

EVOLUTIONARY MORPHOLOGY OF FLIGHTLESSNESS IN THE AUCKLAND ISLANDS TEAL¹

BRADLEY C. LIVEZEY

Museum of Natural History, University of Kansas, Lawrence, KS 66045-2454

Abstract. The morphological bases of flightlessness in the Auckland Islands Teal (*Anas* [a.] *aucklandica*) are described through mensural and qualitative comparisons with its flighted relatives—Grey Teal (*A. gibberifrons*), Chestnut Teal (*A. castanea*), and Brown Teal (*A. chlorotis*)—using 448 study skins, 107 skeletons, dissections of three anatomical specimens, and supplementary data on body mass and wing areas of other dabbling ducks. Limited mensural data also were collected from two skin specimens and 38 skeletal elements of the flightless Campbell Island Teal (*A. [a.] nesiotis*). *Anas aucklandica* is the smallest of the four species, has the smallest relative wing length in the subtribe Anateae, and has tail lengths showing higher variance and sexual dimorphism than those of its closest flighted relatives. Numbers of primary remiges show a modal reduction of one in *A. aucklandica*, but counts varied from seven to 10 per wing and 21% of the specimens were laterally asymmetric in counts; a loss of several secondary remiges also is indicated. *Anas aucklandica* is characterized by a 50% reduction in the mean length of primary remiges and increased variation of the lengths of primary remiges; these changes together result in the highest wing loadings in *Anas* (2.2 g cm^{-2}). Canonical analysis of external measurements confirmed that “relative wing size” of *A. aucklandica* is substantially less than that of its flighted relatives, a proportionality which also characterizes juveniles of all four species; *A. chlorotis* was intermediate in relative wing size. Sexual dimorphism is comparatively great in *A. aucklandica*, despite its smaller overall size. Osteological measurements confirmed a roughly 50-mm reduction in skeletal wing length of *A. aucklandica*, and revealed that the humerus is disproportionately long and the ulna and carpometacarpus disproportionately short in the species; a similar pattern of disproportionately long proximal segments and disproportionately short mid-elements occurs in the leg. Multivariate comparisons of five sternal measurements indicate that *A. aucklandica*, and to a lesser degree *A. chlorotis*, show juvenile characters of shallow carinae and caudal emargination. Canonical analysis of 23 skeletal measurements revealed that the juvenile skeletal proportions of *A. aucklandica* and the intermediate proportions of *A. chlorotis*, relative to *A. gibberifrons* and *A. castanea*, define a complex axis contrasting dimensions of the pectoral girdle, antebrachium, and manus with those of the skull, humerus, leg elements, and other measurements of the manus and sternum. Dissections indicate that *A. aucklandica* is virtually identical (qualitatively) to *A. castanea* and *A. gibberifrons* in its pectoral musculature, but that most pectoral muscles are disproportionately small in the flightless form. The unique morphometrics and presumed genetic isolation of *A. aucklandica* justify its recognition as specifically distinct from *A. chlorotis*; the taxonomy of the group has had significant implications for evolutionary inferences in the past.

Anas aucklandica is the only anatid in which loss of flight was coincident with a derived decrease in body size. Small body size, underdevelopment of the pectoral appendage, and lessened sexual dichromatism of *A. aucklandica*, and to a lesser extent *A. chlorotis*, are interpreted as paedomorphic conditions, adaptive as developmentally economic changes related to year-round residency in a predator-depauperate insular environment, and are most likely the result of progenesis. Correlated changes in life histories, particularly increased egg size and decreased clutch size, characterize both *A. chlorotis* and *A. aucklandica* and distinguish the paedomorphosis of *A. aucklandica* as an exception to the general association between *K*-selection and neoteny.

Key words: Auckland Islands Teal; flightlessness; Australasian teal; *Anas aucklandica*; paedomorphosis; insularity; pectoral myology; morphometrics.

INTRODUCTION

Two skin specimens of a small, drab duck were collected on the Auckland Islands, New Zealand

(51°S, 116°E) in 1840, and these were later described by Gray (1844) as representatives of a new genus and species of duck, *Nesonetta aucklandica*. Gray (1844) described its wings as “. . . very short and pointed, with the second quill the longest . . .” Subsequently, other teal were de-

¹ Received 14 November 1989. Final acceptance 22 February 1990.

scribed from the main islands of New Zealand (*Anas chlorotis* Gray, 1845; later assigned to *Elasmonetta* Salvadori, 1895) and the more southern Campbell Island (*Xenonetta nesiotis* Fleming, 1935). The three taxa were included in the genus *Anas* by Delacour and Mayr (1945), and have been considered in recent decades to be closely related to the Chestnut Teal (*A. castanea*) and Gray Teal (*A. gibberifrons*) (Delacour and Mayr 1945; Delacour 1956; Johnsgaard 1965, 1978; Lack 1970), also of Australasia. *Anas castanea*, *A. chlorotis*, and *A. aucklandica* are monophyletic (Livezey, unpubl. data), and were treated as conspecific by Ripley (1942). Currently all three New Zealand forms are considered to be rare or threatened (Williams 1964, 1986). The taxonomic history of the group was reviewed by Dumbell (1986).

In spite of its relatively drab plumage and extremely limited distributional range, the Auckland Islands Teal became comparatively well-known, principally for its apparent flightlessness (Buller 1888, 1894; Buller and Hector 1896; Wigglesworth 1900). Flightlessness is shared by only three other extant species of waterfowl, the flightless steamer-ducks (*Tachyeres*; Livezey and Humphrey 1986); the extinct Auckland Islands Merganser (*Mergus australis*), formerly sympatric with *A. aucklandica*, was not flightless but appears to have undergone significant reduction of the pectoral apparatus (Livezey 1989a). This notoriety, however, inspired little morphological study of *A. aucklandica*, although adequate descriptions of plumage pattern and soft parts, and compilations of standard external measurements, were published (Buller 1894, Phillips 1925, Fleming 1935, Delacour 1956). Gadow (1902) was the first to consider the anatomical correlates of flightlessness in the species, but his discussion was limited to a footnote concerning the number and relative lengths of primary remiges in nine specimens; a similar condition was noted by Fleming (1935) in *A. (a.) nesiotis*. The only other morphological investigations of pectoral development in *A. aucklandica* were those of Boubier (1934), who compared wing lengths with body lengths in this and several other flightless birds, and Worthy (1988), who compared selected skeletal proportions of austral teal to the subfossil anatid *Euryanas finschi*.

In this paper I present a study of the morphological characters associated, directly or indirectly, with flightlessness in the Auckland Islands

Teal. Although several accounts indicate that *A. aucklandica* occasionally accomplishes weak, short flights (Buller 1905, Waite 1909, Bailey and Sorensen 1962, Scott 1971), the species apparently is not capable of *sustained level flight* (cf. Weller 1975a) and therefore is considered herein to be flightless. The present analysis emphasizes comparisons between the Auckland Islands Teal and three closely related species which are capable of flight (henceforth termed "flighted"). These comparisons include morphometric analyses and qualitative descriptions of skin specimens and skeletons, and myological dissections of the pectoral appendage. The paper concludes with a discussion of the ontogenetic, ecological, taxonomic, and evolutionary implications of flightlessness in the Auckland Islands Teal and a comparison with flightlessness in other waterfowl.

MATERIALS AND METHODS

TAXONOMY

I follow Oliver (1955) in considering the Auckland Islands Teal (*Anas aucklandica*), endemic to the Auckland Islands, as specifically distinct from the Brown Teal (*A. chlorotis*) of New Zealand proper (North Island, South Island, and Stewart Island). *Anas aucklandica* is readily separable from *A. chlorotis* using a number of derived characters, a sufficient condition for the recognition of *A. aucklandica* as a phylogenetic species (McKittrick and Zink 1988). The Campbell Island Teal (*A. [a.] nesiotis*), endemic to Campbell Island and nearby islets, remains poorly known; the few, poorly documented specimens available do not permit a reliable assessment of the differentiation (if any) of *nesiotis* from nominate *aucklandica* (Stead 1938, Delacour 1956, Johnsgard 1978), and it is not known if the population is even self-sustaining (Westerkov 1960, Bailey and Sorensen 1962, Robertson 1976, Williams 1985). Consequently, in the few instances where *nesiotis* is analytically considered, I adopt the tentative taxon *A. (a.) nesiotis*; all references to the binomen *A. aucklandica* concern the nominate form. Phylogenetic relationships of the "Australasian teal"—*Anas gibberifrons*, *A. castanea*, *A. chlorotis*, and *A. aucklandica*—are considered to be as hypothesized by Livezey (unpubl. data), in which *A. chlorotis* and *A. aucklandica* constitute the sister-group of *A. castanea* (Fig. 1).

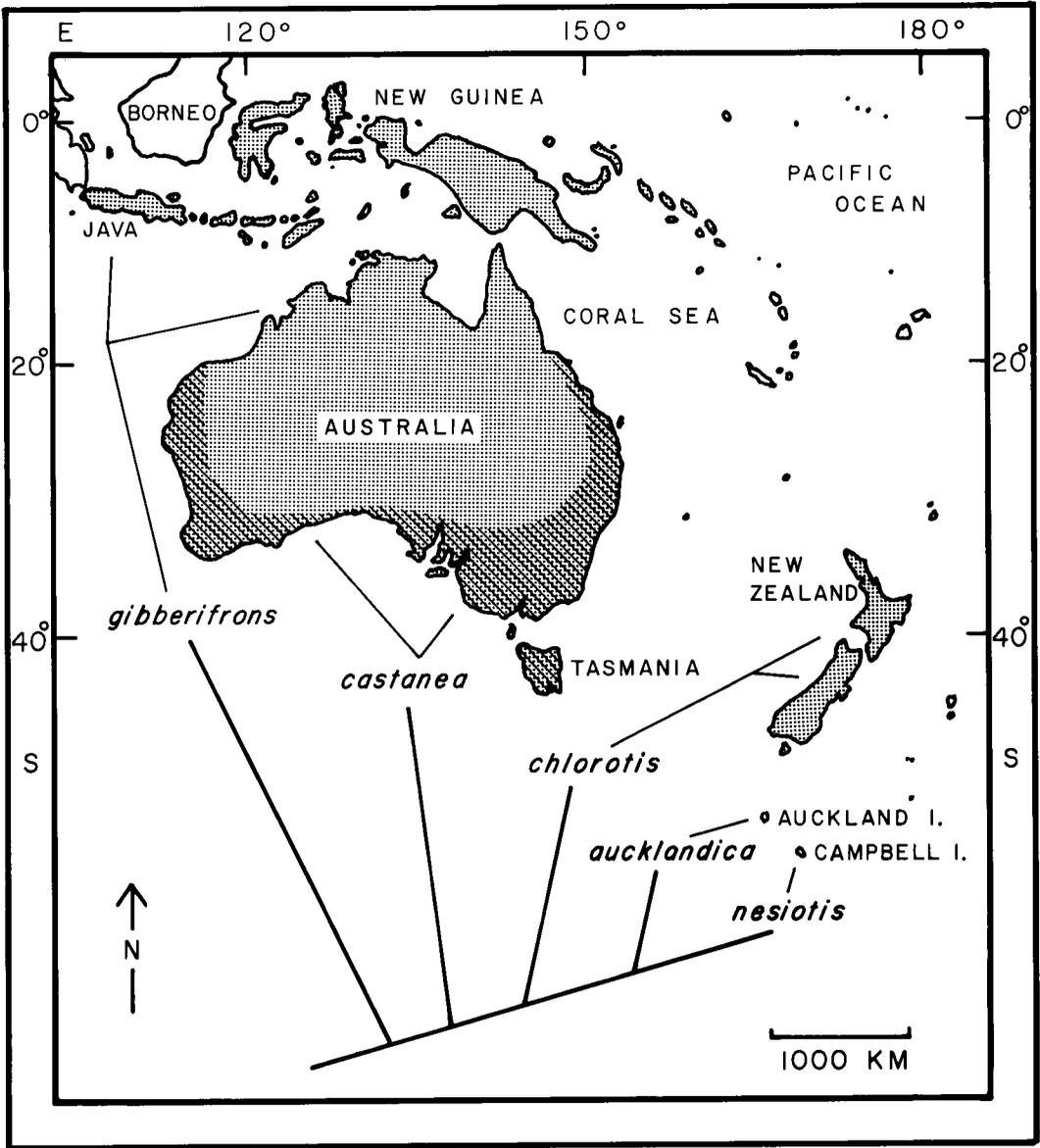


FIGURE 1. Distribution of Australasian teal; *Anas gibberifrons* (stippled) occurs also on the main islands of New Zealand (where sympatric with *A. chlorotis*) and includes an isolated population (*A. [g.] albogularis*) on the Andaman Islands, Indian Ocean (not shown). Substending tree reflects hypothesis of relationships of the five taxa (Livezey, unpubl.).

SPECIMENS AND RELATED DATA

Study skins included in this study were 75 *A. gibberifrons* (excluded *albogularis*), 109 *A. castanea*, 130 *A. chlorotis*, 132 *A. aucklandica*, and 2 *A. (a.) nesiotis*; of these 448 skins, 16 were juveniles and analyzed separately from adults, and the sexes of another 26 remained indeter-

minable using associated data, plumage, or classification functions (see below). A total of 107 associated skeletal specimens—40 *A. gibberifrons*, 37 *A. castanea*, 14 *A. chlorotis*, and 16 *A. aucklandica*—were available for mensural comparisons; of these, 90 provided virtually complete suites of measurements and only three were

from juvenile specimens. Sexes of most skeletons of *A. chlorotis* and *A. aucklandica* were not known or determinable by syringeal bullae or mensural comparisons (see below), therefore sexes within the two species were not distinguished in analyses. In addition, 38 skeletal elements of *A. (a.) nesiotis* (unsexed), some associated, were sampled. One wing and associated girdle of single spirit (anatomical) specimens of *A. gibberifrons* (YAPM 3496, male, wild-taken), *A. castanea* (LSU 99870, male, captive), and *A. aucklandica* (BMNH 1964.51.159, female, wild-taken) were dissected for myological comparisons; no anatomical specimen of *A. chlorotis* was available for study. A complete set of myological illustrations were prepared for *A. aucklandica*, not only to facilitate flightlessness-related comparisons, but because of the inadequacy of available myological studies of Anatidae (see Zusi and Bentz 1978 for review).

