

New Zealand Flycatchers of the genus *Petroica* Swainson (Aves)

PART II

(Concluded from Vol. 78, Part I, page 47.)

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Subgenus MIRO Lesson

Miro Lesson, 1830. *Traite d'Orn.*, p. 389. Type (by monotypy):

Muscicapa longipes Lesson. Bay of Islands, New Zealand.

Muscopus, Reichenbach, 1850, *Syst. Avium*, pl. lxxvii. Type (by monotypy) *Muscicapa longipes* Lesson.

Characters: Medium and large sized flycatchers, similar in general to *Petroica* s.str. but with strong tarsi (36–44% of wing length) and rounder wing; first primary 50 to 60% of second, fifth or fourth longest; third to sixth, emarginate; and seventh, emarginate or cut away; rectrices only slightly graduated; tail lacking pattern and wing bar reduced or absent; plumage soft and fluffy; dorsal surface never glossy black, ventral surface never highly coloured; feet with yellow, not orange, soles.

Range: New Zealand and Chatham Islands.

Remarks: The difference between the birds grouped as *Miro* and any one species of *Petroica* s.str. are greater, in my judgment, than the differences separating any other two species of *Petroica*; on the other hand, there is no doubt that the *Petroica* species are the closest existing relatives of *Miro*, and that the two groups arose from a common ancestor. Phylogenetically, the separation of *Miro* from the main *Petroica* stock seems to have occurred at a much more remote date than did the speciation in *Petroica*. These relationships, structural and phyletic, deserve recognition in the taxonomic scheme if this does not result in an unwieldy nomenclature. The distinctness, morphologically, and the relatively long isolation, from the phylogenetic point of view, that characterise the New Zealand robins, are recognised by the retention of *Miro* as a subgenus; the equally important conclusion that the New Zealand and Australian robins and tomtits are more closely allied to each other than to other flycatchers finds its expression in the use of *Petroica* generically to include them all.

There are no objective criteria for the definition of genera: the grouping of species in genera is a matter of convenience, and, the dictates of convenience vary from person to person and in different contingencies. Nomenclature should be the tool of the student rather than an end in itself, and it is not illogical for different purposes to be served by different interpretations of generic limits. On a lower taxonomic plane, it is general practice to use simple binomial nomenclature where field observations are recorded without study of specimens to justify use of trinomials. For some generations ornithologists have been concerned with emphasizing the differences between one bird and another, and, locally, in emphasizing the distinctness of the

New Zealand avifauna by recognising endemic genera to include the older elements. Latterly, the opposite process, synthesis of related forms into wide genera to emphasize relationships, has resulted in the dropping of many names long current. Both these attitudes to systematics have made important contributions, and if both sets of conclusions can be crystallised in the nomenclature, so much the better. Subgenera have traditional sanction in zoological nomenclature, and, though avoided by some contemporary workers, are used by James Lee Peters in his Checklist of the Birds of the World, which is likely to remain a standard work for some considerable time. Their citation is desirable in the full formal name of a bird, wherever the name is to be used as a basis for phylogenetic or zoogeographic discussion—i.e., in faunal lists generally, though not necessarily in field guides, in life history studies, or on specimen labels.

The nomenclature here adopted is an attempt to indicate both the affinities and distinctness of the New Zealand robins: it is unlikely to appeal to all other students, some of whom will prefer to retain *Miro* as a full genus, others of whom may drop the name altogether and list the robins as *Petroica*. Such variations merely emphasize the subjective nature of supraspecific categories. The most important innovation in the present paper is the attempt to indicate in the nomenclature the diverse affinities of the two black forms, *Petroica macrocephala dannefaerdi* Roths. and *Petroica (Miro) traversi* Buller.

Affinities: With one exception, the structural characters that distinguish the species grouped as *Miro* are all found, chiefly to a lesser degree, in one or more of the forms of *Petroica* s.str. The exception is the emarginate or cut away 7th primary, a feature not seen at all in *Petroica* s.str. This is directly connected with the rounder wing of *Miro*. (Ticehurst, 1938).

Primitive characters of *Petroica*, present in *Miro*, are the general plumage pattern, the small, white frontal spot, yellow soles of feet, streaked fledgling plumage, slightly graduated tail, and persistent alar bar. The specialised characters of *Miro*, large size, loss of tail pattern, reduction of alar bar, loss of sexual dimorphism (through adoption of retarded plumage by males) and the structural characters, are all approached in one or other species of *Petroica* (s.str.). The species of *Miro*, can indeed be regarded as a branch of *Petroica* which have undergone some of the same changes, but to a greater degree, during lengthy isolation in New Zealand, as have species and subspecies of *Petroica* which have colonised islands at more recent dates. This topic is elaborated in another section.

PETROICA (MIRO) AUSTRALIS (Sparrm.)

New Zealand Robins.

Characters: Large races of the subgenus *Miro* with cream, pale yellow, or whitish breasts and dusky dorsal colouration; frontal spot present; wing with reduced alar bar; primary formula $2 = 8/9$,* (usually $5 > 6 = 4 > 3 > 7 > 8 > 2 > 9 > 10$); first primary 52–57% of second; tarsus long, 37–42% of wing. Soft parts: tarsi mauvish horn; soles of feet lemon yellow; rectal membrane and interior of mouth yellow; iris very dark brown (Mamaku)

* Rarely $2 = 9/10$.

Distribution: Main islands of New Zealand and nearer outlying islands.

Moult and Plumages: Available data are quite inadequate for discussing the plumage sequence and moult. May skins (Rotorua) are in fresh feather after completion of the moult; December skins show some wear but no indication of incipient moult. It is impossible to deduce post-juvenal plumage changes because of the persistence of the characteristic streaked feathers of youth into the adult of some races.

Habitat: The New Zealand robins are now chiefly confined to native forest in districts at least moderately remote from areas with high human populations. It is difficult in the present condition of the species to sort out its primitive ecological preferences, but in general it appears to have been fairly tolerant of all habitats where arboreal vegetation existed. It was not absent, for instance, from low rainfall areas. At present the robin occupies a variety of biotopes: kauri and mixed bush (Little Barrier Island); tawa-rimu forest (central North Island); mature *Leptospermum* scrub (Marlborough); *Nothofagus* forest (Otago-Southland); coastal scrub (Stewart Island outliers). Many areas of apparently suitable forest no longer support robin populations: the species has proved less viable during the changes of a century, than has *Petroica macrocephala*.

General Habits: For accounts of the New Zealand robins, the reader is referred to the writings of McLean (1911), Guthrie Smith (1925, 1914), Wilkinson (1927), Moncrieff (1932), and Richdale (1941, 1945). The bird is sedentary and territorial, some pairs at least keeping together and showing aggressive behaviour to other robins even in May (Mamaku). Food is taken chiefly on the ground, and unlike the tit, which sits on a perch and makes darting flights to pick up food, the robin spends quite a lot of time hopping on the forest floor, thrush-like, while feeding. The robin is a bird of the lower stratum of the forest, except that territorial song is sometimes uttered from higher levels. In addition to the normal insect food, crumbs of bread are readily taken. The habit of taking surplus food and "caching" it, noted by several observers, is also characteristic. Stead (1948) notes that worms are robin's favourite food, and are not eaten by the tits.

The pattern of aggressive behaviour, accompanied by erection of crown and frontal feathers, and snapping of the bill, is similar to that of *P. macrocephala*. The cock's feeding of the hen persists throughout the period of mating, nest-building, incubation and even during the fledging of the young.

There is little information on song period: males regularly sing well at Mamaku on frosty mornings in May and in spring (September-November), but were more silent in January (Nelson) and February (Kapiti) in the inferred period of the moult. The song traditionally varies to a great extent from place to place (Guthrie Smith; Wilkinson). In the Rotorua district it consists of a chromatic sequence of clear staccato whistles from about three octaves above middle C, descending for about half an octave and developing into a varied series of trills and thrice repeated whistles which justify comparison with the song of canary and thrush. Anderson (1926) quotes the

beginning of this song, heard at Kapiti, and gives other notes. In September, 1946, male robins at Mamaku bush were singing continuously for periods of 15 and 20 minutes.

Nest site resembles that of *P macrocephala*, but is sometimes almost at ground level, and usually sheltered from above and on one side (but see Stead, 1948). The clutch is 2 or 3: Guthrie Smith (1914) records a nest with 5 eggs, but that is very unusual, and he was not able to confirm their hatching.

Petroica (Miro) australis longipes (Lesson). North Island Robin
Muscicapa longipes Lesson, Voy "Coquille" pl. 19, fig. 1, 1827. (Bay of Islands).

Mynothera novaezelandiae Lesson Man. d'Orn., vol. 1, p. 248, 1828 (new name for above).

Adult Male: Back, scapulars, rump, upper tail coverts, dark mouse grey (R), bases of feathers slate colour, shafts light; some rump feathers with whitish tips; feathers of crown, sides of head, lores, ear coverts, dark mouse grey (R) with lighter shafts and somewhat lighter central areas giving a scalloped effect; small white frontal spot, narrower than gape; cheeks, throat, upper breast, mottled, the bases of feathers slate grey, shafts white, inner parts of vane pale neutral grey, tips deep neutral grey; remiges fuscous black, anterior webs a little paler, alar bar consisting of rounded triangular white areas, on inner webs only, from 6th primary to 5th secondary; lesser coverts dark mouse grey with light shafts; major coverts fuscous black with rare white tips over the secondaries; under wing mouse grey with alar bar conspicuous; under coverts white, lesser coverts dark mouse grey; axillaries white with slate bases; rectrices fuscous black without pattern; lower breast and belly white, faintly washed with ivory yellow, bases of feathers blackish slate, mottling into slate grey on flanks; thighs white (Rotorua District, May).

Adult Female: Differs from male in browner, paler, plumage, mottled paler neck, and ill-defined breast; dorsal plumage fuscous, with darker scalloping, and with pale shaft-streaks extending down on to back; frontal spot as in male; throat and upper breast light olive grey with darker tips of mouse grey producing a mottling which is most pronounced as an ill-defined chest band; lower breast and belly cream ("off-white"), flanks mouse grey; the pale area of the ventral surface is not sharply marked off from the flanks and neck. (Rotorua District, May.)

Fledgling: No adequate material available. A badly "foxed" specimen from Little Barrier, dated November, 1884, and sexed female, juv. (Canterbury Museum 1083.13) has no frontal spot, and more pronounced dorsal streaking than adults; there is a fawny wash across the upper breast, and a pale buff wash on the lower breast.

Variation: The plumage, described above for a freshly moulted male, fades during the year, masking the sex differences, which are, however, usually discernible in a pair of live birds. Inadequate material is available to discern any regional variation in plumage. The skin from Kaitoke Range (Canterbury Museum 1083.4) labelled female, could not be separated from normal males, having less shaft-



FIG. 11—*Petroica (Miro) australis longipes* (Lesson), type of *Miro* Lesson, adult male. Note characteristic stance and long tarsus.

Photographed at National Park by G. A. Buddle.



FIG. 12—North Island Robin (*P. (Miro) a. longipes*). Female on nest, Kapiti Island.

Photo. by A. S. Wilkinson.



FIG. 13—North Island Robin, *Petroica (Miro) a. longipes* Lesson, showing the light-shafted plumage retained by adults of this race, but characteristic of immaturity in most *Petroica*.

Photo. by A. S. Wilkinson.

streaking on the back than many females in addition to a darker plumage tint not customarily present in females. It is the only skin from the southern end of the North Island; and as it might be wrongly sexed no conclusions can be drawn. There is a notable absence in collections of skins from Kapiti where the bird was common even before the island was declared a sanctuary.

The same insufficiency of material prevents adequate assessment of size variation. The 2 males from "Auckland" and Little Barrier have longer wings than the mean of 10 from Rotorua, and the 2 males from Wanganui have shorter wings. This suggestion of a latitudinal cline similar to that found in the South Island must await confirmation by larger series. The Kaitoke skin, for what it is worth, whether male or female, does not fit in with a regular gradient. (Fig. 15.)

Dimensions: See Table 8.

