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Moult and age determination of New Zealand native passerines

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Abstract: Moult is a vital avian process because it allows the renewal of the worn plumage in an organised way. Moult has a circannual periodicity and tends to differ between the first annual cycle (post-juvenile moult) and subsequent ones (post-breeding moult) of passerines, a fact that can be used to determine the age of individuals. We estimated wing-feather and rectrix moult-extent for 17 New Zealand passerines (excluding introduced species), classified each bird according to eight moult patterns, and computed frequency of wing-feather and rectrix replacement. We combined post-juvenile moult information with that of maturation of feathered and unfeathered characters to provide guidelines for age determination. Our results cover an important gap in the knowledge of the natural history of New Zealand passerines, generate reliable age determination criteria, and thus providing essential information for future conservation actions (including translocations) and to test hypotheses on the ecology and evolution of avian moult in the Australasian region.

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INTRODUCTION

The avifauna of New Zealand diversified in the absence of terrestrial predators, a circumstance that drove both the loss of escape instinct and the evolution of flightlessness in several bird groups (Holdaway 1999; Matthews & Triantis 2021). These characteristics made them very vulnerable to hunting and habitat destruction upon arrival of humans, and to predation by the subsequent introduction of other mammals (Duncan & Blackburn 2004). Mainland New Zealand is still home to 20 species of Passeriformes belonging to six of the 12 groups in which the order is divided, including the basal endemic suborder Acanthisitti (Table 1; Winkler *et al.* 2015; Fjeldså *et al.* 2020). Although conservation efforts in the last decades have proven successful for some endemics, several may become extinct in the mid-term as a consequence of the planetary biodiversity crisis (Table 1; Matthews *et al.* 2024). Ongoing conservation challenges will benefit from a better understanding of the biology and population dynamics of New Zealand endemics, which will allow more informed management decisions (Williams *et al.* 2002).

Moult is an important gap in the knowledge of the biology of New Zealand endemic passerines and is currently not described for most species. Moult is a vital trait of avian biology because it allows the necessary renewal of deteriorated plumage. It typically occurs once a year in non-migratory species (all New Zealand passerines except silvereye tauhou *Zosterops lateralis*; Dennison *et al.* 1981), right after the breeding season (between October and January in New Zealand passerines; Higgins *et al.* 2001, 2006; Higgins & Peter 2002), has a circannual periodicity, and tends to differ between the first annual cycle (i.e., the period between hatch and the first post-breeding moult) and subsequent ones; these characteristics are routinely applied to determine bird age (Jenni & Winkler 2020a), which is a crucial parameter for population and ecological studies.

Bird somatic maturation can be assessed using feathered (i.e., plumage) and unfeathered characters. Plumage matures in a discrete way, through moult (Jenni

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Table 1. Data sources and sample sizes for the post-juvenile moult of 17 New Zealand native passerines, and the pre-breeding (pn) moult of New Zealand pipit. We did not gather data from Chatham Islands birds.

Familiy	Species		IUCN category	Source	n
Acanthisittidae	Rifleman Tītipounamu	*Acanthisitta chloris*	Least concern but decreasing	Image libraries Museum	8 5
	Rock wren Pīwauwau	*Xenicus gilviventris*	Endangered	Image libraries	17
Meliphagidae	Tūī	*Prosthemadera novaeseelandiae*	Least concern but decreasing	Museum	14
	Bellbird Korimako	*Anthornis melanura*	Least concern but decreasing	Banding Museum	10 9
Acanthizidae	Grey warbler Riroriro	*Gerygone igata*	Least concern stable	Banding Museum	5 15
Mohouidae	Whitehead Pōpokotea	*Mohoua albicilla*	Least concern stable	Banding Museum Image libraries	5 3 1
Rhipiduridae	New Zealand fantail Pīwakawaka	*Rhipidura fuliginosa*	Least concern but decreasing	Banding Museum Image libraries	8 14 1
Callaeidae	North Is kokako Kōkako	*Callaeas wilsoni*	Least concern and increasing	Museum	4
	North Is saddleback Tīeke	*Philesturnus rufusater*	Near threatened but increasing	Banding Image libraries Museum	2 3 5
	South Is saddleback Tīeke	*Philesturnus carunculatus*	Least concern and increasing	Image libraries Museum	5 1
Notiomystidae	Stitchbird Hihi	*Notiomystis cincta*	Vulnerable	Banding Image libraries Museum	1 9 2
Petroicidae	Tomtit Miromiro	*Petroica macrocephala*	Least concern but decreasing	Banding Image libraries	1 16
	South Is robin Toutouwai	*Petroica australis*	Least concern but decreasing	Banding Museum	1 10
	North Is robin Kakaruai	*Petroica longipes*	Least concern but decreasing	Banding Image libraries	2 1
Hirundinidae	Welcome swallow Warou	*Hirundo neoxena*	Least concern and increasing	Banding Image libraries	6 14
Zosteropidae	Silvereye Tauhou	*Zosterops lateralis*	Least concern stable	Banding	24
Motacillidae	New Zealand pipit Pīhoihoi	*Anthus novaeseelandiae*	Least concern stable	Image libraries	31
	Pīhoihoi (pn)			Image libraries	38

& Winkler 2020b), whereas unfeathered characters (e.g., iris colour and skull pneumatisation) mature in a continuous way, typically over the course of the first 3–6 months of a passerine's life (Yunick 1981; Polakowski *et al.* 2020). In passerines, three features of the maturation process are relevant to age determination. First, the juvenile and the adult aspect differ (i.e., the outer appearance as we perceive it). Second, the definitive adult plumage is acquired either during the post-juvenile moult undergone in the first months of life (which is complete in about 25% species; Delhey *et al.* 2020), or during the first post-breeding moult, with the exception of some manakins that do not acquire the adult coloration during the first post-breeding moult (Doucet *et al.* 2007; Scholer *et al.* 2021) and those Holarctic long-distance migratory species that undergo a complete moult away from the breeding grounds (Jenni & Winkler 2020a; Pyle 2022; Norevik *et al.* 2020). Given that the post-breeding moult of passerines is complete, a mixture of juvenile and non-juvenile feathers in a bird indicates that it has not undergone the post-breeding moult yet. Third, some components of moult are predictable (e.g., sequence of primaries in the complete moult, post-juvenile moult-extent versus post-breeding moult-extent within species; Jenni & Winkler 2020a; Pyle 2022). Therefore, it is only feasible to determine whether a passerine bird is either in its first annual-cycle (which includes the juvenile stage) or in a subsequent one. First-cycle birds (see Glossary Box for technical terminology) of species that undergo a complete post-juvenile moult may be identified until approaching the end of this moult (while the last recognizable juvenile feathers have not been shed yet) or until their unfeathered characters near full maturation, although skull pneumatisation usually ends after the end of the post-juvenile moult. In species undergoing a partial post-juvenile moult, age determination beyond the full maturation of unfeathered characters can be made using moult limits, the contrasting boundaries that appear between the old juvenile feathers and the post-juvenile ones.

We estimated wing-feather and rectrix moult-extent for all mainland native passerines except fernbird mātātā *Poodytes punctatus*, brown creeper pīpipi *Mohoua novaeseelandiae*, and yellowhead mohua *Mohoua ochrocephala*. Along with these estimates, we classified the final moult-phenotype (i.e., identity of feathers replaced after finishing moult) of each bird according to nine patterns (Guallar & Jovani 2020a). We also computed frequency of wing-feather and rectrix-moult to inform where to find moult limits within the flight feathers (Jenni & Winkler 2020a). We combined post-juvenile moult information with that of maturation of feathered and unfeathered characters to provide guidelines for age determination.

GLOSSARY

First-cycle bird. Bird in its first annual cycle, from hatching until the first post-breeding moult, approximately one year later. This term includes birds in juvenile and post-juvenile plumage (i.e., after the post-juvenile moult).

Moult components. Measurable aspects of moult. They can be grouped in process components (feather growth rate, sequence, intensity, and timing) and output components (symmetry, duration, extent, final phenotype, and plumage quality).

Moult episode. Each separate moult event in the annual cycle of birds. Some species can interrupt moult and resume it later (e.g., Hirundinidae). Three main episodes are recognised: post-breeding, which produces the post-breeding plumage; post-juvenile, which produces the post-juvenile plumage; and pre-breeding, which produces the breeding plumage.

Moult extent. Amount of plumage replaced during a moult episode. Here, it has been quantified as number of feathers.

Moult limit. A boundary between moulted and retained feathers after a moult episode is finished. Usually refers to boundaries between feathers of the same tract but can be used for indicating boundaries between feather tracts.

Moult patterns. Classes of moult phenotypes that share some similarity rules (specified in Fig 2).