Data on body mass of the Australasian teal were copied from specimen tags and related files, and taken from published compilations (Gravatt 1966 fide Weller 1980, Frith 1967, Reid and Roderick 1973, Weller 1980, Norman and Hurley 1984), and provided by M. W. Weller (unpubl. data). Wing loadings of *Anas* were taken from Müllenhoff (1885), Magnan (1913a, 1913b, 1922), Poole (1938), George and Nair (1952), Savile (1957), Meunier (1959), Hartman (1961), Raikow (1973), Moulton and Weller (1984), M. W. Weller (unpubl. data), and Livezey (unpubl. data). Mean body masses and wing lengths for other dabbling ducks were based on means compiled by Mudge and Burn (1988), augmented by data given in Dement'ev and Gladkov (1967), Palmer (1976), and Weimerskirch et al. (1988).

MEASUREMENTS

Six measurements were made on study skins: culmen length (exposed, measured medially), nail width, wing length (chord of unflattened wing), tail length (arc length of central rectrix), tarsus length (measured on cranial surface), and middle-toe length (dorsal surface, excluding nail). Skin measurements, except wing length, were made using dividers and a ruler; wing length was measured using an end-stop metric ruler. All external measurements were recorded to the nearest millimeter. In addition, counts of primary remiges were made on both wings of each study skin (for specimens not in wing molt at time of collection). Wing areas of two specimens of *A. chlorotis* (tak-

en from dried, extended wings) and three specimens of *A. aucklandica* (from freshly killed specimens by M. W. Weller) were estimated by doubling the areas of tracings of single wings measured with a compensating polar planimeter. Wing areas for 10 other species of Anateae (sensu Livezey, unpubl. data) were collected by P. S. Humphrey and myself from fresh or frozen-and-thawed specimens using the same techniques. Wing loadings (Clark 1971) were estimated by calculating the ratio of body mass (g) over total wing area (cm²).

Thirty-five measurements were made on skeletal specimens analyzed here; these measurements have been described in previous publications (Livezey and Humphrey 1984, 1986; Livezey 1986a, 1988, 1989a, 1989b, 1989c). All measurements were made with dial calipers to within 0.1 mm.

Myological measurements largely were limited to widths of origins and insertions to avoid the substantial distortions of muscle bellies from preservation of anatomical specimens, although widths and lengths of bellies of some muscles were measured where considered to be representative. Sizes of the two major breast muscles, Mm. pectoralis and supracoracoideus, were compared using lengths and areas of sternal origins, as well as masses of the dried, detached muscle fibers. Relative sizes of other pectoral muscles were compared using interspecific differences between paired muscle measurements, each having been divided previously by the cube root of mean body masses for their respective species-sex groups. These differences in mass-standardized measurements were summarized for groups defined by the primary skeletal elements acted upon by the muscles (based on Raikow 1985; see Appendix). Key myological references consulted were Hudson and Lanzillotti (1964), George and Berger (1966), Hudson et al. (1972), and especially Zusi and Bentz (1978). Myological nomenclature follows Vanden Berge (1979).

STATISTICAL ANALYSES

Univariate comparisons of external and skeletal measurements were made using one-way and two-way analyses of variance (ANOVA), and subsequent pairwise comparisons were based on *t*-tests (based either on pooled or separate variance estimates, conditional on comparisons of sample variances). Variances of selected mea-

measurements were compared across groups using Levene's tests (statistic given as T), and variances of different measurements or groups with substantially different mean measurements were made using coefficients of variation ($CV = s/\bar{x} \cdot 100\%$). The small samples for *A. (a.) nesiotis* were excluded from statistical tests. Univariate tests of linear measurements were performed on raw data; those of body masses were based on log-transformed data (base e).

Bivariate plots of log-transformed data and "geometric-mean" regressions (Ricker 1984) were used to quantify allometric relationships (Gould 1966) between body mass and wing length among species of dabbling ducks. Intra-appendicular proportions of long bones were compared between sexes and among species using ANOVA of log-transformed ratios of bone lengths divided by skeletal limb lengths (skeletal wing length = sum of lengths of humerus, ulna, carpometacarpus, and the two proximal phalanges of major alar digit; skeletal leg length = sum of lengths of femur, tibiotarsus, tarsometatarsus, and the three proximal phalanges of pedal digit III).

Canonical analysis (CA), a technique which defines mutually orthogonal multivariate axes which maximally discriminate predefined groups relative to pooled within-group covariance structure (Pimentel 1979), was used to quantify differences among (1) eight species-sex groups using external measurements, and (2) among four species-sex groups and two species (sexes pooled) using skeletal measurements. Both data sets were log-transformed for multivariate analysis. Skin and skeletal specimens of juvenile birds and of *A. (a.) nesiotis* were plotted separately and not used in derivation of axes. In CAs of skeletal specimens, the lengths of the three proximal phalanges of pedal digit III were summed (referred to as digit-III length) for analysis. Initial CAs, in which variables were backstep-selected from the total data set using F -statistics, indicated that a subset of 23 skeletal variables was sufficient for discrimination of groups; this reduction in dimensionality lessened redundancy among variables and simplified the resultant axes and their interpretation. Multivariate differences among group means in stepwise CAs were tested using Wilks' statistics (λ) and compared using Mahalanobis' distances (D); interspecific D s were estimated between the mean scores of sexes within species. The significance of species, sex, and species-sex interaction effects were tested indi-

vidually for external measurements, for which adequate samples of each species-sex group were available, using stepwise multivariate analysis of variance (MANOVA). Separation of groups on each canonical variate (for both data sets) was assessed using ANOVAs of scores on the axes. Canonical variates for skeletons were interpreted using the standardized coefficients of variables in the complete 23-variable model.

Jackknifed classification procedures based on initial CAs permitted the determination of sex for 28 study skins lacking such data and for which posterior probabilities of assignment exceeded 0.95. Classification functions using skeletal measurements permitted the determination of sex in 11 skeletons of *A. gibberifrons* and *A. castanea* and the revision of species identifications of three inadequately documented skeletons.

Study skins lacking one or two measurements—due to breakage, deformity, or molt—were subjected to a procedure for missing-data estimation prior to CA; each missing datum was estimated using a stepwise regression on available measurements for specimens of the same species. This procedure resulted in 27 estimates (1.0% of data set) involving 21 skin specimens. Similar applications estimated 130 data in a total of 40 complete skeletons (5.8% of data set) and one estimate in each of two sterna (0.4% of data set) prior to corresponding CAs.

All statistical analyses were performed using programs in the Biomedical Computing Programs (Dixon 1985) on an IBM computer at the University of Kansas.

RESULTS

EXTERNAL CHARACTERS

Univariate comparisons. Available data on body mass were not adequate for statistical tests but indicated that *A. aucklandica* is slightly smaller than its sister species, *A. chlorotis*, and moderately less massive than *A. castanea*, the largest of the four species considered (Table 1); the single datum for *A. (a.) nesiotis* suggests that this form is less massive than the nominate taxon. In each species (Table 1), males are more massive than females, and the intersexual difference in *A. aucklandica* (27%) apparently exceeds those in *A. gibberifrons* (8%), *A. castanea* (12%), and *A. chlorotis* (4%).

Culmen lengths showed interspecific and intersexual rankings similar to those of body mass,

TABLE 1. Univariate statistics ($\bar{x} \pm s$ [n]) for body masses (g) and selected external measurements (mm) of the Australasian teal, by sex.

Variable	<i>A. gibberifrons</i>		<i>A. castanea</i>		<i>A. chlorotis</i>		<i>A. aucklandica</i>		<i>A. (a.) nestoris</i>	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Body mass ^a	508 ± 38 (218, 8)	469 ± 36 (153, 15)	660 ± 65 (89)	590 ± 138 (58)	599 ± 107 (13, 5)	574 ± 87 (29, 7)	521 ± 49 (10)	410 ± 94 (6)	426 (1)	
Culmen length	38.8 ± 1.9 (39)	36.9 ± 1.7 (28)	41.5 ± 2.0 (78)	39.3 ± 1.7 (21)	43.3 ± 1.9 (58)	40.4 ± 1.7 (47)	39.8 ± 1.3 (74)	37.0 ± 1.5 (47)	36.0 (2)	
Nail width	5.6 ± 0.8 (39)	5.5 ± 0.7 (29)	5.6 ± 0.5 (77)	5.5 ± 0.6 (21)	5.0 ± 0.6 (59)	4.8 ± 0.7 (50)	4.5 ± 0.6 (74)	4.3 ± 0.5 (47)	4.0 (2)	
Wing length	197 ± 6.6 (40)	186 ± 8.1 (29)	212 ± 6.6 (80)	200 ± 7.2 (20)	200 ± 6.6 (57)	186 ± 6.6 (57)	137 ± 7.2 (74)	123 ± 31 (50)	127 (2)	
Tail length	79.4 ± 6.9 (40)	75.5 ± 6.4 (29)	86.0 ± 6.6 (80)	81.0 ± 6.2 (21)	88.6 ± 7.5 (57)	78.8 ± 7.6 (50)	80.7 ± 12.7 (73)	66.1 ± 8.4 (48)	69.0 (2)	
Tarsus length	38.3 ± 1.8 (40)	35.9 ± 1.5 (29)	39.9 ± 2.2 (81)	38.9 ± 1.7 (21)	41.5 ± 1.9 (59)	39.6 ± 1.6 (50)	36.0 ± 1.9 (74)	33.9 ± 1.6 (48)	33.5 (2)	
Middle-toe length	40.3 ± 1.9 (40)	38.7 ± 1.3 (29)	42.8 ± 2.3 (81)	41.3 ± 2.8 (21)	43.7 ± 1.8 (58)	41.7 ± 2.3 (49)	43.7 ± 1.9 (74)	41.0 ± 2.1 (48)	41.0 (2)	

^a Sample sizes, where two are given, are for estimates of means and standard deviations, respectively.

with significant ($P < 0.0001$) interspecific ($F = 106.7$; $df = 3, 384$) and intersexual ($F = 166.8$; $df = 1, 384$) differences (Table 1). One exception to these mass-related rankings was *A. chlorotis*, in which several external dimensions (especially culmen length) were slightly greater ($P < 0.05$) than those of the more massive *A. castanea*. Variances in culmen lengths also differed among species (Levene's $T = 5.8$; $df = 3, 384$; $P < 0.001$), a result due in large part to the relatively small variances in *A. aucklandica*; variances in males of all species tended to be greater than those in females ($T = 4.7$; $df = 1, 384$; $P < 0.05$). Nail widths also showed significant interspecific differences ($F = 74.4$; $df = 3, 388$; $P < 0.0001$) but rankings deviated from those for body masses and culmen lengths (Table 1). Sex for sex, *A. gibberifrons* and *A. castanea* had equal nail widths (t -tests, $P > 0.45$), which were the largest of the four species (Table 1); nail widths of *A. chlorotis* were intermediate and *A. aucklandica* had the most narrow nails. Variances of nail widths differed significantly among species (Levene's $T = 4.9$; $df = 3, 388$; $P < 0.01$), largely reflecting the relatively low variances in *A. aucklandica*.

Wing lengths differed significantly among species ($F = 2,470.3$; $df = 3, 392$; $P < 0.0001$) and between the sexes ($F = 274.6$; $df = 1, 392$; $P < 0.0001$) and rankings tended to follow those of body mass; the wings of *A. aucklandica*, however, were disproportionately short, and there was no overlap between *A. aucklandica* and the other species in this measurement (Table 1). There were no differences in sexual dimorphism among species (interaction effects, $F = 0.7$; $df = 3, 392$; $P > 0.50$) or differences in variances among species (Levene's $T = 0.2$; $df = 3, 392$; $P > 0.85$) or between sexes ($T = 0.4$; $df = 1, 392$; $P > 0.50$) in wing lengths. Tail lengths also differed among species ($F = 34.8$; $df = 3, 390$; $P < 0.0001$) and between the sexes ($F = 80.0$; $df = 1, 390$; $P < 0.0001$), but showed intergroup rankings divergent from those of wing lengths (Table 1). *Anas castanea* and *A. chlorotis* had the longest tails which, sex for sex, were approximately equal (t -tests, $P > 0.05$). Sexual differences in tail length were comparatively small in *A. gibberifrons* ($t = 2.4$; $df = 63$; $P < 0.05$) and *A. castanea* ($t = 3.2$; $df = 32$; $P < 0.005$), and moderate in *A. chlorotis* ($t = 6.7$; $df = 102$; $P < 0.0001$). Tail lengths of male *A. aucklandica* were comparable to those of male *A. gibberifrons* ($t = -0.7$; $df = 111$; $P > 0.45$), but differed between the species for fe-

TABLE 2. Counts of primary remiges (excluding remicle) in study skins of *A. aucklandica* (not in wing molt), sexes pooled; symmetrical counts shown in boldface.

Number of primary remiges in left wing	Number of primary remiges in right wing				Total
	7	8	9	10	
7	1	0	2	0	3
8	0	11	10	0	21
9	1	10	85	2	98
10	0	0	1	2	3
Total	2	21	98	4	125

males ($t = 5.6$; $df = 71$; $P < 0.0001$), were uniquely variable (especially in males), and showed comparatively great sexual dimorphism ($t = 7.6$; $df = 118$; $P < 0.0001$; Table 1); these characteristics were almost solely responsible for species-sex interaction effects ($F = 7.6$; $df = 3, 390$; $P < 0.0001$) and differences in variances among species (Levene's $T = 12.16$; $df = 3, 390$; $P < 0.0001$) and between sexes ($T = 5.3$; $df = 1, 390$; $P < 0.01$).

