Wing areas and wing loadings of New Zealand land birds

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Abstract: Wing areas and wing loadings of New Zealand land birds are poorly documented in the literature. I therefore report measured wing areas of 84 individual birds belonging to 27 species, with calculated wing loadings. Plotting the data graphically allows some ecological inferences. Heavier New Zealand land birds achieve greater wing loadings than lighter species, as is the case for birds generally. For flying birds, small passerines had the lowest wing loadings (0.12 g/cm² for the New Zealand fantail) and heavier non-passerines the highest wing loadings (0.88 g/cm² for the pukeko). I expected non-migratory, forest-dwelling, endemic song-birds with weak dispersal abilities to have very high wing loadings but this was not the case. Instead, native and introduced song-birds of similar size tended to have fairly similar loadings. Wing loading was slightly elevated in the North Island saddleback and North Island kokako but the whitehead was normal. The tui, a vigorous flier, had a much lower wing loading than expected for its mass. Data for three flightless species suggest that while high wing loading is an important correlate of flightlessness, it is not the only factor.

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INTRODUCTION

The ability to fly, and morphological adaptations for flight, are prominent characteristics of birds. Wing loading is the ratio of body mass to wing area (Pennycuick 1985). Livezey (1992) regarded it as probably the most direct measure of flight-related morphology in birds. The relative wing loading of different species of birds correlates with their evolutionary history and their ecological niche.

Warham (1977) measured wing areas of New Zealand procellariiform seabirds and found that wing loading in petrels, as in birds generally, increased with increasing body size and correlated

with aspects of the birds' ecology. Similar details have not been available for New Zealand land birds. While working as a museum curator I had an opportunity to rectify this by tracing onto paper the wing outlines of land birds from the northern North Island region that were handed in dead to Auckland Museum.

I measured mostly native passerines, but I included a small selection of introduced song birds and native non-passerines for comparison. The samples are small but permit a preliminary overview of the subject. Pennycuick (1985) noted that collections of wing areas were worth publishing, provided that explicit details of the methods of measurement were given.

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Loss of flying ability is a distinctive feature of the New Zealand avifauna (Wilson 2004: 63–66). My expectation was that some of the native passerines in endemic genera that seem to be weak fliers, like the whitehead (*Mohoua albicilla*), North Island kokako (*Callaeas wilsoni*), and saddleback (*Philesturnus rufusater*), would show increased wing loading compared to strong fliers like the tui (*Prosthemadera novaeseelandiae*). This would be consistent with the idea that for some of the non-migratory land birds that live exclusively within forest and scrub, a long evolutionary history in an environment free of mammalian predators had allowed them to reduce their energetic investment in strong flight.

METHODS

From the 1980s to the early 2000s I examined land birds that were received dead by Auckland War Memorial Museum before they were processed into museum specimens. While they were fresh, or after they had defrosted (if received and stored frozen), and while their wings were flexible, I traced the outline of one wing onto millimetre-ruled graph paper using a pencil. I placed the graph paper on a table, and, with the bird on its back, I extended one wing over the graph paper making the wing's leading edge as straight as possible (Mendelsohn *et al.* 1989). This makes the wing fully open, as in flight, and standardises the wing shape. I measured only full-sized (usually adult) wings that did not have moulting flight feathers.

I counted the graph squares within the traced wing outline to estimate the wing area in mm^2 , and divided by 100 to convert the number to cm^2 . Wing loading (or mass loading) can be expressed as body mass per unit of wing area (g/cm²), or as wing area per unit of mass (cm²/g). I used the former, following Clark (1971), Warham (1977), and Mendelsohn *et al.* (1989). I calculated wing loading as body mass (g) divided by twice the area of one wing (cm²). Some authors include in the wing area an estimate of the area of the body between the wings (e.g. Pennycuick 1985), but I followed Warham (1977) and Mendelsohn *et al.* (1989) by ignoring the body.

