

BREEDING HABITS OF THE GREY WARBLER (*Gerygone igata*)

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ABSTRACT

Grey Warblers at Kowhai Bush, Kaikoura, apparently moulted once annually — between January and March. They nested in 19 kinds of trees and shrubs — mostly small-leaved species, especially kanuka, the dominant plant in the study area. Behaviour associated with selection of the nest site is described. A list of materials used in building is given. On average, nests were 14 cm long and just over 7 cm wide. Nearly half the nests hung freely from their upper attachment; others also had attachments laterally and below. The entrances of nests were non-randomly orientated in 1976 but not so as to face away from prevailing winds. Copulation is described. Three eggs in September were laid close to sunrise. Late eggs were wider on average than early ones but no different in length. The constant that related fresh weight of eggs, length, and the square of width was 0.598. Eggs lost about a quarter of their weight during incubation. Grey Warblers hatched with natal down distributed in eight main and two minor patches. The physical and behavioural development of nestlings is described. A sample of 19 nestlings had been fed invertebrates of six orders. Caterpillars occurred in 90% of stomachs and made up 42% of ingested items. Spiders were next most important of total items. Nestlings were parasitised by the blood-sucking mite *Ornithonyssus bursa*. Fledglings had distinctive dark brown irides and yellowish facial plumage until February-March, when they moulted to adult form. Males played the greater role in caring for early fledglings while the female built the late nest. Young males seemed rarely to be successful in holding territory the summer after that in which they were reared. Brood parasitism by Shining Cuckoos was the main cause of failure of late eggs (though a relatively minor factor overall); mammalian predation was the greatest single cause of nestling mortality.

INTRODUCTION

For three seasons beginning 1976-77 I studied the breeding of Grey Warblers (*Gerygone igata*, Muscicapidae: Acanthizinae) in a 30-ha study area at Kowhai Bush, Kaikoura. Elsewhere, I have described the study area (Gill 1980), the brood parasitism of warblers by the Shining Cuckoo (*Chrysococcyx lucidus*) (Gill 1982c and in press) and many aspects of the warbler's breeding (Gill 1982a). In this paper I report some of the more descriptive parts of the study — in particular the morphology of nests and the natal pterylography and development

of nestlings — and I compare the two intensively studied seasons (1976-77 and 1977-78).

By "early" nests, eggs and nestlings, I mean those associated with a clutch started before 23 October. By "late" eggs, I mean those laid on or after 23 October, when the first second clutch in my sample (after the fledging of earlier nestlings) was started. I use the word "fledge" to mean "leave the nest."

METHODS

Identifying the sexes

Male and female Grey Warblers look alike but are distinguishable by behaviour. Only adult males give the full song, whereas females and independent juveniles at most give occasional tuneful subsongs. Males sing all year, although the intensity varies (Cunningham 1955). Males also have a distinctive wing-fluttering display in which they vigorously flap their half-outstretched wings while advancing along a perch. The display occurs at all stages of breeding, mainly in the female's presence. Very rarely females wing-flutter, and so wing-fluttering is not completely diagnostic of males.

Only females collect material and build nests, but males often accompany their mate to and from the nest. Only females incubate eggs and brood nestlings, but both sexes feed the young. Thus, any bird entering the nest, as opposed to merely perching at its entrance, is a female.

Catching adults

I caught adult warblers in small mist-nets (5.5 m long, 2.1 m high) hung between two wooden poles (2 cm in diameter). The poles were held upright in short sections of square iron pipe driven part-way into the ground, and a single guy-rope from the top of one pole was enough to keep the net taut. Nets of about 32-mm mesh (measured knot-to-knot with the netting stretched diagonally) are needed. Warblers can pass through 38-mm mesh.

I lured warblers into nets with recordings of their song. It was advantageous to use twin extension speakers set one on either side of a net and connected by a two-way switch so that the sound could be changed from one speaker to the other. Warblers in an area quickly became accustomed to a tape-recording, and so I changed tapes regularly.

During the breeding season I caught 15 incubating females on their nests by means of a fine hair-net mounted on a wire loop at the end of a stick. The nest had to be approachable from below or behind, and such that the net could be gradually advanced towards it and suddenly pushed over the entrance without catching on twigs. I caught birds only after they had been incubating at least 5 days and released them immediately after banding. None deserted.

Finding nests

The surest way to find a nest was to follow a building female. At intervals, she would break off from foraging to collect material, and once she had a load, would fly directly to the nest, usually with the male close behind. Early nests were easiest to find because they were built slowly, and for a long period early in the season most females were building, accompanied by the vocal and thus easily located male. However, the female does not regularly visit the nest for up to 8 days after she has completed building and during the 7 days needed to lay the clutch of four.

To find nests during incubation, I located the male by his song and followed him until he was joined by his mate after her spell on the nest. However, at this stage she would return to the nest cautiously and indirectly. For the same reason, parents were hard to follow back to the nest when they were collecting food for nestlings.

Late nests were hard to find because breeding was then out of phase, with not all pairs building at a given time, and nests were built quickly with little delay before laying. Also, females were hard to locate late in the season if there were fledglings of a previous brood. The male usually attended these, and so the female built unaccompanied by the vocal male.

Handling eggs and nestlings

I counted eggs by inserting one or two fingers through the nest's entrance, slight enlargement of which did not cause desertion. It was generally too risky to remove eggs for examination, as they are so fragile, but safe removal was possible at low nests with wide entrances. I marked eggs (for later recognition) with an alcohol-based felt-tipped pen. Occasionally I accidentally broke or cracked an egg but only once was this the likely cause of a deserted clutch.

To examine nestlings I removed them by inserting two fingers through the entrance. For broods of four I removed the nestlings in pairs and stood well away so that the parents could feed those left in the nest. I kept one nestling warm in a breast pocket while handling the other.

At the first visit after they hatched I marked nestlings with bright red nail varnish on the toes of one or both feet, leaving the last hatchling unmarked. This identified individuals in a brood until banding at 13-15 days old. The varnish had to be re-applied every 3-4 days, but it lasted well on the claws of older nestlings. Warblers did not fledge prematurely if carefully handled.

No nests at which I handled young were deserted on my account so far as I was aware. One female at a low nest was so tame that I could remove small nestlings from beneath her and replace them, while she continued to brood. Once, when a nest with feathered

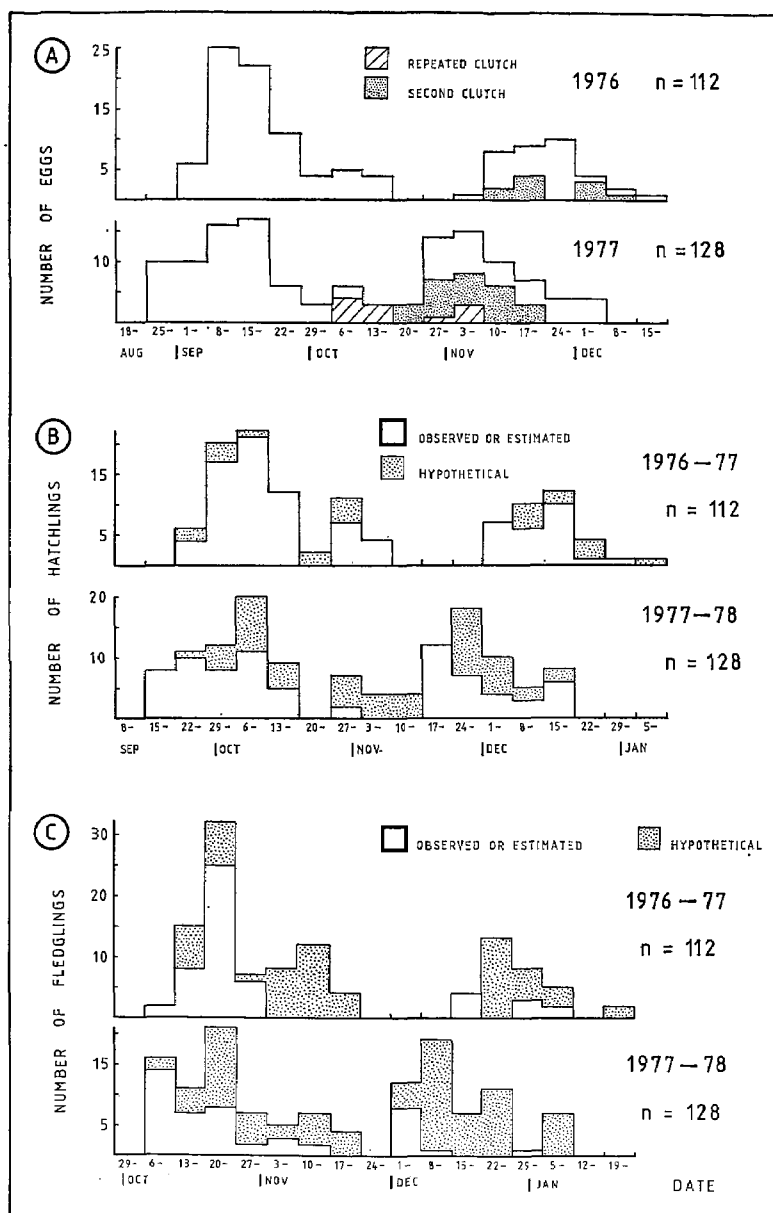


FIGURE 1 — Dates (grouped by week) of (A) laying, (B) hatching and (C) fledging of Grey Warblers at Kowhai Bush

young came away from its attachment, I wired it to a new position 30-40 cm away and the parents continued to feed the nestlings.