Tarsus lengths showed interspecific ($F = 192.3$; $df = 3, 394$; $P < 0.0001$) and intersexual differences ($F = 85.9$; $df = 1, 394$; $P < 0.0001$) which followed body mass in mean rankings (Table 1); tarsus lengths of males were slightly more variable than those of females (Levene's $T = 4.8$; $df = 1, 394$; $P < 0.05$). Middle-toe lengths also differed interspecifically ($F = 37.7$; $df = 3, 392$; $P < 0.0001$) and intersexually ($F = 72.9$; $df = 1, 392$; $P < 0.0001$), but the former were due primarily to the comparatively short toes of *A. gibberifrons*; the other three species, sex for sex, had middle toes of comparable lengths (Table 1). Slight interspecific differences in variances of middle-toe lengths (Levene's $T = 3.3$; $df = 3, 392$; $P < 0.05$) were due in large part to the higher variances in *A. castanea*.

Primary remiges. As indicated by external wing lengths, *A. aucklandica* has disproportionately short wings (Table 1), a condition manifested as well in the primary remiges (flight feathers). Numbers of primary remiges in 125 skins of *A. aucklandica* (not in wing molt) varied from seven to 10 per wing (excluding the vestigial remicle), the pronounced mode being nine (Table 2); within *A. aucklandica* the sexes had similar distributions. The two skins of *A. (a.) nesiotis* had counts of nine left-eight right and eight left-eight right. This contrasts with the invariant count of

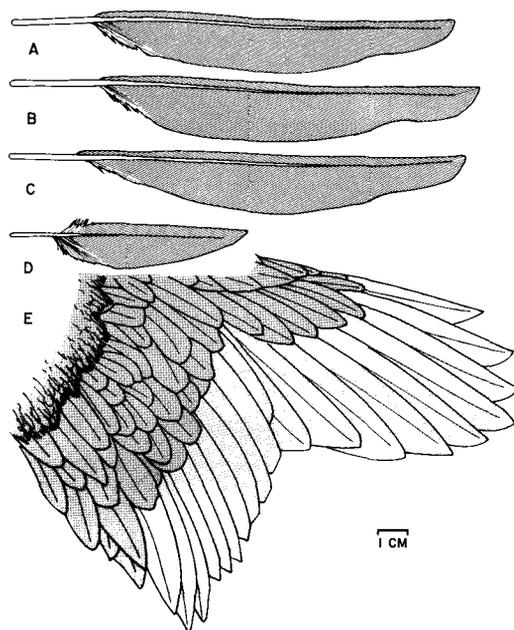


FIGURE 2. Diagrams of right, distal-most functional (10th) primary remiges of (A) *Anas gibberifrons* (YAPM 3496), (B) *A. castanea* (LSU 99870), and (C) *A. chlorotis* (AMNH 424078); and (D) distal-most primary (excluding remicle) remex (BMNH 1964.51.159), and (E) dorsal view of partly extended right wing of *A. aucklandica* (AMNH 731538).

10 functional primary remiges characteristic of *A. gibberifrons*, *A. castanea*, and *A. chlorotis*, and which is the primitive condition for the Anseriformes (Nitzsch 1840). Not only were there fewer primary remiges in *A. aucklandica*, but counts were laterally asymmetric in 26 (21%) of the specimens. The three anatomical specimens dissected confirmed this reduction in the number of primary remiges; also indicated is a loss of several secondary remiges in *A. aucklandica*, in which 11 secondary remiges were found, compared to the 14 found in *A. gibberifrons* and *A. castanea*. No "gaps" between remiges or other clues were detected in skins or anatomical specimens, therefore it was not possible to infer which remiges were lost in *A. aucklandica*.

Lengths of exposed portions of the outermost functional primary remiges of *A. castanea*, *A. chlorotis*, and *A. aucklandica* differed among species ($F = 721.0$; $df = 2, 96$; $P < 0.0001$) and between sexes ($F = 27.4$; $df = 1, 96$; $P < 0.0001$); within sexes, interspecific differences reflected the short primaries of *A. aucklandica* (25 males, $\bar{x} = 71.7$ mm; 20 females, $\bar{x} = 60.3$), which were

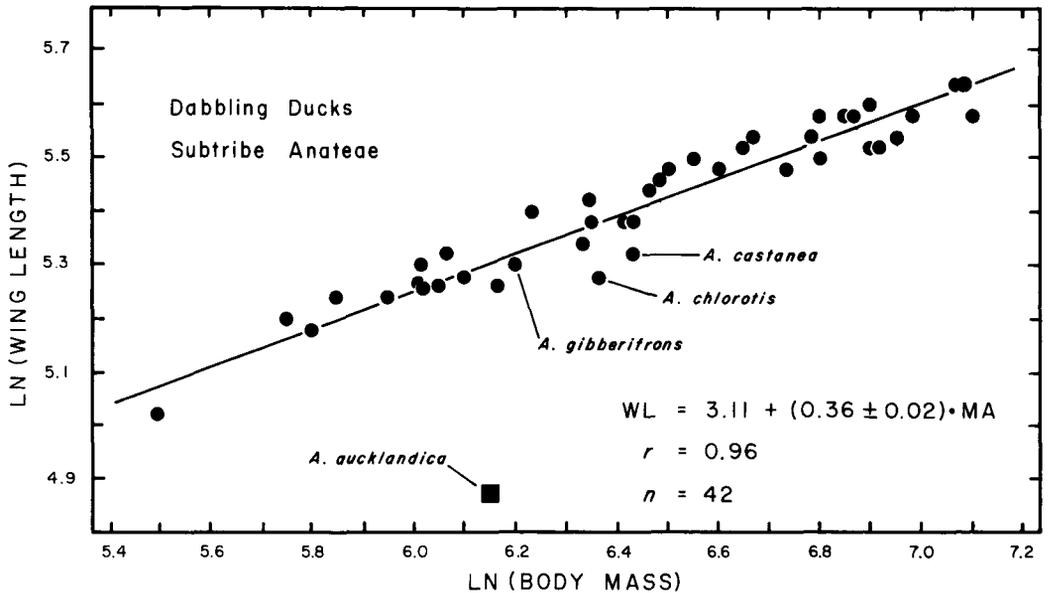


FIGURE 3. Bivariate plot of log-transformed mean body masses (g) and wing lengths (mm) for 43 taxa of dabbling duck (Anateae, sensu Livezey, unpubl.); regression line excludes the datum for flightless *Anas aucklandica*.

approximately half as long as those of *A. castanea* (18 males, $\bar{x} = 125.3$; 12 females, $\bar{x} = 122.0$) and *A. chlorotis* (13 males, $\bar{x} = 122.9$; 14 females, $\bar{x} = 114.3$). Remiges of *A. aucklandica* also were shorter than those of three juvenile *A. castanea* with growing remiges ($\bar{x} = 100.0$). Lengths of remiges also showed marginal differences in variances among species (Levene's $T = 2.6$; $df = 2, 96$; $P = 0.08$) and between sexes ($T = 4.3$; $df = 1, 96$; $P < 0.05$); the former largely reflected the large variances of lengths in *A. aucklandica* (males, $CV = 12.5\%$; females, $CV = 14.3\%$), relative to those within sexes of flighted *A. castanea* (3.9%, 3.8%) and *A. chlorotis* (6.8%, 3.2%). Variation in lengths of remiges in *A. aucklandica* also is manifested in the uniquely rounded wings of the species (Fig. 2). A reduction in asymmetry of the vanes of primary remiges of *A. aucklandica* also is indicated (Fig. 2).

Relative wing size. Wing lengths of flighted dabbling ducks (Fig. 3) were roughly isometric with body mass, i.e., slope not significantly ($t = 1.0$; $df = 32$; $P > 0.05$) different from the 0.33 isometrically relating a length to a mass. *Anas chlorotis*, although capable of flight, appeared as a moderate outlier from the generic curve (residual approximated three standard errors for the regression line), a reflection of its relatively short wings. Flightless *A. aucklandica*, not included in

the fitting of the regression line, was an extreme outlier (residual roughly 12 standard errors) due to its uniquely small relative wing length (Fig. 3).

Wing loadings, an alternate measure of relative wing size and one more directly indicative of flight capacity (Livezey and Humphrey 1986), were available for *A. aucklandica*, *A. chlorotis*, and 18 other species in the subtribe (Table 3). The estimate for *A. chlorotis* indicates that the species has moderately high wing loadings, especially for its size; this estimate, however, is a ratio of means (rather than a mean of directly measured wing loadings) and therefore may be a slight overestimate (Welsh et al. 1988). Although *A. aucklandica* is among the least massive of the species tabulated, it had the highest wing loadings ($\bar{x} = 2.17 \text{ g cm}^{-2}$), exceeding the greatest wing loadings for flighted dabbling ducks by 75% and approaching the theoretical upper limit for wing loadings permitting flight (2.50 g cm^{-2} ; Meunier 1951).

Canonical analysis of external measurements. A canonical analysis of the eight species-sex groups effectively discriminated the groups (Wilks' lambda = 0.01; $df = 6, 7, 394$; $P \ll 0.001$) and significantly incorporated all six measurements into the model (F [to remove] > 7.0 ; $df = 7, 389$; $P < 0.001$). Stepwise MANOVAs

TABLE 3. Mean wing loadings (g body mass·cm⁻² wing area) for 19 species of dabbling ducks, sexes pooled, grouped by mean adult body mass. Estimates based on associated masses and wing areas except for *Anas chlorotis*, which is based on a ratio of means.

Species	n	Wing loading	References*
Small species (mass < 0.5 kg)			
<i>Anas laysanensis</i>	12	0.98	10
<i>A. discors</i>	14	0.85	4, 8, 12
<i>A. cyanoptera</i>	1	0.66	9
<i>A. querquedula</i>	1	0.82	3
<i>A. crecca</i>	5	0.77	2, 3, 4, 7, 12
<i>A. flavirostris</i>	5	0.75	12
<i>A. aucklandica</i>	3	2.17	11
Intermediate species (0.5 kg < mass < 1 kg)			
<i>A. strepera</i>	3	1.05	4, 7, 12
<i>A. sibilatrix</i>	3	0.93	12
<i>A. penelope</i>	3	1.23	2, 3, 7
<i>A. americana</i>	3	1.14	8, 9
<i>A. platalea</i>	3	0.83	12
<i>A. clypeata</i>	8	0.96	2, 3, 4, 6, 7, 9
<i>A. bahamensis</i>	1	0.73	7
<i>A. acuta</i>	11	1.00	2, 3, 4, 5, 8, 9
<i>A. chlorotis</i>	2	1.24	12
Large species (mass > 1 kg)			
<i>A. specularioides</i>	2	1.27	12
<i>A. specularis</i>	1	0.94	12
<i>A. platyrhynchos</i>	20	1.21	1, 2, 3, 4, 7, 9, 12
<i>A. rubripes</i>	3	1.13	4, 6, 7

* 1—Müllenhoff 1885; 2—Magnan 1913a, 1913b; 3—Magnan 1922; 4—Poole 1938; 5—George and Nair 1952; 6—Savile 1957; 7—Meunier 1959; 8—Hartman 1961; 9—Raikow 1973; 10—Moulton and Weller 1984; 11—M. W. Weller, unpubl., nominate race; 12—Livezey, unpubl.

demonstrated significant interspecific ($F = 1,025.9$; $df = 5, 390$), intersexual ($F = 118.6$; $df = 3, 392$), and species-sex interaction ($F = 13.7$; $df = 2, 393$) effects in external measurements ($P < 0.001$ for each). Significant intergroup dispersion was incorporated by each of the first three canonical axes (Table 4). The first canonical variate (CV-I) alone incorporated 93.8% of the total intergroup variance; interspecific differences in scores on this axis were significant ($F = 3,187.5$; $df = 3, 394$; $P < 0.0001$) and largely represent the great morphometric distance between *A. aucklandica* and the three flighted species (Fig. 4). Two skins of *A. (a.) nesiotis*, not used to derive the axes, had scores similar to those for the nominate subspecies. Coefficients of variables for CV-I indicate that this difference is essentially a contrast between wing length and the lengths of the culmen, tail, and middle toe (Table 4). Species differed in variances of scores on CV-I (Levene's $T = 7.3$; $df = 3, 394$; $P < 0.0001$), largely the result of the relatively variable scores of *A. aucklandica*. Significant intersexual differences in scores on CV-I ($F = 165.7$; $df = 1, 394$; $P <$

0.0001) indicate that sexual dimorphism within each species consisted partly of "relative wing length." Various developed juvenile specimens of all four species, not used in deriving the axis, had lower scores on CV-I than their adult conspecifics (Fig. 4).

The second canonical axis (CV-II) for skin

TABLE 4. Standardized coefficients of variables and summary statistics for first three canonical axes of external measurements discriminating eight species-sex groups of Australasian teal.

