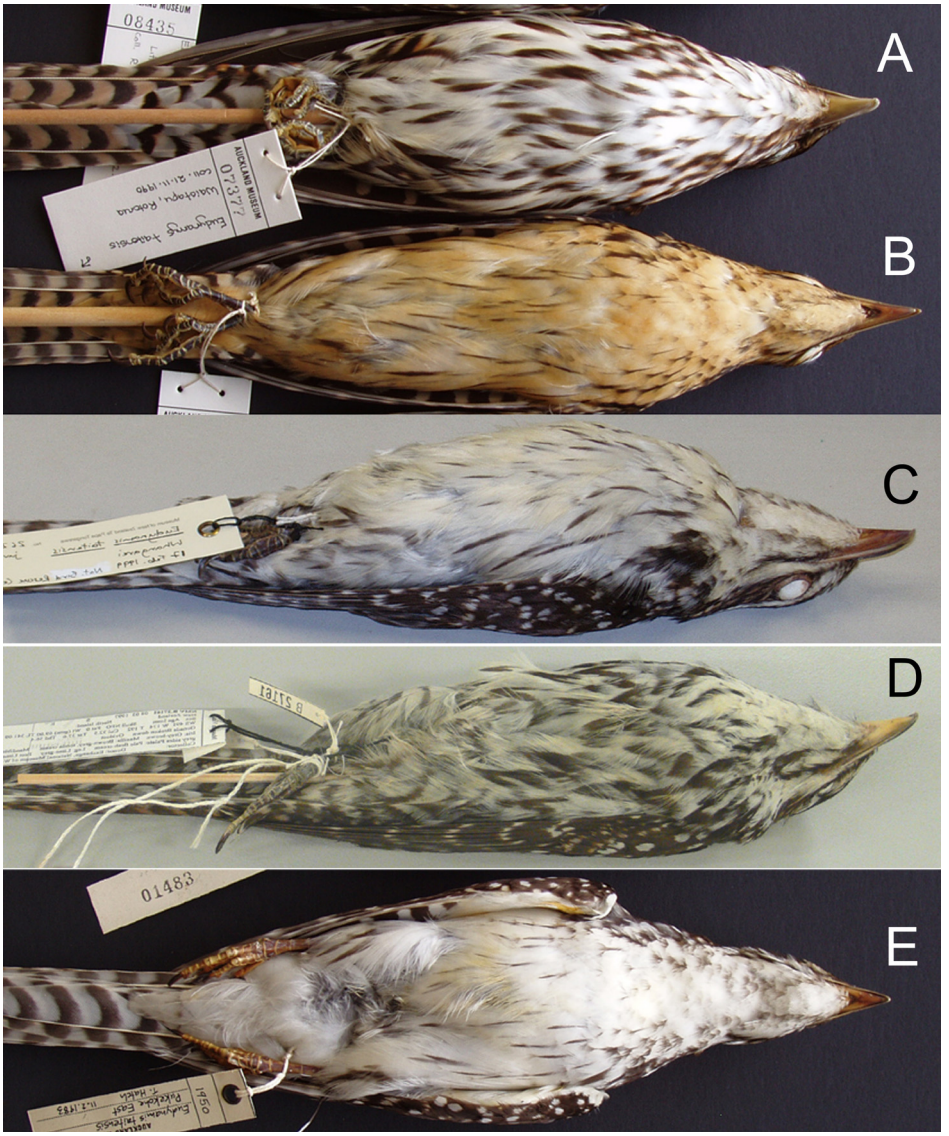

Fig. 2. Study-skins of long-tailed cuckoos (ventral) illustrating different age classes. A, adult (AIM LB7377). B, immature (AIM LB8436). C, possible juvenile (NMNZ 26211). D, possible juvenile (NMV B27161; photo W. Longmore). E, possible juvenile (AIM LB1950).

and are not compared statistically. To quantify the size of the dorsal spots and dark brown ventral streaks, the widths of the narrowest and widest spots and streaks were measured with vernier callipers on 10 adult and 10 immature birds.

RESULTS

Plumages and age

There are clear categorical differences between adult and immature long-tailed cuckoos in the colour and pattern of their plumage, as illustrated and described by Heather & Robertson (1996) and Higgins (1999). However, there is also much individual variability (Bogert 1937; *pers. obs*.). Table 1 summarises plumage differences between the various plumage classes.

Adult plumage. The back and scapulars are dominated by transverse reddish-brown bars (Fig. 1A). The ventral body plumage is white (or white with pale brown suffusions limited to anterior and lateral regions) with dark brown longitudinal streaks (Fig. 2A) that are usually wide (0.9–5.3 mm). There is

Table 1. Summary of plumage characteristics of age/moult classes of long-tailed cuckoos. Transitionals are mostly in the wintering ground; these individuals are presumed to be moulting into adult plumage.