TABLE 8—DIMENSIONS OF *Petroica (Miro) australis longipes* (Lesson)

Collection and number	Locality	Date	Sex	Wing	Tail	Tarsus	Mid-toe	Culmen
C.M.1083.3	Auckland	1886	♂	92	65	36	—	—
C.M.1083.5	Little Barrier Id.	Nov. 1884	♂	95	62	34	25	17
C.M.1083.9	Mamaku, Rotorua	26/4/28	♂	95	61	38	—	17
C.M.1083.17	Mamaku, Rotorua	24/12/24	♂	94	66	38	—	16
C.M.1083.14	Mamaku, Rotorua	22/5/29	♂	92	66	37	25	17
C.M.1083.7	Mamaku, Rotorua	20/5/29	♂	89	60	35	23.5	16
H.G.D.16	Wanganui, River	—	♂	88.5	65	36.5	—	17
A.M.26.6	Mamaku, Rotorua	—	♀	89	60	35	24.5	—
C.M.1083.15	Mamaku, Rotorua	31/8/30	♀	87	61	38	26	16
C.M.1083.8	Mamaku, Rotorua	27/11/27	♀	87	60	36	—	—
C.M.1083.4	Kaitoke Range	1880	♀	95	68	37	24	16

Males (15 measured): wing 85–95 (mean 90.7, $\sigma = 2.9$); tail 59–67 (mean 64, $\sigma = 2.4$); tarsus 34–38 (mean 36.2, $\sigma = 1.36$); middle toe 23.5–25; culmen 15.5–17; bill from skull 19–21.

Females (4 measured): wing 87–95 (mean 89.5); tail 60–68 (mean 64.5); tarsus 24–26.

Proportions: Tail/wing ratio (19 skins), 64–72.9, mean 70%, $\sigma = 2.76$. Tarsus/wing ratio 36–44, mean 40.3%, $\sigma = 2.02$. The tail/wing ratio is significantly different from that of *australis* (mean 74%) ($t = 5$), but significance cannot be claimed for the slight difference in tarsus/tail ratio ($t = 2$).

Distribution: An attempt to summarise the present distribution of *Miro australis* was made in *N.Z. Bird Notes*, vol. 2, no. 2, pp. 24–5. From that paper and from records subsequently received, the present account is compiled. (Fig. 14.)

In 1888 Buller announced that the robin had become one of the rarest of native birds, that it was seldom met with on the mainland, and that its doom was sealed. In 1905 he recorded "that the last heard-of pair" was seen at Papaitonga Lake (Levin), in 1898. Drummond, in 1907 (also Fulton, 1908) listed the robin as surviving in 12 North Island mainland localities, but owing to the frequency with which tits have been reported as robins, it is unsafe to accept any of these records of "robins" that are not also accompanied by records of tits: some 5 localities remain after rejecting such doubtful records. Myers (1923) noted its survival in four mainland localities and two

islands Recently (*Forest and Bird*, No 79, Feb., 1946, pp. 7-8) the statement was made that "The Karioi Bush contains the North Island robin, a confiding little bird found elsewhere only on Little Barrier Island and Kapiti." There was no excuse for the last statement since many other records had appeared in recent issues of *N.Z. Bird Notes*, and the robin is, in fact, in quite as good a position to-day as Drummond and Fulton believed it to be forty years ago.

Although Buller predicted the early extinction of the North Island robin, he has not left us with much precise information on its dis-

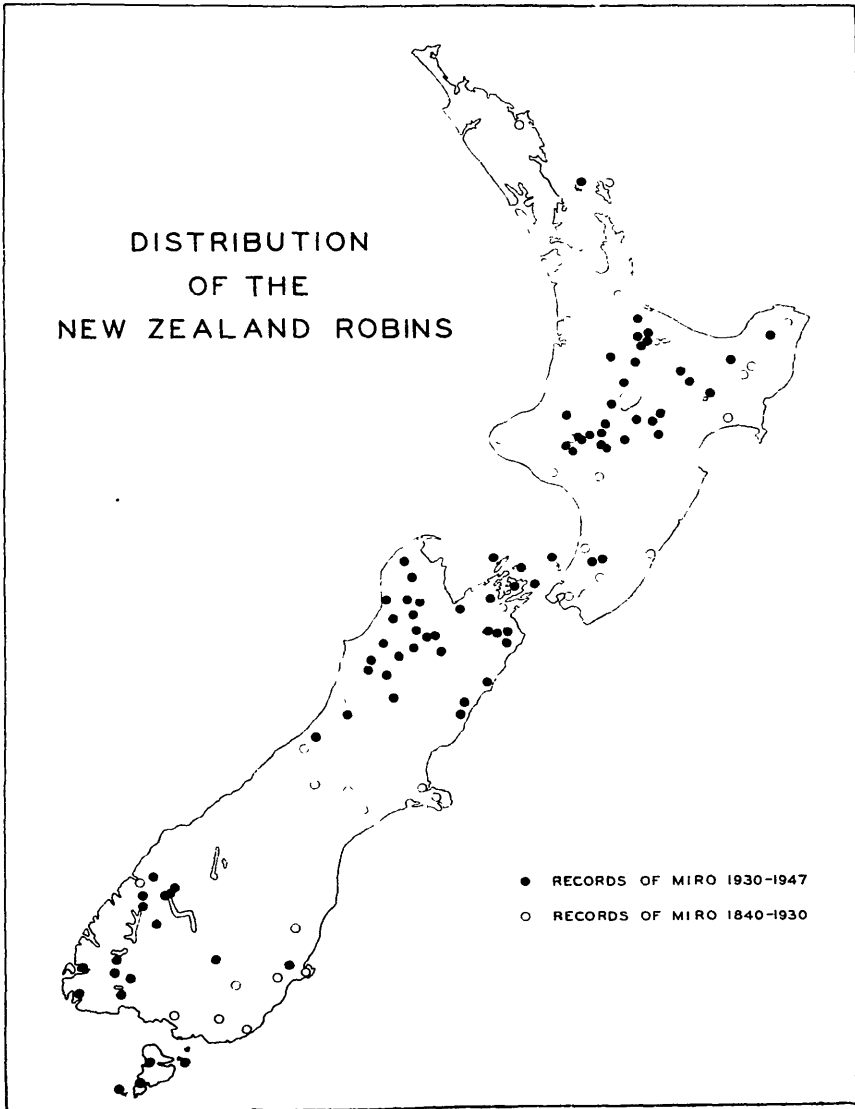


FIGURE 14

tribution in the middle of the nineteenth century, beyond stating that it was very common in all the wooded parts of the country. In his boyhood (say 1850) it was still present at the Bay of Islands, where Lesson had discovered it in 1824. There are few reports from North Auckland: Reischek did not find it in the early eighties, and the skin labelled "Auckland, 1886" (Table 8) may well be from Little Barrier. Hutton recorded the robin from both Barrier Islands in 1868; it has survived on Little Barrier, but there are no contemporary records from Great Barrier. There are no unquestionable North Auckland records in Drummond's (1907) and Myers' (1923) papers. For these reasons I am doubtful of the continued existence of the robin on the mainland north of Auckland. Mr. W. Sanderson, who recorded robins at Takekiwai Hills (Whangarei) writes (29/9/45) that he now suspects that what he saw may have been hedge sparrows. Nor has the report of robins at the Three Kings Islands been confirmed by later visitors to those islands.

From enquiries made by Mr. H. R. McKenzie, it seems unlikely that there have been robins in the country immediately south of Auckland within the last sixty or seventy years: nor are there undoubted earlier records, so that I discount Drummond's Mangatawhiri Valley record as referring to tomtits. His record from Raglan (1907) is accepted, although there have been no subsequent reports published from there. In the bushed ranges extending south from Te Aroha Mountain to the volcanic tableland, robins survive in the south (behind Ngongataha, Mamaku, and Mangarewa Valley), in numbers that seem to have been consistent since at least 1932; further north I have had records which are possibly valid from Kaimai Range (nineteen-thirties) and Dr Falla tells me that the species persisted until about 1926 near Waikino (Waitawhata Valley). East of Rotorua, in the bush around Rotoiti and Okotaina, there are no records, in the experience of Major R. A. Wilson and others: this was the area of bush most affected by the Tarawera eruption of 1886, a fact which may have some significance in view of the observed embarrassment of *Rhipidura* during the mild ash showers from Ruapehu in 1946. South of Rotorua, W. H. Wenham recently saw robins (1945) in afforested hill country on the Tokoroa-Atiamuri Road. Buller's unconfirmed record from Whale Island (1905) is not here accepted.

West of the Waikato valley, robins have persisted on the Hauhangaroa Range and in neighbouring areas, detailed records being: Tihoi and Arataki, West Taupo (R. St. Paul); Maraeroa, east of Mangapehi (R. A. Wilson); Rangitoto Range. Possibly the robin is present more or less continuously from the above localities south to the Main Trunk Railway, where records come from Whakapapa Gorge, National Park, Mangowhero Gorge and Waitaiki Stream (A. C. Henderson and others), Rangataua, and Karioi Forest. Major Wilson notes (*in litt* 9/9/45) that he never heard of a robin being seen south of the railway in the Rangataua district.

From the Main Trunk westward to Cape Egmont, the position of the robin is apparently not so happy, although the "coverage" by observers is not complete. A. C. Henderson and J. M. Heise, Raetahi, provide recent records from the country between the Main Trunk

and the Wanganui River: Raetahi-Pipiriki Road; Waimarino Stream; Makino Road; Murumuru Road, and Kahura Track (Mangonui-a-te-ao). Reischek saw robins on the mainland only at the Tohua (Tuhua) ranges of North Taranaki in 1882. Buller recorded their disappearance prior to 1906 from the forests around Mount Egmont where they were common in 1866. R. H. D. Stidolph recorded robins at Tangarakau Gorge in 1933. Drummond reported them extinct in the Wanganui District and rare in the backblocks of Waitotara (1907). The Wanganui Museum lately received robins alleged to have been taken on Blair Athol Station, Hunterville, between 1881 and 1884, and J. Moreland has collected a number of records from the Wanganui Valley above Jerusalem and from the Upper Waitotara Valley (1947). The latter are not shown on the map.

On the East Cape Peninsula the robin was originally widespread, although early records are scarce. McLean (1892) recorded that the robin was not uncommon in 1889 in an unspecified East Coast locality, Guthrie Smith (1925) noted its abundance in the back country of Poverty Bay in the late "nineties," and in 1911 McLean described a nest found at Waikohu in 1898 and recorded the bird as "present in fair numbers" on the Maungahaumia ridge in 1906 although the bush was then being felled. Myers quotes Elsdon Best as stating that robins had practically disappeared from the Urewera country many years before 1909, but reappeared in limited numbers in 1901-2. At present, the robin is occasionally recorded from the bushed main range at the heads of the Awatere and other East Cape rivers, according to Mr R. H. Metcalfe, and is doubtless present locally all the way down to the north end of the Huiaurau Range (near Rakauroa, present in 1935); it persists, locally in reasonable numbers, in the bush between Waikaremoana and Galatea [recorded from Te Whaiti (H. R. McKenzie), Minginui (R. St. Paul) and Horomaunga Gorge (G. A. Buddle)]. Further south, the robin is reported by Major G. F. Yerex and other officers of the Department of Internal Affairs from the Upper Mohaka River, and in small patches of bush between Rangitaiki and Ahimanawa Range; another deer-stalker stated that they were present at a number of places scattered over the triangular area between the Taupo-Napier, Taihape-Napier, and Desert Roads—i.e., the Kaimanawa and Kaweka Ranges, but Major Wilson failed to find them during several trips to the former range. There is little information about the past status of the species in Hawke's Bay: Guthrie Smith included the robin as one of the species which had disappeared from Tutira before settlement commenced.

Major R. A. Wilson states that he has never seen robins in the Ruahine Range, and there are no other reports. In the Tararua Range the species was plentiful in 1911, but had "disappeared" by 1923 and is now seldom recorded: recent reports come from west of Otaki River, above upper gorge (F. Newcombe, 1934), near Kelliher Creek (Otaki) and Upper Waingawa (E. R. Rye, 1946) and Waipehu Track (1945, A. A. Savell). The beautiful song of robins near Levin in the early days is remembered by Mr. G. H. Snow, and Buller records what he considered the last heard-of pair at Papaitonga in 1898. There is an 1880 skin from Kaitoke Range (Rimutaka); and Drummond lists the robin as persisting at Wainuiomata (1907).