Variable	Canonical variate		
	I	II	III
Culmen length	-0.13	-0.73	-0.13
Nail width	0.05	0.28	0.53
Wing length	1.12	0.15	0.09
Tail length	-0.35	-0.29	0.46
Tarsus length	0.04	-0.29	-0.84
Middle-toe length	-0.13	-0.18	0.80
Eigenvalue	27.6	1.5	0.3
Cumulative variance (%)	93.8	98.8	99.8
Canonical R	0.98	0.77	0.47

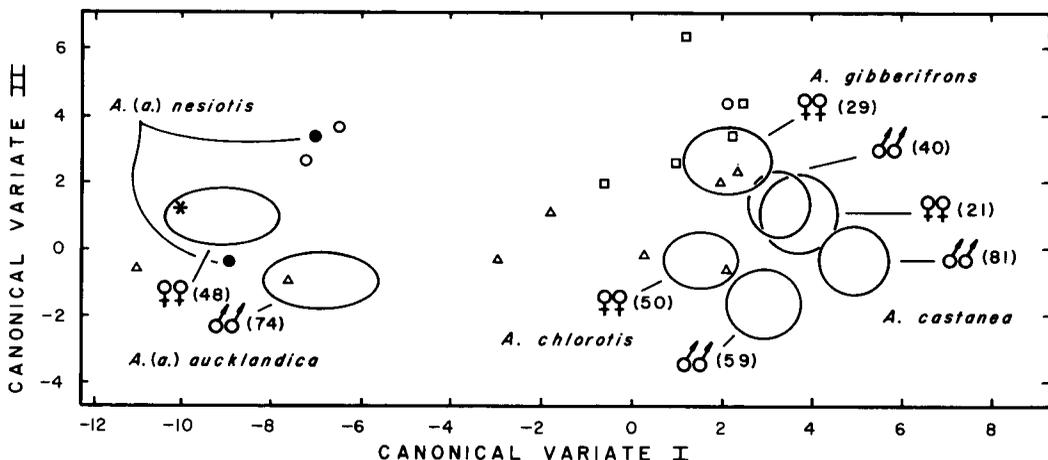


FIGURE 4. Plot of mean scores (\pm standard deviation) of eight species-sex groups of Australasian teal on the first two canonical axes of six external (skin) measurements; also plotted (but not used in derivation of axes) are juvenile specimens of *Anas gibberifrons* (open circles), *A. castanea* (open squares), *A. chlorotis* (open triangles), and *A. aucklandica* (asterisks), as well as two adult specimens of *A. (a.) nesiotis* (solid circles). Axes are interpreted in text.

measurements accounted for another 5.0% of the intergroup dispersion, included significant interspecific ($F = 125.6$; $df = 3, 394$; $P < 0.0001$) and intersexual differences ($F = 177.4$; $df = 1, 394$; $P < 0.0001$) in scores, and essentially contrasted nail width and wing length with the other variables, especially culmen length (Table 4). In large part, CV-II provided additional separation between *A. gibberifrons* and the other three species (Fig. 4). There were no significant differences in variances of scores on CV-II (Levene's tests, $P > 0.10$).

The third canonical variate (CV-III) contributed only 1% to the intergroup dispersion, but included significant ($P < 0.0001$) interspecific ($F = 17.5$; $df = 3, 394$) and intersexual ($F = 16.6$; $df = 1, 394$) differences in scores. Coefficients of variables reveal that this axis contrasted tarsus length with nail width, tail length, and (particularly) middle-toe length (Table 4). Scores indicate that this axis primarily distinguished *A. chlorotis* from the other species by its relatively long tarsi (not figured); scores on this axis also reveal that females tended to have relatively longer tarsi than males, a dimorphism which was substantially greater in *A. chlorotis* and *A. aucklandica* than in the other two species (species-sex interactions, $F = 5.7$; $df = 3, 394$; $P < 0.001$).

Interspecific Mahalanobis' distances (D) on the first three canonical variates underscore the similarity between *A. castanea* and *A. chlorotis* (D

$= 2.7$), and the great morphometric distinctions between flightless *A. aucklandica* and flighted *A. gibberifrons* ($D = 10.9$), *A. castanea* (12.3), and *A. chlorotis* (10.3). Multivariate intersexual distances (within species)—*A. gibberifrons* ($D = 1.8$), *A. castanea* (1.6), *A. chlorotis* (2.1), and *A. aucklandica* (2.9)—confirmed the comparatively great sexual dimorphism of *A. aucklandica* in external measurements.

SKELETAL CHARACTERS

Univariate comparisons. Although adequate numbers of skeletons of known sex were available to analyze the sexes separately in *A. gibberifrons* and *A. castanea*, the smaller samples of typically unsexed skeletons of *A. chlorotis* and *A. aucklandica* precluded this and the latter were pooled within species. The few measurements available for *A. (a.) nesiotis* were tabulated but not included in statistical comparisons. Despite this limitation, however, comparisons of skeletal measurements revealed several strong morphometric patterns among the species, the most notable being unique to flightless *A. aucklandica*. All skeletal measurements showed significant differences among the six groups analyzed (ANOVA, $P < 0.0001$), and, where sexes were distinguished (*A. gibberifrons* and *A. castanea*), males were larger than females (ANOVA, $P < 0.10$) in all but widths of limb elements, sternum, and pelvis.

Skull measurements tended to follow body mass in interspecific rankings, except that three—bill length, cranial height, and cranial width—were largest in *A. chlorotis* (Table 5). Wing measurements followed body mass more closely in interspecific rankings, but those of *A. aucklandica* were disproportionately small, especially those of the midwing elements—ulna, radius, carpometacarpus, and proximal phalanx of the major digit (Table 5). Dimensions of leg elements showed two different interspecific patterns: measurements of the femur, tibiotarsus, and digit III were longest in *A. chlorotis* and *A. aucklandica*, intermediate in *A. castanea*, and least in *A. gibberifrons*; tarsometatarsal dimensions were largest in *A. chlorotis*, intermediate in *A. gibberifrons* and *A. castanea*, and least in *A. aucklandica* (Table 5). Measurements of the pectoral girdle—scapula, coracoid, and sternum—like those of wing elements, followed body mass in interspecific rankings but tended to be disproportionately small in *A. aucklandica*. Interacetabular width, a measurement of pelvic breadth, resembled skull measurements in being largest in *A. chlorotis* and mass-related in the other species (Table 5). Skeletal dimensions of the poorly represented *A. (a.) nesiotis* were slightly smaller than those of (nominative) *A. aucklandica* (Table 5).

Intra-appendicular proportions. Given the interspecific differences in lengths of wing elements, substantial differences among species in total skeletal wing length (sum of lengths of humerus, ulna, carpometacarpus, and major digit) were not unexpected ($F = 171.7$; $df = 3, 68$; $P < 0.0001$). Mean lengths (mm) of the skeletal wing (sexes pooled) were 206.1 in *A. gibberifrons*, 211.6 in *A. castanea*, 195.1 in *A. chlorotis*, and 141.4 in *A. aucklandica*. There also were significant interspecific differences in the proportions of skeletal wing length composed by the humerus ($F = 142.5$; $df = 3, 68$; $P < 0.0001$), ulna ($F = 118.1$; $df = 3, 68$; $P < 0.0001$), carpometacarpus ($F = 69.8$; $df = 3, 68$; $P < 0.0001$), and phalanx II of the major digit ($F = 5.7$; $df = 3, 68$; $P < 0.005$); there were no significant differences in the proportion of phalanx I of the major digit ($F = 1.4$; $df = 3, 68$; $P > 0.25$), and variances of proportions did not differ interspecifically (Levene's tests, $P > 0.05$). *Anas gibberifrons* and *A. castanea* were very similar in intra-alar proportions (Fig. 5), and differed only slightly in those of the humerus ($t = -2.1$; $df = 68$; $P < 0.05$) and ulna ($t = 2.5$; $df = 68$; $P < 0.005$). *Anas*

chlorotis showed substantial shifts in alar proportions, differences which were similar in direction but generally less extreme than those which characterized *A. aucklandica*. The humerus constituted roughly 1.5% more of skeletal wing length in *A. chlorotis* than in *A. gibberifrons* or *A. castanea*, and that of *A. aucklandica* contributed almost 3% more to skeletal wing length than those in the latter two species (Fig. 5). Similarly, the ulna and carpometacarpus of *A. chlorotis* showed a decrease in their contributions to skeletal wing length, relative to those of *A. gibberifrons* and *A. castanea*, and *A. aucklandica* showed an even greater decline in these midwing proportions (Fig. 5). Proportions of the proximal phalanx of the major digit were almost identical in all four species, but *A. chlorotis* showed a decrease in the proportion of the distal phalanx, a shift even greater than that indicated in *A. aucklandica* (Fig. 5).

The pelvic limb also showed striking differences in total skeletal length ($F = 19.7$; $df = 3, 66$; $P < 0.0001$); pooling sexes, the skeletal length (mm) of the leg (femur, tibiotarsus, tarsometatarsus, and digit III) averaged 180.6 in *A. gibberifrons*, 189.7 in *A. castanea*, 202.6 in *A. chlorotis*, and 187.4 in *A. aucklandica*. Interspecific differences in proportions within the pelvic limb were significant in the femur ($F = 26.1$; $df = 3, 66$; $P < 0.0001$), tibiotarsus ($F = 3.0$; $df = 3, 66$; $P < 0.05$), tarsometatarsus ($F = 107.8$; $df = 3, 66$; $P < 0.0001$), and digit III ($F = 4.5$; $df = 3, 66$; $P < 0.01$); and only the femur showed interspecific differences in variance of proportions (Levene's $T = 4.4$; $df = 3, 66$; $P < 0.01$), an effect due to the comparatively large variance in femoral proportions of *A. castanea*. Mean femoral proportions were virtually identical in the three flighted species, but were substantially greater in flightless *A. aucklandica* (Fig. 6). Tibiotarsal proportions were greater in the sister species *A. chlorotis* and *A. aucklandica* than in *A. gibberifrons* or *A. castanea*, and the proportions constituted by the tarsometatarsus were substantially smaller in *A. aucklandica* than in its three flighted relatives (Fig. 6). The proportions of digit III were, relative to those in *A. gibberifrons* and *A. castanea*, small in *A. chlorotis*, and great in *A. aucklandica* (Fig. 6).

Conformation of sterna. The sternum provides the primary anchoring surfaces for the two largest flight muscles—Mm. pectoralis and supracoracoideus—and is the skeletal element most re-

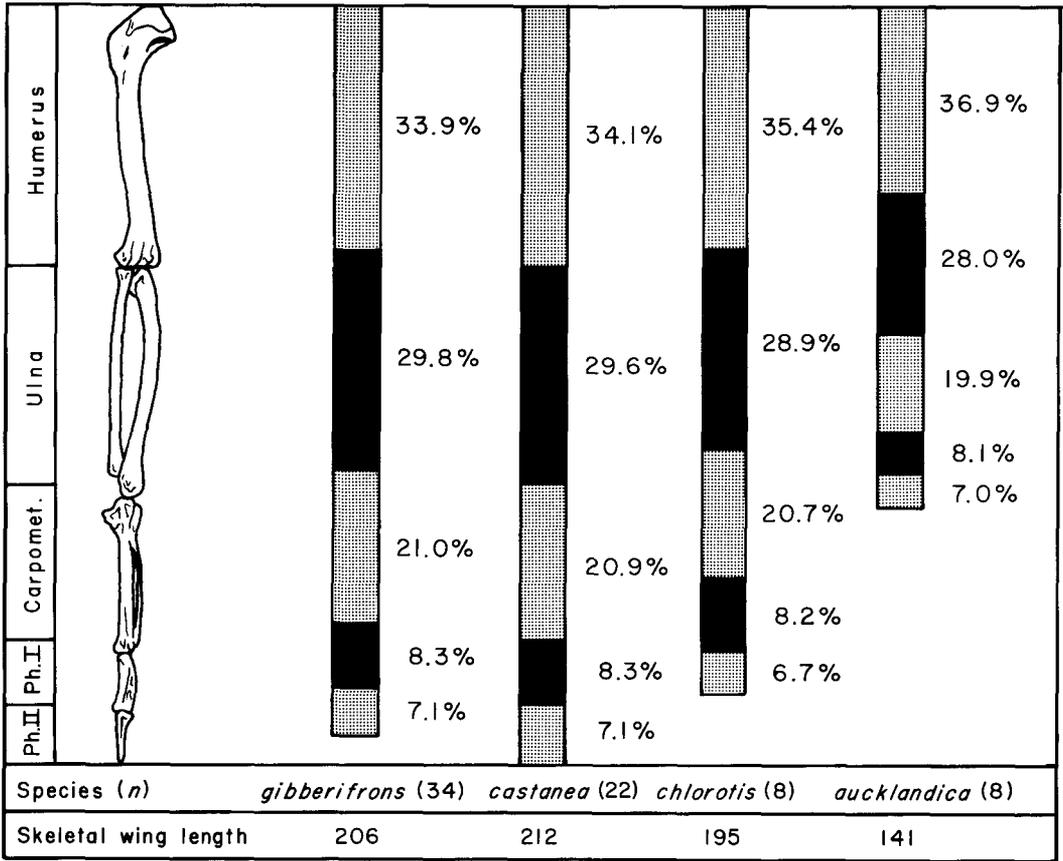


FIGURE 5. Diagrams of mean skeletal wing lengths (mm) and intra-appendicular proportions of four species of Australasian teal (sexes pooled). Outline illustration is of *Anas castanea* (KUMNH 81126).

flective of flight capacity in birds (cf. Olson 1973a; Livezey 1989a, 1989b). *Sterna* of *A. gibberifrons* and *A. castanea* (Fig. 7) are typical of the genus *Anas*, and are characterized by relatively long and deep carinae and by basins showing only moderate caudal widening. *Anas chlorotis* shows a slight reduction in the ventral manubrial process and in the relative size of the sternal carina (Fig. 7). *Anas aucklandica* is characterized by comparatively short and shallow sternal carinae, the absence of a ventral manubrial process, weakly developed caudolateral processes, and by basins which caudally are relatively broad but medially emarginated (Fig. 7).