Individual body masses for most of the museum birds were recorded at examination, but I found that these were usually below the average masses given by Heather & Robertson (1996). This was presumably because birds dried out to some degree before they were found in the field and brought to the museum, and/or during subsequent storage in a deep-freezer (sometimes for many years) before examination. To avoid the bias that these low individual masses would introduce in calculating wing loading, I instead used the average masses that Heather & Robertson (1996) provided. If Heather & Robertson (1996) listed separate masses for males and females, I kept the sexes as separate samples. If a bird of a sexually dimorphic species was unsexed I used the average of the mean male and female masses to calculate wing loading.

In total I traced the outlines of 60 fresh wings belonging to 15 species. To increase the total sample to 84 wings of 27 species I also calculated the areas of 21 dry wings in Auckland Museum's spread-wing collection, and three dry wings in the collection of Museum of New Zealand Te Papa Tongarewa (Wellington). I chose spread wings that had been prepared with a straight leading edge. The sample included three flightless species, i.e. weka (*Gallirallus australis*), South Island takahe (*Porphyrio hochstetteri*), and kakapo (*Strigops habroptila*).

RESULTS

General

Measured areas of single wings vary between 18.4 cm^2 for a grey warbler (*Gerygone igata*) to 646.9 cm^2 for a kakapo (Appendix 1). Wing loadings calculated for each of the 27 species considered (in taxonomic order), with sexes separated for the species dimorphic in mass, are summarised in Table 1.

Representative wing loadings for 24 volant species of New Zealand land birds vary between 0.12 g/cm² for New Zealand fantail (Rhipidura fuliginosa) and 0.88 g/cm² for pukeko (Porphyrio melanotus) (Fig. 1). Small passerines have the lowest wing loadings, and heavier non-passerines the highest wing loadings. The long-tailed cuckoo (Eudynamys taitensis), the only long-distance migrant in the sample, has an intermediate wing loading (0.39 g/cm²). Figure 2 (seven non-passerines and 17 passerines) and Figure 3 (17 passerines only) plot wing loadings as a function of mass. These show that heavier New Zealand land birds achieve greater wing loadings than lighter species. Figure 2 has an inverted j-shaped curve, because wing loading increases steeply with increasing mass and then levels out.

Taxonomic

Wing loadings of volant non-passerines vary between 0.38 g/cm² for the red-crowned parakeet (*Cyanoramphus novaezelandiae*) (a strong flier) and 0.39 g/cm² for the long-tailed cuckoo (which relies on strong flight for its long-distance migration), to 0.88 g/cm² for the pukeko (which flies reluctantly with rather laboured flight). For passerines, wing loadings vary from 0.12 g/cm² for the New Zealand fantail (an acrobatic flier that hawks insects) to 0.62 g/cm² for the North Island kokako (a weak flier). The non-passerines, mostly being heavier than the passerines, tend to have higher wing loadings (Fig. 2).

Table 1. Summary of wing loadings calculated for 27 species of New Zealand land birds. Sexes (and unsexed birds) are combined ("all") in species that are sexually monomorphic in mass. For samples with n = 1, the wing loading is shown in the range column. The data marked with a superscript "F" ($^{\text{F}}$) are used to represent the species in Figs 1–3.