Recently (1946) Mr F. Newcombe told me of two reports from the Orongorongo, and Mr E. W. Hursthouse of an unconfirmed report from the hills behind Mahina Bay. In spite of the present rarity of the robin in southern Wellington, these records, if confirmed, allow hope that the bird may one day recover its position in the areas of bush that remain. East of the range, one of Drummond's correspondents reported that the robin was "almost extinct" in the Castlepoint district (1907) and there have been no subsequent records. The Kapiti sanctuary preserves a healthy robin population.

In summary, it may be stated that the robin persists on two island sanctuaries and in three large bushed areas which form a crude triangle around the central Taupo-Rotorua district (Fig. 14); there is no evidence of decreasing numbers in these central areas, but in the four peninsulas that radiate from them the robins' status is insecure. From the north the species has already gone; from peripheral Taranaki it has almost disappeared; and in East Cape and Wellington it is recorded so seldom or so locally that its position must be considered precarious. Nevertheless, the present summary does not indicate substantial reduction since Myers' review in 1923; on the contrary, the position seems to have improved, but this is certainly in large part due to the greater number of observers now operating in many parts of the country.

Characters and Affinities: There is usually no difficulty in distinguishing adult birds of *australis* from *longipes*; the former have little if any dorsal streaking, a browner tone to the plumage, and are larger; male *longipes* never have the yellowish breasts of adult *australis*. Young birds are more alike, but the differences in plumage tone hold, in my limited experience. *P. australis rakiura* approaches *longipes* in size and in the tone of its dorsal plumage, and in having the light shaft-streaking on the head more persistent than in *australis*, but can be distinguished from *longipes* in lacking the distinctive mottled throat pattern. *P. a. longipes* is the most distinctive of the three races of New Zealand robin here recognised, the light centres of throat and dorsal feathers, in addition to the differences in dimensions and (even more important) proportions, sharply differentiating it from the other two. This emphasises the zoogeographic generalisation (to which I know no exception among birds) that the 21 mile Foveaux Strait is a less important faunal barrier than the 16 mile Cook Strait.

***Petroica (Miro) australis australis* (Sparrman). South Island Robin.**

Turdus australis Sparrman, *Museum Carlson*, pt. 3, no. 69, 1788. (Dusky Sound.)

Turdus albifrons Gmelin, *Syst. Nat.*, vol. i, pt. ii, p. 882, 1789. (Dusky Sound.)

Turdus ochrotarsus Forster, *Descr. Anim. ed. Licht*, p. 82, 1844. (Dusky Sound.)

Miro bulleri Buller, *Supplement, Birds N.Z.*, vol. ii, p. 123, 1906. (Karamea Saddle.)*

* In the Buller Collection, in the Canterbury Museum, are 5 skins from Karamea Saddle, 1895, which constituted some of the original series on which the diagnosis of *Miro bulleri* was based. Of these syntypes I here select a male, Register Number 1082.10 as lectotype.

Buller, in the reference quoted, unintentionally legalised a manuscript name of Sharpe's which was never published by the latter author. Buller claimed that there were two "species" of robin in the South Island, differing in colour of the underparts; one was *albifrons* and the other the Karamea form, which Buller stated agreed with Gray's (1845) figure of *albifrons* but not with his description. But Gray's figure was based on the Forster drawing of *ochrotarsus*, a name given (as Buller pointed out at the bottom of the same page) to the same Dusky Sound specimen as *albifrons*, so that the alleged colour characteristics of *bulleri* are those of the type of *albifrons*. Mathews and Iredale (1913, p. 439) recognised *bulleri* as an "Alpine form." My analysis of the variation in the South Island Robin has not brought out any consistent relationship between breast colour and locality, either altitudinal or geographic. In dimensions, however, there is a fairly regular 'cline,' between larger birds in the extreme north of the South Island and smaller birds in Otago, but the amount of overlap is such that this cannot be used, on the basis of the material available, to separate more subspecies in the South Island. The cline could be recognised in the nomenclature by using *bulleri* for the generally larger northern population, and by calling the South Island robin (in accordance with Huxley's recommendations for the nomenclature of clines, 1939, 1940, 1942), *Petroica (Miro) australis* cl. *australis-bulleri*. This may be the best procedure if the nomenclature of clines becomes generally accepted, but it is not adopted here because (a) no exact topotypes of *australis* have been seen, (b) the name *bulleri* was not applied to the population at the extreme north of the cline but to birds of somewhat smaller mean size (c) because recognition of the two extreme forms of the South Island robin would tend to suggest that the differences between them were of equal rank to the differences between either one of them and *P. australis longipes*. Therefore, I group all the South Island robins under one subspecific name, presenting below the evidence for an intra-racial cline.

Adult Male: Crown, sides of head, ear coverts, back, rump, upper tail coverts, fuscous to chaetura drab (R.) feathers of crown with narrow terminal edges of blackish brown giving a subdued scalloped effect; feathers light-shafted only at their bases, which are slate-coloured; white frontal spot, about as wide as base of bill and not as high, separated from bill by narrow dark band; lores and throat a shade lighter than upper parts, with persistent light shafts; tail blackish brown without pattern; wing blackish brown, an obscure white alar bar confined to the inner webs of secondaries and inner five primaries, extended on to outer webs as ill-defined slate grey areas; under coverts faintly flecked with whitish; breast maize yellow (R.), apparently varying with age, with a clear line of demarcation from the dark plumage of the neck; flanks fuscous; vent and under tail coverts white; thighs fuscous with whitish tips. (Winton, Southland, April).

Adult Female: Dorsal plumage fuscous, scalloped on head, with light shafts showing on crown only; throat hair brown with pale shafts, decreasing towards shoulders and breast; sides of head hair brown

with light shaft streaks grading into the fuscous of dorsal plumage; ear coverts fuscous, streaked with light shafts; wing and tail as in male but browner, remiges with paler (drab) outer webs; alar bar ill-defined. Breast whitish, more restricted than in male. (Otago, undated.) In the field, the female of a pair appears paler and duller than a male, and many skins marked female agree. However, there are a number of skins marked female which cannot be distinguished from males: most of such anomalous skins are from Nelson (collected Travers).

TABLE 9—DIMENSIONS OF *Petroica (Miro) australis australis* (Sparrmann)

Collection and number	Locality	Date	Sex	Wing	Tail	Tarsus	Mid-toe	Culmen
Dom. Mus.	D'Urville Id.	13/4/05	♂	102	76	38.5	26.5	18.5
C.M.1082.19	Chetwode Id.	10/5/25	♂	101	73	38	26	19
E.F.S.	Chetwode Id.	16/10/26	♂	102	75	39	28	19
H.G.D.56	Chetwode Id.	—	♂	102	77	39.5	—	18.7
P.619	Pickersgill Id.	6/11/15	♂	99	69	39.5	25.5	19.5
H.G.D.14	Pickersgill Id.	—	♂	97	77	39.5	—	18.7
C.M.1082.24	Pickersgill Id.	26/5/15	♂	102	75	39	26	19
Dom. Mus.								
A.249	Nelson	May, 1897	♂	97	71	37	—	—
Dom. Mus. —	Nelson	Apr., 1905	♂	103	79	40	—	—
Dom. Mus. —	Nelson	Apr. 1905	♂	92	69	38	—	—
C.M.1082.16	Pelorus Woods	1894	♂	101	76	41	—	—
C.M.1082.20	Owen Junction	30/5/29	♂	99	72	40	26	18.5
C.M.1082.21	Owen Junction	30/5/29	♂	96	75	40	26	19
C.M.1082.10	Karamea Saddle	1895	♂	96	72	40	27	19
C.M.1082.13	Karamea Saddle	1895	♂	98.5	71	41	26	19
C.M.1082.25	Akaroa	—	—	102	79	38.5	25	18
P.737	Akaroa	—	—	97	76	38.5	—	—
C.M.1082.14	Otago	1892	♂	95	68	37.5	26	18
A.M.27.1	Otago	—	♂	97	65	39.5	23	19
P.254	St. Martins Bay	—	♂	96	72	36.7	26	19.5
E.F.S.	Winton, St. land.	14/4/01	♂	101	70	42	26	20
Dom. Mus.	Nelson	May, 1897	♀	93	68	38	—	—
Dom. Mus.	Nelson	Mar., 1904	♀	98	72	37.5	—	—
C.M.1082.7	Karamea Saddle	1895	♀	96	70	38.5	26	19
C.M.1082.15	Karamea Saddle	1895	♀	97	71	39	23.5	18
C.M.1082.6	Otago	1892	♀	92	71	36	24	17
A.M.27.2	Otago	—	♀	93	67	36	24	17.5

Note: The skins from Karamea Saddle are syntypes of *Miro bulleri* Buller; of them, C.M.1082.10 is here selected as lectotype.

Fledgling: No accurately sexed specimens seen. Obviously immature skins resemble adult females, but some have light shafts more prominent on crown, nape, scapulars; the breast is not coloured, but whitish, and is more restricted than in adults, streaked with hair-brown. A known fledgling from Matakita River (just flying on November 29) is streaked dorsally, has virtually no frontal spot; throat pale, breast and flanks irregularly washed with buff, and alar bar buff, not grey, on outer webs.

Variation: Plumage variation within the sexes is difficult to assess because of lack of confidence in the sexing of a number of museum skins. Breast in adult males varies from whitish to cream buff and maize yellow; as fledglings all have whitish breasts, this may be merely a matter of age. Frontal spot varies, as in other *Petroica*, and can be accentuated or minimised in skins by different methods of taxidermy.

Variation in size is more definite, and is related to locality: there is a cline of decreasing wing length from the Marlborough Sounds, in the North, to Otago-Southland, and similar clines in tail and tarsus lengths, with a few discrepancies perhaps due to the smallness of the series available from some areas. The data may be summarised as a table. (See also Fig. 15.)

Area.	Number.	Mean Wing.	σ	Mean Tail.	σ	Mean Tarsus.	σ
Marlborough ..	7 males	100.7	1.98	74.6	2.8	39.0	1.1
Inland Nelson ..	20 males	98.2	3.35	72.9	3.38	38.6	1.25
Banks Peninsula	3 skins	97.0	—	75.3	—	37.7	—
Otago-Southland	5 males	96.4	2.97	67.8	3.1	38.1	2.7

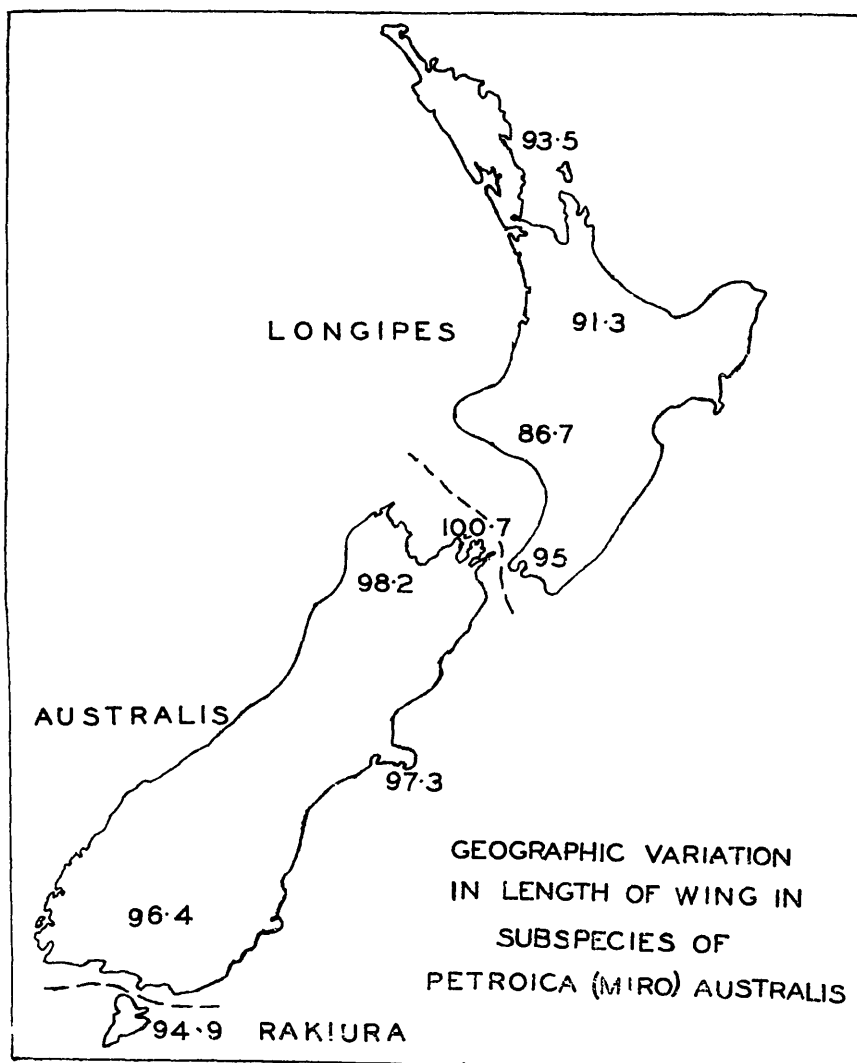


FIGURE 15

The differences between the wing and tail measurements of the extreme populations are probably significant ($t = 2.7$ and 2.5) but it is likely that fuller material from the intervening areas would bridge the gap even more fully than do the skins measured. For over half a century there have been no robins on the east side of the Alps, except for the small relict population on Banks Peninsula (which is possibly now extinct), so that the chances of obtaining further data on the Canterbury side are small. On the west side of the Alps robins persist locally in reduced numbers, but no skins have been seen.