	Dorsal plumage (back, scapulars)	Ventral plumage (breast, belly)
Adult	Dark brown with numerous red-brown transverse bars (Fig. 1A). Variant individuals may also show small white spots (Fig. 1B).	White with dark brown longitudinal streaks (Fig. 2A). Streaks (0.9–5.3 mm wide) usually thick.
Transitional	Mixed; areas of adult-type and immature-type plumage side-by-side (Fig. 1C).	Either pale brown or white, presumably depending on the stage of transition.
Immature	Dark brown with numerous large rounded cream-coloured spots (Fig. 1D). Transverse bars few and pale red-brown.	Light or intense pale brown, with dark brown longitudinal streaks (Fig. 2B). Streaks (0.3–3.8 mm wide) usually thin.
Juvenile?	Dark brown with numerous large rounded white spots (Figs 1E–F). Transverse bars few and very pale red-brown.	White or suffused with pale lemon-yellow, with dark brown longitudinal streaks (Figs 2C–E). Streaks usually thin.

Table 2. Museum specimens of long-tailed cuckoos considered to be possibly in juvenile plumage, with their weights and length measurements. L, length.

Specimen	Locality	Collecting date	Weight (g)	Wing L (mm)	Tail L (mm)	Bill L (mm)
AIM LB1950, skin, Fig. 2E	Pukekohe	11 Feb 1983	–	171	178	13.3
AIM LB9229, spread wing	Howick	30 Jan 1997	100	180	188	16.1
AIM LB14021, spread wing	West Auckland	Mar 2008	79	177	187	15.5
NMNZ 26211, skin, Figs 1E, 2C	Whangarei	17 Feb 1999	128	176	207	16.6
NMV B27161, skin, Figs 1F, 2D	New Zealand	8 Mar 1997	69	174	192	14.7

much variation in adult plumage, for example in the presence or absence of white spots on the dorsal plumage (Fig. 1B); some 34% of 112 adult study-skins at AIM and AMNH were scored as having white dorsal spots. These spots in adults tend to be small (*c.* 3 mm diameter) and intensely white, unlike the larger, cream-coloured spots (*c.* 5 mm diameter) on the dorsal plumage of immatures (Fig. 1D).

Immature plumage. Dorsally, immatures (Fig. 1D) have fainter red-brown transverse bars than adults and the back is dominated by large pale, cream-coloured spots. In immatures the ventral coloration (Fig. 2B) is pale brown with narrower dark brown streaks (0.3–3.8 mm wide) than in adults. The ventral pale brown coloration varies from faint to intense.

Transitional plumage. Some cuckoos exhibit a 'transitional' plumage (Fig. 1C) in which the back and scapulars show a mosaic of regions of immature plumage (with large pale, cream-coloured spots) and adult plumage (with transverse reddish-brown bars). They are presumably moulting their body plumage from the immature to the adult condition. We scored as transitionals about 13% of study-skins collected in the Pacific island wintering grounds. We also know of one transitional specimen collected on mainland New Zealand (AIM LB11963, Auckland; Fig. 1C). It was collected on 26 Mar 2003 (*i.e.*, in autumn), suggesting that a few immatures may begin some moult, perhaps just of body feathers, at about the time they migrate north. Another transitional (NMNZ 1905) was collected on Raoul I, Kermadec Is, on 1 May 1913.

Possible juvenile plumage

In 2008, BJG examined a recently-dead long-tailed cuckoo (now AIM LB14021) that was clearly non-adult from the large spots dominating the back and scapulars but which was strikingly pale below. It lacked pale brown coloration on the chest and belly, and the underwing coverts were tinged with pale yellow rather than pale brown. The bird had a low weight (79 g) and a noticeably short bill (15.5 mm), so it may have been a recent fledgling. Looking more closely at museum specimens, BJG found 2 others with the pale ventral condition at AIM, one at NMNZ and one at NMV (Table 2). All were collected from late Jan to Mar (*i.e.*, towards the end of the breeding season when fledgling cuckoos would be expected). They were low in weight—94 g on average compared with a mean of 122 g for immatures and 131 g for adults (Table 3). Their wing, tail, and bill lengths were much shorter than for adults, but similar to those of immatures.