Moult phenotype. The identity of feathers replaced by a bird after finishing a moult episode.

Secondary coverts. All upper wing coverts except the primary coverts.

MATERIALS AND METHODS

Moult extent and pattern

We gathered moult data of New Zealand passerines (excluding the Chatham Islands) from three sources: banding, specimens in the collection of Te Papa and Auckland museums, and online image libraries, excluding birds from the Chatham Islands (Table 1; Guallar *et al.* 2025). Moult scoring was essentially the same, although in photos, rectrices tended not to be visible; and spread wings were easier to score than folded ones in specimens (Carrillo-Ortiz *et al.* 2021). We assigned the (finished) moult of birds to each of three moult episodes defined from stage of the annual cycle: (1) post-juvenile, the moult of the juvenile plumage undergone during the first months of life; (2) post-breeding, the moult undergone after breeding by birds hatched in previous years; and (3) pre-breeding, a second annual moult undergone by some species usually at the end of the wintering period (Salewski *et al.* 2004; Jenni & Winkler 2020b). We scored each feather on one wing (Fig. 1) and one half of the tail from 291 birds that had finished moult or were in the last stages of the post-juvenile and pre-breeding moults (i.e., no more wing or tail feathers were likely to be moulted): 1 when moulted (new feather) and 0 when retained (old feather). We scored the proportion of replaced marginal coverts as a decimal between 0 and 1 (Guallar *et al.* 2021). We also scored the percentage of moulted body feathers.

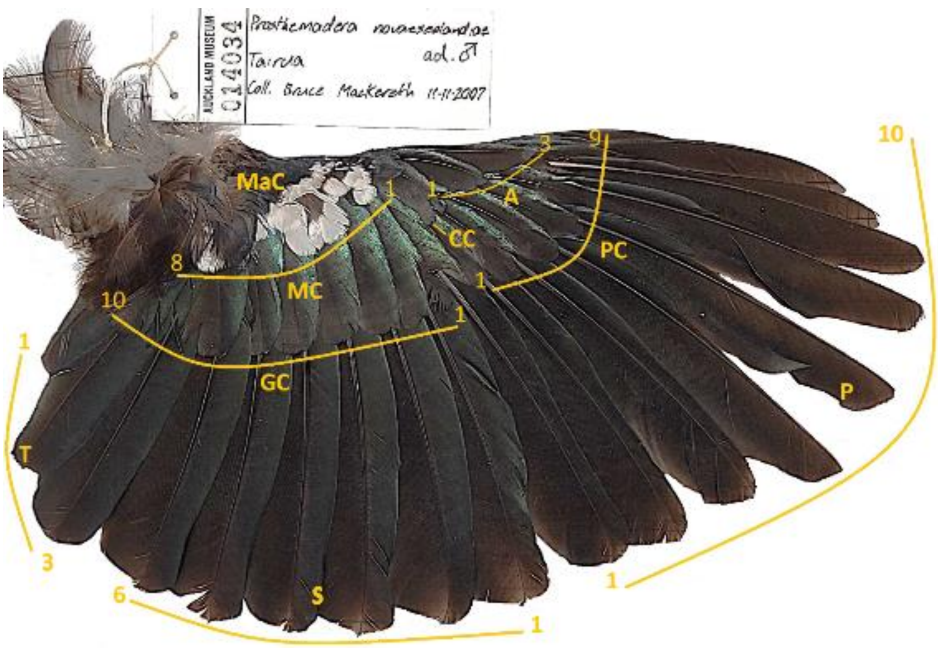
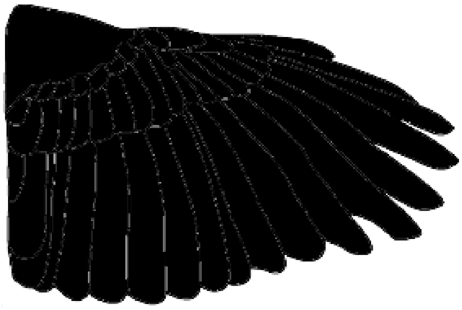
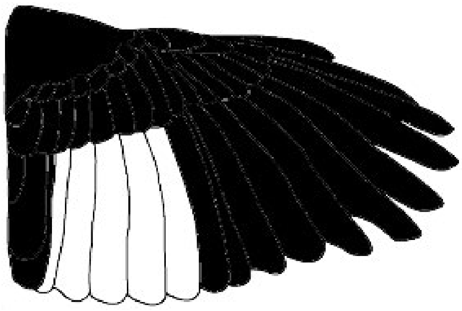
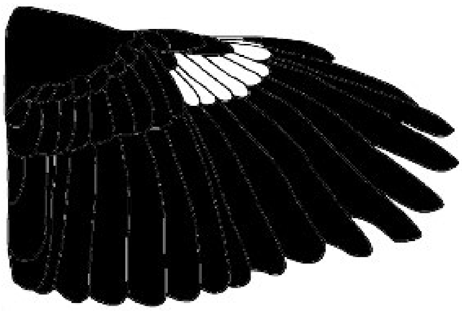
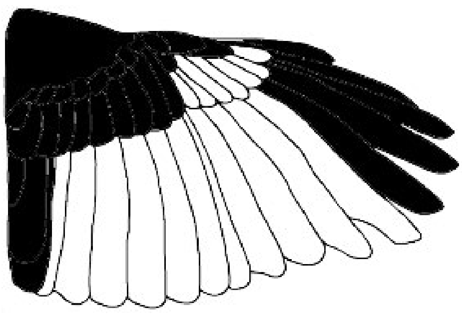


Figure 1. Feather tracts and numbering on the right wing of a tui. GC10 and four inner median coverts not visible. We adhered to the numbering system proposed by Jenni & Winkler (2020b) save for the tertials, whose moult timing and sequence clearly differs from that of the secondaries. P: primaries, S: secondaries, T: tertials, PC: primary coverts, GC: greater coverts, A: alula feathers, CC: carpal covert, MC: median coverts, MaC: marginal coverts. Photo by the authors.

Table 2. Observed moult patterns in New Zealand native passerines. Except the complete pattern, the remaining patterns show variation in the feathers moulted (always within the rules of similarity). The first three patterns include all rectrices, and the eccentric usually too. We only show a typical example per moult pattern. Replaced (new) feathers shown in black, retained (old) feathers in white.

Moult pattern	Definition
	Complete: Full feather moult. Primaries are moulted by accompanying primary coverts when underway.
	Abridged1: An otherwise complete moult with a variable number of retained secondaries.
	Abridged2: An otherwise complete moult with a variable number of retained primary coverts.
	Eccentric: Retention of a variable number of inner primaries and outer secondaries, and most to all primary coverts.

Individual moult extent was calculated as the mean number of wing feathers and rectrices moulted. Therefore, the score for a completely moulted wing (all feathers replaced) was 51 (including species with nine visible primaries; Hall 2005) and the complete rectrix-moult extent was 6 (4 for Acanthisittidae species, which only have eight rectrices). Mean and 95% confidence intervals of wing-feather and rectrix moult extent for each species were estimated applying Bayesian bootstrapping as implemented in library *bayesboot* (Bååth 2016; R Core Team 2025), an adequate method for small datasets and/or variables which do not reasonably fit a known distribution.

We classified each bird's final moult phenotype into one of nine moult patterns defined by rules of similarity (Table 2; Guallar & Jovani 2020a). Frequency of wing-feather and rectrix replacement was computed as the mean score for each feather across birds for every species.