BREEDING SEASON AND MOULT

Figure 1 shows for 1976-77 and 1977-78 the distribution of dates of laying (Fig. 1A), hatching (Fig. 1B) and fledging (Fig. 1C) of individual eggs, hatchlings and fledglings at Kowhai Bush. The data are grouped by weeks beginning 18-24 August. Some dates of laying, hatching and fledging were not determined accurately in the field and so were estimated from other known dates. To counteract the effect of mortality in reducing sample sizes, "hypothetical" dates of hatching and fledging were calculated for eggs which did not hatch and young which did not fledge.

All first nests, and most second attempts at building after an unsuccessful first nest, were completed by mid-October. New nests for true second clutches (following the fledging of at least one nestling from the earlier brood) were started from mid-October to November. The earliest and latest eggs in my sample were laid on 25 August 1977 and c. 17 December 1976, the earliest and latest nestlings hatched on 20 September 1977 and c. 6 January 1977 and the earliest and latest nestlings fledged on 8 October 1977 and c. 22 January 1977. Repeated clutches after loss of a first, and true second clutches, are shown in Fig. 1A when known. The earliest egg of a true second clutch was laid on 23 October 1977.

Figure 1 suggests that warblers bred earlier in 1977 than in 1976. My greater experience in finding nests in the second year may have biased results, but information from banded birds supports the trend. Table 1 gives dates of completion of clutches in the two years by pairs with at least one partner banded. In all five cases laying was earlier in 1977, by 7-20 days. Snow, which is rare on the Kaikoura Plain, fell at Kowhai Bush during a four-day southerly storm in late

TABLE 1 — Dates of clutch-completion at Kowhai Bush for banded Grey Warblers (H, B, 9, 13 and 2) in two years. U = unbanded bird; * = late clutches — all others early

Male	Female	Date		Difference (days)
		1976	1977	
U	9	19 Sep	12 Sep	7
H	U	27 Sep	14 Sep	13
U	13	16 Sep	5 Sep	11
B	2	17 Sep	31 Aug	17
B	2	9 Dec*	19 Nov*	20

June 1976. The cold winter and cool wet spring of 1976 may have delayed breeding that year.

Grey Warblers at Kowhai Bush apparently moulted only once annually, after breeding. Both rectrices and body plumage were moulted from January, and by March most birds had complete unworn tails. In early January a male was moulting 30 days after his brood had fledged, and in late January a female was moulting while her mate was still feeding their single young, which had fledged 18 days before. In mid-January I saw three separate non-moulting adults attending fledgling Shining Cuckoos, while elsewhere a male was moulting whose cuckoo had fledged 24 days before.

NESTS

Selection of the site

Occasionally I saw behaviour at Kowhai Bush which I assumed to be associated with selection of the Grey Warbler's nest site. The female, constantly twittering, flew excitedly in wide circles with the male close by. Then she collected nesting material and flew to a twig, closely followed by the male who perched 10-20 cm away. The female leaned backwards and held an almost hanging position for 4-5 seconds with head and body vertically aligned, tail spread and wings outstretched. The male did likewise while the female, still hanging, wound material around the twig with her bill and resumed a normal perching position. After the male perched normally again he sang and both departed, often repeating the sequence after a few minutes.

Sometimes I later found a nest in the shrub at which this behaviour took place, but indecision in siting nests also occurred. In three instances a pair began building at one site but began again a few days later 30, 36 and 52 m away.

Spreading of the wings and tail, as here described, was a common display at all stages of the nesting cycle, perhaps to reinforce the pair bond and synchronise the pair's activities.

Plants used

At Kowhai Bush Grey Warblers nested in 19 kinds of trees and shrubs (Table 2), all but five of them natives. Most nests (69%, $n = 129$) were in plants with leaves < 2 cm long, especially kanuka (33%), the physiognomic and numerical dominant at Kowhai Bush. Three small-leaved exotic legumes (Montpellier broom, broom and gorse) accounted for another 26% of nests. Small-leaved species were favoured for nesting probably because attachment was easier and camouflage better where branching was dense, and because spines (gorse) and needle-leaves (*Leptospermum* and mingimingi) deterred predators.

Grey Warbler nests reported to the OSNZ Nest Record Scheme from throughout New Zealand were in plants of at least 40 species (16 exotic). Of 130 nests recorded, 35% were in manuka, 11% in

TABLE 2 — Trees and shrubs that Grey Warblers nested in at Kowhai Bush; n = 129; * = exotic species

	Frequency (%)
Leaves > 4 cm long	17.8
Karamu <u>Coprosma robusta</u>	5.4
Tutu <u>Coriaria arborea</u>	0.8
Akeake <u>Dodonaea viscosa</u>	6.2
Mahoe <u>Melicytus ramiflorus</u>	2.3
Akiraho <u>Olearia paniculata</u>	2.3
Tarata <u>Pittosporum eugenioides</u>	0.8
Leaves 2-4cm long	13.2
Putaputaweta <u>Carpodetus serratus</u>	1.6
* Traveller's Joy <u>Clematis vitalba</u>	1.6
<u>Coprosma propinqua</u> x <u>robusta</u>	1.6
Kohuhu <u>Pittosporum tenuifolium</u>	7.6
* Sweet Brier <u>Rosa rubiginosa</u>	0.8
Leaves < 2 cm long	69.0
<u>Coprosma propinqua</u>	3.9
Mingimingi <u>Cyathodes fasciculata</u>	1.6
* Montpellier Broom <u>Cytisus monspessulanus</u>	10.1
* Broom <u>C. scoparius</u>	4.7
<u>Helichrysum aggregatum</u>	2.3
Kanuka <u>Leptospermum ericoides</u>	32.5
Manuka <u>L. scoparium</u>	2.3
* Gorse <u>Ulex europaeus</u>	11.6

gorse, 5% in matagouri (*Discaria toumatou*) and 7% in species of *Coprosma*. The average height above ground of these nests was 2.7 m ($n = 135$, s.d. 2.80, range 0.3-21.3 m), compared with 3.2 m ($n = 103$, s.d. 1.93, range 0.7-9.0 m) for all nests found at Kowhai Bush (Gill 1982a).

Dimensions, form and attachment

I measured the dimensions (Fig. 2) of a sample of nests at Kowhai Bush to the nearest 0.5 cm. The results (Table 3) show that entrances were just under 3 cm in diameter. The deepest entrance (6.0 cm) was also one of the widest (3.5 cm), and the smallest was 2.0 x 2.0 cm. The outside depth of an exceptionally low-slung nest

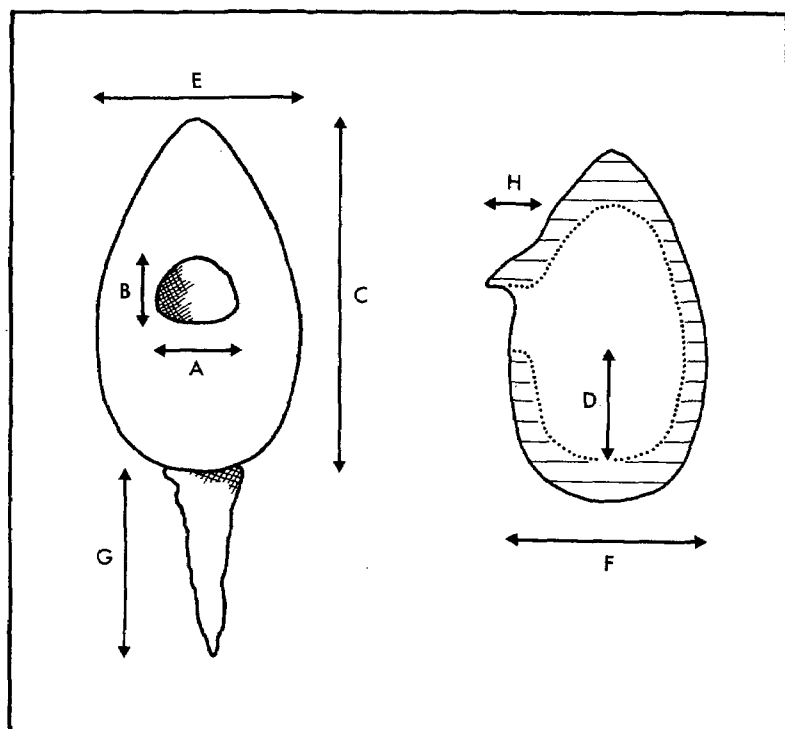


FIGURE 2 — Dimensions of Grey Warbler nests: (A) width of entrance, (B) depth of entrance, (C) outside depth, (D) inside depth below entrance, (E) outside frontal diameter, (F) outside lateral diameter, (G) length of "beard," (H) length of hood

was 21.0 cm. Lengths of "beard" (or "tail") and of hood varied greatly and usually had to be measured approximately because the base of the hood often merged imperceptibly with the body and the beard was sometimes extended by one twig or straw to a misleading length.