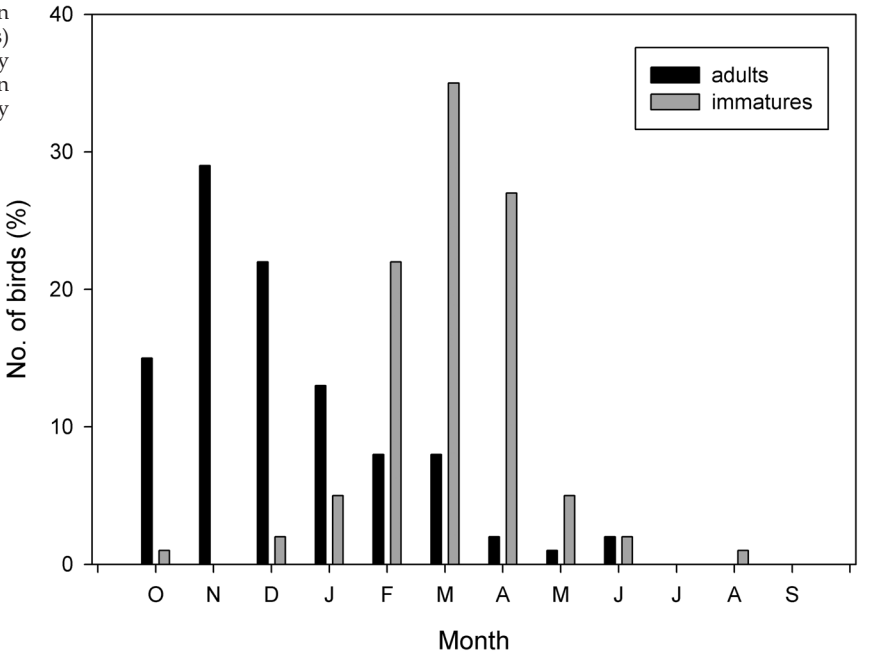

Fig. 3. Monthly distribution of adult records (black bars) and immature records (grey bars) of long-tailed cuckoos in New Zealand (n = 192; mostly museum specimens).

Table 3. Average weights and length measurements of long-tailed cuckoos of different age classes: mean (s.d., n) range. L, length.

	Juvenile?	Immature	Adult
Weight (g)	94.0 (26.09, 4) 69–128	121.8 (23.70, 47) 73–172	131.4 (21.74, 15) 109–183
Wing L (mm)	175.6 (3.36, 5) 171–180	171.2 (8.53, 33) 134–182	185.5 (5.73, 31) 176–202
Tail L (mm)	190.4 (10.60, 5) 178–207	191.6 (11.80, 40) 169–214	227.9 (8.94, 16) 217–244
Bill L (mm)	15.24 (1.295, 5) 13.3–16.6	15.26 (1.223, 33) 12.7–17.3	18.11 (0.740, 31) 16.5–19.3

These 5 pale birds may be juveniles (recent fledglings) in a distinctive juvenile plumage. If so, this juvenile plumage is similar in nearly all respects to the immature plumage, differing principally in the general paleness in the paler parts (as opposed to the dark brown parts) of the juvenile plumage. On the back and scapulars (Figs 1E–F) the transverse bars have only a faint hint of red-brown, and the large spots are white rather than cream-coloured (as in immatures). On the throat, breast, belly and flanks the juvenile lacks the pale brown plumage of the immature, and is instead white like the adult (Figs 2C–E). The white is sometimes suffused with pale yellow. The dark brown longitudinal streaks on the ventral body may be thick (Fig. 2D), resembling an adult, but are more usually thin (Fig. 2C, 2E) as in the immature. The underwing coverts have a pale yellow tinge rather than a brown tinge as in immatures.

Seasonality and distribution

Seasonality

Fig. 3 summarises monthly records of adult and immature cuckoos in New Zealand, and shows the lag between the arrival of adults in spring-summer and the production of immatures in summer-autumn. One of the clearest findings from our study is that virtually all cuckoos in New Zealand between Oct and Dec are in adult plumage, meaning that they have returned to New Zealand as adults. Immatures are evident in New Zealand almost only between Jan and May, which means that they are mostly never more than a few months old and have fledged in the current summer. We presume that immatures undergo moult into adult plumage on the wintering ground. Our data suggest that most birds moult quickly into adult plumage during their first year

Table 4. Summary of events in the long-tailed cuckoo's annual cycle. C = common occurrence, r = rarer occurrence.

	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Migration south	r	C										
Egg-laying		r	C	C	r							
Dependent fledglings					r	C	r					
Migration north by adults					r	C	C					
Migration north by immatures							r	C	C			
Immatures in Pacific	r						C	C	C	C	r	r
Transitionals in Pacific	r							r	r	r	C	C
All birds in adult plumage	r	C	C	C								

(Gill & Hauber 2012) but whether they return to New Zealand to breed in their second summer, or cryptically remain for their second year in the Pacific (in adult plumage) is not known. Whatever the case, immature plumage is (almost) only ever seen in New Zealand in hatch-year birds. The rare immatures seen in New Zealand between Oct and Dec (Fig. 3) are likely to be early fledglings rather than migrants returning in immature plumage.

Table 4 summarises the timing of the breeding and migratory events in the cuckoo's yearly cycle, based on this paper, Gill & Hauber (2012), and summary accounts of the species by Heather & Robertson (1996) and Higgins (1999).

Total distribution

Appendix 1 summarises published accounts of the distribution and seasonality of the long-tailed cuckoo throughout its range. Fig. 4 plots the distribution of all records compiled for this study and confirms the cuckoo's fan-shaped total distributional range, first plotted by Bogert (1937). The most northerly known record is on Wake I at 19.3°N (Peale I, Jul 1939, MVZ 79443). The most westerly record is also in Micronesia, at Palau (134.5°E, before Mar 1873, spirit specimen, now lost; Finsch 1875). The eastern-most record is for Henderson I (Pitcairn Is group) at 128.3°W (based on bones; Wragg 1995). At 48.0°S, records from the Snares Is south of Stewart I, New Zealand, are the species' most southerly confirmed records (several sight-records). The arc of the cuckoo's wintering range extends 11,000 km from Palau to Henderson. Wake and the Snares lie at the same longitude and are 7,450 km apart. The distances from central New Zealand (say, Nelson) are 5,680 km to Henderson I, 6,640 km to Palau and 6,700 km to Wake I, so the outer radius of the cuckoo's fan-shaped distribution is about 6,000 km.