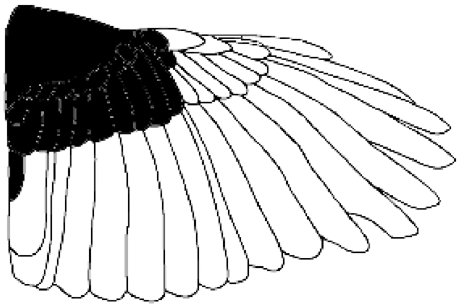
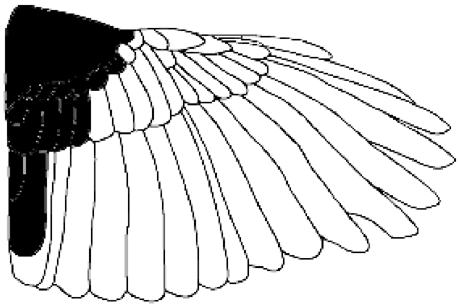
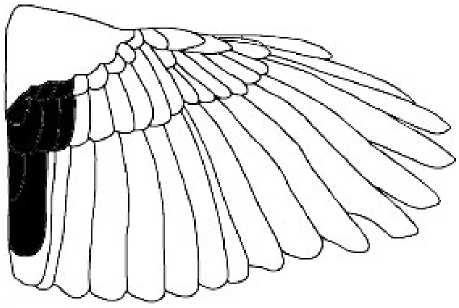
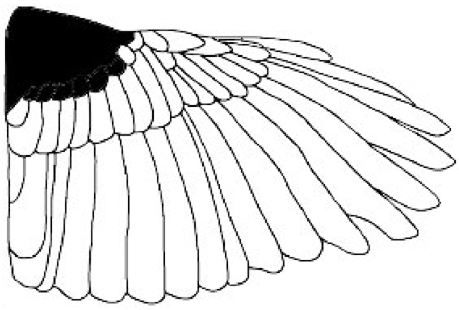
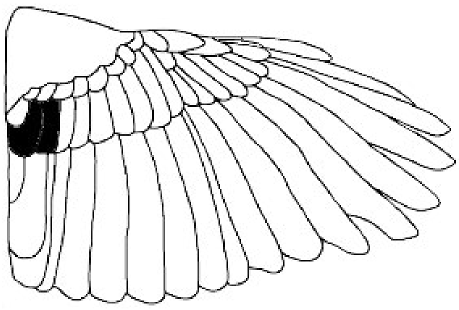
Age determination

We used the following plumage and moult characters to determine the age of birds: juvenile plumage, moult sequence in actively moulting birds, moult limits in birds that had finished moult, and dynamics of feather deterioration (largely fade and wear) throughout the annual cycle for all birds (Fig. 2).

Passerine juvenile feathers differ from adult ones largely by three features: shape, which tends to be shorter and narrower, with more pointed tips; colour, which tends to be duller; and structure, which tends to be looser, of a worse quality, and therefore more prone to fade and wear.

Partial and complete moults can be identified by the sequence of activation of wing-feather tracts. Thus, the complete moult typically starts at the inner primaries with their corresponding primary coverts. Primary moult proceeds outward and usually finishes when the last 1–3

Table 2. *continued*

Moult pattern	**Definition**
	General: Replacement of secondary coverts. Tertials moulted only if all secondary coverts are moulted. Prioritisation from leading to trailing edge of wing.
	Proximal: Prioritisation of wing feathers closer to the body over those of the outer wing. Tertials replaced with retention of outer secondary coverts.
	Inverted: Prioritisation of feathers closer to the body from trailing to leading wing edge, ie., tertials, inner secondaries, and inner greater coverts over median and marginal coverts (the latter tending to 0%). Body moult tends to be incomplete.
	Limited: Moult of marginal coverts. This usually includes median coverts.
	Reduced: 2-4 wing feathers (secondaries, tertials, median, or greater coverts) and rectrices, without a clear priority. Incomplete body moult.

innermost secondaries are still growing (Zeidler 1966; Guallar & Quesada 2023). Partial moults (except the abridged2 pattern (Table 2), which can only be identified at late stages of the moult progress) will show neither of these, rather an intense body and wing-covert moult without primary moult. Eccentric moults can be confused with complete moults; however, moulting primaries are not accompanied by primary coverts and the sequence of activation of other wing-feather tracts will also differ (Fig. 3; Guallar 2024).

Detectability of moult limits vary within and among species, as well as with timing within the annual cycle.

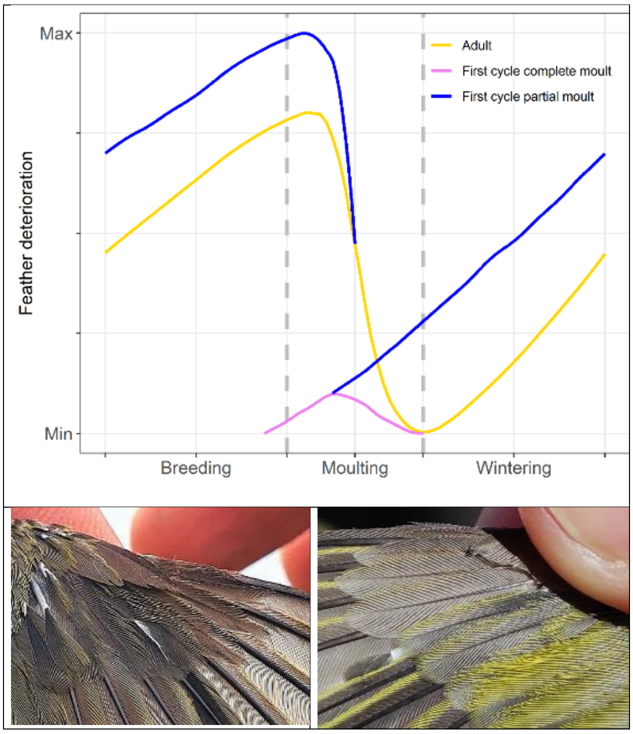


Figure 2. Theoretical dynamics of plumage deterioration by age throughout the annual cycle. Below: differences in deterioration between one adult (left; 20 Mar 2022) and one juvenile silvereye (right; 3 Feb 2025). The outer four primary coverts are old in both birds, but notice that they are faded and ragged in the adult and still fresh in the juvenile. Photos by the authors.

The feather tracts showing moult limits and conspicuousness of the latter tend to be species-specific (e.g., very subtle in North Island kokako *Callaeas wilsoni* and obvious in grey warbler riroriro *Gerygone igata*). We looked for contrasts within and among wing-feather tracts (also among rectrices) using differences in shape, colour, and wear between the retained and the moulted feathers. Considering that contrasts between juvenile and post-juvenile feathers are often subtle, we calibrated our search using museum specimens and online images of the juvenile plumage.

Feather deterioration is expected to peak at the end of the annual moult cycle (Rogers 1990; Guallar *et al.* 2009; Fig. 2) and is aggravated in the retained juvenile feathers of first-cycle birds for two reasons: the juvenile plumage grew several weeks before the adults started their post-breeding moult (the juvenile plumage is worn longer) and the quality of juvenile feathers is generally inferior (Pap *et al.* 2007). This was the main criterion used for determining age in species with a complete post-juvenile moult: moulting adults and first-cycle birds will be readily aged because the retained adult feathers will be one year old and hence worn, and the juvenile feathers will still be fresh (Fig. 2).

We used all potential unfeathered characters to determine the age of banded and photographed birds, including presence of a soft bill gape, palate colour, wattle development, iris colour, and skull pneumatisation. Since we neither scored nor recorded these variables, we will only comment on their qualitative use as complementary ageing criteria.

RESULTS

Moult extent and pattern

The post-breeding moult was complete, although it could be suspended in welcome swallows warou *Hirundo neoxena* (Guallar *et al.* 2025). We found that most New Zealand pipits pīhoihoi *Anthus novaeseelandiae* underwent a pre-breeding moult, which was characterised by partial retention of body feathers and by the presence of wing-feather moult-patterns not found in the post-juvenile moult of any other New Zealand passerine species. In subantarctic islands (e.g., Campbell, Enderby), the pre-breeding moult of Auckland Island pipits *A.n. aucklandica* was frequently lacking or restricted to a few body feathers (Table 3).

All species in our sample replaced body and marginal coverts during the post-juvenile moult. Mean post-juvenile wing-feather moult-extent ranged from 9.5 in South Island robin kakaruai *Petroica australis* to 50.9 in welcome swallows and silvereye (median across species= 18.7). Nine species replaced one to all rectrices during the post-juvenile moult. Individuals in 15 species did not replace rectrices, whereas individuals from seven species replaced them all (Guallar *et al.* 2025; Table 3).

We found nine patterns associated with the post-juvenile moult (Table 2). The abridged patterns were found at low frequencies in the welcome swallow and silvereye, two species that otherwise mostly undergo complete post-juvenile moults. We also found the abridged2 pattern in the post-breeding moult of two rifleman tītipounamu *Acanthisitta chloris* and one tūī *Prosthemadera noveaeseelandiae* (Guallar *et al.* 2025). The general pattern was present in all species except welcome swallow and silvereye, which mostly undergo a complete post-juvenile moult. The inverted and reduced patterns were only present (and were predominant) in the pre-breeding moult of New Zealand

Figure 3. Differences between the complete- and the eccentric-moult sequences in two first-cycle birds. Left (complete): primary P9 finishing growth, secondaries S5 and S6 still growing (silvereye, Nelson 14 Mar 2025). Right (eccentric): primaries P8 through P10 growing in, all secondaries old, and tertials T1 and T3 growing in (bellbird, Tiritiri 20 Feb 2025). Photos by the authors.

Table 3. Bootstrapped estimates (mean and 95% bootstrapped confidence intervals) of post- juvenile and pre-breeding moult-extents on the wing and tail and presence of species showing every moult pattern (nine columns on the right) in New Zealand native passerines.