Dimensions: See Table 9 for measurements of individual skins. For the whole South Island population the figures for 35 males are: wing, 93–103 (mean 98.3, $\sigma = 3.16$); tail, 65–79 (mean 73.1, $\sigma = 3.8$); tarsus, 35–42 (mean 38.6, $\sigma = 1.5$); middle toe 23–27; culmen, 16.5–20; bill from skull, 20–22.

Females (19 measured): wing 91–100 (mean 96, $\sigma = 2.7$); tail 67–77 (mean 71, $\sigma = 2.5$); tarsus 36–40 (mean 37.4, $\sigma = 1.35$).

The sexual differences in mean wing and tail lengths are significant.

Proportions: Tail/wing ratio in 33 skins, 70–97, mean 74%, $\sigma = 2.1$; tarsus/wing ratio, 36–41, mean 39%, $\sigma = 1.7$.

Distribution: In Marlborough, the robin still exists in a large number of localities, the records from dry manuka scrub of valleys through land mainly in tussock grassland being particularly notable. Robins were reported very common in the Picton-Blenheim district as late as 1894 (J. Walling Handly); they have largely gone from the Sounds area, where Dieffenbach saw and collected them in 1839, but persist on Little Mount Stokes, above Manaroa (A. C. O'Connor), near Pelorus Bridge, and on the outlying islands (D'Urville, Chetwode, Pickersgill). In the dryer district of eastern Marlborough, Messrs. Kean, Barra, Vercoe and Rye (Department of Internal Affairs) supply the following records:—Omaka Valley, confluence with Dillon Creek (1946), Waihopai River, below Benopai Station (1926 and later), Wairau Valley, 1 mile above Rainbow Accommodation House (1931, 1937), Ure Valley (1936–7), Lower Awatere, above junction of Taylor's Pass Road. Mona Gordon, in 1938, reported that the robin was "still found" at Kaikoura. All told, the robin's present status in Marlborough is satisfactory.

Although, in Nelson Province, as elsewhere, the robin "has become less plentiful than of yore" (Moncrieff, 1932), yet it is generally distributed in the forested areas, including bush near the city of Nelson. Detailed locality records are: Dun Mountain (1936 and later), Onekaka-Aorere Valley; Mokihiui River (1935), Wangapeka River (P. Moncrieff, 1934), Owen Junction (A. C. O'C.), Buller Valley, from Tophouse to Inangahua (R. H. D. Stidolph, 1945), Karamea Saddle, Tarakohe to Mt. Arthur, Capleston (A. C. O'C.), head of Lake Rotoroa, Mt. Travers, Abel Tasman National Park (F. Newcombe), Fenian Creek (branch Oparara River, 1932–33, R. J. Scarlett), Mangles Valley (1946), Matakitaki Valley (E. F. Stead), Lanky's Gully, Reefton (M. Gage), Rahu Saddle (W. A. Watters, 1945).

From Westland there are few detailed records, although the robin is believed to persist in many suitable areas west of the Alps. Taramakau Valley (E. F. Stead, "nineteen-forties"), and Totara Saddle, behind Ross (M. Gage, 1940), are the only actual localities I have received. From the lowland bush areas of North Westland from the Taramakau to the Hokitika River, the robin has long been absent; nor does it persist near Lake Brunner, where W. W. Smith recorded it in 1888.

The robin has fared worse in Canterbury than elsewhere in the South Island. On Banks Peninsula it was abundant in the "seventies" when Haast supplied skins to Otto Finsch, was "still to be seen" there in 1907 (Drummond) and persisted until a comparatively late date in the Akaroa district: indeed Dr R. A. Falla suspects that the species may still exist, although there are no actual reports in the last few years. On the Canterbury Plains robins may never have been widely distributed, and I have seen no records.* In the bushed gorges of the foothills, however, robins were abundant in the "seventies" (Potts, 1870); according to Mr. E. F. Stead they disappeared from districts east of the main range at the end of the century. In the Ashburton-Springburn district of South Canterbury, Mr. W. W. Smith informed Buller in 1903 that the robin was "almost extinct" and "very rarely seen." The only definite reports of robins in Canterbury during the past 15 years come from the Boyle Hut, on the Canterbury side of Lewis Pass (R. A. Falla, 1945) and Parnassus and the Conway River near the Marlborough Boundary (R. A. F., 1946).

In Otago the robin seems to have been fairly widespread, though perhaps always localised to some extent by the incompleteness of forest cover. There are a number of skins collected by Smythe and labelled vaguely, "Otago, 1892". In 1907 Drummond's correspondents reported its presence at Waihemo (North Otago), and Tautuku (South Otago), but extinction at Woodside (West Taieri), where previously common. Major R. A. Wilson remembers robins in a garden on the east shore of Dunedin Harbour in about 1893. The persistent occurrence of robins at Whare Flat, within 10 miles of Dunedin, in the last few years, suggests that there may be unreported small robin populations surviving in eastern Otago† Other recent records from the province are all from a fairly restricted area near the head of Lake Wakatipu in western Otago; Dart, Routeburn, Rees Valleys, Sylvan Lake, Diamond Lake, foot of Mount Earnslaw [Arcadia] (several observers).

The status of the robin in Southland appears to have changed for the better after a decline early in the present century. Presumably the bird was initially well distributed and abundant in forested areas. The earliest collected specimens came from Dusky Sound, Reischek reported their presence in Fiordland in 1884, R. Henry reported increasing scarcity of small birds from 1894 to 1908, and Stuart

* In Drummond's summary (1907, p. 40) the record of the robin from Riccarton is taken to mean the tit, which is not listed.

† See *N.Z. Bird Notes*, vol. 3, no. 8 p. 217, 1950, for reports of increasing numbers near Dunedin.

Sutherland did not list the robin from Puysegur Point in 1919, yet the bird was seen at several of the Sounds during the 1946 expedition of the Department of Scientific and Industrial Research in the ketch *New Golden Hind*. In the coastal forest from beyond the Waiau to Preservation Inlet Philpott (1919) reported that the robin had disappeared but that it was still to be found in certain other Southland localities closer to towns. He recorded rapid disappearance from the Titiroa Forest (Hunter Mountains) from 1914 to 1917, but persistence, locally, on the Monowai Flat. Professor James Park noted the robin's absence from Western Southland during extensive explorations in 1919-20, but saw one pair near Lake Gunn in 1921. In late years, however, there have been records of the robin's comparative abundance in the forested country immediately west of the Waiau: Lillburn Valley, Hope Arm, Manapouri, Upper Waiau Basin (between Monowai and Manapouri, Dept. of Internal Affairs), and Mavora Lake (W. A. Watters); Eglington Valley and west of Te Anau (several observers). Further East, the species was present at Winton in 1901, at Wyndham and Mataura in 1907, and Waianiwa in 1907, and there have been late records from Piano Flat (a persistent locality since 1913) and Glenavy, Waikaia and Golden Downs (1940).

In summary, it may be stated that, instead of the eight localities where Fulton (1908) was able to record the South Island robin as common, there are some dozens of places where the bird is reasonably abundant. Part of this apparent improvement in status must be due to the operation of a greater number of observers, but, on the other hand, the only large area where robins have disappeared since 1908 is Banks Peninsula, and there is some evidence, in Nelson and in Otago and Southland, of a definite improvement.

Characters and Affinities: Of the three races of *Petroica* (*Miro*) *australis*, the nominate one is the largest in average dimensions, and has the most "advanced" male plumage, with appreciable ventral pigment and with dorsal shaft streaking absent in the adult. In plumage, dimensions and proportions *australis* is closer to *rakiura* (Stewart Island), than to *longipes* (North Island).

***Petroica* (*Miro*) *australis rakiura*, new subspecies. Stewart Island Robin.**

The six male robin skins available from Stewart Island and three of its outlying islands are smaller in their average dimensions than the South Island series. When the figures are compared with those for the generally smaller birds inhabiting the southern end of the South Island, the difference, in wing and tarsus, is still evident (though reduced), and leads to the conclusion that the cline of decreasing size from north to south is continuous across Foveaux Strait. But in addition to the difference in size between robins from opposite sides of Foveaux Strait (a difference which cannot be shown, on the basis of the small series available, to be statistically significant), there are differences in plumage that allow taxonomic separation of the Stewart Island birds.

Holotype: Adult male, Jacques Lees Island, off east coast of Stewart Island, December, 1932. In the collection of Edgar F. Stead,

Esq., Christchurch.* Dimensions: length of skin, 180; wing, 98; tail, 74; tarsus, 38; mid toe, 25; culmen, 18; bill from skull, 21 mm. The descriptions that follow are based on a series of five skins from Jacques Lees (including the type), on two from Pukeweka and one from Solomon Island (South Cape Group, off the south of Stewart Island), and three labelled "Stewart Island" in the Dominion Museum.

Adult Male: Similar to the nominate race, but with a smaller frontal spot, dorsal surface darker, dark mouse grey rather than fuscous (R.), and whitish, uncoloured, breast.

Adult Female: The limited material suggests that the dorsal colour is slightly darker than in females of the nominate race.

Variation: One male (Pukeweka, June) has no dorsal streaking, and the type is a similar bird with few light feather shafts on the head and neck. It has been selected in case further material should show that light feather shafting is confined to immature birds. But over half the series available have more or less pronounced light shafts to the feathers of the crown and neck, although only one of them seems to be other than adult. Mr Stead told me that he collected a fair representation of the adult population at Jacques Lees at a season when juvenal birds are readily recognisable as such. Furthermore, Mr Stead noted that the Stewart Island robin resembled the North Island bird rather than the South Island one in its plumage and dorsal streaking. It seems, therefore, that a tendency to retardation, the retention in the adult of the light feather shafts of the dorsal surface, is characteristic of *rakiura*.

TABLE 10—DIMENSIONS OF *Petroica (Muo) australis rakiura* subsp. nov.

Collection and number	Locality	Date	Sex	Wing	Tail	Tarsus	Mid-toe	Culmen
E.F.S.1	Jacques Lees Id.	17/12/32	♂	94.5	70	36	25.5	16
E.F.S.2	Jacques Lees Id.	Dec, 1932	♂	98	74	38	25	18
E.F.S.6	Solomon Id.	—	♂	90	65	35	25	18
P.413	Pukeweka	13/6/38	♂	95	73	37	25.7	—
Dom. Mus.	Stewart Island	July, 1899	♂	98	75	39	27	18
Dom. Mus.	Stewart Island	July, 1907	♂	94	71	37.5	26	17
E.F.S.3	Jacques Lees Id.	17/12/32	♀	93	70	37.5	23.5	16
E.F.S.4	Jacques Lees Id.	17/12/32	♀	90	69	37	24	—
E.F.S.5	Jacques Lees Id.	12/2/33	♀	89	64	36.5	—	—
P.412	Pukeweka	13/6/38	♀	87	66.5	34	25.3	18.2

Note: Specimen E.F.S.2 is the holotype of the subspecies.

Dimensions: See Table 10. Males (six measured): Wing, 90–98 (mean 94.9, $\sigma = 2.98$); tail, 65–75.5 (mean 71.8, $\sigma = 3.82$); tarsus, 35–39 (mean 37.1, $\sigma = 1.43$). Females (4 measured): wing, 87–93, mean 91.5; tail, 64–70, mean 67.4; tarsus 34–37.5, mean 36.2. The difference in wing length between males of *rakiura* and males of *australis* is statistically significant, but significance cannot be demonstrated for the differences between *rakiura* and the small series of Otago-Southland specimens of *australis*.