New Zealand distribution

Fig. 5 shows the geographic distribution of 753 records of long-tailed cuckoos in New Zealand grouped by months. Fig. 6 shows the relative proportions of these records from the North and South Is throughout the year. There is a bias towards North I records (74% of total). This may largely be because there are more observers in the North I, and this may confound any seasonal tendency the cuckoo may have to be more common in the north.

In Sep (Fig. 5A) and Oct (Fig. 5B) it is possible that long-tailed cuckoos are more numerous in the North I, and that this reflects frequent landfall in the north after migration from the Pacific wintering grounds. However, even in Sep there are already records in the far south of New Zealand. Over summer, from Nov to Feb, the cuckoo is widespread throughout New Zealand (Figs 5C–D). In Dec and Jan there is an increase in the relative numbers of South I records (Fig. 6). There are almost no immatures in Nov and Dec (2 of 45 known-age records; Fig. 5C), because even Dec is too early in the annual breeding cycle for many of the cuckoo's hosts to have fledged young parasites (Table 4). In Jan and Feb (Fig. 5D) there are few adults (18 of 47 known-age records), meaning that they have already begun to depart the country, and immatures are beginning to dominate (29 of 47 known-age records).

From Mar to May (Figs 5E–G), adults are rare, implying that most have departed, and cuckoos in New Zealand are mostly immature (young of the current season). Increasingly over these 3 months cuckoos are far more evident in the North I and the maps show a gradual retreat of cuckoos towards the north of the country, or a progressive wave of direct departures of birds from areas beginning in the south. Northland may be a pre-migratory staging area in May (Fig. 5G). North I records account for 74% of the total records of long-tailed cuckoos in New Zealand. Fig. 6 shows a surge in North I records, beyond the 74% line, in Mar, Apr and May at the time of the northward migration of immatures. The proportions (North I vs. South I) are significantly different from expected (74% in North I) in Mar ($\chi^2 = 11.74$, $n = 99$, $df = 1$, $P < 0.001$) and Apr ($\chi^2 = 8.52$, $n = 60$, $df = 1$, $P < 0.01$). All 15 May records are from the North I. Data for Jun to Aug are

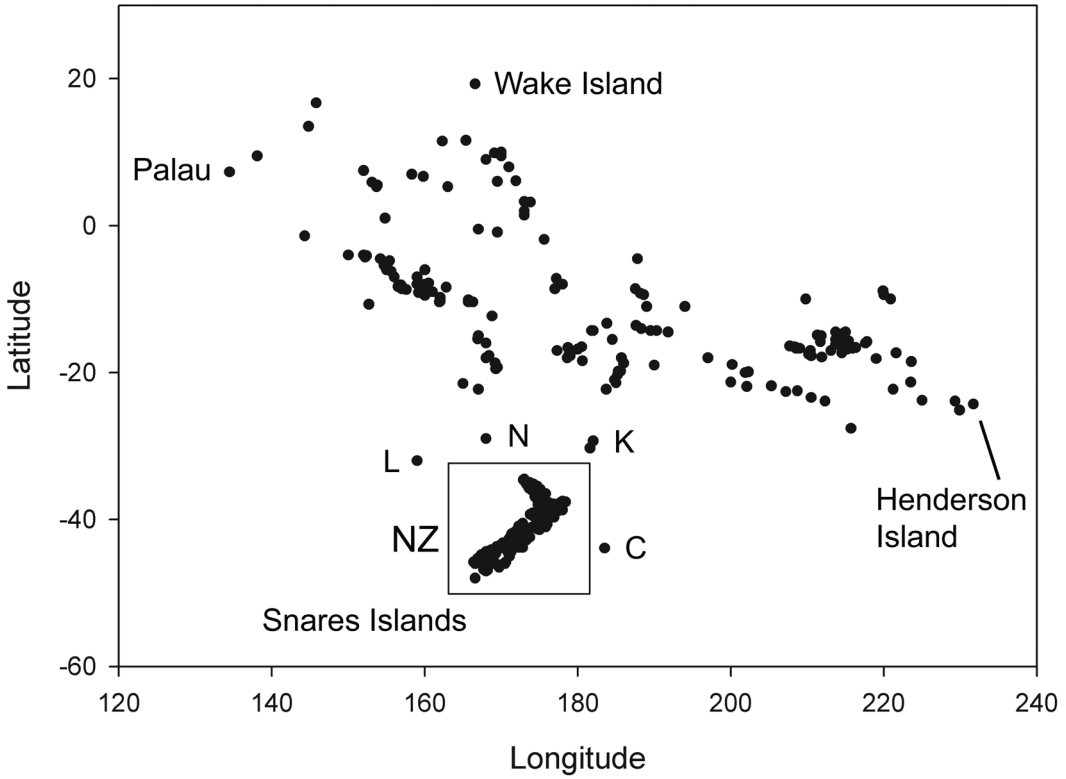

Fig. 4. Geographic distribution of all 1120 long-tailed cuckoo records in this study. The dots north of New Zealand are records of cuckoos on Pacific islands. C = Chatham Is; L = Lord Howe I; N = Norfolk I; K = Kermadec Is. The rectangle shows the area covered in Fig. 5.