These interspecific differences in sternal shape were summarized by the first canonical variate (CV-I) of six species-sex groups of adult Australasian teal based on five sternal measurements (Wilks' lambda = 0.0326; df = 5, 5, 91; $P \ll$

0.001). This linear combination of the (log-transformed) measurements maximally discriminated the groups from each other in these dimensions, accounted for 86.7% of the total intergroup dispersion in sternal dimensions, and was defined as follows:

$$\begin{aligned} \text{Canonical score} = & 17.72 (\text{carina length}) - \\ & 8.21 (\text{basin length}) - 2.10 (\text{least basin width}) \\ & + 1.44 (\text{caudal basin width}) + 9.95 (\text{carina depth}) - 68.52. \end{aligned}$$

This variate placed flightless *A. aucklandica* at one extreme, reflecting shallow carinae and relative caudolateral broadening, and the more typical *A. castanea* and *A. gibberifrons* (not shown) at the other; *A. chlorotis* was positioned between these two groups in sternal conformation, but was more similar to *A. aucklandica*. In addition, juveniles of *A. chlorotis* and *A. aucklandica* (plot-

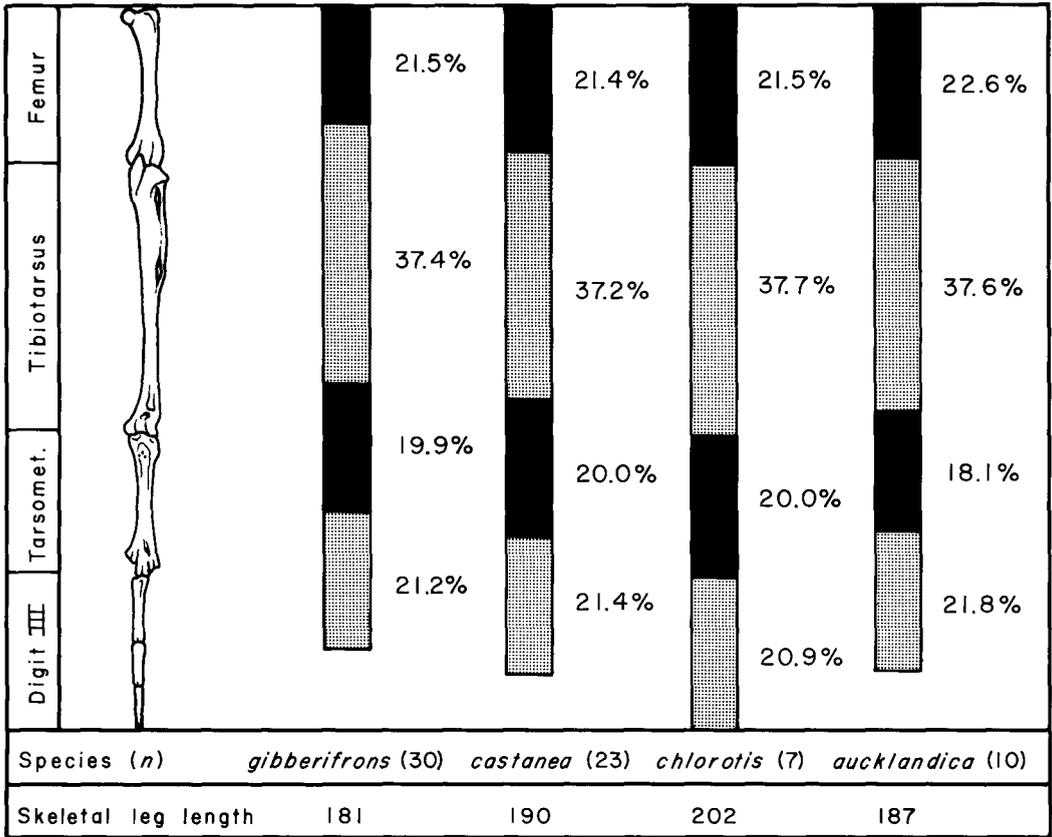


FIGURE 6. Diagrams of mean skeletal leg lengths (mm) and intra-appendicular proportions of four species of Australasian teal (sexes pooled). Outline illustration is of *Anas castanea* (KUMNH 81126).

ted a posteriori) were more “*aucklandica*-like” in sternal shape than their adult conspecifics (Fig. 7).

Canonical analysis of complete skeletons. A canonical analysis of 87 adequately identified skeletons effectively separated the six species-sex groups using 23 skeletal measurements (Wilks’ lambda = 0.0002; df = 14, 5, 79; $P \ll 0.001$). Interspecific Mahalanobis’ distances (D) on the five canonical variates reflected: (1) the close similarity between *A. gibberifrons* and *A. castanea* ($D = 3.3$), one of comparable magnitude to intersexual distances within the two species ($D = 2.9$ and 4.5 , respectively); (2) the moderate similarity between *A. chlorotis* and these two flighted species ($D = 14.9$ and 13.1 , respectively); (3) the large difference between flightless *A. aucklandica* and its sister species *A. chlorotis* ($D = 24.1$); and (4) the even greater differences between *A. aucklandica* and the more distantly re-

lated *A. castanea* and *A. gibberifrons* ($D = 34.8$ and 36.3 , respectively).

A full-dimensional CA of the 23 skeletal measurements permitted the interpretation of these multivariate differences (Table 6, Fig. 8). The first canonical variate (CV-I) incorporated 92.7% of the total intergroup dispersion (Table 6; ANOVA of scores, $F = 1,995.7$; df = 5, 79; $P \ll 0.0001$), and largely discriminated *A. aucklandica* from its flighted relatives (Fig. 8). Signs and magnitudes of coefficients indicate that CV-I primarily contrasted skull lengths, humeral head width, lengths of the carpometacarpus and leg elements, and caudal sternal width with lengths of the ulna, radius, phalanx II of the major alar digit, coracoid, and the sternal basin (Table 6). The low scores of *A. aucklandica* (Fig. 8) accordingly reflected the relatively short distal and antebrachial elements and small dimensions of the pectoral girdle characteristic of the species as

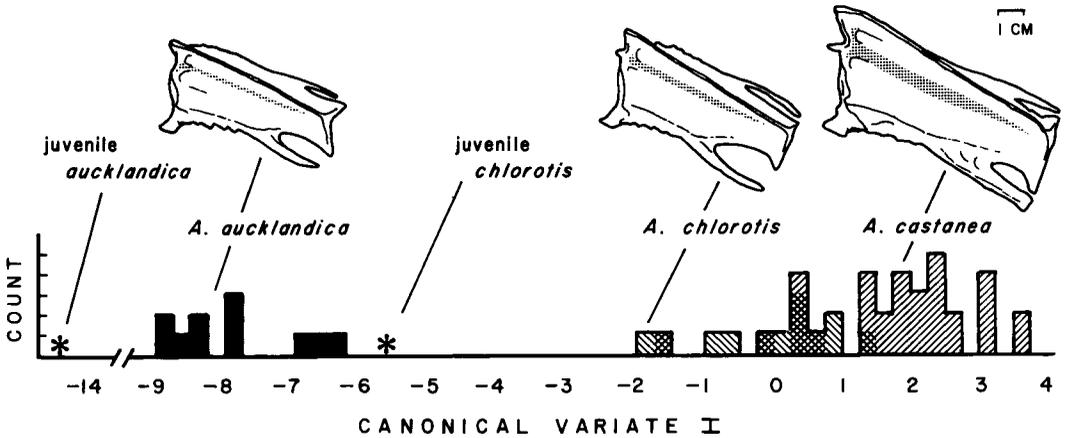


FIGURE 7. Plot of scores of *Anas castanea*, *A. chlorotis*, and *A. aucklandica* on first canonical axis of five sternal dimensions; also plotted (but not used in derivation of axes) are single juvenile specimens of *A. chlorotis* and *A. aucklandica*. Sterna are figured at equal reduction (*A. castanea*—KUMNH 81126; *A. chlorotis*—AIM 386; *A. aucklandica*—USNM 500620).

compared to its flighted relatives. The intermediate scores of *A. chlorotis* suggest that the species shares, to a lesser degree, the pectoral reduction evident in *A. aucklandica*. Two poorly ossified skeletons of juvenile specimens—one *A. chlorotis* and one *A. aucklandica*—had substantially lower scores on CV-I than their adult conspecifics (Fig. 8).

The second canonical axis for skeletal measurements (CV-II) accounted for another 4.0% of the intergroup dispersion (Table 6) and incorporated significant differences among groups in scores ($F = 69.3$; $df = 5, 79$; $P < 0.0001$). This axis mostly discriminated the low-scoring *A. chlorotis* from its flightless sister species *A. aucklandica*; the other flighted species had intermediate scores on the axis (Fig. 8). Coefficients of measurements show that CV-II essentially contrasted humeral dimensions and tarsometatarsus length with femur length, dimensions of the coracoid, and sternal lengths (Table 6).

The three remaining canonical variates for skeletons (CV-III through CV-V) together accounted for the remaining 3.2% of the total intergroup dispersion, but each included significant ($F > 5.0$; $df = 5, 79$; $P < 0.001$) differences among groups in scores. CV-III, an axis primarily contrasting lengths of the bill, carpometacarpus, and coracoid with lengths of the forewing elements and sternal basin (Table 6), identified residual distinctions between *A. chlorotis* and *A. aucklandica* and displayed sexual dimorphism common to *A. gibberifrons* and *A. castanea*. CV-

IV and CV-V revealed additional sexual differences in *A. castanea* and *A. gibberifrons*, respectively, and will not be discussed further.

PECTORAL MUSCULATURE

Qualitative myology. Based on dissections of single specimens, the pectoral musculature of flightless *A. aucklandica* is qualitatively identical to those of *A. gibberifrons* and *A. castanea*. One possible exception, the apparent lack of an abdominal dermal component (Pars abdominalis) of *M. pectoralis* in *A. aucklandica* (Fig. 9), detected in both of its flighted relatives, requires confirmation; however, the absence of this component in *A. aucklandica*, if genuine, would be inconsequential for flight capacity. Furthermore, the pectoral musculature of all three austral teal agrees qualitatively with that described by Zusi and Bentz (1978) for a partial specimen of the Labrador Duck (*Mergini*; *Camptorhynchus labradorius*), with the following exceptions: (1) the insertion of *M. pronator profundus* extends almost to the distal end of the radius in the teal, whereas in *Camptorhynchus* it extends only two-thirds of the length of the radius; and (2) the insertion of *M. entepicondylo-ulnaris* is dorsad (deep) to the belly of the proximal terminus of *M. flexor digitorum profundus* in the teal, whereas in *Camptorhynchus* the former is ventrad (superficial) to the latter. Also, the three teal possessed the accessory pars of *M. pronator profundus* (see George and Berger 1966), a small, fleshy belly immediately distad to the origin of

TABLE 6. Standardized coefficients and summary statistics for the first three canonical variates for 23 skeletal measurements discriminating six species-sex groups of Australasian teal.

Variable	Canonical variate		
	I	II	III
Bill length	-0.60	-0.26	-0.07
Cranium length	-0.54	-0.23	-0.94
height	0.16	-0.35	0.07
Humerus length	0.34	-0.89	-0.35
head width	-0.45	-0.53	-0.04
Radius length	0.68	0.42	0.88
Ulna length	1.18	-0.39	0.97
Carpometacarpus length	-0.38	0.10	-1.17
Major digit, phalanx I length	-0.20	-0.41	-0.02
phalanx II length	0.69	0.35	-0.40
Femur length	-1.37	0.50	-0.06
Tibiotarsus length	-0.45	0.19	-0.03
Tarsometatarsus length	-0.13	-1.54	0.54
Middle-toe length	-0.98	0.07	0.09
Scapula length	-0.29	0.02	0.48
Coracoid length	0.50	0.68	-1.02
basal width	-0.02	0.51	-0.40
Sternal carina length	0.38	0.93	-0.57
basin length	1.45	0.68	1.03
least basin width	0.12	-0.35	0.21
caudal basin width	-0.38	-0.14	0.16
carina depth	-0.13	-0.35	-0.27
Interacetabular width	-0.06	-0.07	0.33
Eigenvalue	140.79	6.12	3.15
Cumulative variance (%)	92.7	96.7	98.8
Canonical <i>R</i>	0.99	0.93	0.87

the muscle and ventrad to the main muscle body, but this feature was not mentioned in the myological study of *Camptorhynchus* by Zusi and Bentz (1978). As did the specimens of *A. gibberifrons* and *A. castanea*, *A. aucklandica* retains: (1) three subcutaneous slips of *M. pectoralis* (Fig. 9); (2) two-parted *Mm. serratus profundus* and *serratus superficialis caudalis* (Fig. 10); (3) a complete patagial musculature including *Mm. latissimus dorsi metapatagialis* and *serratus superficialis metapatagialis*, both *Tendo longa* and *Tendo brevis* of *M. proapatagialis*, a well-developed *M. biceps proapatagialis*, and an evidently functional *M. expansor secundariorum* including both proximal (scapular) tendon and distal belly (Figs. 11, 12); and (4) identically positioned and robust muscles and tendons of the antebrachium and manus, including both parts of *M. extensor longus digiti majoris* and both heads of *M. extensor longus alulae* (Figs. 13–16). None of the six minor qualitative changes noted in the pectoral musculature of some flightless grebes (Livezey 1989a) was detected in *A. aucklandica*.

Quantitative myology. Most muscle measure-

ments for *A. aucklandica*, however, were smaller than those in its flighted relatives, a condition related in part to its smaller overall size (Table 1). Absolute differences in the large *Mm. pectoralis* and *supracoracoideus*, the muscles primarily responsible for powering the wing strokes, were comparatively pronounced (Table 7). The smaller dimensions of at least *M. pectoralis* in *A. aucklandica* exceeded those expected simply on interspecific differences in body mass (Table 7). However, the relative size of breast muscles in *A. castanea* (based on a captive bird) approached those of *A. aucklandica*, indicating an effect of exercise on the overall bulk of breast muscles, although this effect was not evident in measurements of origins and insertions.