Nearly every nest at Kowhai Bush (94% of 92 nests) was attached to living vegetation, and the exceptions, although attached to dead twigs, were often surrounded by live foliage from adjacent branches. All nests ($n = 88$) had an upper attachment beneath which they were slung, and 46% were truly pensile in having no, or negligible, other connections. However, 41% of nests had significant lateral attachments and 28% were secured below. Considered another way, of the 88 nests, 25% had lateral attachments but none below, 13% were attached below but not laterally, and 16% had both attachments.

TABLE 3 — Measurements (cm) of Grey Warbler nests at Kowhai Bush; see Fig 2

	Mean	n	s.d.	Range
(A) Width of entrance	2.9	61	0.33	2.0-3.5
(B) Depth of entrance	2.8	61	0.68	2.0-6.0
(C) Outside depth	14.0	58	1.65	10.0-16.5 (21.0)
(D) Inside depth below entrance	4.0	27	1.08	2.0-6.0
(E) Outside frontal diameter	7.2	56	0.72	5.5-8.5
(F) Outside lateral diameter	7.5	55	0.81	6.0-9.0
(G) Length of beard	6.6	35	3.85	2.0-19.0
(H) Length of hood	2.9	49	0.87	1.5-4.5

In general, nests either hung more or less freely, or were secured in a matrix of surrounding twigs.

"Beards" were present on 63% of nests ($n = 89$). They either hung freely, perhaps helping to make the nests cryptic, or were involved in attachment. A hood was a feature of 94% of nests ($n = 88$), and in 14% ($n = 81$) a sort of threshold (Andersen 1926: 49) or ledge extended from the lower rim of the entrance.

Figures 3 and 4 illustrate a range of nests from Kowhai Bush. In Fig. 3, nests a, b, g and h were truly pensile, whereas c, from the crown of a kanuka, was securely stayed by the beard. Nests d, e and f had many lateral attachments and were built in thickets of leaves and twigs.

Direction of entrance

According to Maori folklore, Grey Warblers direct the entrances of their nests opposite to the direction of prevailing winds (Andersen 1926). At Kowhai Bush I noted the orientation of entrances and compared this with wind roses for the Kaikoura Peninsula (Figure 5). I used the frequency of winds of force 4 (Beaufort Scale) or stronger recorded at 0900 h for the four months during which warblers built (August-November; data from Kaikoura Meteorological Office, Ministry of Transport).

Directions of entrances were significantly different from random in 1976-77 (chi-squared = 28.35 for 7 d.f.; $P < 0.001$) and for the two seasons combined (chi-squared = 31.80 for 2 d.f.; $P < 0.001$). However, direction did not differ significantly from random in 1977-78 (chi-squared test; $P > 0.1$). To see if the frequencies of orientation of entrances varied in proportion to the frequencies of winds from the opposite direction, I had to group E-SE-S in 1976-77 and 1977-78, SE-S in both seasons combined and SW-W-NW in every case. Results for 1976-77 (chi-squared = 16.01 for 3 d.f.; $P < 0.005$), 1977-78 (chi-squared = 13.85 for 3 d.f.; $P < 0.005$) and seasons combined

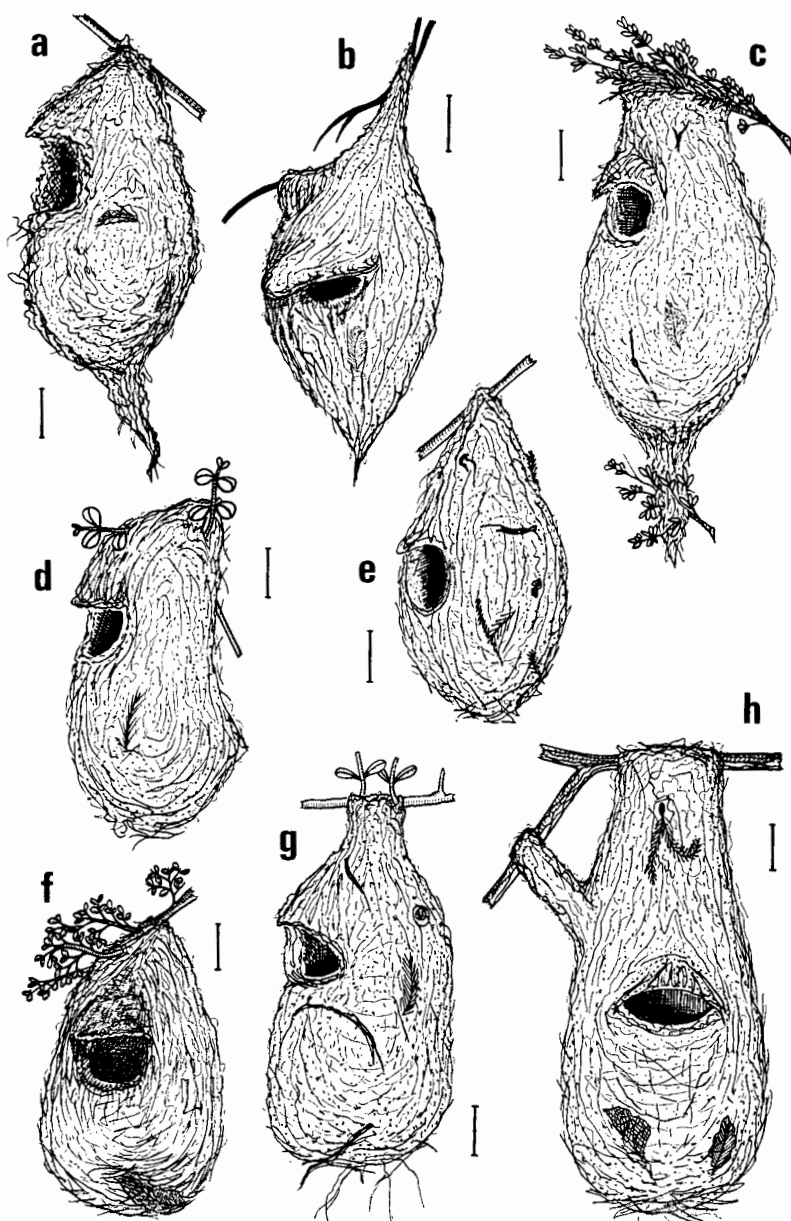


FIGURE 3 — Nests from Kowhai Bush; scale line = 2 cm

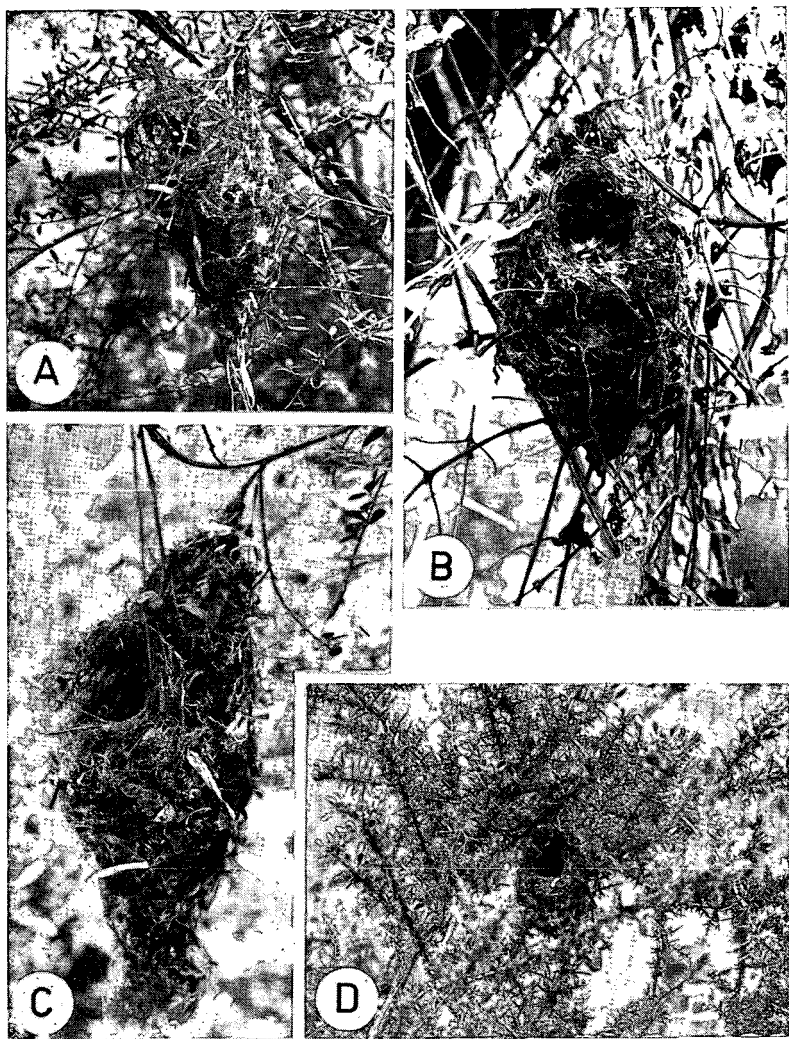


FIGURE 4 — Nests from Kowhai Bush. (A) Pensile nest with prominent hood (in *Coprosma propinqua*; 2 m above ground). (B) Semi-pensile nest (*Clematis vitalba*; 3.5 m) containing four nestlings (8-9 days old; two visible at entrance). (C) Precariously attached pensile nest (*Cytisus monspessulanus*; 1.5 m). (D) Pensile nest without "beard" (*Ulex europaeus*; 1 m)

(chi-squared = 124.58 for 4 d.f.; $P < 0.001$) show that there was always a significant difference between observed orientations of nests and orientations expected from the occurrence of winds.