unreliable (low sample sizes) since cuckoos are rare in New Zealand in winter.

Sex ratio

In our samples of sexed museum specimens there was a pattern for males to predominate, which was statistically significant in 2 cases. From the eastern Pacific (Cook Is, French Polynesia, etc.; n = 54), 74% of the sample were males (χ^2 = 12.52, df = 1, P < 0.001), whereas the corresponding figures for other Pacific regions were closer to parity (all P > 0.05): central, 56% (Tuvalu, Tokelau, Fiji, Wallis and Futuna, Samoas, Tonga, Niue, *etc.*; n = 54); northern, 60% (Caroline Is, Marshall Is, Kiribati, *etc.*; n = 20); and western 41% (Papua New Guinea, Solomon Is, Vanuatu, New Caledonia; n = 39). Adults in the Pacific generally (excluding the Kermadec, Norfolk and Lord Howe Is) were 59% male (n = 110), while immatures were 70% male (n = 20). Across all Pacific specimens (n = 167) males made up 59% (χ^2 = 5.04, df = 1, P < 0.05). In New Zealand samples, the sex ratios were closer to even (all P > 0.05): North I, 52% males (n = 93); South I, 58% (n = 33); adults, 53% (n = 73); immatures, 55% (n = 53).

DISCUSSION

Higgins (1999: 779–780) gives the most detailed description of the long-tailed cuckoo's plumage, based on examination of a large sample of museum study-skins from New Zealand (but not from the Pacific wintering grounds). The non-adult plumage (spotted above; pale brown below; here referred to as "immature"), was regarded as the juvenile by Higgins (1999) who stated that the cuckoos "fledge in juvenile plumage". No birds thought to be immatures were found among the study-skins, and it was considered unknown whether immatures were separable from adults by their plumage.

If the pale, non-adult cuckoos listed in Table 2 are indeed juveniles, then this is the plumage in which they fledge, and those with pale brown underparts are the immatures. Immatures form a large proportion of the cuckoo population observed in New Zealand in late summer and autumn. The scarcity of "juveniles?" in museum collections may testify to a short juvenile phase and a rapid transition to the immature condition by a post-juvenile moult. In the common koel (*Eudynamys scolopacea*), a "post-juvenile moult to immature (first basic) plumage"