Measurements of other pectoral muscles confirmed that many were disproportionately small in *A. aucklandica* (Table 8). Differences between *A. aucklandica* and its two flighted relatives in relative muscle dimensions were largest and most consistent in muscles primarily acting on the scapula and carpometacarpus, intermediate in those responsible for moving the humerus bra-

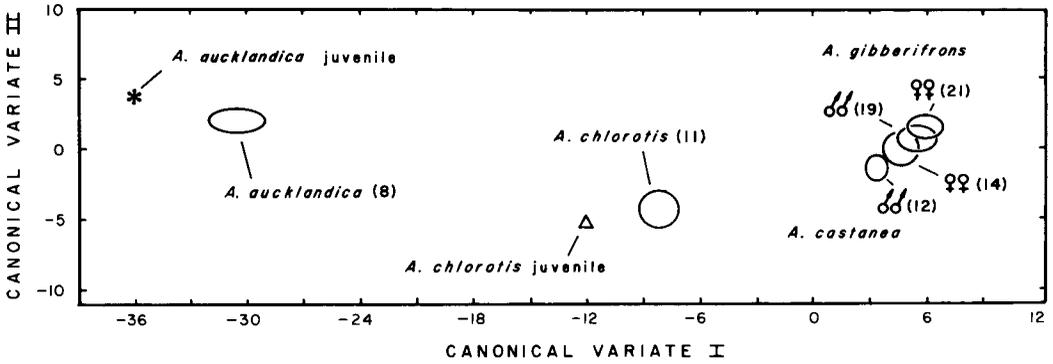


FIGURE 8. Plot of mean scores (\pm standard deviation) of six species-sex groups of Australasian teal on first two canonical axes of 23 skeletal measurements; also plotted (but not used in derivation of axes) are juvenile specimens of *Anas chlorotis* and *A. aucklandica*.

chium, antebrachium, and digits, and virtually nonexistent (i.e., completely accounted for by body size) in the metapatagial slips (Table 8).

DISCUSSION

BODY SIZE AND ALLOMETRY IN ANATIDS

Flight capacity of dabbling ducks. Typical dabbling ducks (Anateae, sensu Livezey 1986b, unpubl. data), like other Anseriformes, are powerfliers, birds characterized by relatively heavy wing loadings (Table 3) which must employ rapid wing beats to attain and maintain flight (Hartman 1961, Greenewalt 1962); diving Anatinae (Aythyini, Mergini, and Oxyurini) have even heavier wing loadings (Raikow 1973, Livezey and Humphrey 1986, Bethke and Thomas 1988). Mei-

nertzhagen (1955) recorded higher wing-beat frequencies (5 sec^{-1}) in four species of *Anas*—Gadwall (*A. strepera*), American Wigeon (*A. americana*), Mallard (*A. platyrhynchos*), and Northern Shoveler (*A. clypeata*)—than in most other birds sampled, with the notable exceptions of diving ducks, grebes, loons, alcids, and gallinaceous birds. Relatively large breast muscles (Mm. pectoralis and supracoracoideus), constituting 17–21% and 2–3%, respectively, of body mass in *Anas*, are functionally related to the energetically demanding, rapid aerial locomotion of the members of the genus, in which flight is typically attained by an almost vertical take-off (Hartman 1961, Bethke and Thomas 1988). De-

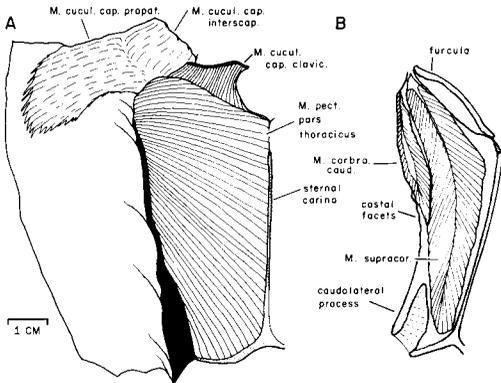


FIGURE 9. Ventral views of right breast muscles of *Anas aucklandica*: A—superficial layer; B—deep layer, with moderate lateral perspective. Abbreviations given in Appendix.

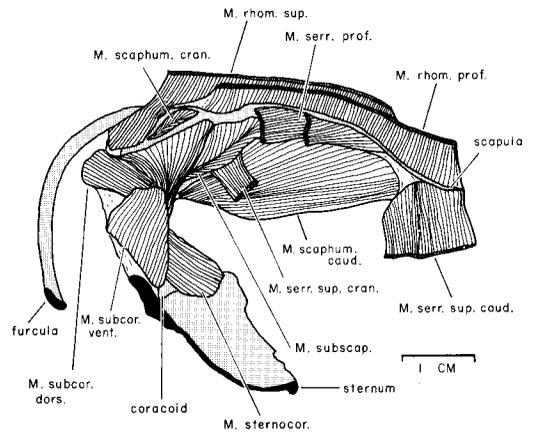


FIGURE 10. Medioventral views of muscles in triosseal region of pectoral girdle of *Anas aucklandica*, right side, Mm. pectoralis and supracoracoideus removed. Abbreviations given in Appendix.

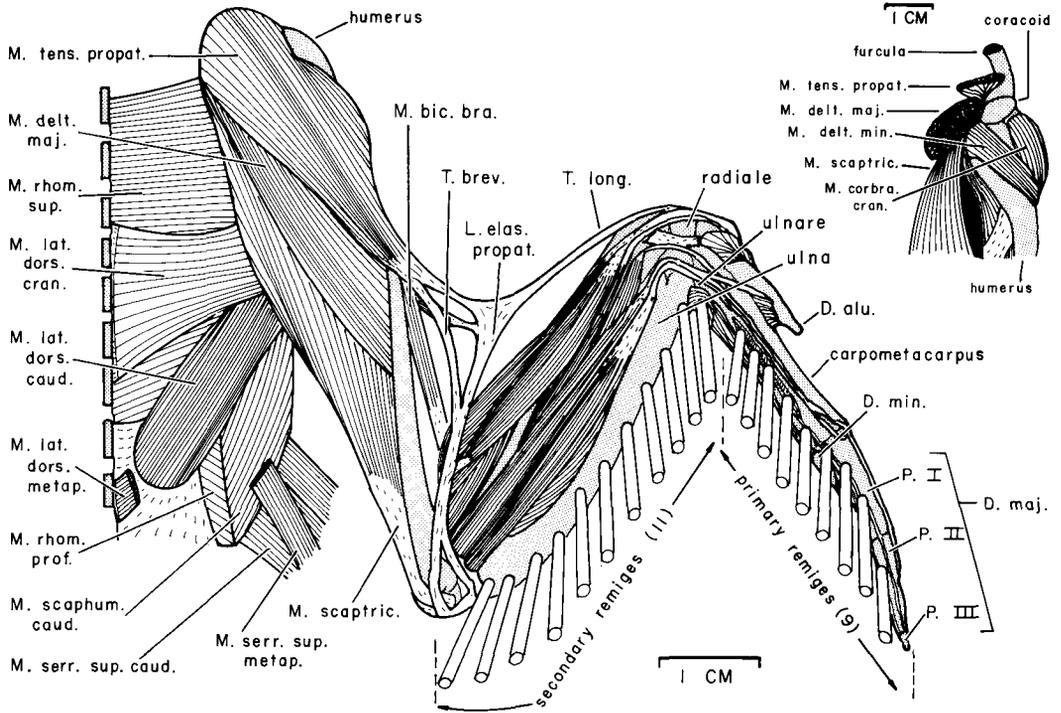


FIGURE 11. Dorsal view of right pectoral limb of *Anas aucklandica*, superficial layer. Inset—lateral view of head of humerus, deep layer. Abbreviations given in Appendix.

spite the allometry of wing size with body mass in *Anas* (Fig. 3) and other anatids (Livezey and Humphrey 1986, Livezey 1989b), an (allometric) size increase alone eventually would not render an *Anas* lineage flightless (i.e., produce a wing loading in excess of 2.5 g cm⁻²; Meunier 1951) until a body mass of roughly 13 kg was attained (based on a regression of data in Table 3); this approximates the body mass of the Trumpeter Swan (*Cygnus buccinator*), the most massive anseriform and among the largest of flying birds (Pennycuik 1975). The threshold estimated by Meunier (1951), however, did not consider accompanying changes in pectoral musculature; reductions in muscle mass, like those evident in *A. aucklandica*, effectively lower the threshold of flightlessness to smaller body masses.

Body size and flightlessness. Pennycuik (1975, p. 70) stated: "No case is known of a bird having lost the power of flight through selection for small size . . . [emphasis added]." Although this observation remains correct at this writing, in part because of an inadequate understanding of the

selective causes of avian flightlessness, there are instances known in which the loss of flight is coincident with decreased size. *Anas aucklandica* is an example of a flightless lineage which is smaller than its closest flighted relatives (Table 1, Fig. 2), and the phylogeny adopted here (Fig. 1; Livezey, unpubl. data) indicates that this difference in size is the result of a *derived decrease* in body mass within the *A. castanea-chlorotis-aucklandica* clade. This inference is contingent on this specific phylogenetic hypothesis; for example, if the phylogeny of the Australasian teal given in Figure 1 were modified by a reversal of the relationships proposed within the *A. castanea-chlorotis-aucklandica* clade (i.e., *A. aucklandica* as the sister-group to *A. chlorotis* and *A. castanea*), then the small mass of *A. aucklandica* would be most parsimoniously interpreted as the retention of a primitive condition. No hypothesis has been advanced, however, which attributes the loss of flight in *A. aucklandica* to the evolutionary advantage(s) of small body size. The diminution of *A. aucklandica* is also noteworthy

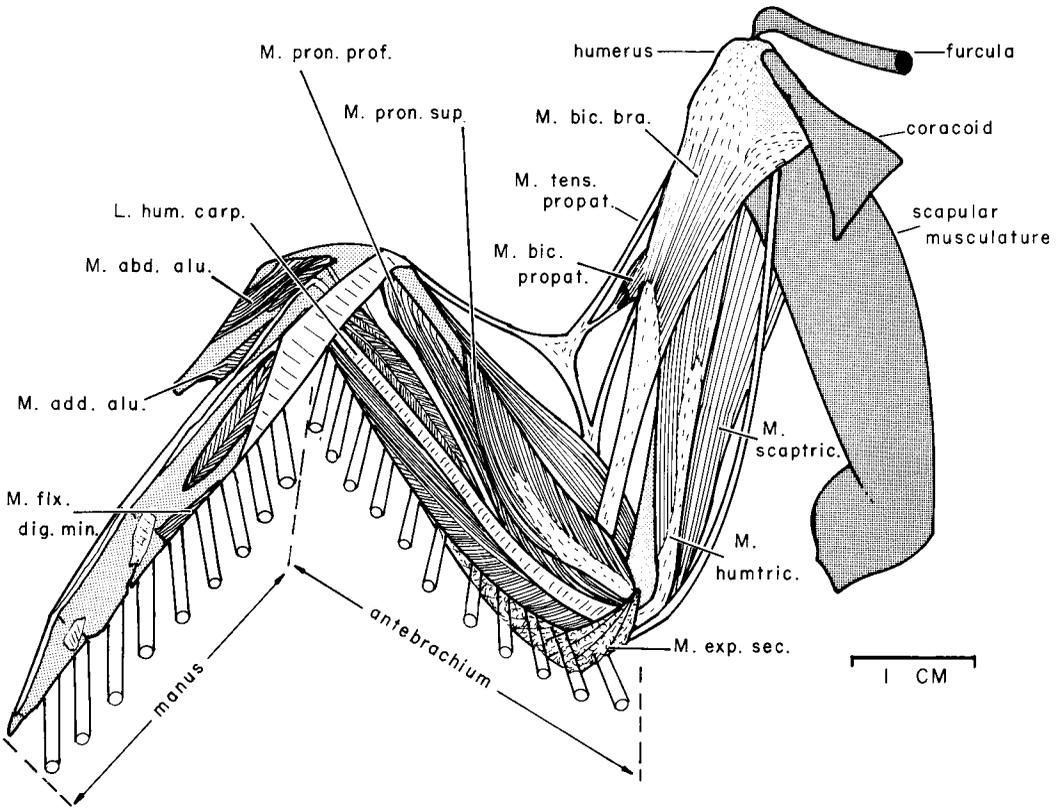


FIGURE 12. Ventral view of right pectoral limb of *Anas aucklandica*, superficial layer. Abbreviations given in Appendix.

in that it contradicts the prediction of Bergmann's Rule, i.e., the tendency for body size to increase with latitude (Rensch 1960); however, even evaluated at the phylogenetic level originally intended (populations within species), Bergmann's Rule is only weakly corroborated (Zink and Remsen 1986). Moreover, although large body size is advantageous for endotherms in cold climates through a reduction in relative rate of heat loss and increased tolerance for fasting, increased bulk also results in a higher total heat loss (Calder 1974).