Post-juvenile	n	wing mean[95% CI]	tail mean[95% CI]	complete	abridged1	abridged2	eccentric	general	proximal	inverted	limited	reduced
Rifleman	13	24.7 [20.5-28.6]	2.5 [1.4-3.4]	0	0	0	7	3	3	0	0	0
Rock wren	17	19.6 [18.3-20.9]	0.1 [0-0.3]	0	0	0	0	16	1	0	0	0
Tui	14	23.5 [20.0-27.2]	0.6 [0.1-1.5]	0	0	0	2	12	0	0	0	0
Bellbird	19	23.6 [19.7-27.0]	1.4 [0.5-2.4]	0	0	0	11	8	0	0	0	0
Grey warbler	20	17.0 [15.1-18.9]	1.0 [0.1-1.9]	0	0	0	0	12	7	0	0	0
Whitehead	9	19.8 [17.8-21.5]	0	0	0	0	0	9	0	0	0	0
New Zealand fantail	23	19.1 [17.7-20.5]	4.79 [3.9-5.8]	0	0	0	0	10	11	0	0	0
NI kokako	4	9.3 [1.3-17.4]	0	0	0	0	0	2	0	0	2	0
SI saddleback	6	11.8 [8.5-14.0]	0	0	0	0	0	5	1	0	0	0
NI saddleback	10	16.1 [11.7-20.0]	0	0	0	0	0	8	0	0	2	0
Stitchbird	12	18.8 [17.0-20.6]	0	0	0	0	0	12	0	0	0	0
Tomtit	17	13.5 [11.8-15.0]	0	0	0	0	0	13	2	0	2	0
NI robin	3	13.6 [11.1-15.7]	0	0	0	0	0	2	1	0	0	0
SI robin	11	9.5 [7.3-11.6]	0	0	0	0	0	5	0	0	6	0
Welcome swallow	20	50.9 [50.8 - 51]	6	18	2	0	0	0	0	0	0	0
Silvereye	24	50.9 [50.8 - 51]	6	23	0	1	0	0	0	0	0	0
New Zealand pipit	31	11.6 [9.5-13.7]	0.4 [0.2-0.6]	0	0	0	0	4	24	0	3	1
Presence (%)				16.4	0.8	0.4	8	48.4	20	0	5.6	0.4
Pre-breeding												
New Zealand pipit	38	3.6 [2.5-4.6]	0.1 [0-0.2]	0	0	0	0	0	2	10	3	23

pipit (Table 3). Intraspecific variation in moult pattern was much lower, with only three species showing up to three patterns (median= 2; Table 3).

Because of the low sample sizes, the absolute frequencies at which moult patterns are present in our dataset should be taken with caution.

Age determination

Ageing guidelines for each species are provided below (summarised in Table 4). Greater coverts (15 species) and tertials (14 species) were the feather tracts that exhibited moult limits most frequently. They were followed by the alula feathers (eight species) median coverts (seven species), rectrices (five species) marginal covert (three species) (Table 3).

Rifleman tītipounamu: mottled juvenile body plumage was age diagnostic until the end of the post-juvenile moult (Fig. 4). Afterwards, moult limits were found between the blacker outer moulted primaries and the browner inner retained ones (seven of 13 cases, which underwent eccentric moults) or within the greater coverts and the tertials (six birds that did not moult primaries). Juvenile primary coverts were browner than the adult black ones, contrasting with adjacent post-juvenile greater coverts, alula feathers and primaries.

Rock wren pīwauwau *Xenicus gilviventris*: the juvenile plumage did not contrast starkly with the post-juvenile one (Fig. 4). Moult limits were typically found between the duller brown moulted outer greater coverts and the retained greener inner ones. Also, between brown retained primary coverts and the moulted black alula feathers.

Tūī: the dull juvenile body plumage, with reduced throat tufts and lacking specialised mantle feathers, was age diagnostic until the end of the post-juvenile moult (Fig. 5). Afterwards, moult limits were typically found between the dull retained tertials and alula feathers contrasting starkly with the iridescent post-juvenile ones. The notch on primary P8 was still lacking in most tūī after the post-juvenile moult (because they retained the juvenile primaries); however, two of 14 birds underwent an eccentric post-juvenile moult that included P8, which acquired the notched shape.

Bellbird korimako *Anthornis melanura*: the juvenile plumage did not obviously contrast with the post-juvenile one, although tertials had buffy margins and the face lacked the purple iridescence. The narrower (or absent) and paler margins on the primary coverts were useful to determine the age after the end of the post-juvenile moult. Moult limits were typically found within primaries, tertials, alula feathers, greater coverts, and rectrices. The notch on the outer primaries was lacking in seven of 18 cases individuals after the post-juvenile moult; however, 11 of 18 individuals had undergone an eccentric post-juvenile moult and their outer primaries had the notched shape.

Grey warbler riroriro: the juvenile plumage was similar to the post-juvenile one. Moult limits were typically found within tertials, greater coverts, and rectrices (Fig. 6). Moulted wing feathers had darker vanes with wider and greener margins. The iris of first-cycle birds was still brownish in March.

Whitehead pōpokatea *Mohoua albicilla*: the juvenile plumage was extremely similar to the adult one, only distinguished by less white on the crown and nape. Moult limits were very hard to discern. Moult sequence and the freshness of retained plumage were the main detection aid of the post-juvenile moult (Figs 2 & 6). Birds that were undergoing a complete moult and did not show noticeable

Table 4. Summary of guidelines for ageing 17 New Zealand passerine species. The column moult limits indicates which feather tracts are more likely to have them. Tracts abridged following Fig 1 (R: rectrices).

species	moult limits	moult patterns	other ageing tips
Rifleman	P, R, A GC, T	eccentric general, proximal	
Rock wren	GC, A	general, proximal	
Tui	P, R GC, T, A	eccentric general	some first-cycle birds have notched p
Bellbird	P, R GC, T, A	eccentric general	some first-cycle birds have notched p
Grey warbler	GC, T, R	general, proximal	iris colour useful until March or later
Whitehead	GC, T	general	
New Zealand fantail	GC, T, A	general, proximal	do not rely solely on colour of gc tips
NI kokako	GC, T MC, MaC	general limited	
SI saddleback	GC	general, proximal	delayed plumage maturation
NI saddleback	GC, T	general limited	
Stitchbird	GC, T, A	general	bill colour useful until March or later
Tomtit	GC, MC MC	general, proximal limited	bill colour useful until March or later
NI robin	GC, T, MC	general, proximal	bill and palate colour useful until March or later
SI robin	GC MC	general limited	bill and palate colour useful until March or later
Welcome swallow	no S	complete abridged1	
Silvereye	no PC	complete abridged2	
New Zealand pipit	GC, T, MC, R MC, MaC	general, proximal limited, reduced	most individuals have moult limits after the pre-breeding moult. Ageing based on shape and wear of PC is recommended

differences in degree of deterioration among remiges and greater coverts were likely hatched in the penultimate breeding season.

New Zealand fantail pīwakawaka *Rhipidura fuliginosa*: the dusky juvenile plumage strongly contrasted with the post-juvenile one. The small spots on the tips of tertials and greater coverts changed from the juvenile tawny to the adult whitish (Fig. 6). Moult limits were typically found within the tertials and greater coverts (carpal covert replaced in six of 23 cases), although five of 19 individuals had moulted all the greater coverts.

North Island kokako kōkako: the juvenile plumage was loose textured but very similar to the adult one both in colour and texture. Moult limits may be found within the secondary coverts (Fig. 7). Some kokako might have a post-juvenile moult restricted to the body. No first-cycle birds had developed adult-type wattles by March.

North Island saddleback tīeke *Philesturnus rufusater*: the juvenile plumage was extremely similar to the adult one. Moult limits were found within tertials and greater coverts, with the post-juvenile feathers being larger and having deeper red and black tones. No first-cycle birds had developed adult-type wattles by March.

South Island saddleback tīeke *Philesturnus carunculatus*: showed delayed plumage maturation. The overall brown juvenile colouration was retained after the post-juvenile moult, contrasting strikingly with the adult one. Moult limits were found among the slightly larger and darker inner greater coverts and the juvenile outer ones (Fig. 7).

Stitchbird hihi *Notiomystis cincta*: the juvenile plumage was similar to the adult-female plumage. Bill melanisation of juveniles was incomplete at least until March. Moult limits were found within greater coverts (54% birds), tertials (38% birds), and alula feathers (23% birds). We did not find moult limits within the rectrices (*contra* Smith *et al.* 2015).

Tomtit miromiro *Petroica macrocephala*: the juvenile plumage was paler, with smudged underparts and the head showing thin pale streaks resembling those of the next two robin species. Bill melanisation of juveniles was incomplete at least until March. Moult limits were subtle, typically found within greater coverts and occasionally (three of 17 birds) within median coverts (Fig. 9). Plumage of Petroicidae species wears very little.