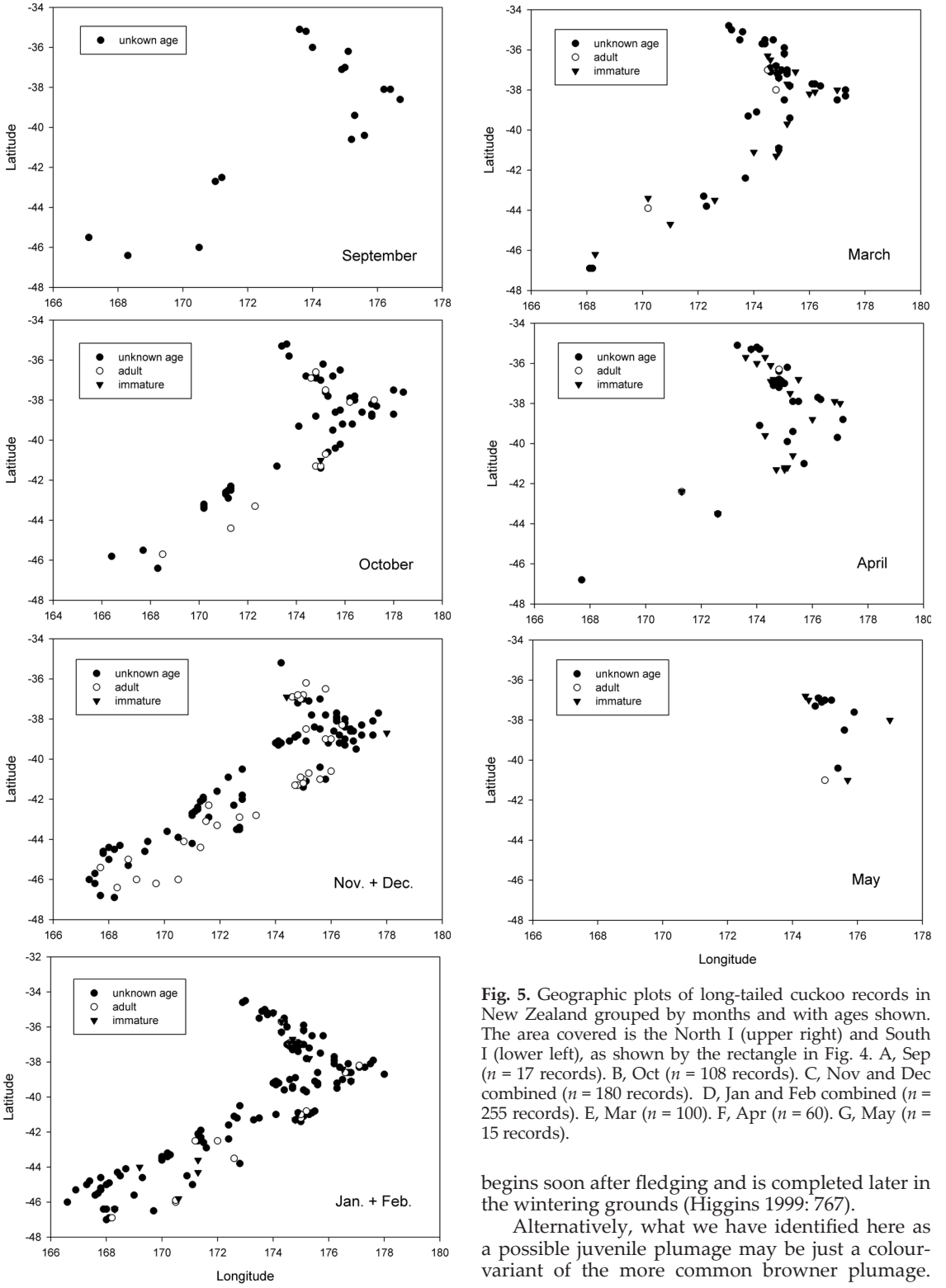

Fig. 5. Geographic plots of long-tailed cuckoo records in New Zealand grouped by months and with ages shown. The area covered is the North I (upper right) and South I (lower left), as shown by the rectangle in Fig. 4. A, Sep (n = 17 records). B, Oct (n = 108 records). C, Nov and Dec combined (n = 180 records). D, Jan and Feb combined (n = 255 records). E, Mar (n = 100). F, Apr (n = 60). G, May (n = 15 records).

begins soon after fledging and is completed later in the wintering grounds (Higgins 1999: 767).

Alternatively, what we have identified here as a possible juvenile plumage may be just a colour-variant of the more common browner plumage.

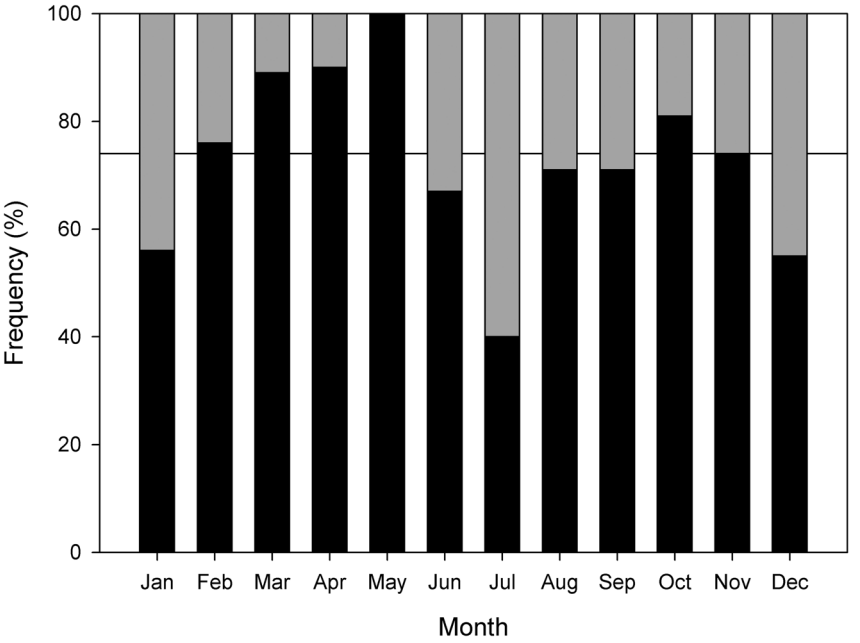

Fig. 6. New Zealand records of long-tailed cuckoos (*n* = 753) showing monthly distribution between the North I (black bars) and South I (grey bars). Some 74% of all records were from the North I and the 74% line is shown. There are fewer than 8 records in each month from Jun to Aug; for other months, *n* = 15–135.

We note that in a recent colour photograph (by T.G. Lovegrove; cover of the May 2011 issue of *Ethology*) showing a long-tailed cuckoo nestling in a whitehead nest (*Mohoua albicilla*), the section of the cuckoo's throat visible above the nest rim is pale brown and not white as in the pale forms we have described.