Other flightless waterfowl are the comparatively huge subfossil *Cnemiornis* of New Zealand (Owen 1866, 1875; Hector 1873; Howard 1964; Livezey 1989d), the subfossil anserine *Thambetothen* of Hawaii (Olson and Wetmore 1976, Olson and James 1982), three extant species of steamer-duck (Livezey and Humphrey 1986), a teal-sized subfossil *Anas* from Amsterdam Island

(Martinez 1987), and the fossil sea-duck *Chenydytes* of California (Miller 1925; Howard 1955, 1964). With the possible exception of the unnamed *Anas* from Amsterdam Island, each of these exceeds its flighted relatives in general size, the best-known example being the steamer-ducks (Humphrey and Livezey 1982, Livezey and Humphrey 1986). Worthy (1988) inferred that the subfossil duck *Euryanas finschi* of New Zealand had undergone modest alar reduction during the period 11,000 to 1,000 BP, changes which culminated in proportions similar to those of *A. chlorotis*; he concluded that *Euryanas* was capable of flight, however, and that there was no evidence for a correlated increase in overall size in the same subfossil samples. In addition, the extinct Auckland Islands Merganser (*Mergus australis*), formerly sympatric with *A. aucklandica* (Kear and Scarlett 1970), appears to have undergone significant morphological changes to-

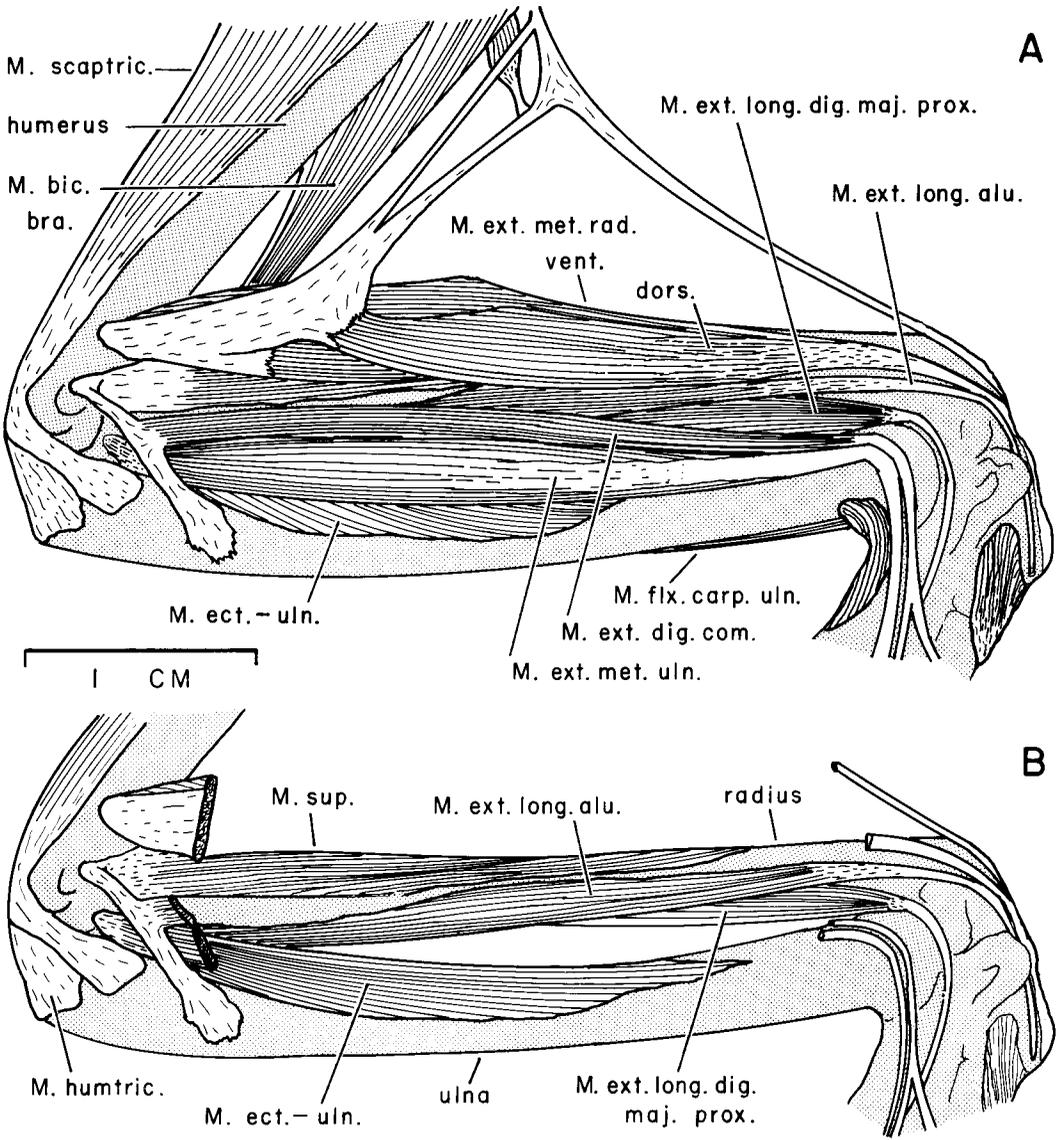


FIGURE 13. Dorsal view of right antebrachium of *Anas aucklandica*, remiges removed: A—superficial layer; B—deep layer. Abbreviations given in Appendix.

ward flightlessness; however, its comparatively small size, at least in large part, appears to be a primitive condition not associated with these pectoral modifications (Livezey 1989a). Therefore, the general inference that insular waterfowl have undergone a decrease in size (Lack 1970, Weller 1980) evidently does not pertain either to terrestrially specialized forms (e.g., *Cnemiornis*, *Thambetothen*) or benthic-diving *Tachye-*

res, and finds only equivocal support in the pursuit-diving *Mergus*.

MORPHOLOGICAL CHANGES IN *ANAS AUCKLANDICA*

Reductions in the pectoral limb. External measurements clearly demonstrate that *A. aucklandica*, and to a lesser extent *A. chlorotis*, have disproportionately short wings (Table 1, Fig. 3).

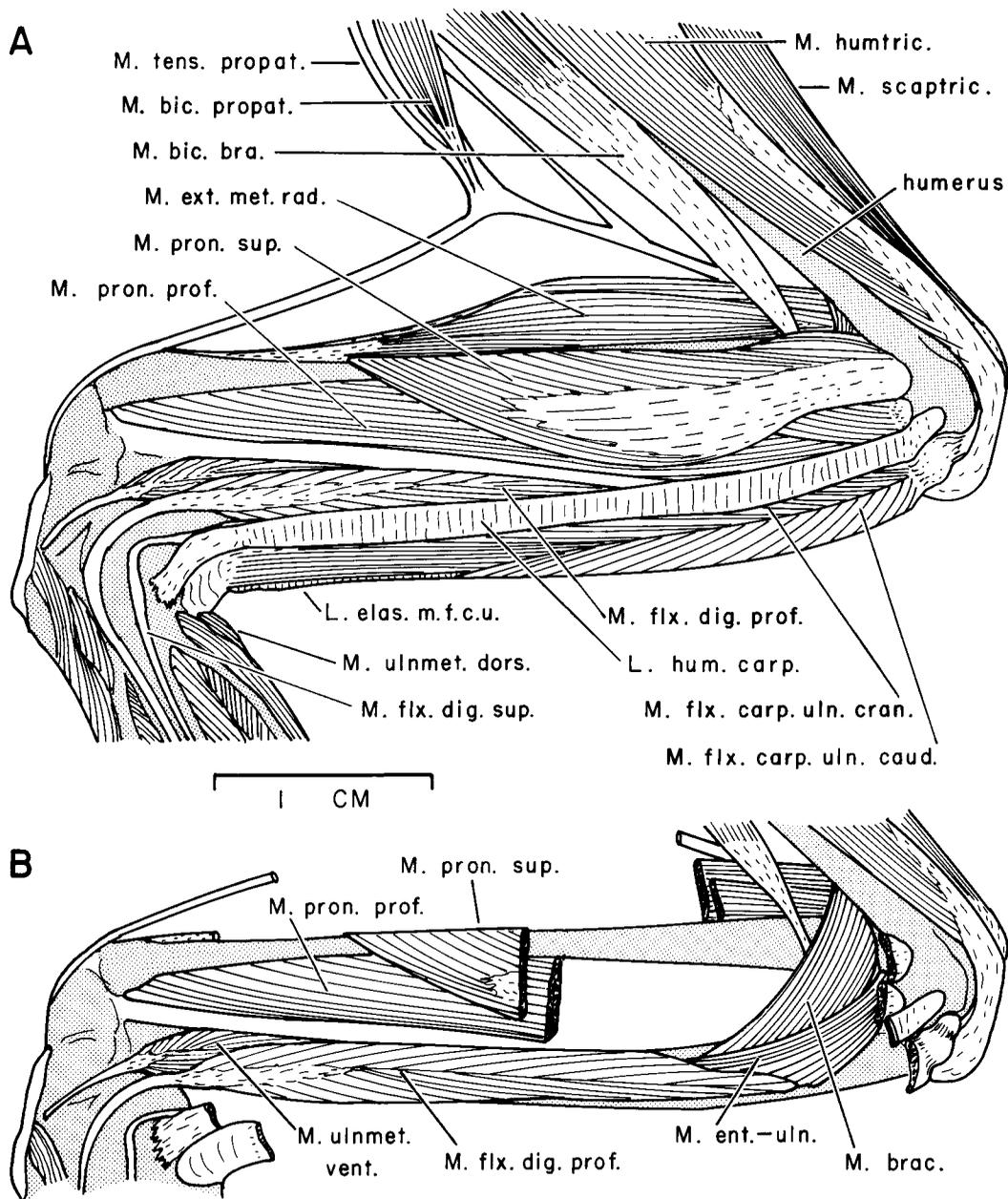


FIGURE 14. Ventral view of right antebrachium of *Anas aucklandica*, remiges removed: A—superficial layer; B—deep layer. Abbreviations given in Appendix.

Based on the regression line for flighted dabbling ducks (Fig. 3), wing lengths of *A. chlorotis* are approximately 27 mm shorter than that predicted on the basis of body mass, whereas those of *A. aucklandica* are shortened by 74 mm. Evident truncation of external wing lengths in *A.*

aucklandica primarily reflects shortening of the primary remiges (Fig. 2), and is associated with losses of one or more primary remiges in most specimens (Table 2). "Gaps" between calami of remiges in *A. aucklandica*, features which would indicate which remiges have been lost in the pro-

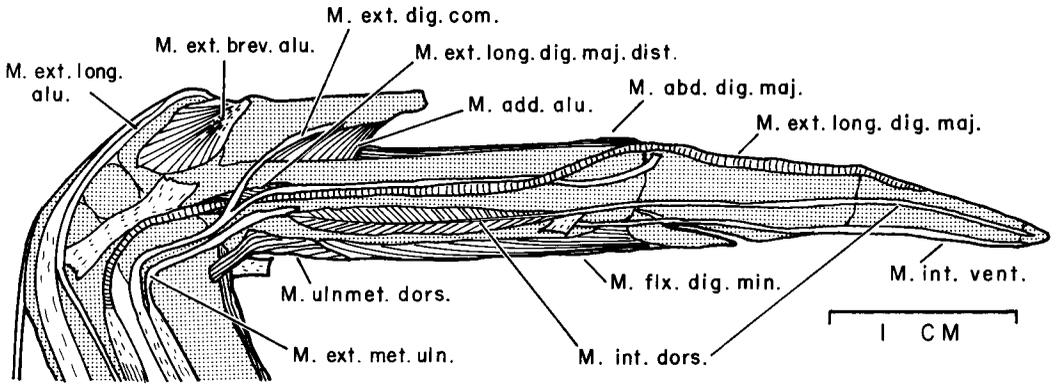


FIGURE 15. Dorsal view of right manus of *Anas aucklandica*, remiges removed; tendon of *M. extensor longus digiti majoris* is crosshatched for clarity. Abbreviations given in Appendix.

cess of alar reduction, were not evident in study skins (Fig. 2) or the dissected specimen (Figs. 11, 12); this finding suggests that either the outermost or innermost remiges were aborted. Comparisons with the positions of remiges in specimens of *A. gibberifrons* and *A. castanea* dissected in this study, and the positions shown for the Mallard (*A. platyrhynchos*) by Humphrey and Clark (1961), suggests that carpometacarpal remiges are missing in *A. aucklandica* (Fig. 11). Gadow (1902) speculated that the missing remiges in *A. aucklandica* were the outermost members, and went on to suggest that the process of reduction was analogous to that evident in the non-functional remicle and that this process might actually progress during development of individual birds. The last suggestion, which proposes the truncation of feather growth with age and seems to invoke a Lamarckian inheritance of shortened wings, seems particularly unlikely.

Loss of primary remiges is known also in the Laysan Duck (*A. laysanensis*) (Moulton and Weller 1984), an insular endemic not characterized, however, by the heavy wing loadings of *A. aucklandica* (Table 3). The intermediate alar reduction of *A. chlorotis*, second only to *A. aucklandica* in magnitude within *Anas* (Table 3, Figs. 3, 4), was inferred earlier by Falla (1953). Primary remiges of *A. aucklandica*, however, retain the asymmetry of vanes characteristic of flighted species (Feduccia and Tordoff 1979), but there appears to have been some reduction in this asymmetry, one confounded with a shortening of the remiges (Fig. 2). Also, there is no gross evidence of a (genetically based) alteration of fine structure of remiges in *A. aucklandica*, a phenomenon observed in several variants of domestic fowl and hypothesized to have been a possible factor in the evolution of flightlessness in the ratites (Provine 1981), species character-

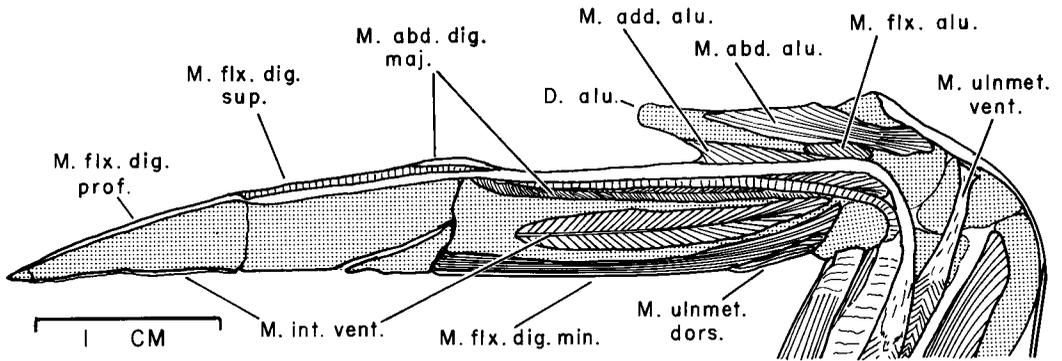


FIGURE 16. Ventral view of right manus of *Anas aucklandica*, remiges removed; tendon of *M. flexor digitorum superficialis* is crosshatched for clarity. Abbreviations given in Appendix.

TABLE 7. Selected measurements of the two largest pectoral muscles, Mm. pectoralis and supracoracoideus, for three species of Australasian teal (*Anas*).