Species	Sex	Mean	S.D.	п	Range
New Zealand pigeon (kererū)	Ŷ	0.674 ^F	0.00880	2	0.67-0.68
long-tailed cuckoo	all	0.391 ^F	0.0378	3	0.37-0.44
banded rail	ď	-	-	1	0.56 ^F
weka	ď	_	_	1	1.19
pukeko	ď	-	-	1	0.88 ^F
South Island takahe	ď	_	_	1	2.98
New Zealand dotterel	?	_	_	1	0.58 ^F
kakapo	ď	_	_	1	1.62
kaka	?	_	_	1	0.59 ^F
red-crowned parakeet	Ŷ	0.379 ^F	0.0412	2	0.35-0.41
red-crowned parakeet	?	_	_	1	0.37
rifleman	?	_	_	1	0.16 ^F
bellbird	ď	_	_	1	0.35
bellbird	Ŷ	0.371 ^F	0.0764	3	0.31-0.46
tui	ď	0.312 ^F	0.0691	2	0.26-0.36
tui	?	_	_	1	0.24
grey warbler	all	0.164^{F}	0.0175	2	0.15-0.18
North Island kokako	ď	_	_	1	0.62 ^F
North Island saddleback	?	0.528 ^F	0.0523	7	0.45-0.62
North Island saddleback	ď	0.532	0.0557	3	0.49-0.59
stitchbird	ď	0.317 ^F	0.0450	3	0.28-0.36
stitchbird	Ŷ	0.272	0.0305	2	0.25-0.29
stitchbird	?	_	_	1	0.31
whitehead	ď	0.278 ^F	0.0615	3	0.21-0.33
whitehead	Ŷ	0.234	0.0163	3	0.22-0.24
whitehead	?	_	_	1	0.29
New Zealand fantail	all	0.118^{F}	0.0130	5	0.10-0.13
tomtit	ď	0.197 ^F	0.0222	8	0.17-0.23
North Island robin	all	0.334 ^F	0.0427	13	0.26-0.41
welcome swallow	all	0.178^{F}	0.0222	4	0.15-0.20
silvereye	ď	-	_	1	0.28 ^F
Eurasian blackbird*	ď	_	_	1	0.43 ^F
song thrush*	?	-	_	1	0.48^{F}
house sparrow*	ď	_	_	1	0.35 ^F
European goldfinch*	?	_	_	1	0.21 ^F





Figure 1. Wing loadings (g/cm²) of 24 species of volant land birds from New Zealand. Bars show means or single values (see Table 1). Introduced species are marked with an asterisk (*).



Figure 2. Wing loading (g/cm²) as a function of mass (g) for 24 New Zealand volant land bird species. Plotted points are means or single values (see Table 1). Non-passerines are labelled: banded rail (BR), kaka (K), long-tailed cuckoo (LTC), New Zealand dotterel (NZD), New Zealand pigeon (NZP), pukeko (P), red-crowned parakeet (RCP). Unlabelled points are for passerines, shown separately in Fig. 3.



Figure 3. Semi-log plot of wing loading (g/cm²) as a function of mass (g) for 17 New Zealand passerine species (see Table 1): bellbird (Be), Eurasian blackbird* (EB), European goldfinch* (EG), grey warbler (GW), house sparrow* (HS), New Zealand fantail (NZF), North Island kokako (NIK), North Island robin (NIR), North Island saddleback (NIS), rifleman (Ri), silvereye (Si), song thrush* (ST), stitchbird (St, tomtit (To), tui (Tu), welcome swallow (WS), whitehead (Wh). Introduced species are marked with an asterisk (*).

The highest wing loadings for passerines (>0.4 g/cm²) are held by the heavier species (North Island kokako, North Island saddleback, song thrush *Turdus philomelos*, Eurasian blackbird *T. merula*; Fig. 3). The tui seems to have a much lower wing loading than expected for its mass and the North Island kokako and saddleback a slightly greater wing loading than expected (Fig. 3). In general, the native passerines in the study have wing loadings that are similar to those of similar-sized introduced song-birds, e.g. tomtit (*Petroica macrocephala*) and European goldfinch (*Carduelis carduelis*), bellbird (*Anthornis melanura*) and house sparrow (*Passer domesticus*) (Fig. 3).

Flightlessness

The weka is flightless at a wing loading of 1.19 g/ cm^2 , the kakapo at 1.62 g/ cm^2 and the South Island takahe at 2.98 g/ cm^2 (Table 1). The wing area of the takahe specimen is 503.3 cm^2 , while that of a pukeko, its close relative, is similar at 594.5 cm^2 . However, the takahe is about three times heavier than the pukeko, giving the flightless bird the greatly elevated wing loading.