The long-tailed cuckoo winters in all available tropical Pacific island groups north-northeast of New Zealand (Fig. 4), with little but open ocean beyond the northern and eastern boundaries of this wintering range. The cuckoo also migrates a similar distance to Pacific islands northwest of New Zealand, but it notably avoids Australia, mainland New Guinea and the Philippines, where there could be competition from other species of cuckoos of similar size and dietary requirements (Payne 2005). Baker (1951) suggested that the long-tailed cuckoo winters on oceanic islands because there is less competition for food and habitats than would be encountered westwards in Malaysia and Melanesia. Indeed, on some more remote islands and atolls, the cuckoo is the only land-bird, albeit only a part-time resident.

Furthermore, even in the larger tropical Pacific archipelagos of the Solomon Is and Fiji, the long-tailed cuckoo is said to be mainly on smaller outer islands rather than the larger central islands (Galbraith & Galbraith 1962; Clunie 1984; Watling 2001). A resident congener, the common koel, is widespread in the Bismarck Archipelago and Solomon Is (del Hoyo *et al*. 1997; Doughty *et al*. 1999). In Fiji, the resident fan-tailed cuckoo (*Cacomantis flabelliformis*) lives mainly in forested and heavily wooded areas (Watling 2001). Long-tailed cuckoos may be competitively excluded by the presence of these resident cuckoos, and thus limited to outer islands, or it might be that long-tailed cuckoos, often difficult to observe unless calling, are simply more readily seen on smaller islands with sparser vegetation and more forest edge. Direct tagging and remote tracking (Wikelski *et al*. 2007) of the migratory flights and the wintering distribution of individual cuckoos would test these alternative explanations (*e.g.*, Ismar *et al*. 2010).

Fig. 6 shows a stronger-than-average North I bias in cuckoo records for New Zealand in Mar–May, suggesting that birds may retreat gradually to the north of the country to stage prior to the northward migration. However, there is no equivalent stronger-than-average northern bias in records for Sep and Oct at the spring influx. This suggests that cuckoos in spring may arrive directly throughout the 2 main islands of the country, or if they arrive in the north first, they rapidly move onto their breeding grounds further south. The skewed curve for the monthly distribution of adult cuckoos in New Zealand (Fig. 3) suggests a fast arrival before breeding and a more gradual departure after breeding.

In the departure of long-tailed cuckoos from New Zealand between Jan and May there is a timing lag of several months between adults (first to depart) and immatures (Fig. 3; Gill & Hauber 2012). A picture therefore emerges of a rather diffuse, unhurried northward migration, with birds of 2 age-classes migrating at separate times. Indications are of a more intense or urgent southward spring migration to New

Zealand (Sep–Oct) with birds of a single plumage-class perhaps arriving and settling over a much shorter period. It seems unlikely that the Chatham Is are a staging-post for cuckoos flying east; if this were so, they would be recorded more regularly on this island group than is the case (Appendix 1).

Among Pacific island museum specimens, we detected a statistically significant uneven sex ratio in favour of males (59%), which was particularly extreme in the eastern region (74%). Holyoak & Thibault (1984) also found that 72% of long-tailed cuckoos in their regional sample from eastern Polynesia were males. In contrast, the sex ratio in New Zealand was more even. There may be some behavioural traits or habitat factors in the Pacific that make males more liable to be collected. Direct tagging and remote monitoring of known-sex individuals will be critical to ascertain any sex differences in the migratory patterns and behavioural dynamics of the long-tailed cuckoo.

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Appendix 1. Review of the recorded distribution of long-tailed cuckoos.

Breeding grounds

New Zealand mainland

Widespread on North, South and Stewart Is in spring and summer, mainly in areas of native forest coinciding with the hosts' distributions (Higgins 1999; Robertson *et al*. 2007). In the North I the distribution matches closely that of the cuckoo's host the whitehead (*Mohoua albicilla*), but in the South I the distribution of the brown creeper (*M. novaeseelandiae*) is wider than the cuckoo's (Robertson *et al*. 2007). The most southerly records are those from the southern end of Stewart I (e.g. Robertson *et al*. 2007). Known to breed only on the New Zealand mainland (North, South and Stewart Is) and its inshore islands such as Little Barrier (McLean 1988), Kapiti (Wilkinson & Wilkinson 1952) and Codfish (Robertson *et al*. 2007).

Stragglers south and east of New Zealand

Three records from the Snares Is (48.0°S): Nov–Dec 1976, Jan 1986 and Dec 1986 (Sagar 1977; Miskelly *et al*. 2001). Reports from the Auckland Is (50.8°S) are unsubstantiated and trace back to a tabular listing with no supporting data (Travers 1883). Five records from the Chatham Is (44.0°S; 900 km east of mainland New Zealand): Mar 1946, Dec 1982, Jan 1996, Sep 2003 and Nov 2003 (Anonymous 1947; Nilsson *et al*. 1994; Miskelly *et al*. 2006). These records show that the cuckoos can overshoot the New Zealand mainland and straggle to islands further to the south and east. These islands lack host species and the cuckoos cannot breed there.