Proportions: Tail/wing ratio in 6 males, 72–79.5, mean 75.7; tarsus/wing ratio, 38–40, mean 39.1. Tail/wing ratio is not significantly higher than in *australis* (mean 74%).

* Now in the Canterbury Museum.

Distribution: Specimens examined and attributed to this subspecies come from "Stewart Island" (collected between 1899 and 1907; probably from main island); from Jacques Lees Island, off the north-east coast; and from Pukeweka and Solomon Islands, off South Cape. For the present it seems reasonable to draw the boundary between the range of *australis* and *rakiura* at Foveaux Strait, and the following records of robins in the Stewart Island area may be listed under *rakiura*: main island, Port Pegasus; behind Mason Bay (W. Dawbin); Lower Freshwater Valley (W. A. Watters); Green Island; Big South Cape Island (W. P. Wardlaw).

Characters and Affinities: The Stewart Island race of the robin is a "weak" subspecies, differing from the South Island one, *australis*, in its smaller mean size, darker, "mouse grey," dorsal plumage, paler ventral surface, and more persistent light feather shafts. Although, in its smaller size and in some of its plumage characters, *rakiura* approaches *longipes*, the latter differs more fundamentally in tail/wing proportion (70% compared with 74% in *australis* and 75.7 in *rakiura*).

***Petroica (Miro) traversi* (Buller).** Chatham Island Robin.

Miro traversi Buller, *Birds New Zealand*, p. 123, June, 1872 (Chatham Islands)

Petroica traversi Hutton, *Ibis*, 1872, p. 245. (Chatham Islands)

Characters: A monotypic species of the subgenus with entirely brownish black plumage, smallish size, and distinctive proportions. The wing is short and rounded, the first primary disproportionately long, about 60% of second. Primary formula: $2 = 9/10$ or $2 = 10$; usually $5 > 6 > 4 > 3 > 7 > 8 > 9 > 2 > 10$. Tarsus 38% of wing. Soft parts: tarsi brownish black, soles of feet "bright yellow," iris dark brown (Little Mangare, January.)

Moult and Plumages: In reporting a visit to Little Mangare Island on 2 January, 1938, it was noted that "immature birds of the year, with fresh plumage and short tails were . . . present" (Fleming, 1939, p. 507). A correction is necessary, since examination of a January skin of an immature male shows that its tail is not much below average, but an adult collected in the same month has new rectrices (in sheath) only 15 mm long; the sixth and tenth primaries are short and new, and the bird is in double contour feather. A January female is, however, in faded plumage without sign of moult. At the date mentioned, therefore, short tailed birds were probably moulting adults. The only juvenal-plumaged skin seen is described below

Adult Male: Crown, forehead, sides of head, lores, ear coverts, scapulars, rump, lesser coverts, upper tail coverts, fuscous black, fading with wear to bone brown (R.); wing fuscous without pattern; tail blackish brown; throat, breast, belly, flanks, vent blackish brown, all feathers with slate coloured bases and light basal shafts. (Little Mangare Island, January.)

Adult Female: No sexual differences have been found, the difference between sexes in plumage tone being less than the difference between fresh and faded males

Fledgling Male: Similar to adult but crown, neck and scapulars with light shafted feathers, and contour feathers of both upper and lower surfaces with faint light brown tips. (Little Mangare, January.)

Dimensions: See Table 11. Males (11 measured): wing 81-86 (mean 82.6, $\sigma = 1.87$); tail 61-68 (mean 63.7, $\sigma = 1.97$); tarsus 30-32 (mean 31.5, $\sigma = 0.74$); mid toe 21.8-25, mean 23.3, culmen 13.4-14.5, mean 13.9; bill from skull 16-17.2. Females (10 measured): wing 79-85, mean 81.4; tail 62-66, mean 64; tarsus 30-33, mean 31.2. The sexual differences in dimensions are not statistically significant.

TABLE 11—DIMENSIONS OF *Petroica (Miro) traversi* Buller

Collection and number	Locality	Date	Sex	Wing	Tail	Tarsus	Mid-toe	Culmen
C.M.1084.3	Little Mangare Id.	18/8/01	♂	83	61	30	24	14
Auck. Univ.	Little Mangare Id.	—	♂	81	61	33	25	14
P.385	Little Mangare Id.	—	♂	81	63	31.6	22.5	13.4
Dom. Mus.	Little Mangare Id.	18/8/1900	♂	81	64	31.5	23	14
„ A.259	Tapuaenuku (= Little Mangare I.)	—	♂	83	64	31.5	23.5	14
„ A.265	Tapuaenuku	Sept., 1907	♂	82	63	30.5	22	14
Dom. Mus.	“Pitts Island”	16/9/1871	♂	83	68	31.5	22.7	14
„ A.264	“Chatham Is.”	—	♂	81	63	31.5	24	13.5
„ A.258	Mangare	Sept., 1871	♂	86	64	31.5	23	14
„ A.257	Mangare	Dec., 1871	♀	81	63	30	22	13.5
„ A.262	“Pitts Island”	16/9/1871	♀	81	66	31.5	24	13.5
Dom. Mus.	Little Mangare Id.	18/8/1900	♀	85	65	32	24	13.5
Dom. Mus.	Little Mangare Id.	18/8/1900	♀	82	64	30	21	13.5

Note: The specimens collected in 1871 by H. H. Travers are those by which the species was first made known. Buller received a pair which became the co-types of *Miro traversi*, and these apparently reached the Dominion Museum with the rest of his first collection. Other specimens collected by Travers were described by Hutton as *Petroica traversi*; Hutton was, in 1872, attached to the Colonial Museum and Geological Survey, Wellington, and the specimens labelled “Pitts Island” may be the type material of his name.

Proportions: Tail/wing percentage in 18 skins, 73.7-82 (mean 77.7); tarsus/wing percentage 36.1-40.8, mean 38.2.

Distribution: It is inferred that the species at one time ranged throughout the Chatham Islands, but it had become extinct on the main Chatham Island before 1871. Of the four Dominion Museum skins collected in 1871 by H. H. Travers, two are marked “Pitts Island” (dated September 16, 1871), and two Mangare (dated September and December, 1871). Other localised skins seen are all from Little Mangare Island (Tapuaenuku) where the species has persisted in a very small area of scrubby forest (Fleming, 1939). The existing Chatham Island robins, estimated at 20 to 35 pairs in 1937, must constitute one of the smallest populations of a bird species in the world.

Habitat: The remaining robins on Little Mangare occupy a small area of coastal forest and the ledges of scrubby vegetation on the surrounding cliffs.

General Habits: The species has the same erect posture as *P. australis*, a character perhaps related to the long tarsus shared by both species. From the hour's observations in 1938, I concluded

that it behaves like the New Zealand robin in its flights from perch to ground, where it was seen to feed in the fresh soil of collapsed petrel burrows. "Their song was somewhat similar to that of *Miro longipes*, but not nearly so full in tone nor so varied in composition." Elaborating this statement, I would emphasise that nothing was heard that could be compared with the song of *P. macrocephala*. My impressions were that the song heard (given, it must be noted, by birds approaching, or in, the moult) was like the first three notes of the descending chromatic song of *longipes*, but set lower. Little is known of breeding habits, except that the species is territorial; an empty nest was "low down at the base of a branch and almost sheltered above by a higher branch" (Fleming, *loc. cit.*).

Affinities: The black colour and size give a superficial resemblance to *Petroica macrocephala danneferdii* which is quite misleading. The colouration is attributed to the development of racial melanism at a comparatively late stage in the history of the species. The small wing length (compared with that of mainland robins) is believed secondary, for the very long first primary suggests that the wing, at least, has at one time been longer than it is. Affinity with the robins is attested by the emarginate seventh primary (Fig 7), the long tarsus, and by what is known of the live bird's posture and song. Nevertheless, the differences between *P. traversi* and *P. australis* point to a much longer period of separation than that which has resulted in the differentiation of races in *P. australis* and *P. macrocephala*.

The suggestion that the characteristic long first primary of *traversi* indicates a phyletic reduction of wing length may be supported by the following line of reasoning. In most dimensions *traversi* is not much smaller than *longipes*, the smallest New Zealand robin. It is difficult to suppose that the first primary, rudimentary in so many Passeres, has lengthened in response to selection pressure (or through any other evolutionary process): it seems more probable that that feather has lagged behind in a general reduction in length of wing elements. If, now, we suppose that the short, rounded wing of *traversi* is the result of negative heterogony affecting chiefly the longest primaries, we may reconstruct a hypothetical ancestor by increasing the length of the longest primary (or alternatively of the whole wing) until it bears the same proportional relationship to the first primary as does that of *longipes*,* as in the following table—

	<i>P. (Miro) traversi</i>	Hypothetical ancestor of <i>P. traversi</i>	<i>P. (Miro) a. longipes</i>
First primary	30	30	30
Second primary	50	51	51
Longest primary	67	72	72
Wing length	82.6	87.6–90.7	90.7
Tail	63.7	63.7	64
Tarsus	31.5	31.5	36.2
Tail/wing %	77%	72.5–70%	70%
Tarsus/wing %	38%	36–35%	40.3%

* The race *longipes* is selected for this purpose on account of its small size, but it is not intended to suggest that *traversi* is more closely related to *longipes* than to any other race of *P. (M.) australis*.

It may be noted that, even if no other dimensional changes were involved, an ancestral longer wing would result in a tail/wing percentage approaching that of *P. australis* (70–75%). The tarsus/wing percentage would be reduced below that of *australis* (37–42%) and would approach the proportions characteristic of *Petroica* s.str. (23–37%). If, as is otherwise evident, *P. traversi* was isolated from *P. australis* at a fairly remote period, it is reasonable to suggest that the tarsus had not then gained the extreme length it now has in the latter species

THE PHYLOGENY OF THE NEW ZEALAND TITS AND ROBINS

1. Correlated Characters.

Variability: Table 12 presents the co-efficient of variation ($V = \frac{100 \times \sigma}{\text{mean}}$) for three dimensions of males of the New Zealand races of *Petroica* other than *dannefaerdi*, for which there are insufficient sexed skins to allow compilation of similar data. Scrutiny of the table shows that the lowest figures in each column pertain to insular races, but the correlation is not complete for wing and tail, perhaps because unsuspected moult and wear contribute to the variability of those dimensions. For tarsus, however, the co-efficients are in every case higher for the races inhabiting the three main islands of New Zealand than for the related insular races, and there is justification for a generalisation that the insular races tend to have a smaller store of variability than the wider ranging mainland populations.

The inferred greater genetic uniformity of small island populations is in accord with the theoretical conclusions of Sewall Wright (and others) on the relation between total population size and the loss or fixation of gene allelomorphs, resulting in nonadaptive divergence in insular races.