DISCUSSION

Wing loading is difficult to quantify accurately, as it varies for individual birds with daily and seasonal

changes in their body masses (e.g. fullness of the stomach, development or regression of the gonads, state of fatness in connection with migration) and wing areas (e.g. wear and moult of the remiges; Warham 1977). Wing area is difficult to measure (Mendelsohn *et al.* 1989) and it varies with slight changes in how far the wing is spread. Wing loadings calculated for single birds (as for many species in Table 1) are indicative rather than definitive, and we need more measurements of wing areas to provide more reliable data based on the averages of good samples. This study is therefore a preliminary foray into the wing loadings of New Zealand land birds.

The data show that wing loading in New Zealand land birds increases with body size as is the case in birds generally (Warham 1977). The lowest wing loadings in the study are for small passerines with strong powers of flight (Fig. 1). The New Zealand fantail (0.12 g/cm²) flies acrobatically, and the welcome swallow (*Hirundo neoxena*) (0.18 g/cm²) extremely rapidly, to catch insects on the wing. The grey warbler (0.16 g/cm^2) is able to hover to glean insects from the outermost leaves of twigs and branches. The tomtit (0.20 g/cm^2) catches insects by sallying forth quickly from a perch. Durmuş (2022) confirmed that birds with higher wing loadings tend to perform unpowered flight styles such as soaring and gliding, while birds with lower wing loadings tend to have powered flight styles, such as flapping and hovering.

Wing loadings compiled by Poole (1938) for numerous North American birds (and which I recalculated in g/cm²) varied between 0.11 for both the golden-crowned kinglet (Regulus satrapa) and Leach's storm petrel (Hydrobates leucorhous), to 1.89 for the long-tailed duck (Clangula hyemalis). Bird (1999: 249) gave wing loadings for 44 volant Northern Hemisphere species, mostly land birds. When re-calculated in g/cm2 the wing loadings varied between extremes of 0.11 for Leach's storm petrel and 0.14 for the barn swallow (*Hirundo rustica*) to 2.01 for the Canada goose (Branta canadensis). In procellariiforms, Warham (1977) showed that wing loading varied between 0.15 g/cm² for the least storm petrel (Hydrobates microsoma) to 1.75 g/cm² for the southern royal albatross (Diomedea epomophora). Wing loadings were 0.21–1.09 g/cm² in 66 species of African raptors (Mendelsohn et al. 1989). The volant New Zealand land birds reported here all have wing loadings within the range known for other comparable birds.

I predicted that some of the endemic New Zealand song-birds, being non-migratory, living within the forest and scrub, and having had a long evolutionary history without mammalian predation, would show high wing loadings that suggested they were on the path towards flightlessness. The weak-flying North Island kokako had the highest wing loading (0.62 g/cm²) of any passerine in this study, but it was also the heaviest passerine and the wing loading was not extremely high.

Similarly, the North Island saddleback "bounds from branch to branch rather than flies" (Heather & Robertson 1996) and was ranked by Innes *et al.* (2022) as moderately gap limited in terms of its ability to cross gaps between forest fragments. From wing loadings it showed a small tendency towards flightlessness, with a value of about 0.53 g/cm², the second-highest of the passerines recorded in this study. However, the saddleback's wing loading is only slightly higher than for the song thrush and Eurasian blackbird (Fig. 3) which are birds of a similar size.

When studying whiteheads on Little Barrier Island (Gill & McLean 1992) I noticed that they fly quite weakly, often losing height if they are forced to fly more than a few tens of metres across open ground between trees. Innes *et al.* (2022) ranked the whitehead as strongly gap limited. Yet there is no exaggeration of the whitehead's wing loading, with a value similar to that of the strong-flying silvereye (Fig. 3). The tui, with a wing loading of about 0.31 g/ cm², has a much lower wing loading that expected for its mass. This is consistent with it being a strong flier, that makes long and fast trips between food sources and often flies high above the forest canopy.