North Island robin toutouwai *Petroica longipes*: the juvenile plumage was similar to the post-juvenile one, although the white belly patch was small and ill-defined. Bill and palate melanisation of juveniles was incomplete at least until March. Moult limits were typically found within the greater coverts, less often within the median coverts, and occasionally within tertials (very low sample size). Moult limits were revealed as a noticeable step between the inner moulted greater coverts (which were larger, darker, and greyer) and the retained juvenile ones (Fig. 9).

South Island robin kakaruai: like North Island robin although moult limits were typically found within the median coverts (six of 11 birds) and the greater coverts (four of 11 birds; Fig. 9).

Welcome swallow warou (Fig. 10): juveniles had less forked tails (due to shorter outer rectrices) and a paler face and throat. Since the head is moulted in the late stages of the moult progress, face colouration was useful to age welcome swallows until late in the wintering season.

Silvereye tauhou: the juvenile plumage was slightly paler than the adult one. Silvereyes could be easily aged using degree of feather deterioration (before and during moult), with juvenile birds showing fresh juvenile feathers and adults showing faded and worn ones (Fig. 10).

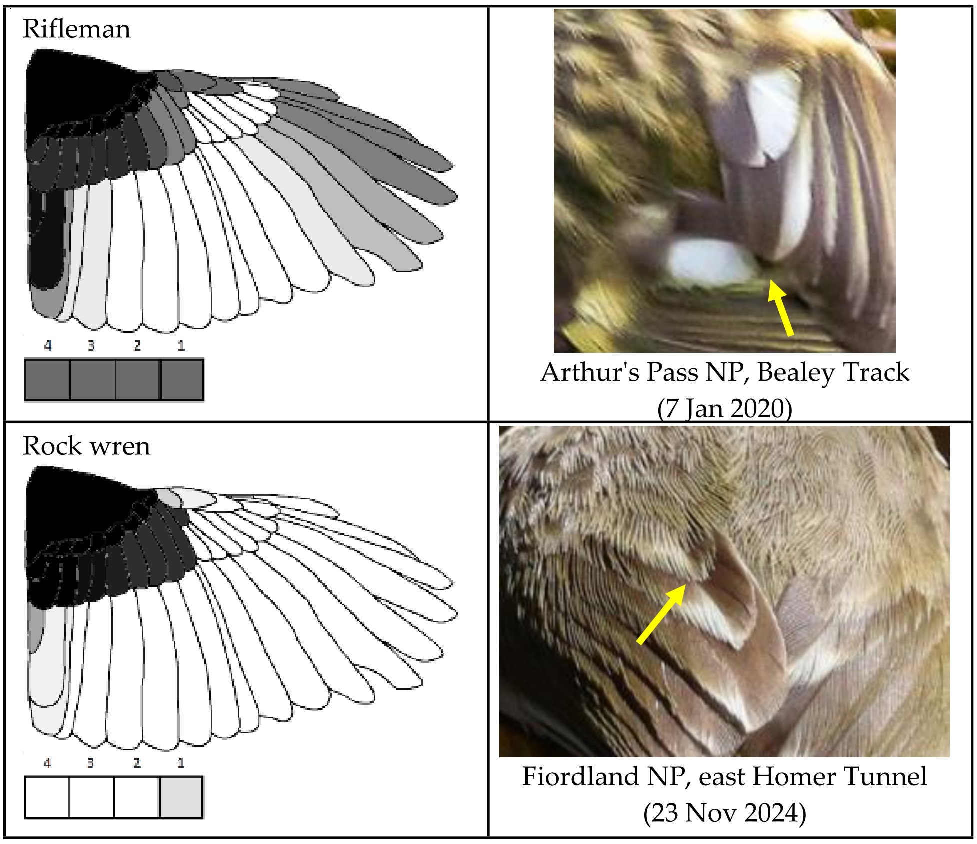


Figure 4. Feather replacement frequency in the post-juvenile moult of New Zealand wrens. Left column: Frequency of wing-feather replacement (top diagram) and of rectrix replacement (bottom squares). Grey shades depict observed percentage of replacement (white = 0%, black = 100%). Right column: Examples of moult limits (indicated by yellow arrows) with localities and dates. Photos used by license agreement from the Macaulay Library.

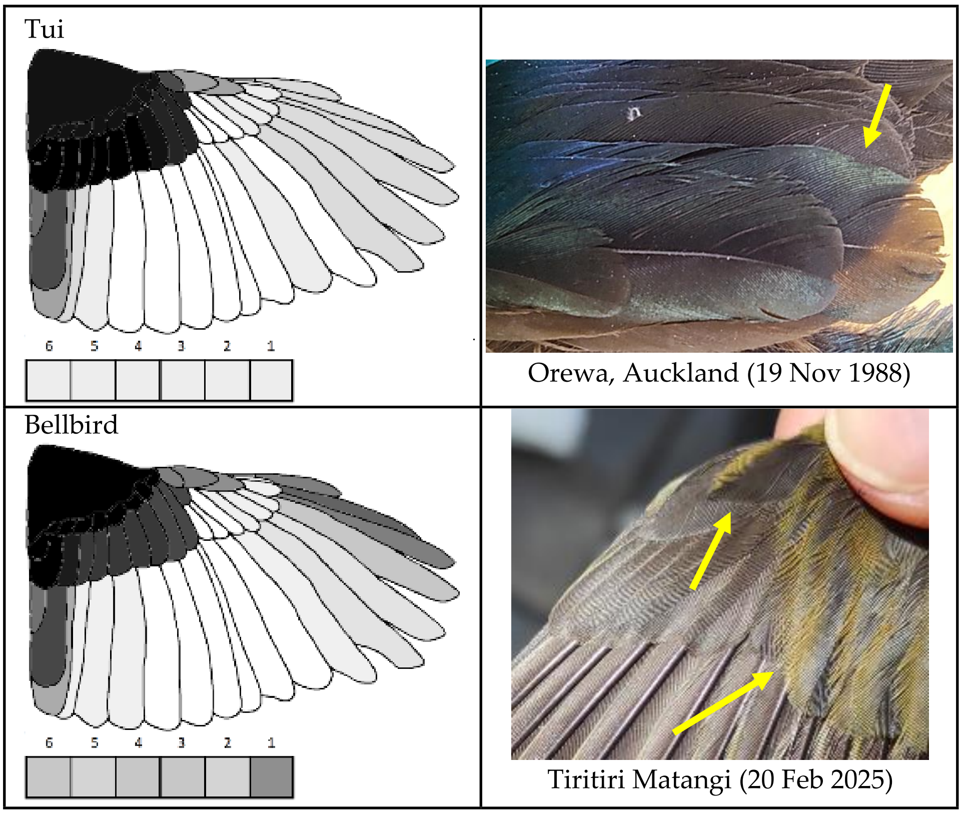


Figure 5. Feather replacement frequency in the post-juvenile moult of New Zealand honeyeaters. Left column: Frequency of wing-feather replacement (top diagram) and of rectrix replacement (bottom squares). Grey shades depict observed percentage of replacement (white = 0%, black = 100%). Right column: Examples of moult limits (indicated by yellow arrows) with localities and dates. Photos by authors.