TABLE 12—COEFFICIENTS OF VARIATION ($V = \frac{100 \times \sigma}{\text{mean}}$) IN MALE *Petroica*

	Locality	N	Wing	Tail	Tarsus
<i>P. m. macrocephala</i>	South Island	26	2.1	3.8	6.0
<i>P. m. toitoi</i>	North Island	38	3.1	3.5	8.0
<i>P. m. chathamensis</i>	Chatham Island	12	1.4	3.0	4.1
<i>P. m. marrineri</i>	Auckland Island	9	2.2	2.1	2.7
<i>P. a. australis</i>	South Island	35	3.1	5.2	3.9
<i>P. a. longipes</i>	North Island	15	3.2	3.7	3.8
<i>P. a. rakiura</i>	Stewart Island	6	3.1	5.3	3.8
<i>P. traversi</i>	Chatham Island	11	2.1	3.1	2.3
Races on main islands of New Zealand			2.1–3.2	3.0–5.2	3.8–8.0
Races on small islands:			1.4–2.2	2.1–3.1	2.3–4.1

Size: In *Petroica* in general, and in *P. macrocephala* in particular, there is a fairly strong correlation between size and temperature (i.e., latitude), in accordance with Bergmann's "rule". This is illustrated in Figs. 16, 17. The notable exception is *P. m. dannefaerdi*, of the Snares, which is slightly longer in the wing than *marrineri* (Auckland Islands). Without body weights it is difficult to assess the importance of this exception, which may be related to the Sewall Wright effect operating on a small population (of *circa* 500 breeding

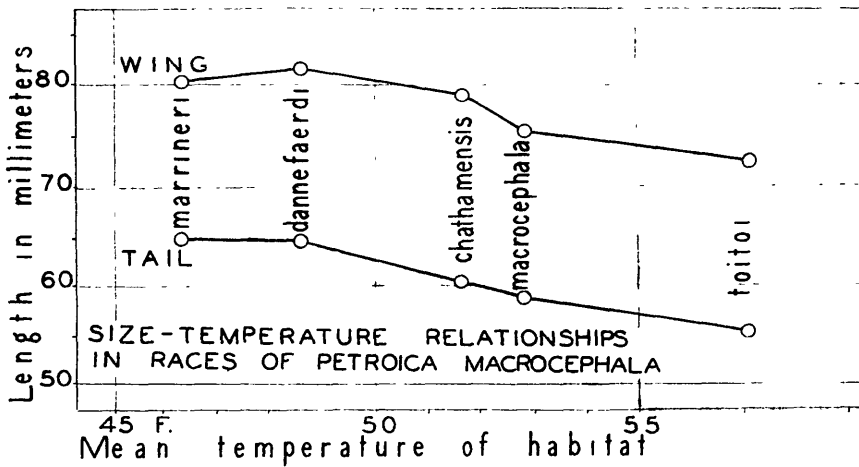


FIG 16—*Petroica macrocephala*. Mean wing and tail length of males of the five geographic subspecies plotted against mean temperature of habitat. See text for further explanation.

pairs). Current interpretation of the mechanism governing such intra-specific clines correlated with geographic gradients is that they are selectively determined. There is a *prima facie* case for believing that response to a geographic rule may be fairly rapidly attained by races of a far-flung species, granted that the species is initially obedient to it: should members of a species already exemplifying a geographic rule invade a new thermal environment, selection pressure will immediately tend to modify the invaders in terms of that rule. The adaptational control of size in accordance with Bergmann's rule is significant, because absolute size may determine allomorphic differences in proportions, differences that appear important functionally and which are doubtless under selective control, but which are due primarily to the correlation of body size with climate.

In *Miro* there is no consistent obedience to the Bergmann principle on the contrary, while the North Island *longipes* is smaller than the South Island *australis*, the evidence points to intra-racial clines with slope opposed to the Bergmann rule, with an abrupt discontinuity in the character gradient at Cook Strait. It must be noted that the differences between the means on which figures 15 and 18 are based are not in all cases statistically significant (the single aberrant skin from Wellington district is omitted): nevertheless the phenomenon seems worth recording, if only as a stimulus for the acquisition of more complete data. Mayr (1942, p. 90) notes that "the reasons for exceptions" (to the Bergmann rule) "are seldom apparent": no guess is hazarded for this case, but the discrepancy between intra-group and inter-group slopes is not without parallel (see Falla, 1940, p. 229, for cases in seabirds)

Tail/Wing Ratio: In *Petroica* there is a tendency, illustrated in Fig. 17, for the tail to be shorter, in relation to the wing, in tropical races and longer in sub-Antarctic races. Lack of information about body weight hinders interpretation,

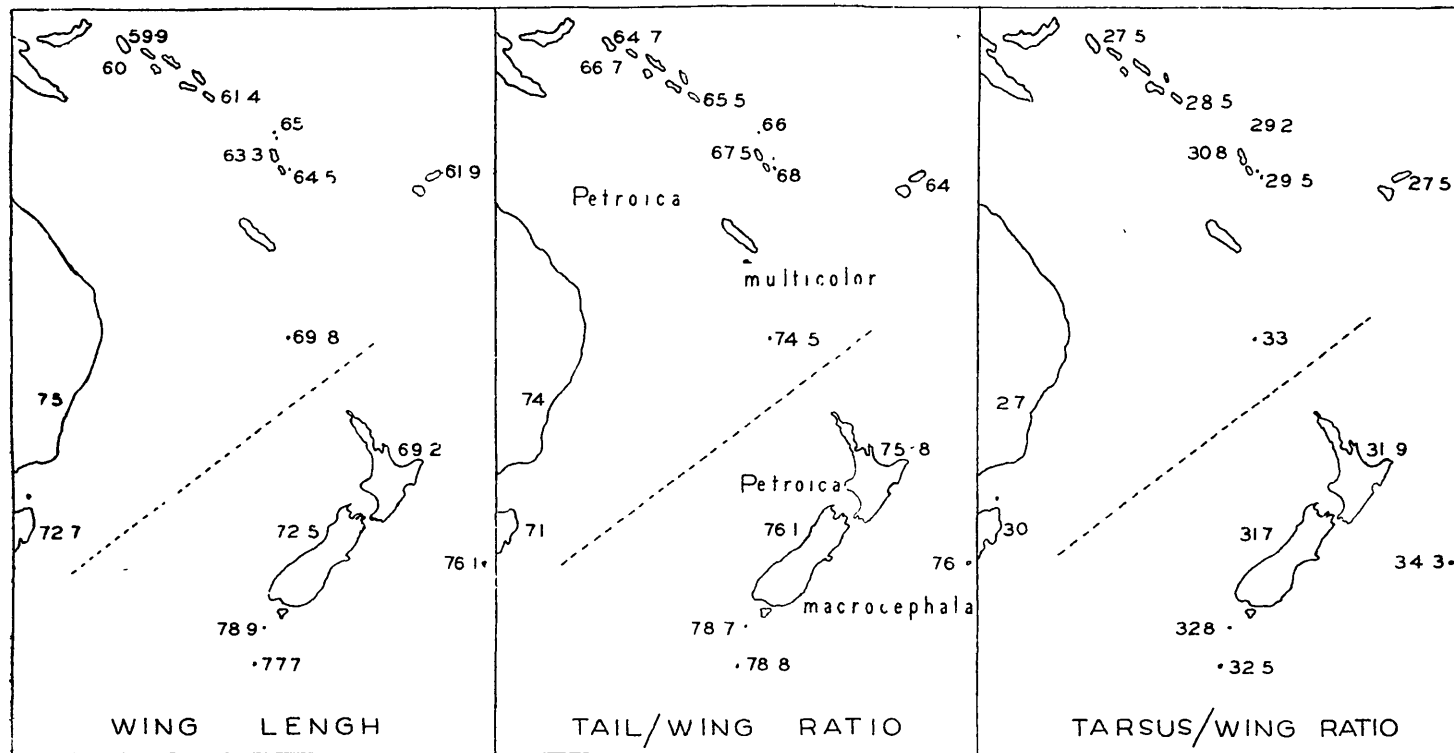


FIG. 17—Geographic variation of unit characters in the superspecies *Petroica multicolor* (Gould).
Mean wing length in millimetres, ratios as percentage of wing length.

The question that arises is: which, if any, of the linear dimensions is correlated with general size? Amadon (1943) has made a cogent plea for the recording of weights in the routine examination of bird specimens, because "we cannot fully evaluate the biological significance of geographical variation in measurements of appendages without first relating these measurements to general size." An attempt to use the dimensions "body length" obtained by subtracting "tail length" from "length of skin" was fruitless because of the variation in methods of taxidermy, and because of the smallness of the differences involved. When mean values for each dimension are plotted graphically against each race (the method used by Miller, 1941) some

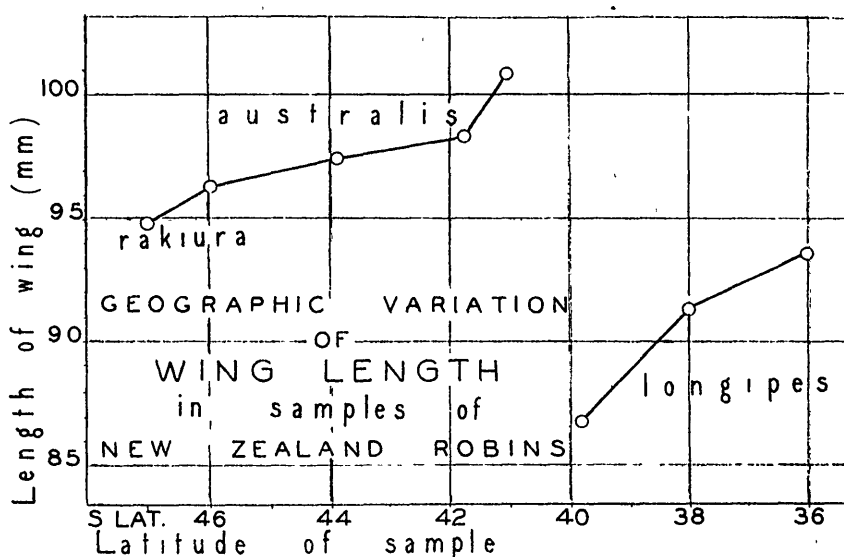


FIG. 18—Clines in wing length in races of *Petroica (Miro) australis* (Spar.).

general correlations are evident, but it is impossible to tell by inspection whether such correlations are isometric or allometric. The most satisfactory method of demonstrating the relationship between the size of one organ and that of another in a related group of races is by plotting the information on a double logarithmic graph when, if the points for several different forms fall on a straight line "curve," a constant growth rate (in this case phylogenetic and not ontogenetic) may be inferred. If the curve slopes at an angle of 45° with abscissa and ordinate, the relationship between the two organs is isometric—i.e., change in one is in direct proportion to change in the other, but if the slope of the curve is at any other angle, the relationship is allometric—i.e., changes are differential. Allometry between adults of different races, implying phylogenetic, rather than ontogenetic changes, is known as allomorphy (Huxley, Needham and Lerner, 1941) or heteragony.

The wing and tail measurements* of races of *P. macrocephala*, plotted on a log-log grid, fall on a reasonably straight line "curve" indicating allomorphic relationship. (Fig. 19C) Now, when the tarsus/tail and tarsus/wing relationships are plotted in the same way (Fig. 19, A, F) they also indicate, with an exception to be noted, definite relationships leading to the following argument:

1. The tarsus and tail bear an isomorphic relationship to each other—i.e., the curve slopes at 45° (exception: *chathamensis*).
2. The slopes of the tarsus/wing and tail/wing curves are parallel and allomorphic, sloping at an angle of about 52° .
3. There seems no reason why changes in tarsus and tail lengths should be isomorphic unless both are isometric with body size, although this statement can hardly be proved without body weights.
4. If tarsus and tail are isometric with body size as they are with each other, then the wing in *Petroica macrocephala* exhibits negative allometry. In the formula for the allometry involved ($y = bx^k$) the constant $k = 0.81$ and $b = 1.85$.

The wing and tail measurements of the Australian, Norfolk Island and Pacific races of *P. multicolor* have not been found to bear any simple relationship to each other. In the subgenus *Miro* there is an

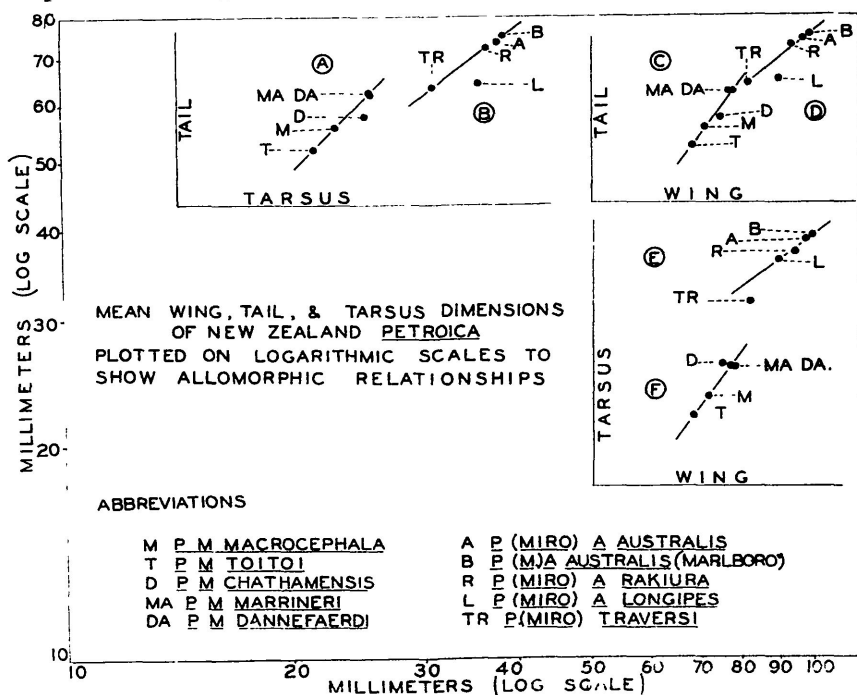


FIGURE 19

* The means for males, as presented in previous sections, and, for *dannefaerdi*, means for a series of both sexes, are the basis of these and other calculations. Most of the differences between the means are significant; where this is not the case it does not affect the argument offered.

increase in tail/wing ratio from 70 in the North Island *longipes* to 74 in the South Island *australis* and 75.7 in the Stewart Island *rakiura*: as in *P. macrocephala* the tail is relatively longer (or the wing relatively shorter) in the south, but in this case there is no simple allomorphy since the size-latitude relationship is irregular. This suggests that the tail/wing ratio may be selectively controlled by environment independent of the allomorphic relationship demonstrated in *Petroica*. New Zealand *Petroica* are exceptions to the generalisation of Rensch and others that wings of races that live in a cold climate are relatively longer than those of races that live in a warm climate.