Thus, although warbler nests were often non-randomly orientated, there was no correlation with winds from the opposite direction. Responses to direction of sunlight may have been involved, but there was no obvious trend (Fig. 5). Alternatively, orientation may have been to aspects of the nest site, rather than to any gross environmental factor.

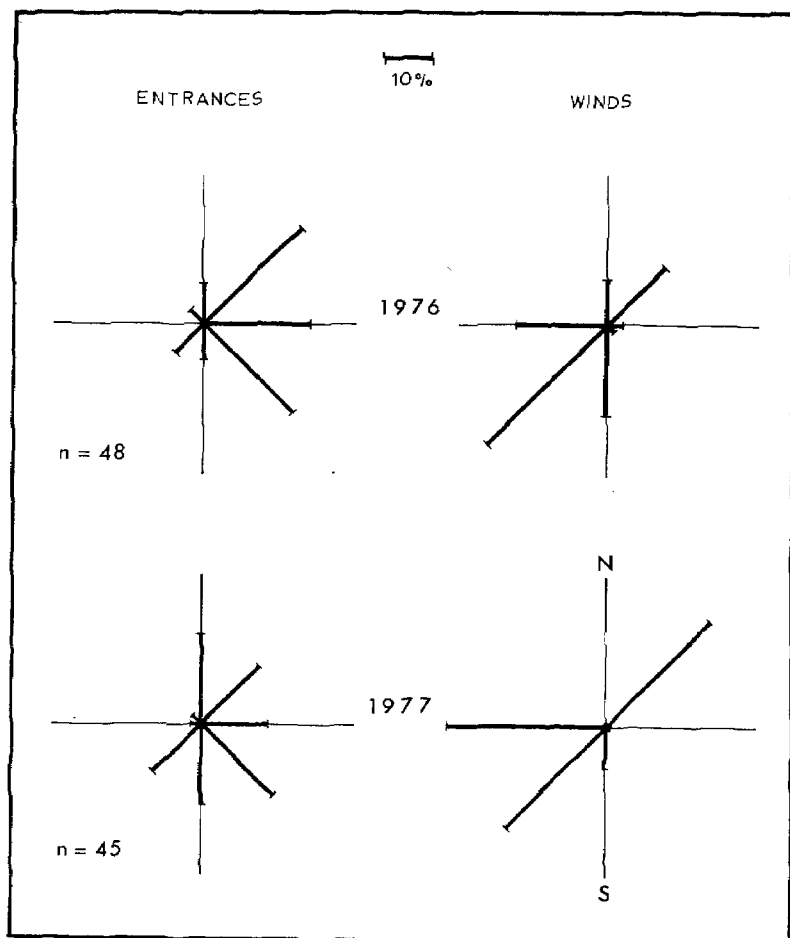


FIGURE 5 — Directions which nest entrances faced at Kowhai Bush, and from which winds blew on the Kaikoura Peninsula

Composition

The nest's exterior, including points of attachment, was a dark brown-grey-green fabric comprising a framework of stout material (rootlets and grass stems) filled out with fine matter (e.g. moss and sheep's wool) intimately bound together with cobwebs. Many nests at Kowhai Bush simply had an outer shell of this material and a lining, whereas others had an intermediate layer of wool or *Clematis* seeds. I dissected two nests (after removing the lining) but was left with residues (10% and 36% by weight) of intimately bound cobwebs, moss and other fine matter that I could not separate further. Otherwise the nests comprised roughly equal amounts by weight of moss, rootlets or grass stems, and spiders' webbing or egg cases.

The composition of nests depends partly on what materials are available. Nests at the edge of Kowhai Bush near farmland, for example, contained large amounts of sheep's wool. Moss and *Leptospermum* bark were found everywhere at Kowhai Bush, and both adorned the exterior of most nests. The following list of the nesting materials of Grey Warblers was compiled from the present study and from about 50 cards of the Nest Record Scheme:

Moss; cobwebs and spiders' egg cases; lichen; sheep's wool; hair of horses, cows, deer and humans; feathers; leaves, pine needles and leaf skeletons; scales and fibres from ferns; twigs; bark; rootlets; thistledown and willow catkins; decayed wood; scraps of paper; fine creepers.

Nests are lined with feathers (one at Kowhai Bush had 255), downy seeds and tree-fern scales.

Similarity of nests of a pair

At Kowhai Bush, a late nest was often strikingly similar in form to the same pair's earlier nest, and I considered this for up to 22 pairs of nests. The degree to which nests were pensile was the same in 9 of 14 pairs; presence of a hood was consistent in all of 13 pairs and of a ledge in 8 of 10 pairs; direction of entrance was the same in 13 of 15 pairs (adjacent eighths of the compass considered equal); and outside depth was identical to within 1 cm in 6 of 7 pairs. However, as many pairs of nests were consistent in the presence of a "beard" as were inconsistent ($n = 12$), and the nests of only 8 of 22 pairs were in the same species of tree. Sixteen of 22 late nests were lower than their earlier counterpart; 13 of 17 were in shorter trees; 10 of 17 were lower in relation to tree height; and 14 of 17 were lower relative to canopy height. This trend towards late nests being low was general for Grey Warblers at Kowhai Bush (Gill 1982a).

EGGS

Copulation

Six times (between late October and mid-December) I saw Grey Warblers copulate. I saw one pair copulate 14 days before

the first egg was laid. Another pair copulated on about the same day that they produced the first egg (nest undiscovered at the time) and another on about the day that they laid the third egg of four. One instance of copulation (apparently fruitless) preceded moulting in the male by only a month.

Mounting lasted less than 10 seconds but was usually repeated, the male alternately balancing on the female's back by constantly fluttering his wings, and perching beside her. The female displaced her tail to the left (two instances) for cloacal contact, and sometimes held nesting material or food in her bill. A harsh chattering was given, at least on one occasion by the female. Birds copulated on the ground or on perches, some nearly vertical.

Time of laying

In September 1977 I determined for three eggs in two early clutches the times at which they were laid. All were laid within an hour of first light (c. 0600 h), probably, in two cases, a few minutes after sunrise (0640 h). In the best-documented example (12 September), the unbanded female entered the nest (containing two eggs) 36 minutes after first light, followed to the entrance by ♂-H, which had been singing repeatedly nearby. After 9 minutes (at 0645 h) the female reared up and held this position for 1.5 minutes, except for a brief lowering at 0646 h. This period was presumably the actual moment of laying, at which time birds typically raise the body (Welty 1975). The male sang but also gave short down-slurred calls. The female stayed in the nest for 7.5 minutes more, fidgeting occasionally, and then flew off at 0654 h after ♂-H sang. She had spent 18 minutes in the nest, which then contained three eggs.

Two mornings later the female was on the same nest when I inspected it only 14 minutes after first light. I flushed her to be sure there were only three eggs. She re-entered after 15 minutes (at 0629 h), and 25.5 minutes later, she reared up in the nest, peering from side to side with her head extended through the entrance. This lasted a minute and was followed by 9 minutes more in the nest. The male sang as close as 1 m from the nest, but for much of the time he was elsewhere driving an intruding warbler from the territory. When the female departed at 0704.5 h (after 35.5 minutes in the nest) there were four eggs.

In the third case (12 September), at a neighbouring nest, I flushed ♀-9 from three eggs at 0618 h. When I inspected the nest 48 minutes later the female was off but the clutch was complete (four eggs). Grey Warblers may not always lay at sunrise. Card 6435 of the Nest Record Scheme reports the laying of a fourth and final egg between 0800 h and 1600 h on 30 November 1967.