In the New Zealand flying species studied, the wing loadings of up to 0.88 g/cm² (pukeko) gave no strong indication that any of these species have

seriously constrained flying ability. Meanwhile, the weka, kakapo and South Island takahe are flightless at wing loadings of 1.19–2.98 g/cm² (Table 1). However, the highest wing loadings for Northern Hemisphere flying birds listed by Bird (1999: 249) are 1.56 g/cm² for great bustard (*Otis tarda*), 1.70 for mute swan (*Cygnus olor*), 1.76 for whooper swan (*C. cygnus*), 1.79 for great northern diver (*Gavia immer*) and 2.01 for Canada goose. Meunier (1951) gave a wing loading of 2.5 g/cm² as a threoretical maximum that still permits flight.

The kakapo is the world's most massive parrot with the smallest relative wing size of any parrot (Livezey 1992). In the absence of wing area measurements for the kakapo, Livezey (1992) made estimates based on a regression line for other parrots and predicted wing loadings of 1.89 g/cm² for male kakapo and 1.17 g/cm² for females. The current study now provides the first measured wing loading for a male kakapo (1.62 g/cm²) and it is close to Livezey's estimate. Livezey (2003) estimated the takahe's wing loading with the suggestion that it would exceed Meunier's "threshold of flightlessness". This is now confirmed by my measured wing loading of 2.98 g/cm² in that species.

The takahe is a flightless bird that has passed Meunier's threshold, but the weka and kakapo are flightless well below it. Wing loading is clearly not the only determinant of flightlessness and flightless birds can retain large wings for purposes other than flight, such as display. Rails are a family in which reduction of pectoral musculature is critical to flightlessness (Livezey 2003). Similarly, Livezey (1992) showed that the kakapo's pectoral skeleton had reduced (with regard to adaptations for flight, like size of the sternal keel) compared with that of the kea (*Nestor notabilis*).

New Zealand birds show extremes of high and low dispersal ability. In line with this, Sheard *et al.* (2020) found that New Zealand was one of several regions of the world in which birds had highly variable hand-wing indices, an expression of the wing's aspect ratio that correlates with dispersal ability. The large range of wing loadings for New Zealand land birds – between 0.12 for the New Zealand fantail and 2.98 for the South Island takahe – also reflects the great variation in dispersal ability of New Zealand birds.

Since Word War II, New Zealand museums have relied on the salvage of dead birds to augment their collections and this paper shows the value of the biological information that can be gleaned from salvaged birds.