When the mean dimensions for wing, tail and tarsus in *Miro* are plotted on a double logarithmic grid* there are approaches to straight line curves in some cases, but notable departures in others (Fig. 19, B, D, E). The tarsus/tail curve (B) approaches the isometric slope (45°) but *longipes* is off the line suggesting an excessively short tail, and *traversi* is also aberrant with a tarsus shorter than the rest of the series (*ante* p 146). The wing/tarsus curve (E) is allometric (slope 38°) but *traversi* is divergent, again because its tarsus is not long enough to put it into the series. The tail/wing ratio curve (D) is also allometric, with a slope not greatly different from that of wing/tarsus; *longipes* is again aberrant in the direction of shorter tail. There are almost as many exceptions as there are points for the drawing of these "curves" so that the situation is capable of more than one interpretation. The inferences affecting wing and tail are:

1. Wing tends to be positively allomorphic in *Miro*—i.e., larger forms have longer wings. Since the wing of *traversi* is believed degenerate for other reasons than its shortness, the generalisation might be better expressed as a tendency to reduction of relative wing length in smaller forms. That the allomorphy is in the opposite sense from that in *P. macrocephala* is inevitable since the size gradients in the two groups slope in opposing directions, whereas the gradients in tail/wing ratio have the same direction of slope.

2. *Petroica (Miro) australis longipes* has acquired a short tail by departure from the general rule (in New Zealand *Petroica*) that tail tends to vary isomorphically.

3. The high tail/wing ratio of *P. (M.) traversi* could have been acquired by reduction of tail and wing in accordance with the same allomorphic formula that pertains among the robin populations of the South Island and Stewart Island.

Tarsus Length: The tarsus/wing ratios in *P. multicolor* and *P. macrocephala* at first sight show no regular geographic correlation. However, the highest values for *multicolor* all occur in insular races; *macrocephala* has a higher value than continental *multicolor* and for the insular races of *macrocephala* the values are higher still, that of *chathamensis* being highest of all. The plotted data (Fig. 19, A, E) suggests that the discrepantly long tarsus of *chathamensis* is due to phylogenetic positive allometry of that bone; the alternative that wing

* Because of the geographic variation within *P. a. australis* the extreme populations can provide additional points for plotting.

and tail have undergone correlated negative allometry is not in accord with the sum total of evidence.

In the subgenus *Miro* the tarsus is relatively longer than in other *Petroica* (indeed than in other Muscicapidae). Not only are tarsus/wing and tarsus/tail ratios high, but the mean toe/tarsus ratio, which ranges from 76 to 83 in races of *P. macrocephala*, is 74 in *P. traversi* (supporting other evidence that the high tarsus/wing ratio of that species is in part the result of wing degeneration) and only 65-68 in *australis*. It is apparent that the long tarsus of *Miro* is the result of positive allometry in the history of the group just as in *P. m. chathamensis*. If the environment on islands is in some way selective for long tarsus, that character of *Miro* may be the result of the same adaptive trend whereby *P. m. chathamensis* and *P. multicolor multicolor* (for instance) acquired longer tarsi than their nearest relatives. The forest environment of New Zealand had in common with such oceanic islands as Norfolk and the Chathams an almost complete freedom from mammalian and other predators; and, in *P. australis* at least, the habit of forest-floor feeding gives a plausible adaptive significance to the long tarsus.

Wing Shape: Wing formula in *Petroica* varies from $2 = 6/7$ to $2 = 10$: in the following table the figure in parentheses is the number of skins examined for this character.

<i>Petroica goodenovii</i> (3, Australia)	$2 = 6/7$
<i>P. multicolor</i> (6, Australian races)	$2 = 6/7, 2 = 7$
<i>P. m. multicolor</i> (1, Norfolk Island)	$2 = 7/8$
<i>P. m. kleinschmidti</i> (2, Fiji)	$2 = 7/8$
<i>P. m. pusilla</i> (2, Samoa)	$2 = 7/8$
<i>P. macrocephala</i> (all races, 10)	$2 = 7/8$ (rare), $2 = 8/9$
<i>P. (Miro) australis</i> (7)	$2 = 8/9, 2 = 9/10$
<i>P. (Miro) traversi</i> (3)	$2 = 9/10, 2 = 10$

In the "continental" races, the tip of the wing is relatively long; in the insular races shortening of the tip reduces the second primary below the 7th, and, in *macrocephala*, below the 8th. In *Miro* the process has gone further. The shortening and rounding of the wing in Neozelandic *Petroica* may also be illustrated by comparison of the actual and relative lengths of the rudimentary first and the second primaries.

	First Primary	Second Primary	First as % of Second
<i>Petroica goodenovii</i> (3)	17 mm.	41-42 mm.	40-41%
<i>P. multicolor campbelli</i> (3)	18-19	45-50	38-41%
<i>P. multicolor boodang</i> (3)	20-21.5	48-50	42-43%
<i>P. multicolor multicolor</i> (1)	20	44	45%
<i>P. multicolor kleinschmidti</i> (2)	17-18	36-37	47-48%
<i>P. multicolor pusilla</i> (2)	17	35-37	46-48%
<i>P. macrocephala</i> (all races, 10)	18-25	40-50	48-55%
			(mean 51%)
<i>P. (Miro) australis</i> (7)	28-33	53-62	51-57%
<i>P. (Miro) traversi</i> (3)	30-32	48-51	61-63%

It seems likely that the vestigial first primary has not taken part in the reduction of the wing in insular forms, and there is incomplete evidence that it has a roughly isometric relationship with general body size: at any rate it is a fair generalisation that shortening and rounding of the wing in insular races has resulted in a relatively

longer first primary than is present in the continental forms, and that the wing of *Miro* is an extreme result of the same process. The long first primary of *traversi*, with the most degenerate wing of all, is a feature not only exceptional in Muscicapidae, but in the Passeres in general. The emargination of an additional primary in *Miro* is functionally related to the rounder, shorter wing (Ticehurst, 1938).

Other Characters: In *P. macrocephala* the two southern races (*marrineri* and *dannefaerdi*) are darker in plumage, and the northern race (*toitoti*) is paler than the intermediate races. The North Island *Miro* is also paler breasted than the South Island form. The same tendency is found in several other New Zealand passerines, and no feasible hypothesis has yet been suggested to account for the phenomenon: it does not seem to be a case of Gloger's rule. Murphy's generalisation (1938) that insular birds have longer bills than their continental relatives has no general application in *Petroica*, but *P. m. multicolor* (Norfolk Id.) and *P. m. dannefaerdi* (Snares) may be cases.

Summary.

1. The races of *Petroica* on small islands tend to be less variable than those on the larger islands of the New Zealand Archipelago.

2. Bergmann's rule applies in a general way in *Petroica*, with notable exceptions in *P. (Miro) australis*.

3. Wing is relatively shorter in races inhabiting cooler regions, the differences in proportions being due to negative allomorphy of the wing in *P. macrocephala*, but perhaps to the opposite tendency in *P. australis* and in the degenerate *P. traversi*.

4. Tarsus generally has an isomorphic relationship with general body size, but departure from this relationship has resulted in longer tarsi in certain insular *Petroica*, and, by inference, in the subgenus *Miro*.

5. The New Zealand *P. macrocephala* and other insular *Petroica* have shorter, rounder wings than most Australian *Petroica*, the subgenus *Miro* has a still rounder wing, and *P. (M.) traversi* has the most degenerate wing of all: the roundening of the wing is apparently related to conditions of the predator-free insular environment.

6. Most of the structural and dimensional differences in the group are adaptive, in the broad sense, although the superficially striking plumage characters may be, in part, non-adaptive

2. Evolutionary History.

The morphological affinities and geographic distribution of the forms discussed in this paper point to a phylogenetic history which has been suggested, in part, under different headings in earlier sections. The suggested history infers no mechanism of speciation other than that of geographic isolation followed by morphological differentiation of the separated populations and by eventual physiological isolation in some instances. Geographic speciation seems entirely adequate to account for the characteristics of the avifauna of the Neozelandic Archipelago.

Petroica, it is inferred, developed in the Australian continent and has on several occasions invaded the peripheral islands of New Guinea, Western Polynesia, Norfolk Island and New Zealand (Fig. 2).

At a relatively early date an invasion of New Zealand provided the ancestors of the forms here grouped under the subgenus *Miro*. In the forest biotopes of New Zealand, virtually free from predators, *Miro* developed its somewhat degenerate wing, long tarsus, large size and other characteristics. But before these processes had gone very far, the Chatham Islands were colonised by the ancestors of *traversi*, which eventually underwent extreme wing degeneration and acquired melanic plumage. Within New Zealand *P. (Miro) australis* subspeciated at a fairly late date: the North and South Island forms show evidence of earlier separation than is indicated by the slight differences between South Island and Stewart Island forms.

The evolutionary history of *Petroica* in Australia is beyond the scope of this paper. Nevertheless, the concentration of species around Bass Strait suggests that this feature (irrespective of its geologic age or youth) has been of great importance in the speciation process: by repeated crossing of Bass Strait, by differentiation of the populations on either side, and then by re-invasion of the mainland from Tasmania, most of the features of the existing distribution pattern could be accounted for. A similar process has been invoked by Mayr and Serventy (1938) to account for certain relationships in *Acanthisa*, and, more recently, by Hindwood and Mayr, in their review of *Pardalotus* (1946). I may repeat the opinion that *P. goodenovii* may have arisen from *P. multicolor* and attained a partially sympatric relationship at a late date, either by the northward re-invasion of *multicolor* after a period of isolation in Tasmania, or, more probably, after isolation within the continent. However that may be, *P. multicolor* has been a most successful coloniser, invading in succession New Zealand, New Guinea, Norfolk Island, and the western Pacific as far east as Samoa.

In New Zealand the colonising stock of *P. multicolor* diverged as *macrocephala*, following several of the adaptive paths which *Miro* had taken at an earlier date in the same area, and, inferentially, for the same reasons: the wing became shorter and rounder, general body size larger, the tarsi somewhat longer. Other changes, in plumage, for instance, were apparently non-adaptive.

From New Zealand the outlying islands were populated and subspeciation occurred on them and on either side of Cook Strait. The Snares and Auckland Island races, with their large size and distinctive plumage patterns, appear superficially to have diverged more from mainland stock than has the Chatham Island *chathamensis*; but the long tarsus of the latter is a more fundamental difference, indicating departure from an allomorphic relationship common to the other races, and it is interpreted here as evidence for perhaps longer isolation. The chief characteristics of *marrineri* are large size and "advanced" female plumage: the former is directly correlated with latitude and the latter is the expression of a by no means rare tendency in the genus—neither demands lengthy isolation. Nor does the melanism of *dannefaerdi* necessarily imply longer isolation than does the loss of pigment in the breast of *toitoti*. Certainly the divergence of *toitoti* from the nominate race is to be judged the latest event in the

history of the species. From the similarity of *dannefaerdi* and *marrineri* it seems likely that the Snares supported a race which had diverged from *macrocephala* to some extent prior to the population of the Auckland Islands and that the melanism of *dannefaerdi* post-dates that event. Alternatively, *marrineri* may have arisen by reversion to a pale-breasted plumage by wholly black birds derived from the Snares, or, less probably, from the point of view of dispersal factors, the Snares may have been colonised from the Auckland Islands by *marrineri*, and have later gained its wholly melanic characters.