Morphology

The Grey Warbler's egg is white with reddish-brown speckles. The speckling varied, both within and between clutches, from almost

none to intensive, and the blotches ranged from minute to about 1.5 mm wide. Figure 6 shows large-speckled and finely speckled eggs from two different clutches. Speckles were usually concentrated into a dense band at the egg's larger end, but a few eggs were nearly uniformly speckled. Early writers reported pure white eggs, attributed to young birds (Potts 1869) or to a possibly separate species (Buller 1870), but they are not mentioned in recent literature and I found none.

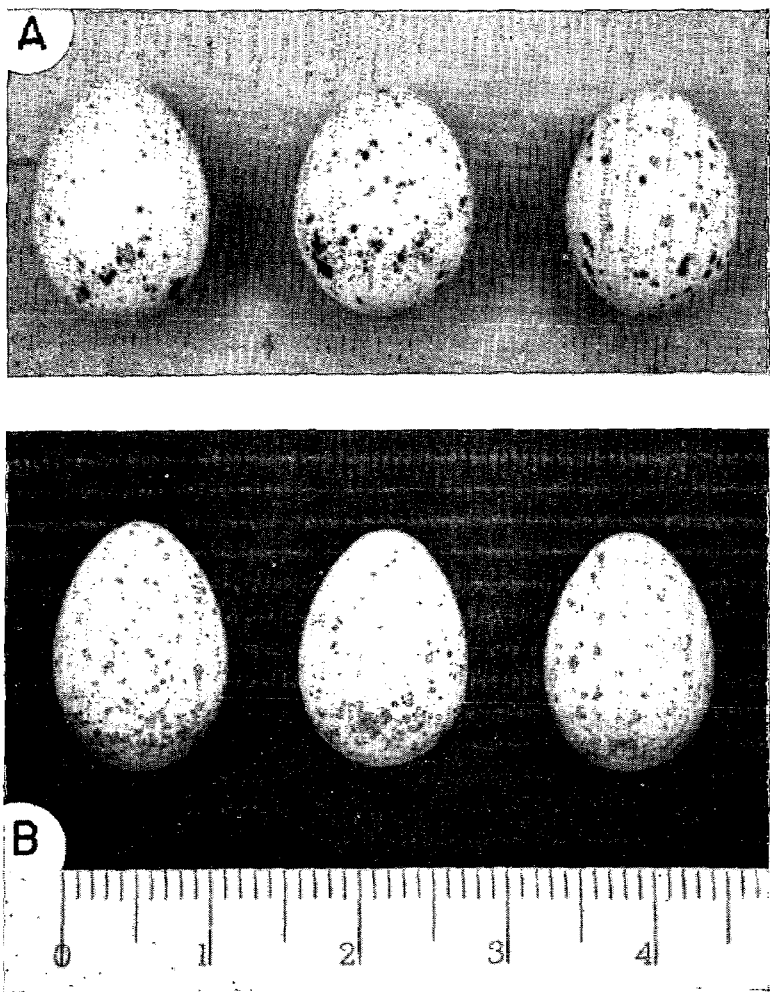


FIGURE 6 — Eggs from two Grey Warbler clutches showing variation in pattern; scale in mm. In (A) the angle of view is slightly oblique, favouring the larger end.

The shell was translucent and slightly pink in the fresh egg but became chalky-white and opaque with incubation.

The longest egg I measured at Kowhai Bush was nearly the narrowest (18.8 x 11.4 mm), and the shortest was nearly the widest (15.8 x 12.8 mm), but there was no statistical correlation between length and width ($r^2 = 0.01$, $n = 35$). On average, eggs of early clutches were 16.95 mm long ($n = 16$, s.d. 0.638), compared with 17.21 mm ($n = 15$, s.d. 0.895) for late eggs, the difference being not significant (t-test). However, the difference in width between early eggs (mean = 11.96 mm, $n = 17$, s.d. 0.381) and late eggs (mean = 12.23 mm, $n = 15$, s.d. 0.362) was highly significant ($t = 5.50$ for 30 d.f.; $P < 0.001$). By contrast, early eggs of the Robin (*Petroica australis*) at Kowhai Bush were longer than later ones, but widths were similar (R. Powlesland, pers. comm.).

The weight (W), length (L) and width (B) of avian eggs are related by the expression $W = kLB^2$. Average values for Grey Warblers at Kowhai Bush were: fresh weight 1.49 g, length 1.708 cm and width 1.208 cm. Therefore $k = 0.598$. This is close to the value ($k = 0.546$) that Romanoff & Romanoff (1949) gave for 14 altricial species. The mean weight of seven warbler eggs on the day before hatching was 1.13 g (s.d. 0.04, range 1.10-1.20 g), showing an average loss during incubation of 0.36 g or 24% of fresh weight.

NESTLINGS

Natal pterylography

The young of some passerines are naked at hatching, but many sport a natal down, especially on dorsal surfaces. The down feathers (neossophtiles) are pushed from their follicles by the ensheathed teleoptiles ("pin feathers") that develop later, and to which the down remains attached until the juvenile feathers unfold (Pettingill 1970). Not all teleoptiles are preceded by neossophtiles. Therefore, the tufts and rows of down feathers only roughly match the arrangement of pterylae, and separate naming is required. I followed the nomenclature of down-patches used by Saunders (1956) for North American passerines.

The natal down of Grey Warblers occurred in eight main patches: ocular, coronal and occipital patches on the head; dorsal, humeral, femoral and abdominal patches on the body; and secondary patches on the wings (Figure 7). Occipital and dorsal patches were median; all others were bilaterally paired. In addition to the above patches, 10% of nestlings had a minute tuft (on one or both thighs) of crural down, and nearly 80% ($n = 45$) had single or multiple tufts of down to one or both sides of the throat. This throat patch was not noted by Saunders and I called it the jugular patch. It occurs also in Willie Wagtails (*Rhipidura leucophrys*) in Australia (Gill 1982b). Crural and jugular down was insignificant and variable in Grey Warblers, and I overlooked it during the first breeding season.

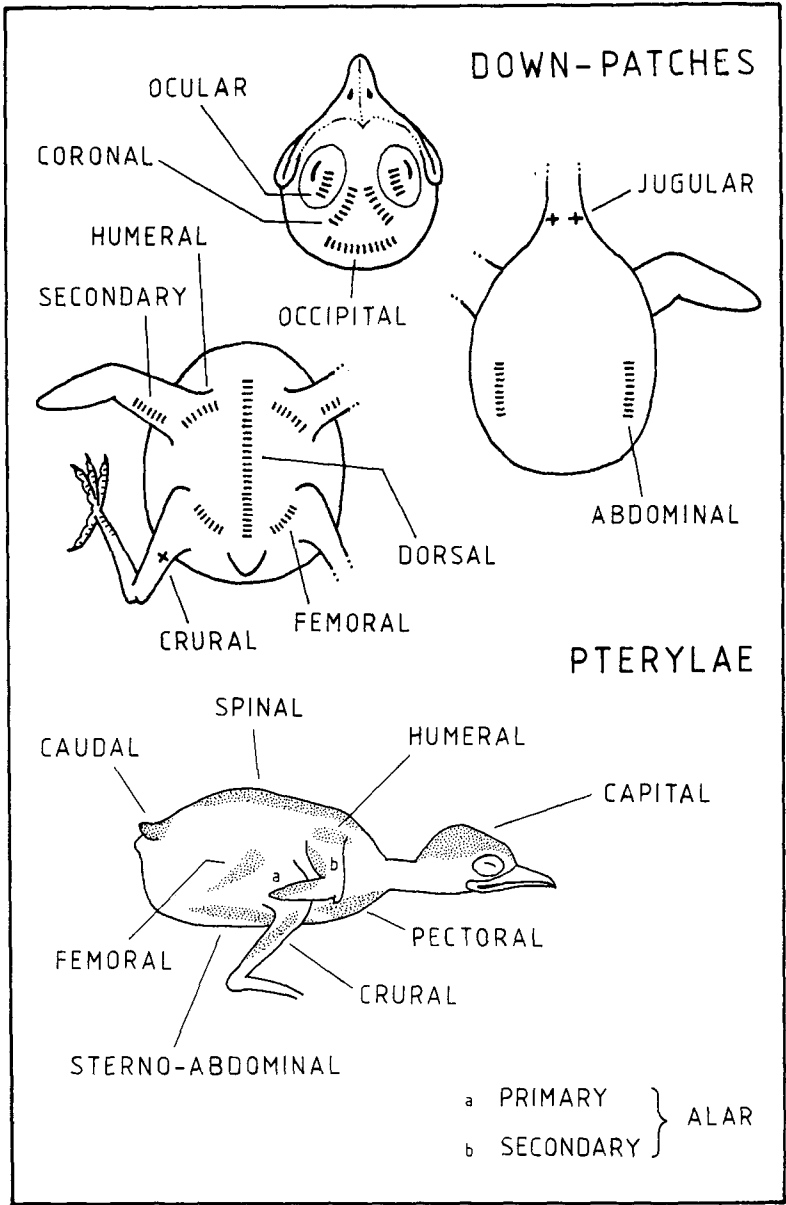


FIGURE 7 — Names and positions of the down-patches and pterylae of nestling Grey Warblers

Of the 12 down patches described by Saunders, three (the primary, caudal and lateral patches) were absent in Grey Warblers. The ocular patch (just above the eye; see Figure 8A), was seen only in a tyrannid flycatcher by Saunders, who predicted wrongly that it would not be found in song birds.