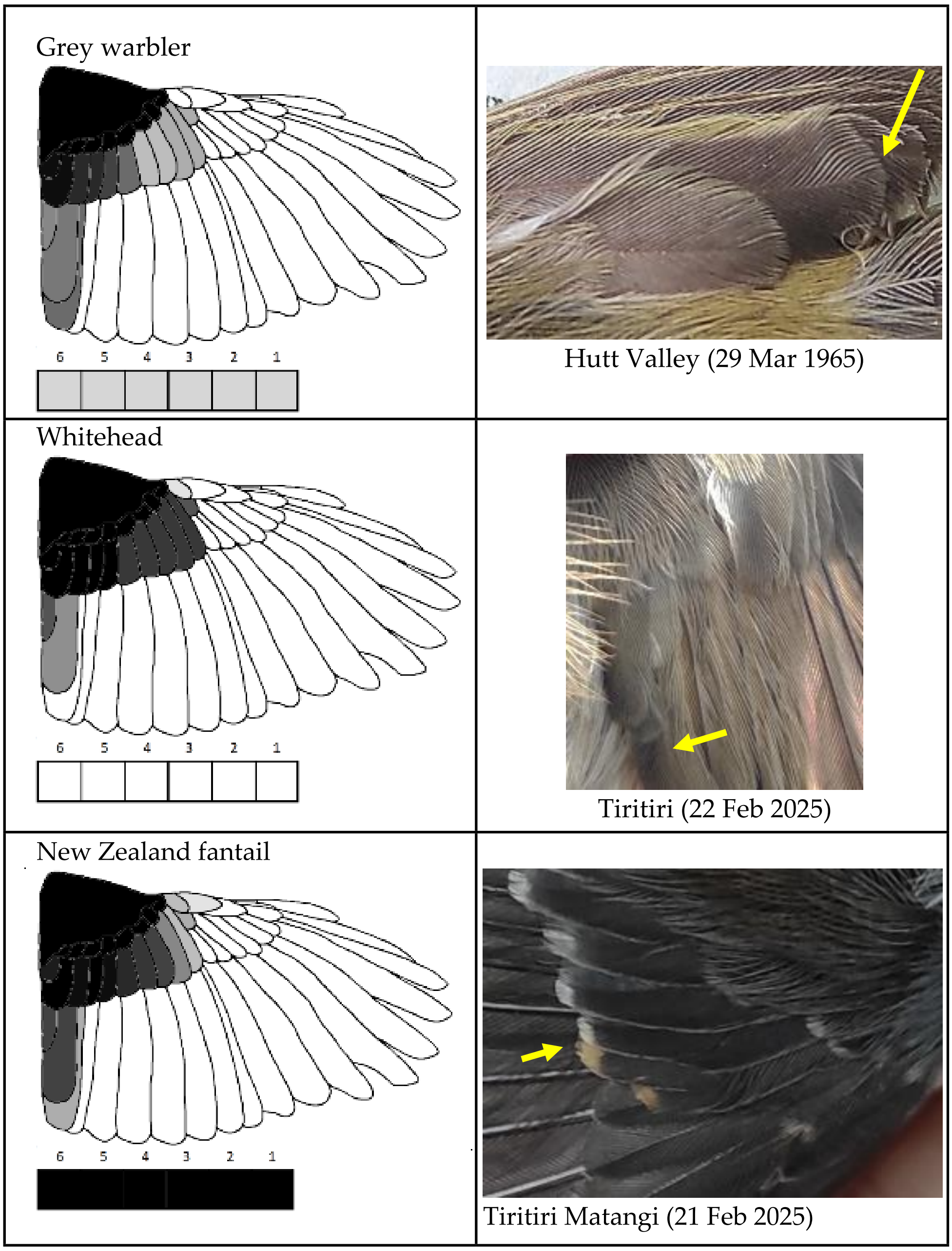


Figure 6. Feather replacement frequency in the post-juvenile moult of grey warbler, whitehead, and New Zealand fantail. Left column: Frequency of wing-feather replacement (top diagram) and of rectrix replacement (bottom squares). Grey shades depict observed percentage of replacement (white = 0%, black = 100%). Right column: Examples of moult limits (indicated by yellow arrows) with localities and dates. Photos by authors.

New Zealand pipit pīhoihoi: the juvenile plumage was paler overall with whitish margins to wing feathers that contrasted with the rufous margins of adults. Post-juvenile moult-limits were found within greater coverts (30 of 31 birds) and tertials (27 of 31 ones (Fig. 11). Pre-breeding moult limits were found within greater coverts and tertials also, with strong contrast between the fresh new feathers and the very deteriorated retained ones (Fig. 11). Age determination after the pre-breeding moult should rely on the shape and wear of feathers and not on the presence of moult limits (Jenni & Winkler 2020a).

DISCUSSION

Moult extent and pattern

Some New Zealand passerines show noticeable within-species differences in post-juvenile moult-extent (e.g., bellbirds moult from 11 up to 42 wing feathers; Guallar *et al.* 2025; Table 3). Considering that hatching date is negatively correlated with moult-extent (Bojarinova *et al.* 1999), this variation could be largely explained by the span of the breeding period. Moult extent is known to affect the social life of passerines because first-year males with larger post-juvenile moult-extent receive more aggression from adult ones, and this can have fitness consequences as seen in North Island robins (Berggren *et al.* 2004; Senar 2006). In this sense, the effect of post-juvenile moult-extent on the social life of the two Meliphagidae species of New Zealand merits further study, particularly how acquisition of notched primaries affects interactions with adults, winter survival, and mate selection in relation to changes in environmental conditions over the years (Craig 1984; Senar *et al* 1998, López *et al.* 2005).

Post-juvenile moult-extent estimates for four New Zealand passerines were obtained from very small sample sizes and should be taken with caution

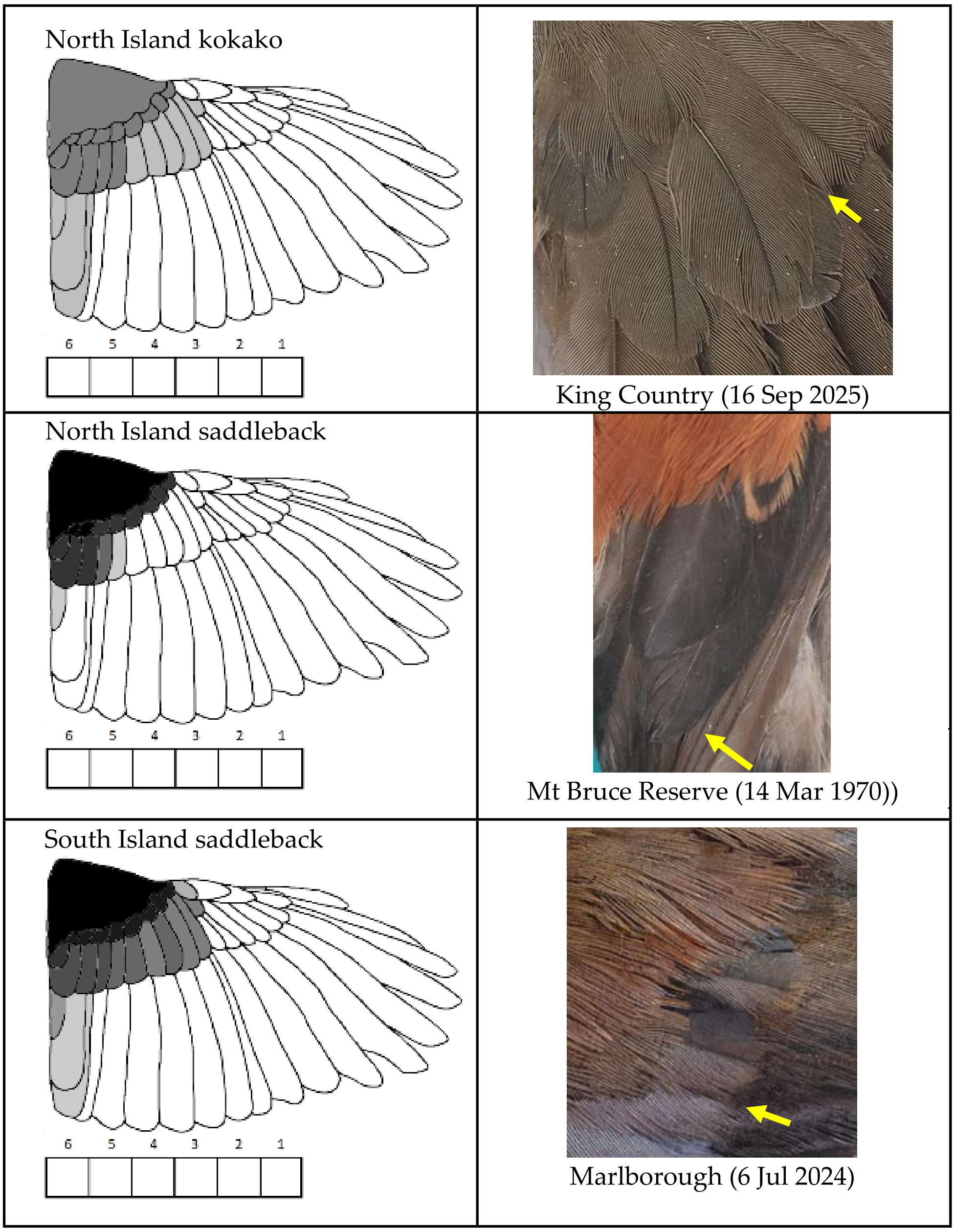


Figure 7. Feather replacement frequency in the post-juvenile moult of New Zealand wattlebirds. Left column: Frequency of wing-feather replacement (top diagram) and of rectrix replacement (bottom squares). Grey shades depict observed percentage of replacement (white = 0%, black = 100%). Right column: Examples of moult limits (indicated by yellow arrows) with localities and dates. Saddleback photos used by license agreement from the Macaulay Library; kokako photo by authors.