Wintering grounds

Micronesia

More numerous in the Marshall Is than in the Caroline Is to the west; no records for the Mariana Is to the north (Baker 1951). In the Carolines, it is a vagrant to Yap (1 record; Wiles 2005) but a regular migrant to Chuuk. One specimen from Wake I, north of the Marshalls. More common in the wetter islands of Tuvalu (Ellice Is) than in the drier islands of Kiribati (Gilbert Is; Child 1960). Regular visitor to Nauru (Buden 2008), and recorded at Ocean I (Banaba), Kiribati (Pearson 1962). Winter straggler to Caroline Atoll, Line Is, Kiribati (Ellis *et al*. 1990).

Melanesia

At western end of cuckoo's range there are no records for mainland New Guinea (Beehler *et al*. 1986), nor any confirmed records for mainland Australia (Higgins 1999). However, it is a rare migrant to New Britain and other islands in south-eastern Papua New Guinea (Coates 1985; Beehler *et al*. 1986). Listed as 'very rare' for Bougainville and Buka (North Solomons Province of PNG; Hadden 1981); seen in 2001 on Nissan Atoll, North Solomons Province (Hadden 2004). Widespread winter visitor to Solomon Is, but mainly on smaller outer islands (Galbraith & Galbraith 1962; Doughty *et al*. 1999), such as the atoll Ontong Java (Bayliss-Smith 1972). Common migrant on the Three Sisters off San Cristobal (French 1957). Not recorded on New Georgia by Blaber (1990), nor on Santa Isabel by Webb (1992).

A 'rather rare' visitor to Vanuatu, mainly Apr to Sep, with no records from the Banks Is at the north of the archipelago (Bregulla 1992). Layard & Layard (1882: 523) stated that the cuckoo was very rare in New Caledonia, but 2 of 4 obtained from street-vendors in Nouméa in Mar and Apr 1879–1881 'exhibited nestling-plumes'. They thought the cuckoos were probably 'migrants visiting us for breeding-purposes about Christmas'. These observations and conclusions seem dubious and the modern view is that the cuckoo is an occasional migrant on passage in New Caledonia between May and Sep (Delacour 1966; Hannecart & Létocart 1983). In Fiji, more frequently encountered on smaller islands; seems to avoid larger ones (Watling 2001).

Western Polynesia

In Western Polynesia (and Fiji) most arrive in Apr and depart in Sep or Oct; some remain through to Dec and fewer all year (Watling 2001). Regular migrant to Wallis and Futuna, especially from Jun to Sep (Guyot & Thibault 1987). Apparently a regular migrant to the Tokelau Is (Thompson & Hackman 1968). In American Samoa an 'uncommon year-round visitor, reported from all islands' (Amerson *et al*. 1982). Clapp (1968) reported the cuckoo on isolated Swains I (north of the Samoas) at each of his brief visits in Feb, Aug, Oct and Nov 1966 and in Apr 1967. Fewest birds were seen in late Nov, but around 15 were seen in Oct. Small numbers regularly visit Niue in winter (Kinsky & Yaldwyn 1981); Powlesland *et al*. (2000) recorded them in Sep and Dec.

Eastern Polynesia

Observed all year in eastern Polynesia, but most common from Mar to Aug (Holyoak & Thibault 1984). Recorded from most of the Cook Is; commonest from Mar to Aug but also seen in other months (Holyoak 1980). In French Polynesia widespread but in low numbers; most numerous in the Society, Austral and Tuamotu groups; little recorded in the Marquesas Is (Holyoak & Thibault 1984). In Tahiti 'present throughout the year, but most common from June to September' (Thibault & Rives 1975). In the Pitcairn I there are second-hand reports on Pitcairn itself (Williams 1960), records of bones from Henderson I (Wragg 1995) and sightings from Oeno I (Brooke 1995). Not recorded from the Line Is and Easter I (Holyoak & Thibault 1984).

Middle latitudes

Lord Howe I

Rare with just 5 reports, only 3 of them with times of year: 'spring' 1905, Jan–Feb 1967 and Feb 1989 (McAllan *et al*. 2004).

Norfolk I

First recorded in the early 1800s and considered to have declined since settlement (Schodde *et al*. 1983). A few recorded Dec 1978 (Schodde *et al*. 1983). Since then, recorded Dec 1991, Apr 1994, and repeatedly between Sep 1996 and Jan 1997 (Higgins 1999; Moore 1999).

Kermadec Is

Recorded throughout the year (Veitch *et al*. 2004). Iredale (1913) spent nearly a year on Raoul I, noting the bird in every month (except perhaps Dec) and finding it most numerous in Oct. Sorensen (1964) saw cuckoos in most of the winter months of 1944. The 'Bird Sightings' book at the Department of Conservation field station on Raoul I recorded cuckoos in Jan, Feb, Apr, May, Sep–Dec for 2002–10 (I. Thorne, *pers. comm*., to BJG, 31 May 2010). Suggestions of breeding on the Kermadec Is are discussed and dismissed by Gill & Hauber (2012).