The neossophtiles of Grey Warblers (as seen in full-term embryos from unhatched eggs; Fig. 8A) were in rows rather than patches, many at the ends of rows being shorter than the rest. Ocular, coronal and abdominal neossophtiles were in a single row, whereas those of the occipital, secondary, humeral and femoral patches were in a double row, though not always paired off. Neossophtiles were paired in the anterior part of the dorsal patch but formed one row posteriorly. Three-quarters of nestlings had a dorsal patch in two sections separated by a gap, but in some it was continuous and in others nearly absent.

Physical development

I described the superficial development of Grey Warblers from repeated examination in the field of 40-60 nestlings. The developmental sequence was uniform, but the rate varied greatly among individuals — the nestling in Fig. 8D, for example, developed much more slowly than those in Fig. 8C & E. The description that follows is composite and generalised. Day 0 was the day of hatching. The nomenclature of major pterylae (Fig. 7) follows Lucas & Stettenheim (1972: 74-75).

Day 0 (Fig. 8B): Two warblers at hatching weighed 0.80 g and 1.15 g, and of 83 nestlings weighed within 24 hours of hatching, 14 were 1.00 g and a further seven were 0.85-0.95 g, these presumably having recently hatched. Thus newly hatched warblers weighed about 1 g, often a little less. The skin colour of nestlings at hatching was either distinctly grey (32% of the 87 examined) or pink. Most nestlings were clearly assignable to one or other category but others suggested continuous variation. Sometimes both forms were in the same brood. The significance of the two skin colours is obscure, and both forms developed the same plumage. Natal down and rictal flanges were white. The grey bill had a black tip and claws were dark grey. Bristles less than 1 mm long were on the caudal tract and primary and secondary alar tracts.

Day 1-2: The skin darkened on all dorsal surfaces and on the legs. Skin covering the eyes slit in many cases. Some rictal flanges turned pale yellow.

Day 3-4: Emerging pin feathers were visible along the pectoral and sternoabdominal tracts, and on the alar tracts they were up to 2 mm long (including terminal bristle). Skin over the eyes slightly parted (i.e. widened beyond a slit) in some cases. Rictal flanges were mostly yellow or bright yellow (with buccal skin and tongue to match); only a few remained white.

Day 5-6: Capital, caudal, femoral, humeral and crural pin

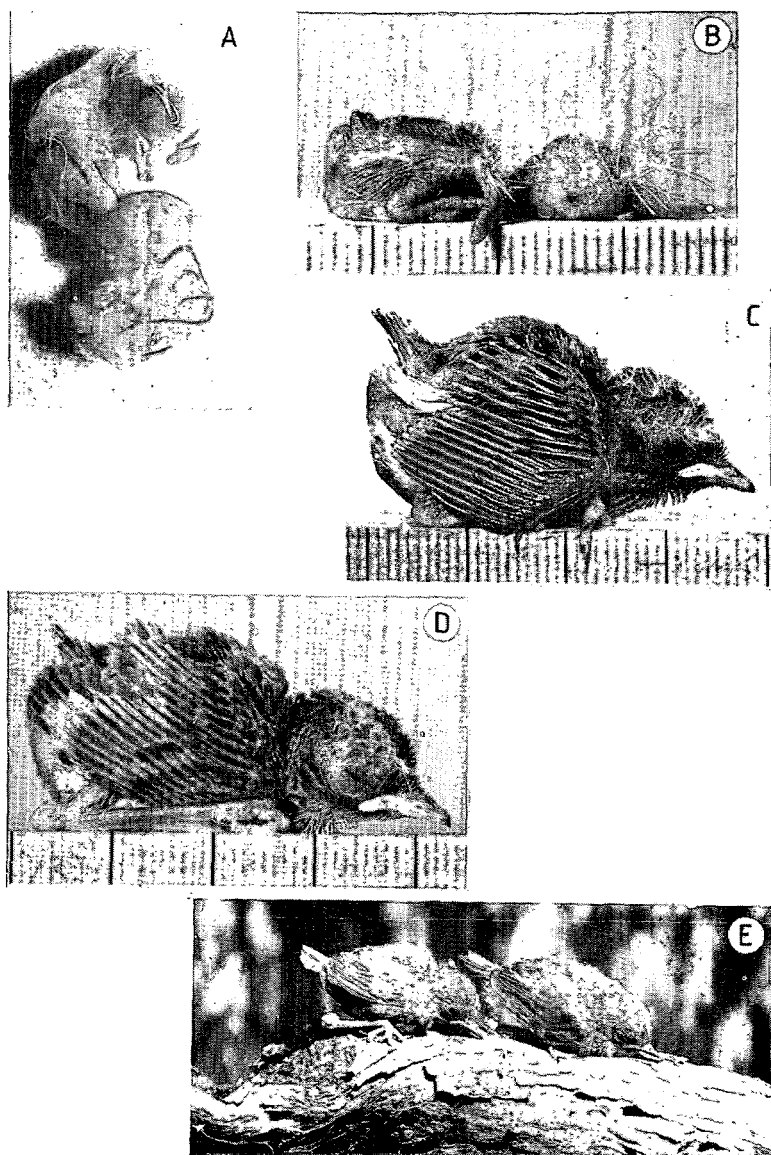


FIGURE 8 — Developmental stages of nestling Grey Warblers; scales in mm.
(A) Full-term embryo (under water) showing yolk-sac and natal down. (B) Day of hatching. (C) c. 8 days old. (D) 12 days old. (E) 15 days old

feathers were less than 1 mm long; others reached 1 mm (spinal, pectoral and sternoabdominal tracts), 4 mm (secondary tract) or up to 5 mm (primary tract). The opaque sheaths showed the grey of the underlying feathers except in the sternoabdominal and femoral pterylae, where they showed pale. All rictal flanges were cream to bright yellow.

Day 7-8 (Fig. 8C): Spinal, pectoral, sternoabdominal and femoral feathers were first to erupt from their sheaths. Sometimes, primary and secondary remiges and capital, humeral and crural feathers also emerged. Sternoabdominal and femoral feathers were white, and the others grey. Rectrices remained ensheathed. The longest primary pin feather was 10-12 mm before the sheath started to disintegrate, and the longest secondary was a little shorter. Spinal, pectoral, sternoabdominal, femoral and humeral pin feathers did not exceed about 3 mm, and capital and crural pin feathers reached up to 1.5 mm. Some nestlings lost the egg tooth; most had half-open eyes. Legs were dark grey-pink but for conspicuously pale ankles.

Day 9-10: Caudal feathers erupted before the intact sheaths exceeded about 4 mm. Most feathers in all pterylae were at least partly unsheathed, but much natal down persisted, presumably at the tips of intact pin feathers.

Day 11-12 (Fig. 8D): White keratinous flakes were shed profusely as the sheaths disintegrated. Remiges extended to 20 mm from base to tip, whereas the longest rectrix was barely 10 mm. The bill (progressively from tip to base) and legs darkened. Many nestlings had yellowish ankles and a pale stripe along the hind edge of the tarsometatarsus. Some nestlings retained the egg tooth.

Day 13-17+ (Fig. 8E): No sheaths or apteria were externally visible on nestlings resting with folded wings. The ventral apterium and much of the nakedness under the wing were occluded before fledging. The longest remex approached 30 mm and the longest rectrix 15 mm. The tail was conspicuously short at fledging, at which time natal down sometimes persisted on the head. Small yellow feathers developed in the orbital region. At fledging, claws were black, legs distinctly grey with paler soles, and the bill dark grey with a black tip. Eyes opened fully revealing dark brown irides. Warblers could fly when they left the nest.

Behavioural development

The following simplified composite description of behavioural development refers mainly to nestlings in the hand, their behaviour in the enclosed nest being hard to see. Although influenced by disturbance these details show the main events.

Newly hatched nestlings rested on their abdomen in the foetal or "egg" position characteristic of most altricial birds (Banks 1959). They did little other than raise their head to gape, often when their bill was touched. After 2-3 days, they struggled during handling by

stroking with their legs, and as dexterity developed, by clenching and unclenching their toes. Day 4 was the earliest that a nestling showed signs of grasping the nest's lining, and from that time I noted faint cheeping (begging calls) in the hand. From day 5, nestlings squealed (protest calls) when taken from the nest. On day 7, nestlings were just able to right themselves when inverted, and at rest they gripped with the toes, held the wings folded against the body and hunched the head without raising it. From day 8, I saw nestlings shuffling in the nest and could hear them cheeping when I was within 5 m. Between days 8 and 12, nestlings began to raise their head and look from side to side, obviously responsive to visual stimuli.