(Table 3; McCarthy 2007). However, comparison with the scarce information published on the post-juvenile moult of their closest relatives show clear similarities. For example, a portion of New Holland honeyeaters *Phylidonyris novaehollandiae* (Meliphagidae) exhibit an eccentric pattern, while the regent honeyeater *Anthochaera phrygia* undergoes a partial moult (Paton 1982; Munro & McFadden 2005). Grey warbler's congeners also undergo a partial moult (Higgins & Peter 2002). Like New Zealand fantail, the rufous fantail *Rhipidura rufifrons* retains greater coverts (Radley *et al.* 2011). Petroicidae species apparently undergo a partial moult (Higgins & Peter 2002). Welcome swallow's and silvereye's congeners also undergo a complete moult (Melville 1988; Radley *et al.* 2011). Incidentally, both species colonised New Zealand in recent times (Higgins & Peter 2002). Welcome swallow also shows the typical moult suspension of species in the family Hirundinidae (Niles 1972; Wilson *et al.* 2006). New Zealand pipit's congeners exhibit similar moult patterns (Guallar & Figuerola 2016), and is the only species in which we detected a pre-breeding moult. These similarities suggest that, despite their evolution in relative isolation, the post-juvenile moult of New Zealand passerines presents a phylogenetic inertia, in accordance with studies based on larger avifaunas (Delhey *et al.* 2020; Guallar & Jovani 2020a).

Low sample sizes may have also prevented detection of infrequent or occasional wing-feather moult patterns across New Zealand passerines. For example, we did not observe any partial post-juvenile moult in silvereye, as seen in Australia for birds hatched at the end of the breeding season (Swanson 1971; Scott *et al.* 2023). As found in previous studies, 'General' is the commonest post-juvenile moult-pattern (Table 2), while the inverted and reduced ones are associated with the pre-breeding moult (Guallar *et al.* 2018, 2020; Guallar & Jovani 2020a). The biological meaning of post-juvenile moult-pattern variation within species is unclear (Guallar *et al.* 2014).

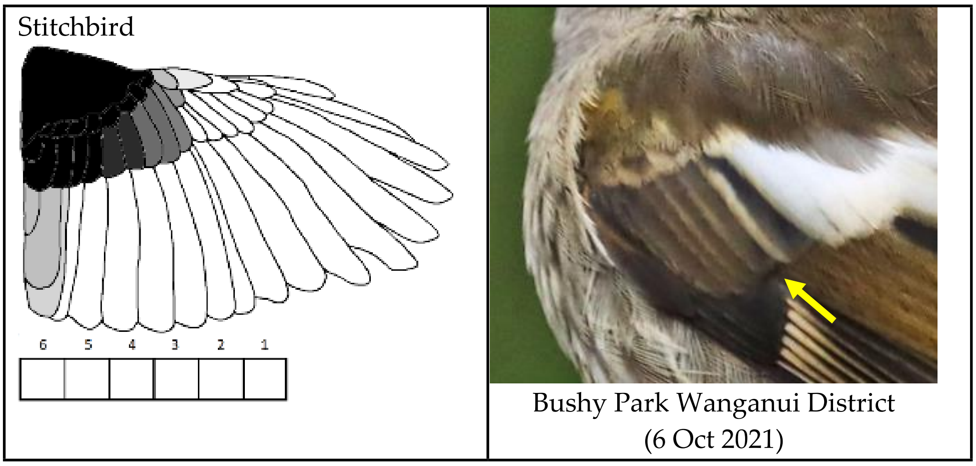


Figure 8. Feather replacement frequency in the post-juvenile moult of stitchbird. Left column: Frequency of wing-feather replacement (top diagram) and of rectrix replacement (bottom squares). Grey shades depict observed percentage of replacement (white = 0%, black = 100%). Right column: Examples of moult limits (indicated by yellow arrows) with localities and dates. Photo used by license agreement from the Macaulay Library.

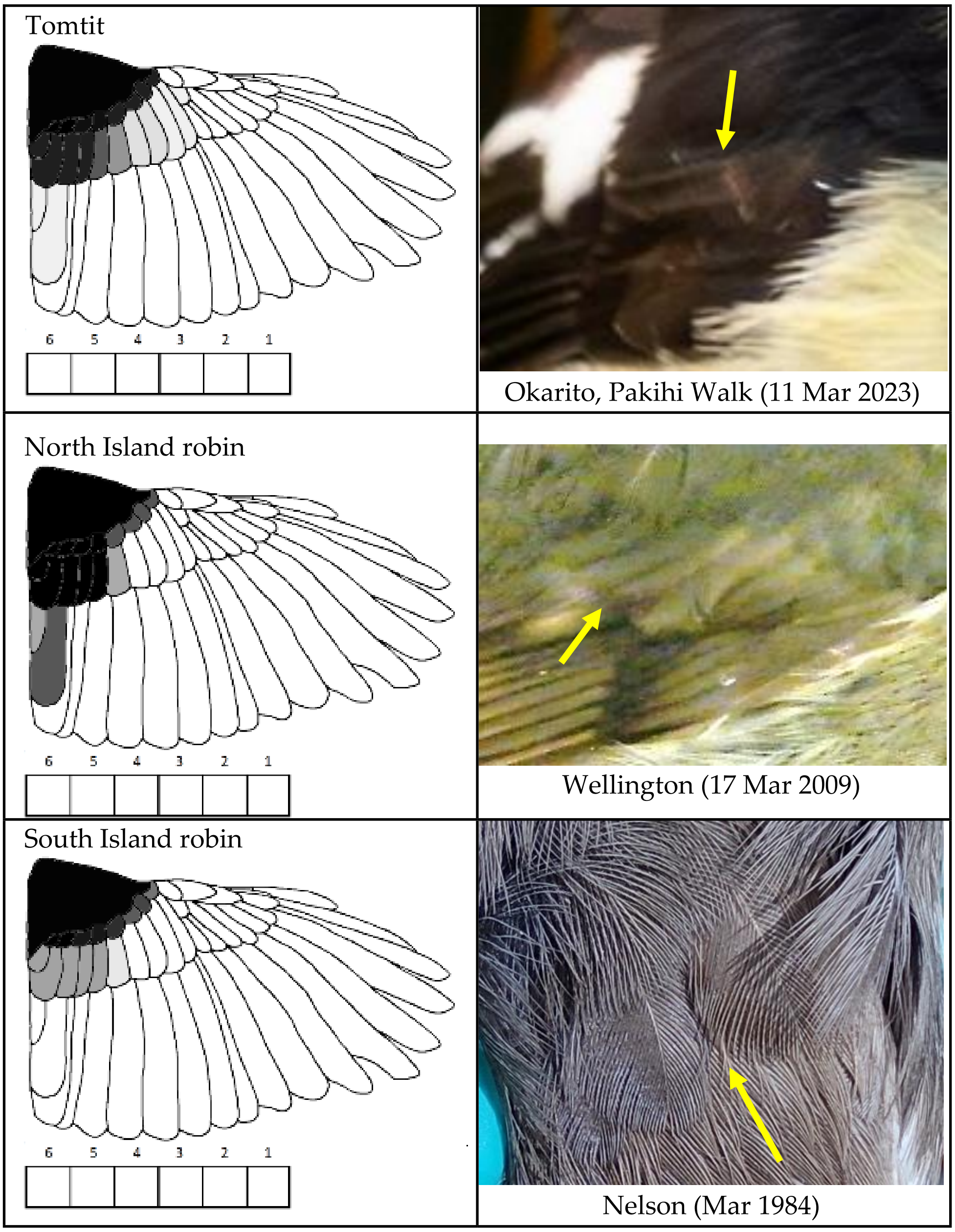


Figure 9. Feather replacement frequency in the post-juvenile moult of New Zealand robins. Left column: Frequency of wing-feather replacement (top diagram) and of rectrix replacement (bottom squares). Grey shades depict observed percentage of replacement (white = 0%, black = 100%). Right column: Examples of moult limits (indicated by yellow arrows) with localities and dates. Photos used by license agreement from the Macaulay Library.