Mayr (1939) has made the generalisation that the New Zealand avifauna "consists primarily of old and young Australian elements," in the present case "*Miro*" and *P. macrocephala* respectively. A further generalisation is that where a passerine species ranges from New Zealand to the outlying islands, the insular races are "stronger" subspecies than those of North and South Islands. Further, the "strongest" of such insular subspecies usually occupies the Chatham Islands, but this last generalisation is more clearly exemplified in other genera—*Bowdleria*, *Anthornis*, *Gerygone*, *Cyanorhamphus (auriceps)*—than in *Petroica*, in which *P. m. chathamensis* is, at least superficially, no more distinctive than the two sub-Antarctic races.

3. Dates in the Phylogenetic History

There is no fossil evidence as to the time when the events outlined in the previous section occurred, but certain deductions can be drawn from the geological history of the various islands of the New Zealand Archipelago.

Certainly land has been present in the New Zealand area during the whole Tertiary, so that no earliest limit can be placed on the first event: the invasion of New Zealand by the ancestors of the subgenus *Miro*. During the latter Tertiary, the positions and outlines of the islands comprising the New Zealand Archipelago changed many times and bore little relation to their present form. In the lower Pliocene, for instance, straits divided the North Island in a number of places, but land was probably continuous across Cook Strait.* Little is known of the age of Foveaux Strait except that it was probably in existence in the Pleistocene, but as it is in general less than 20 fathoms in depth it could have been bridged if there was a 300 feet withdrawal of water at each glaciation.† Cook Strait, and many other major geographic features of modern New Zealand are believed to have been formed in post-Pliocene, pre-later Pleistocene times (see, e.g. Cotton, 1918, on the late origin of Cook Strait).

* It is not possible to quote references to support all the statements made in this section, some of which are based on unpublished geological information. For recent accounts of the Tertiary history of New Zealand see Macpherson, 1947, and Fleming, 1949.

† Since Mount Anglem (3,200 ft.) was slightly glaciated (Williams, 1936), there can have been little if any arboreal vegetation on Stewart Island in glacial times, so that forest birds may have been unable to take advantage of any glacial bridging of Foveaux Strait. The chain of islands connecting Stewart Island with the South Island has been a more important factor in the post-glacial population of Stewart Island by birds, the recency of which event is emphasized by the slight taxonomic differentiation shown by Stewart Island land birds.

Now, if the ancestors of *Miro* had been in New Zealand prior to the post-Pliocene deformation that delineated the present cartographic units, the existing forms might have shown evidence of subspeciation related, not to the present geography, but to Pliocene geography. Such evidence would be the occurrence of at least partially sympatric forms brought together by the obliteration of the inter-island straits that conditioned their separation, or the failure of the taxonomic, or other morphological categories to correspond with geographic units. There is no evidence of this in *Miro*: on the contrary, adjustment to the present geography is fairly complete. This negative evidence does not, of course, preclude a Pliocene, or earlier, entry of *Miro* into New Zealand, but it suggests that the subspeciation of *P. (Miro) australis* is to be regarded as a late event.

At the Chatham Islands, littoral deposits of early and mid-Pliocene age suggest that land was available for colonisation during the Pliocene, and the history of the islands as land may well go much further back into the Tertiary.* There is thus no direct evidence on the date of colonisation by the ancestors of *P. (Miro) traversi*.

The second invasion of New Zealand by *Petroica* cannot be directly dated, but the history of subspeciation of *P. macrocephala* allows more definite conclusions.

The Snares Islands are the reduced remnant of a granite mass which has been base-levelled at a fairly uniform height of less than 650 ft above present sea-level: their terrace-like summits are well shown in photographs (e.g. Marshall, 1909, p. 703) and by their aspect from the sea. Marshall (*op. cit.*, p. 704) plausibly interprets this planed summit as a "plain of marine erosion" formed when the land stood lower than now. It is at least possible that the Snares were completely reduced to a submarine shoal at that time, for any unreduced land is unlikely to have suffered complete subsequent removal while the terrace remnants persisted. Marine benches indicating stillstand at 500–600 ft. above present sea-level are reported from Stewart Island (Williams, 1936), and are widespread in New Zealand where Henderson (1924) has grouped and correlated them as products of his Charleston Cycle. Although there are difficulties in correlating terraces in an area where differential diastrophic movements have occurred late in the geological history, the consensus of opinion on the age of raised shorelines at such heights is that they are Younger Pleistocene (Henderson, *op. cit.*) or Middle Pleistocene (Morgan, 1926, p. 280). Thus the Snares may owe their form as islands to an elevation which is not older than Mid-Pleistocene.†

But even after the Snares became land they were not immediately available for colonisation by the shrubby vegetation necessary to provide a habitat for *Petroica*. At least one, and probably two periods of glaciation were of later date than the Charleston Cycle shorelines

* The amount of endemism in the fossil shallow water mollusca (Marwick, 1928) may be interpreted as indicating insular conditions at the Chathams in the Pliocene.

† Observations at the Snares since the above paragraph was written suggest that the erosion surface may be tilted, and thus difficult to correlate with any confidence: nevertheless the relatively undissected nature of the surface makes it unlikely that the islands' present form is geologically old.

It has been noted in New Zealand that "the greatest extension of the glaciers was at the period of maximum land depression," when the strand line was from 500 ft. to 600 ft. higher than at present (Henderson, 1917, p. 98); the same author (1932) notes a second glaciation widely separated in time from the first and related to present base levels. Morgan (*op. cit.*, p. 281) concludes that in Westland "the Piedmont ice sheet did not retreat into the mountains until a late period in the Pleistocene," and, more recently, Wellman and Willett (1942A, p. 304; 1942B, p. 217) have considered that elevated coastal beaches at 400 ft. above sea-level were "probably cut before the main advance of the ice." Thus the Snares must have gone through at least one period of glaciation since their emergence. Griffiths Taylor (1926) and Zotov (with direct reference to vegetation, 1938) have given diagrams to show the position of the snowline in New Zealand. By interpolating in these diagrams it can be deduced that the present altitude of the snowline at the latitude of the Snares is at from 4,000 to 5,500 feet. Griffith Taylor plots the Pleistocene snowline at about 2,500 feet below its present position, i.e. 1,500 feet at the Snares. Since the Tararua Range and Stewart Island both show minor glacial effects, the approximate position of the Pleistocene snowline can be drawn on Zotov's diagram, which shows those features, and its projection crosses the Snares at about 2,000 feet.* During the Pleistocene glaciations any land at sea-level at the Snares had the approximate temperature characteristics of a mountain belt within 2,000 ft. of permanent snow,† and from Zotov's diagram it is clear that the optimum possible conditions at such times would be those of the "warm sub-polar" belt, supporting a vegetation probably homologous to that at present living on the heights of Auckland and Campbell Islands. Before scrubby vegetation, and *Petroica*, could populate the Snares, the amelioration of climate after the last glaciation must have proceeded to a considerable extent, and I conclude therefore, that colonisation by the ancestors of *P. m. dannefaerdi* cannot have been earlier than latest Pleistocene.

The Auckland Islands arose as shield volcanoes on a basement of Tertiary and older rocks some time before the Pleistocene glaciation. There is evidence from marine benches and deposits that the group has been insular since before the last glacial advance, and probably for a much longer time. Glaciation brought the snowline well below the 1,000 ft. contour and conditions for life were then even more severe than at the Snares: any glacial period vegetation must have been comparable with that of Macquarie Island at present. The ancestors of *P. m. marrineri* cannot have arrived at the Auckland Islands until some arboreal vegetation was established, at a date which cannot have been much earlier than the beginning of the Recent era: if, as has been suggested, *marrineri* and *dannefaerdi* are monophyletic and not independently derived from *macrocephala* stock, the common ancestor

* For the principles involved in reconstructing the Pleistocene snowline see R. W. Willett (in press), "The Pleistocene Snowline and Glacial Control in New Zealand," a paper presented to the Geological Section of the Sixth Science Congress of the Royal Society of New Zealand, Wellington, May, 1947.

† A 300 ft. retreat of sea-level during glaciation would not materially alter the position.

of these two races may have spent some time at the Snares prior to colonising the Aucklands.

If, then, the race *dannefaerd* is no older than latest Pleistocene and has been differentiated from *marrineri* at a later date (say, early Recent), this gives us a unit of measurement by which we may interpret the degree of morphological differentiation in other races in terms of a rough time scale. Differentiation is unlikely to have proceeded at a uniform rate in all cases, for the Sewall Wright effect may have operated to hasten divergence in isolated small island populations, and incomplete isolation, by geographic proximity, may have delayed it.

The Chatham Island *chathamensis* has departed from the isomorphic tarsus-tail relationship common to the other races, and this is interpreted (somewhat subjectively, it must be admitted) as evidence of equal if not longer isolation than has been operative in the cases of the subantarctic subspecies: yet in other characters *chathamensis* is conservative, and (in view of the amount of differentiation in post-Pleistocene races) it would not be justified to allow the race a greater antiquity than Pleistocene. There were no glacial conditions to bar colonisation of the Chathams.

The separation of *P. m. toitoi* from *P. m. macrocephala* cannot have occurred prior to the formation of Cook Strait, an event usually associated with the post-Pliocene Kaikoura orogeny, which antedated both the formation of elevated beaches and the glaciations discussed above.* It is unlikely that Cook Strait was bridged by any Pleistocene retreat of sea-level, but the two races concerned are so close morphologically that it may be fairly inferred that the formation of the strait did not finally and completely isolate the separated populations. This leads to the conclusion that the species was at first more "vagile," i.e. had greater dispersal ability, and that a subsequent loss of flight capability eventually rendered Cook Strait an effective barrier. The field naturalist would doubt the ability of the New Zealand tomtits to cross Cook Strait (let alone the distances between New Zealand and the Chatham and Auckland groups) and the fact that in a century of experience *toitoi* has never been observed in the range of *macrocephala* (and *vice versa*) supports the inference of the low vagility of these races at present. The implied greater vagility and subsequent restriction in post-Pleistocene times is in keeping with the seemingly facile colonisation of such distant islands as the Chathams and Aucklands and the rapid development of subspecies on them in effective isolation.

In the late Pleistocene or early Recent era, when *Petroica macrocephala* was colonising the outlying islands of New Zealand, the species probably retained to some extent the longer, sharper wing of its Australian relatives, and since the wing characters are the chief functional differences between *macrocephala* and *multicolor*, it is unnecessary to postulate any very great interval between the arrival of ancestors of *macrocephala* in New Zealand and the colonisation of the outlying islands: that is to say, the initial colonisation from Australia could well have been as late as earliest Pleistocene, though it may have been earlier.

* The possibility of still earlier glaciation does not concern us here

Miro has proceeded much further along the path of specialisation and loss of dispersal ability than has *P. macrocephala*, and an earlier derivation from Australia is inferred: how much earlier we can hardly judge, but since the moderately strong differentiation of *P. (Miro) australis longipes* from *P. (M.) a. australis* cannot be older than the early Pleistocene origin of Cook Strait, a fairly rapid evolutionary rate is indicated, and it may well be that the original invasion of New Zealand by the ancestors of this subgenus was not earlier than Pliocene. Such a date would allow a period over ten times as long for the development of *Miro* as for the evolution of *P. macrocephala* from its Australian ancestors, and over 400 times as long as for the differentiation of *dannefaerdi* from *macrocephala*, the latter divarication being the point of departure in discussion of the time factor in the evolution of *Petroica* in New Zealand. The point to be made is that there is no necessity to place the origin of such an endemic group as *Miro* far back into the Tertiary, and that such "older elements" in the New Zealand passerine avifauna, although rightly so designated, are not necessarily "old" in the geologic sense.

Summary: (1) The ancestors of *Miro* may have arrived in New Zealand in the Pliocene, and have populated the Chatham Islands before the loss of dispersal ability which accompanied specialisation to the New Zealand forest floor environment.

(2) Subspeciation of *P. (Miro) australis* is not older than Pleistocene.

(3) The ancestors of *P. macrocephala* probably colonised New Zealand in the early Pleistocene.

(4) Occupation of the Snares and Auckland Islands by *macrocephala* cannot have been before the latest Pleistocene, and most of the subspeciation in *P. macrocephala* must have occurred in the Recent era.

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