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Appendix 1. Wing areas (cm ²) of New Zealand land bird collection (NINNZ); all others have Auckland Museum re body. Sex is given where known. If there are subspecies, i (*); all other wings were fresh when measured.	s reported in this study, showing the Latin names of the species. Three wing specimens were in the Te Papa gistration (or taxidermy) numbers assigned to them. Areas are of one extended wing, excluding the adjacent all birds (except weka) are from the North Island subspecies. Dried spread-wings are marked with an asterisk
Species	Wing area (cm²)
COLUMBIDAE	
New Zealand pigeon Hemiphaga novaeseelandiae	477.7 (Tax. 02-028, 9). 486.6 (Tax. 02-030, 9).
Long-tailed cuckoo Eudunamus taitensis	143.7 (LB11809, imm). 168.2 (LB14020*, ad ơ). 170.1 (LB8981*, ad Չ).
RALLIDAE	
Banded rail Gallirallus philippensis	152.6 (LB7758*, ♂).
Weka Gallirallus australis	418.8 (NMNZ OR24133*, σ).
Pukeko Porphyrio melanotus	594.5 (LB1543*, ♂).
South Island takahe P. hochstetteri	503.3 (LB8980, d).
CHARADRIIDAE	
New Zealand dotterel Charadrius obscurus	125.2 (LB3664).
STRIGOPIDAE	
Kakapo Strigops habroptila	646.9 (NMNZ OR25733*, σ).
Kaka Nestor meridionalis	381.6 (Tax. 98-032).
PSITTACULIDAE	
Red-crowned parakeet Cyanoramphus novaezelandiae	85.8 (LB3588, ♀). 100.1 (LB7763*, ♀). 101.1 (Tax. 00-002).
ACANTHISITTIDAE	
Rifleman Acanthisitta chloris	20.3 (LB1633*).
MELIPHAGIDAE	
Bellbird Anthornis melanura	28.4 (LB3594, ♀). 37.8 (LB3589, ♀). 41.6 (LB9439, ♀). 49.2 (LB9168, ♂).
Tui Prosthemadera novaeseelandiae	166.4 (LB6798*, ♂). 215.9 (LB13208*). 228.3 (LB13209*, ♂).
ACANTHIZIDAE	
Grey warbler Gerygone igata	18.4 (LB10851). 21.4 (LB14075*, ơ).
CALLAEIDAE	
North Island kokako Callaeas wilsoni	186.7 (NMNZ OR30770*, ♂).
North Island saddleback <i>Philesturnus rufusater</i>	60.8 (LB11771). 66.7 (LB10837). 67.3 (Tax. 94-066, σ). 69.8 (LB9845). 71.8 (LB11073). 73.8 (Tax. 98-207). 74.8 (reg. no. uncertain). 78.0 (LB10722, σ). 82.0 (LB8610, σ). 83.4 (reg. no. uncertain).

Appendix 1. continued	
Species	Wing area (cm²)
NOTIOMYSTIDAE	
Stitchbird Notiomystis cincta	50.7 (LB7087*, ơ). 51.1 (LB3618, ♀). 53.3 (LB10357). 59.6 (LB7086*, ơ). 59.9 (LB12952, ♀). 67.1 (LB10748, ơ).
MOHOUIDAE	
Whitehead Mohoua albicilla	27.8 (LB13949, σ). 28.0 (LB9846). 29.8 (LB1575*, γ). 29.8 (LB10194, φ). 31.8 (LB10838, σ). 33.7 (LB3597, φ). 43.7 (LB3596, σ).
RHIPIDURIDAE	
New Zealand fantail Rhipidura fuliginosa PETROICIDAE	30.3 (LB11817). 31.7 (LB1558*, ơ). 32.9 (LB8432, ơ). 37.7 (Tax. 92-063). 39.3 (Tax. 98-076).
Tomtit Petroica macrocephala	23.6 (LB3671, ơ). 24.4 (LB11800, ơ). 26.6 (LB7844, ơ). 29.7 (LB12682, ơ). 29.9 (LB9292, ơ). 30.1 (LB12085, ơ). 30.2 (LB7843, ơ). 31.6 (LB12864, ơ).
North Island robin P. longipes	42.3 (LB7121*). 46.1 (LB7765). 47.1 (LB11095, imm). 48.4 (LB9293). 48.9 (LB7762). 50.3 (LB12039). 52.4 (LB12728). 56.2 (LB3666). 56.7 (LB11790). 57.9 (LB12039). 58.2 (LB9192). 60.8 (LB1666). 66.7 (LB11810).
HIRUNDINIDAE	
Welcome swallow <i>Hirundo neoxena</i> ZOSTEROPIDAE	35.1 (LB5811*, ơ). 36.7 (Tax. 97-197). 40.6 (LB12396). 46.9 (LB3592).
Silvereye Zosterops lateralis TURDIDAE	22.9 (LB1544*, ơ).
Eurasian blackbird Turdus merula	105.8 (LB1560*, ơ).
Song thrush T. philomelos	73.6 (LB1545*).
PASSERIDAE	
House sparrow Passer domesticus	42.3 (LB1563*, ơ).
FRINGILLIDAE	
European goldfinch Carduelis carduelis	36.1 (LB1566*).