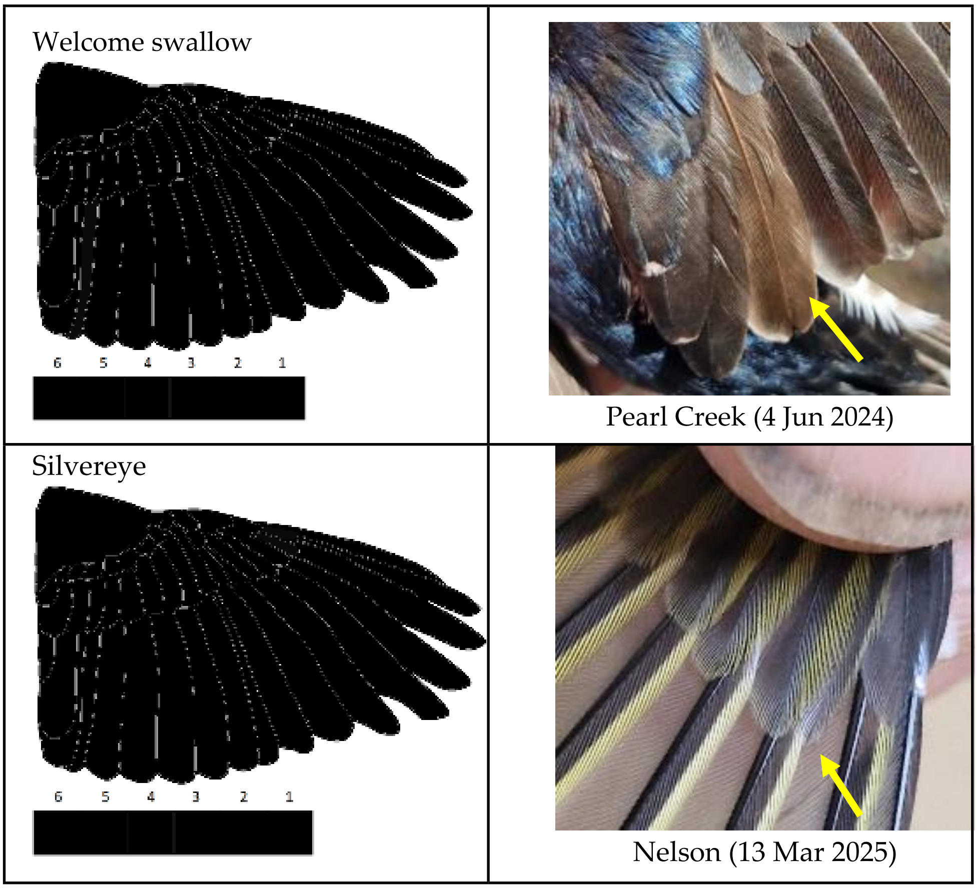


Figure 10. Feather replacement frequency in the post-juvenile moult of welcome swallow and silvereye. Left column: Frequency of wing-feather replacement (top diagram) and of rectrix replacement (bottom squares). Grey shades depict observed percentage of replacement (white = 0%, black = 100%). Right column: Examples of moult limits (indicated by yellow arrows) with localities and dates. Photos by authors.

However, moult patterns suggest that the feathers finally replaced during the post-juvenile moult are controlled by rules that balance moult extent increases with the general needs and constraints of each species (Barta *et al.* 2008; Guallar & Jovani 2020b; Guallar 2024). For example, increase in the post-juvenile moult-extent of bellbirds prioritises outer (notched) primaries over rectrices, whereas New Zealand pipits prioritise tertials and even rectrices over outer greater coverts (Fig. 4).

Age determination

Accurate age determination demands integrative use of morphological information. Timing within the annual cycle determines how to carry out this task, implying that the ageing guidelines may differ before, during, and after the moulting season. Differences in appearance between the adult and the juvenile should be used throughout the whole first annual cycle, albeit their applicability diminishes as the bird passes through new stages of the annual cycle. Indeed, these differences blur in the moulting season as the juvenile plumage gets replaced, during which moult sequence becomes diagnostic to distinguish between partial and complete moults. Once moult is finished, differences in appearance between the adult and the juvenile are at its minimum, and once unfeathered characters are fully mature, moult limits become the only guideline left (provided that the post-juvenile moult is not complete).

Technological advances may allow ageing of long-lived birds throughout their life time with a small error (De Paoli-Iseppi *et al.* 2019; Roman *et al.* 2024); however, age determination of birds in the field currently relies entirely on human assessment (although see Weidensaul *et al.* 2011). We caution that insufficient experience or training may lead to too much weight to morphological traits considered to be age diagnostic, without critical appraisal. For example, adult but not juvenile outer primaries of tui and bellbird have pronounced notches (Onley 1986; Bartle & Sagar 1987). If this character is used *prima facie*, without assessing moult limits, about 15% first-cycle tuis and 60% first-cycle bellbirds would be incorrectly classified as adults (Table 3). Similarly, about 25% first-cycle New Zealand fantails moulting all greater coverts would be incorrectly classified as adults if age determination relied solely on the presence of tawny tips on the greater coverts (Table 3; Radley *et al.* 2011). Conclusions from any analysis based on data obtained from this method would be incorrect. This is potentially relevant for managing New Zealand passerine populations, given that the success of translocations can be influenced by the age of the released birds, with young birds being more likely to settle, survive, and breed in the translocated areas (Miller *et al.* 2024; Morkvėnas *et al.* 2025).

Our results cover an important gap in the knowledge of the natural history of New Zealand passerines, generate reliable age determination criteria, and provide essential information to test hypotheses on the ecology and evolution of avian moult in the Australasian region. Nevertheless, since some of our findings are based on a very low sample size, we encourage New Zealand ornithologists and bird banders to accrue more moult information, both quantitative and photographic, and to refine the ageing criteria here outlined with larger sample sizes and more comprehensive descriptions.

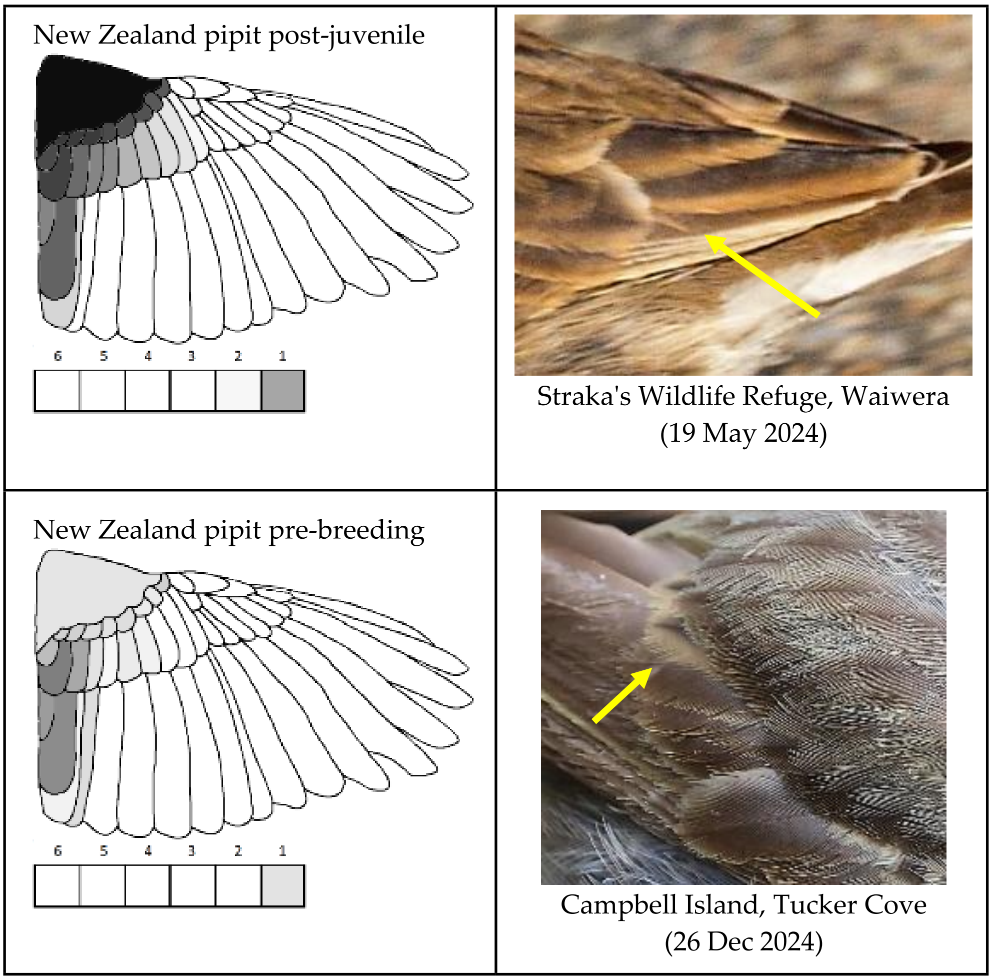


Figure 11. Feather replacement frequency in the post-juvenile and pre-breeding moults of New Zealand pipits. Left column: Frequency of wing-feather replacement (top diagram) and of rectrix replacement (bottom squares). Grey shades depict observed percentage of replacement (white = 0%, black = 100%). Right column: Examples of moult limits (indicated by yellow arrows) with localities and dates. Photos used by license agreement from the Macaulay Library.

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ETHICS

Mist-netting and banding were undertaken under the Ornithological Society of New Zealand's Wildlife Act Authorisation 48320-FAU issued by the Department of Conservation.

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