At 12 days, many nestlings could grasp twigs but could not raise their own weight, and so, if made to perch, they rested on their belly. From about 13 days, the crown feathers were erectile and nestlings raised them (as did adults) when I measured their bill. Older nestlings gave single cheeps almost continuously in the nest but broke into rapid cheeping whenever a parent arrived with food. Sometimes nestlings so crowded the entrance and begged so vigorously that a parent could not perch there and had to deliver food from an adjacent twig. When removed from the nest older nestlings sought cover in dark cavities, but nearer fledging they remained in the light and gaped at objects thrust close to their bill. When I approached them, nestlings never left the nest suddenly, unless about to fledge anyway. Thus, this species does not have the explosive response to disturbance noted for many north-temperate passerines (Pettingill 1970).

Young nestlings rose up in the nest only when an adult brought food; otherwise they lay prostrate, pressed against one another. The natal down of nestlings at rest formed a dense layer which blended with the lining in the nest. Thus, the young nestlings' first defence against predation was camouflage. If molested, nestlings clung to the floor of the nest, and if dislodged, they squealed loudly. The parents usually responded at once, and both presented the human intruder with a repertoire of beak-clicking, growling and agitated trilling while they hovered, perched and swooped to within centimetres of the squealing nestlings. When a nestling fledged the watchful parents followed it immediately and, as occasion demanded, fed it or attempted its defence by the above displays.

Stomach contents

I investigated the diet of nestling Grey Warblers at Kowhai Bush by removing the stomachs from 19 nestlings that had died. All were 10 days or older, collected from October to January. I examined the contents of the gizzard and proventriculus (though the latter was usually empty) under a dissecting microscope, and identified items of food to order (Table 4). I measured or estimated the length of the longest axis of items to the nearest whole millimetre.

TABLE 4 — Classification by order of 173 invertebrates collected from the stomachs of 19 nestling Grey Warblers at Kowhai Bush

	Stomachs		Total items		Items/stomach	
	No.	%	No.	%	Mean	Maximum
Hemiptera	3	16	6	3.5	0.3	4
Coleoptera	9	47	9	5.2	0.5	1
(caterpillars)	(17)	(90)	(72)	(41.6)	(3.8)	(16)
(moths)	(2)	(11)	(5)	(2.9)	(0.3)	(4)
Lepidoptera	18	95	77	44.5	4.1	16
Diptera	12	63	21	12.1	1.1	3
INSECTA	19	100	113	65.3	6.0	21
Araneae	12	63	38	22.0	2.0	8
ARACHNIDA						
Unidentified arthropods	8	42	16	9.2	0.8	5
ARTHROPODA	19	100	167	96.5	8.8	31
Stylommatophora	3	16	6	3.5	0.3	3
MOLLUSCA						
INVERTEBRATES	19	100	173	100	9.1	31

Grey Warblers fed their nestlings solely on invertebrates; *Leptospermum* leaves and small pieces of grass in some stomachs were probably ingested accidentally. The maximum number of items in a single stomach was 31. On average there were 9.1 invertebrates per stomach, but several held only finely comminuted remains.

The proportion of stomachs in which a category of food appears indicates selectivity and/or the availability of food. All stomachs contained insects and most held caterpillars. Dipteran flies and spiders were well represented. In general, however, the diet was rather narrow, comprising members of only six invertebrate orders. By comparison, nestling parid tits in Britain were fed invertebrates of 14 orders (Betts 1955).

Of all items ingested, 45% were lepidopterans, 20% other insects and 20% spiders. On average there were six insects (including four lepidopterans) per stomach and two spiders. Three stomachs contained small discoid snails 1-2 mm in diameter, showing that warblers may

collect prey that is neither large nor fast-moving. Silvereyes (*Zosterops lateralis*) in New Zealand also eat small snails (Kikkawa 1966). Nearly half the ingested items were 5 mm long or less (Figure 9), even though the data refer to nestlings at least half-grown. In my sample, nearly all items longer than 10 mm were caterpillars.

Sanitation and mites

After delivering food at the nest, parents removed faecal sacs if the nestlings produced any. The enclosed nest made observation difficult, but often adults seemed to prod to stimulate defecation, and nestlings revolved in the nest and presented their rump at the entrance. The gelatinous faecal sac was carried to a perch 6-15 m from the nest and some, perhaps all, were dropped. Adults at the nest sometimes made repeated swallowing motions, but whether they ate faecal matter or were clearing their bill of the food just brought was not clear.

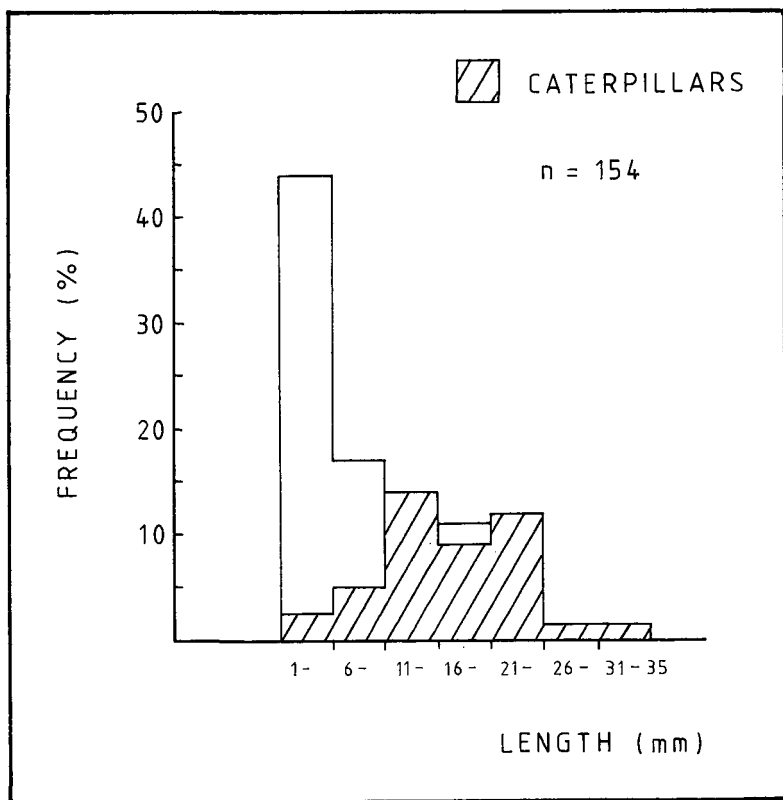


FIGURE 9 — Distribution of items from the stomachs of nestling Grey Warblers according to length of the longest axis

Nests were clean initially, but as the nestlings grew, dried faecal sacs accumulated in the lining along with flakes of keratin from the pin feathers. Nearly 40% of 37 nests at Kowhai Bush developed infestations of red or brown mites (Acarina), which I usually noticed after the young were half-grown. I may have transmitted mites from nest to nest by the polythene bags in which I weighed young, and so the incidence quoted here may be inflated. Sometimes, mites were so numerous that they swarmed over the nest's exterior and over adjacent vegetation, after the nestlings fledged.

Samples of mites from several nests were examined by Dr R. Domrow (Queensland Institute of Medical Research, Brisbane) and found to be *Ornithonyssus bursa* (Berlese 1888), which is known also from Starlings (*Sturnus vulgaris*), House Sparrows (*Passer domesticus*) and Domestic Fowls (*Gallus gallus*) in New Zealand (Powlesland 1977).

FLEDGLINGS AND JUVENILES

Fledgling Grey Warblers were recognisable in the field at Kowhai Bush until about mid-March, two months after the last fledged. The irides were dark brown (red in adults), the legs dull grey (black in adults) and the buccal lining yellowish (black in adults). The facial plumage was suffused with yellow, and a pale yellow circum-orbital ring was often apparent, even at a distance. The tail was paler than in adults. Two banded young developed adult appearance in early February, 12 and 15 weeks after fledging. At this time other banded juveniles had moulting tails and red irides. Young apparently became indistinguishable from adults at their first moult, which seemed to coincide with the post-nuptial moult of adults (January to March). Juveniles dispersing from their natal areas could often be distinguished by their quietness and secretiveness. Sometimes they were chased from territories by resident adults; often they were tolerated.

For 1-3 weeks after fledging, warblers of early broods usually stayed together and were fed by both parents, but the male often did most feeding when only two young fledged. Then, during the next 1-3 weeks, the male often attended the juveniles alone, while the female left the group intermittently to build a second nest. When with the group at this time the female often ate the food she collected and ignored or drove off fledglings that begged to her.

In two of nine families that I watched regularly, the male cared for two of four, and two of three, juveniles, and the female attended to the rest. Both parties within the family were always nearby, but each juvenile begged to, and received food from, only one parent. Twice at Kowhai Bush I saw an adult warbler feeding an unrelated juvenile in addition to its own.

At Kowhai Bush less than 10% of fledglings (six birds) were recruited to the breeding population during my study (Gill 1982a). One was probably a female — I saw it in November 1978 near the

TABLE 5 — Fates of Grey Warbler eggs at Kowhai Bush that did not hatch

Cause of mortality	1976-77		1977-78		Early		Late		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%
Infertility	4	12	4	9	6	17	2	5	8	10
Death of embryo	6	20	7	15	6	17	7	16	13	17
Cuckoo-parasitism: removal	5	16	6	13	0		11	26	11	14
Cuckoo-parasitism: eviction	3	9	3	6	0		6	14	6	8
? : disappearance	9	28	16	34	11	30	14	32	25	31
? : eviction	4	12	10	21	12	33	2	5	14	18
? : broken in nest	1	3	1	2	1	3	1	2	2	2
	n 32		47		36		43		79	

TABLE 6 — Fates of Grey Warbler nestlings at Kowhai Bush that did not fledge

Cause of mortality	1976-77		1977-78		Early		Late		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%
? : death in nest	10	25	7	22	14	43	3	8	17	23
? : disappearance	14	34	3	10	9	27	8	20	17	23
Cuckoo-parasitism: eviction	3	7	9	29	0		12	31	12	17
? : eviction	0	-	4	13	0		4	10	4	6
Predation	12	29	8	26	8	24	12	31	20	28
Competition?: "runts"	2	5	0		2	6	0	-	2	3
	n 41		31		33		39		72	

natal territory from which it had fledged in October 1976. The others were males that I saw proclaiming territory. Two males were singing on territories (0.8 km and 2.3 km from their natal sites) in the season after that in which they had been raised. Another held a territory (0.6 km from the natal site) in the second summer after it had been raised, although it may also have done so in the first summer. I did not determine whether any of these three males had mates and bred.

The fourth, ♂-K, was netted, probably as a juvenile, in July 1977 and seen repeatedly on a territory 0.4 km away from August to October 1977. It sang regularly and fought neighbouring males but probably did not breed because I did not see a mate. It apparently lost its territory for the second half of the 1977-78 breeding season, but in 1978-79 ♂-K held a territory throughout the summer and bred at least twice with an unbanded mate. The fifth male held a territory 9 months after fledging. The unbanded mate built a nest 0.7 km from that in which the male had been raised. I did not determine whether eggs were laid, and later in the season an unbanded pair were occupying the area.

Nearly all territorial birds begin reproduction in the first season after that in which they are raised (Lack 1968). The evidence is meagre but it seems that male Grey Warblers at Kowhai Bush were rarely successful in holding territory and breeding in this first year.

MORTALITY OF EGGS AND NESTLINGS

Tables 5 and 6 give the known or inferred causes of death at Kowhai Bush of 79 eggs and 72 nestlings. Infertility of eggs was more common in early clutches than late ones, suggesting poor behavioural or physiological synchronisation during some initial copulations. Parasitism by Shining Cuckoos destroyed eggs in two ways: a warbler's egg was apparently removed in substitution for the cuckoo's and nestling cuckoos evicted warbler eggs (Gill, in press). Parasitism affected only late clutches but it was the main cause of loss of late eggs (40%). Eggs that disappeared without trace vanished all at once or sporadically, and sometimes only part of a clutch was lost. Eviction of eggs (other than by cuckoos), as indicated by their presence on the ground beneath nests, was particularly common for early clutches in 1977 when strong winds seemed responsible for the loss of 9 eggs. Most eggs that disappeared, that were broken in the nest, or that were evicted (other than by cuckoos) were probably destroyed by ship rats (*Rattus rattus*) or stoats (*Mustela erminea*).

The greatest single cause of mortality of nestlings was predation (presumably mammalian), indicated by a destroyed nest and/or mutilated nestlings. Unrecognised predation may have contributed to the disappearance of nestlings, which for reasons unknown was more common in 1976-77 than in 1977-78. More nestlings died in the nest without obvious cause in early broods than in late ones. Food supply early in the season may have been involved, but some of the dead nestlings

I dissected had full stomachs and so they had not starved. The last nestlings hatched in two broods of four in 1976 did not gain weight and died, whereas their siblings were healthy. These "runs" that apparently starved were from early broods. The eviction of nestling warblers by young cuckoos was a major cause of mortality for late broods but a relatively minor one overall. In Table 6, eviction (other than by cuckoos) refers to four nestlings in two late broods of 1977-78 found unharmed on the ground beneath their nests, perhaps after disturbance by a predator.

The average number of young to fledge per nest was similar in 1976-77 (1.74) and in 1977-78 (1.71), but whereas 3.3 nestlings on average hatched per nest in 1976-77, only 2.4 did in 1977-78. This suggests high mortality of eggs in 1977-78 but of nestlings in 1976-77.

Of 65 early eggs (in 18 nests) in 1976-77, 92% hatched, whereas of 70 early eggs (in 18 nests) in 1977-78 only 64% hatched. Of 60 early young hatched in 1976-77, only 63% fledged, whereas of 45 early young in 1977-78, 80% fledged. The success of late eggs and nestlings was similar in the two seasons, as was the overall proportion of eggs (early and late) that yielded fledglings (43% of 109 eggs in 1976-77; 34% of 123 eggs in 1977-78).

DISCUSSION

Several factors combine to make Grey Warblers very suitable for study in the field. They are common and widespread; breeding adults are sedentary and long-lived (Gill 1982a); adults are relatively easily caught in mist-nets for banding; females may be caught on the nest; and observations and manipulations at the nest bring little risk of desertion. The biology of this species deserves to be fully explored.

The arrangement of natal down in neonate passerines warrants more attention than it has received because it is a potential taxonomic character that may help resolve generic and familial relationships. A start has been made here for New Zealand species. Further records of natal pterylography may lead to a better understanding of the relationships between, for example, the Acanthisittidae and New Zealand song-birds, and between *Mohoua*/*Finschia* and the malurid and acanthizid warblers of Australia.

The developmental sequence (physical and behavioural) that nestling Grey Warblers follow is very similar to that of other song-birds. However, I suspect that the rate of development in warblers varies more among individuals than is so for most north-temperate species. Also, warblers are physically very advanced at fledging compared with Northern Hemisphere species with shorter nestling periods. In North America, White-crowned Sparrows (*Zonotrichia leucophrys* Emberizidae) fledge at 9-10 days old, often with partly ensheathed feathers and a partly exposed ventral apterium (Banks 1959), and newly-fledged Rufous-winged Sparrows (*Aimophila carpalis* Fringillidae), which are 8-9 days old, hide in grass because they cannot fly

(Austin & Ricklefs 1977). It is interesting that Grey Warblers shun the light for part of the nestling period. This presumably befits life in an enclosed nest, but the opposite tendency must be developed for fledging to occur.

Some of the eggs and nestlings that failed to survive at Kowhai Bush may have been taken by avian (rather than mammalian) predators, though none is known to rob warbler nests. Fulton (1910) was convinced of Shining Cuckoos being predatory, which is realistic because European Cuckoos (*Cuculus canorus*) avidly prey on eggs and nestlings (Wyllie 1975). Michie (1948) apparently saw a Shining Cuckoo eating the contents of a warbler egg but this may have been removed during parasitism rather than by deliberate predation. In Australia, Fien (1970) saw a Horsfield's Bronze-cuckoo (*Chrysococcyx basalis*) remove a host nestling. Magpies (*Gymnorhina*) may prey on the contents of Grey Warbler nests (Moon 1960). Another possible predator is the New Zealand Kingfisher (*Halcyon sancta*), which may attack warblers (Hay, pers. comm.), and which I saw at Kowhai Bush provoking alarm in adult warblers.

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Note added in press

Female-14, caught and banded as an adult in September 1977 (see territory plotted in Gill 1982a) was seen in the same part of Kowhai Bush by G. Sherley in August 1981, giving a minimum life span of about 4 years.

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SHORT NOTES

DAY-SLEEPING BIRDS

I have a horizontal stick outside my kitchen window on which I hang tins of syrup in winter time.

On 23 July 1982, I noticed a Silvereye (*Zosterops lateralis*) apparently asleep on the stick with its claws over the hook of the feeding tin. I stroked the Silvereye gently but it made no move. I was able to put a finger under its claw and roll my finger until the bird was perching on it. The empty tin was removed and a full one put on the hook, and I replaced the Silvereye by hooking its claws over the stick and removing my finger. It remained on the stick for another hour and ten minutes, even though other birds came to feed. Eventually it opened its eyes, flew down to feed a little, and then flew off. I did not know how long it had been asleep on the stick before I saw it.

While I was working in the garden on 15 October 1982, a Starling (*Sturnus vulgaris*) landed on the lawn about 2 metres away and laid an egg immediately. The Starling then moved as if to cover the egg, but instead folded its wings and sat on the grass beside it and went to sleep.

Half an hour later the Starling had not moved. I stroked it, with no response from the bird. I covered bird and egg with a large box and inspected it at about half-hourly intervals. On the fourth inspection I noted that the bird had changed its position a little, and so I stroked it gently. Presently the Starling opened its eyes and a moment later took a little run and flew off.

M. LANE, *Ashburton*