Variable*	Species		
	<i>A. gibberifrons</i>	<i>A. castanea</i>	<i>A. aucklandica</i>
M. pectoralis thoracicus			
Dry mass (g)	14.4	11.6	8.2
Area of sternal origin (mm ²)	800	760	340
Perimeter of belly (mm)	260	272	191
M. supracoracoideus			
Dry mass (g)	6.5	6.4	5.7
Length of opaque aponeurosis (mm)	9.0	8.5	6.0
Length of belly (mm)	86	102	67
Maximal width of belly (mm)	20	24	16

* Measurements for one side of one specimen.

ized by uniquely modified, aerodynamically dis-functional plumage (Feduccia 1980).

Skeletal changes in the pectoral limb of *A. aucklandica* were more profound, affecting most elements of the wing and girdle (Table 5), and are reflected in absolute decreases in lengths not proportional to the interspecific differences in body size. As in comparisons of external measurements, *A. chlorotis* was intermediate between *A. aucklandica* and other Australasian teal in these characters. Intra-alar proportions indicate that the greatest reductions occurred in the midwing elements (Fig. 5), a pattern of skeletal change which characterizes flightless steamer-ducks (Livezey and Humphrey 1986), flightless grebes (Livezey 1989b), the Auckland Islands Merganser (Livezey 1989a), and the Galápagos Cormorant (*Compsohalieu* [*Phalacrocorax*

harrisi) (Livezey, unpubl.). Smaller size but similar intra-alar proportions are indicated in the flightless subfossil duck from Amsterdam Island (Martinez 1987). The sternum of *A. aucklandica* differed conspicuously from those of its flighted relatives in conformation (Fig. 7); these characters are qualitatively convergent with sternal modifications of the Auckland Islands Merganser, flightless grebes, and Galápagos Cormorant, but there are differences in detail (e.g., relative basin widths) and degree, especially in reduction of the carina (Livezey 1989a, 1989b, unpubl.). A reduction in carinal depth also was noted in a domesticated strain of the Mallard (Wiglesworth 1900). In contrast, sterna of flightless *Tachyeres* are qualitatively similar to those of the Flying Steamer-Duck (*T. patachonicus*) (Livezey and Humphrey 1986), whereas those of flightless,

TABLE 8. Summary statistics (mean, range) for *p* interspecific differences in standardized muscle measurements (linear measurements [mm] divided by cube root of mean body masses [g] for respective species-sex group).

Muscle group (<i>p</i>)*	<i>Anas aucklandica</i> ^b vs.	
	<i>A. gibberifrons</i>	<i>A. castanea</i>
Scapular (6)	-1.06 ⁰	-0.71 ⁰
Humeral (18)	(-2.43, -0.01)	(-1.72, 0.24)
	-0.42 ⁰	-0.52 ³
Antebrachial (19)	(-1.49, -0.11)	(-1.06, 0.13)
	-0.61 ²	-0.61 ¹
Carpometacarpal (17)	(-1.90, -0.15)	(-2.00, 0.07)
	-0.88 ¹	-1.02 ¹
Digital (6)	(-1.93, 0.01)	(-2.45, 0.04)
	-0.60 ¹	-0.71 ⁰
Patagial (8)	(-1.49, 0.06)	(-1.18, -0.16)
	-0.11 ³	0.10 ⁴
	(-0.95, 0.58)	(-0.27, 0.55)

* Muscles grouped according to primary skeletal element(s) acted upon (see Appendix).

^b Superscripts indicate number of measurements in which *A. aucklandica* was (relatively) larger.

largely terrestrial *Cnemiornis* retained but a vestige of a carina (Hector 1873, Owen 1875). Clearly the retention of a reduced sternal carina and associated flight muscles in *A. aucklandica* is related to the capacity for the short "flights" recounted by Phillips (1925) and Oliver (1955); the utility of short ascents to nesting sites in cliffs (Bollons fide Waite 1909) may impose a selectively maintained limit on pectoral reduction in *A. aucklandica*. The extreme morphometric position of *A. aucklandica* among Australasian teal (Fig. 8) reflects, in large part, a constellation of unique pectoral proportions that dwarfs skeletal differences among its flighted relatives or those related to sexual dimorphism in the group.

Although *A. aucklandica* retains a complete complement of pectoral muscles (with the possible exception of *M. pectoralis abdominalis*; Figs. 9–16), the relative sizes of most muscles (i.e., sizes of muscles corrected for mean interspecific and intersexual differences in body mass) were smaller in the flightless form than in its flighted congeners (Tables 7, 8). The specimen of *A. castanea*, a captive bird, provides apparent underestimates of some dimensions for the species (especially masses and widths of bellies; Table 7), but also indicates that some of the decreased muscle bulk indicated in *A. aucklandica* may have resulted from disuse as well as from changes prescribed by genetic alterations. Relative sizes of the metapatagial slips remain virtually unchanged in *A. aucklandica* (Table 8); this stasis presumably reflects the probable importance of these slips in functions other than flight, particularly for adjustment of tension of the patagium for purposes of thermoregulation. Generally, however, the overall change in pectoral musculature in *A. aucklandica* is characterized by small to moderate decreases in relative size without losses of muscles or parts thereof.

Skeletal changes in the pelvic limb. Coincident with the more conspicuous changes in the pectoral limb in *A. aucklandica* are significant shifts in the proportions of skeletal elements of the leg (Fig. 6). *Anas aucklandica* is characterized by disproportionately long femora and toes and relatively (very) short tarsometatarsi (Fig. 6). The functional significance of these proportions is not clear; they may represent a compromise between specializations for climbing (long femora and short tarsometatarsi) and swimming (long toes). *Anas chlorotis* also shows significant differences in pelvic proportions relative to the more typical

A. gibberifrons and *A. castanea*, but these differences are distinct from those of *A. aucklandica* and are accompanied by a 1-cm increase in skeletal leg length. The pelvic limb of *A. chlorotis* is characterized by relatively long tibiotarsi and short toes (Fig. 6), proportions generally associated in waterbirds with specialization for terrestrial locomotion (Raikow 1985).

The unexpectedly wide interacetabular width of *A. chlorotis* also conforms with a specialization for terrestrial locomotion (Table 5). The distinctive pelvic proportions of *A. aucklandica*, and to a lesser degree, those of *A. chlorotis*, were important in the definition of the first canonical variate (CV-I) for skeletons, whereas those unique to *A. chlorotis* contributed principally to skeletal CV-II (Fig. 8).

ONTOGENETIC BASIS OF FLIGHTLESSNESS IN *ANAS AUCKLANDICA*

Pedomorphosis, the occurrence of ancestrally embryonic or juvenile characters in the (reproductive) adults of descendent lineages (McNamara 1986), has been inferred only rarely for birds (Gould 1977). An important avian example of this is the morphology of selected flightless birds, for which neoteny was proposed as the developmental mechanism responsible for the "degenerate" pectoral apparatus and body plumage characteristic of the Inaccessible Island Rail (*Atlantisia rogersi*) (Lowe 1928), several other flightless rails (Olson 1973a, 1973b), and some subfossil anserines from Hawaii (James and Olson 1983). There is strong evidence for pedomorphosis in the Auckland Islands Teal. The irregularly shortened primary remiges of *A. aucklandica* resemble the partly grown primaries of juvenile *Anas* in the prejuvenal molt (Humphrey and Parkes 1959), and the shorter wings of juvenile *A. gibberifrons*, *A. castanea*, and *A. chlorotis* primarily account for the morphometric similarity between the younger birds and adult *A. aucklandica* (Fig. 4). Remiges have been found to be shorter in juvenile Eurasian Coots (*Fulica atra*) (Fjeldså 1977) and steamer-ducks (Livezey and Humphrey 1986), and the less robust vanes of remiges of *A. aucklandica* (Fig. 2) are clearly suggestive of aborted development. Reductions in numbers of primary remiges in *A. aucklandica*, however, are not pedomorphic in that this condition is not considered to be the plesiomorphic state for juvenile *Anas*.

Plumage patterns of adults in the *Anas cas-*

tanea-chlorotis-aucklandica clade also exhibit a directional evolutionary trend toward sexual monochromatism and paedomorphosis. All three species, as is typical of *Anas*, have two molts and plumages per annual cycle (Falla and Stead 1938, Frith 1967, Reid and Roderick 1973, Johnsgard 1978), in which the alternate plumages (i.e., nuptial plumages) of males are variably more colorful than the homologous plumages of female conspecifics (Buller 1894, 1905; Phillips 1925; Oliver 1955; Delacour 1956; Weller 1975b; Todd 1979; Madge and Burn 1988). In *A. castanea*, adult males have largely iridescent green heads, rich chestnut breasts and sides, conspicuous white flank spots, and deep black undertail coverts, and adults of both sexes have bright red irides and conspicuously bordered, metallic wing specula; females and juveniles are dark mottled brown, and juveniles have dark brown irides. Adult males of *A. chlorotis* have the greenish iridescence limited to the nape and postocular regions of the head, the chestnut wash is limited to the breast, the flank spot and undertail coverts are less distinct and the wing speculum is slightly less brightly colored; adults of both sexes and juveniles lack red irides, and adult females differ from juveniles only in the clarity of ventral vermiculations.

Adult males of *A. aucklandica* have but a vestigial greenish postocular iridescence, the chestnut tones of the breast and sides are obsolete, the whitish flank spots and dark undertail patches are faint or indistinguishable, and adults of both sexes resemble juveniles in their brown irides and virtually nonchromatic wing specula. The few available skins of *A. (a.) nesiotis* confirm that this population is at least as derived in its plumage pattern as the nominate race (Fleming 1935, Oliver 1955). Accordingly, it seems justified to refer to the progressive sexual monochromatism in this species-group, a plumage character noted earlier by Falla (1953) and which is frequent among insular waterfowl (Lack 1970, Weller 1980), as paedomorphic. The white eye-rings shared by *A. chlorotis* and *A. aucklandica*, a character found in some other insular waterfowl (Weller 1980), constitutes a synapomorphy not attributable to developmental heterochrony.

Skeletal modifications in *A. aucklandica* offer particularly persuasive evidence of paedomorphosis, and these "juvenile" characters of the skeleton have obvious functional impacts on the capacity for flight. Several investigations of avian embryology have shown that: (1) the develop-

ment of the pectoral limb in birds lags behind that of the skull and pelvic girdle; (2) growth of proximal wing elements proceeds more quickly than that of distal elements; and (3) the sternum is among the last skeletal elements to ossify (Latimer 1927, Marples 1930, Schinz and Zangerl 1937, Montagna 1945, Maillard 1948, Fujioka 1955, Klima 1962). The shallow sternal carinae and differentially shortened wing elements of flightless rails (Lowe 1928, Olson 1973a), steamer-ducks (Livezey and Humphrey 1986), grebes (Livezey 1989b), and alcids (Livezey 1988) have been interpreted as paedomorphic. Reductions in dimensions of pectoral-alar elements (Table 5), shifts in intra-alar proportions (Fig. 5), conformational changes in sterna (Fig. 7), and multivariate similarities between adult *A. aucklandica* and juveniles of its flighted congeners (Figs. 4, 8) conform well with the expectations for paedomorphic skeletal modifications. The generalized "under-development" (Tables 8, 9) of an otherwise typical, complete pectoral musculature (Figs. 9–16) also accords with an hypothesis of paedomorphosis. The finding that midwing elements have undergone greater reductions in proportions than the distal-most elements in *A. aucklandica* (Fig. 5), however, does not agree with the comparatively proximal-distal developmental gradient characteristic of embryonic birds, and apparently reflects a derived, nonpaedomorphic state.

Although there is abundant evidence of paedomorphosis in the integument, skeleton, and pectoral musculature of *A. aucklandica*, diagnosis of the underlying ontogenetic mechanism (neoteny, progenesis, or postdisplacement) is not possible with currently available data. Neoteny, the deceleration of growth of one anatomical structure relative to the general developmental state of an organism, is the most frequently hypothesized of the three heterochronic mechanisms which produce a paedomorphic condition (Gould 1977, McNamara 1986). Postdisplacement, in which onset of development is delayed relative to other ontogenetic schedules, was suggested as the mechanism underlying the subtle skeletal paedomorphosis inferred for flightless steamer-ducks (Livezey and Humphrey 1986) and the Titicaca Grebe (*Rollandia microptera*) (Livezey 1989b). Progenesis, the early onset of sexual maturity, is a particularly likely candidate in *A. aucklandica* in that the condition is characterized by a generalized underdevelopment,

TABLE 9. Parameters of reproduction^a for three species of Australasian teal (*Anas*).

Species	Clutch size	Egg size ^b	Egg mass ^c	Brood size
<i>A. castanea</i>	10+	53 × 38	44 (8%)	8 ^d
<i>A. chlorotis</i>	6	61 × 43	64 (11%)	4
<i>A. aucklandica</i> ^e	4	64 × 44	72 (18%)	1–2

^a Data compiled from Oliver (1955), Delacour (1956), Lack (1967, 1970), Reid and Roderick (1973), Weller (1975a, 1980), Norman (1982), and Norman and McKinney (1987).

^b Mean length × width (mm).

^c Mean mass (g) and % of mean body mass of females.

^d At departure from nest.

^e Nominate subspecies.

including reduced body size (McNamara 1986). Morphological study of series of developing birds of known age in *A. chlorotis* and *A. aucklandica* (including prehatching embryos) should permit this differentiation.

EVOLUTIONARY CONSIDERATIONS

Inferences from phylogeny. As detailed above, interspecific differences in plumage pattern within the *A. castanea-chlorotis-aucklandica* clade (Fig. 1) are interpretable as a unidirectional trend toward progressive pedomorphosis with increasing insularity; decreasing body size parallels this pattern (Table 1). In addition, a number of flightlessness-related characters of *A. aucklandica*—including relative wing length (Fig. 3), wing loading (Table 3), intra-alar proportions of skeletal elements (Fig. 5), sternal conformation (Fig. 7), and multivariate trends in external and skeletal dimensions (Figs. 4, 8)—were found to a lesser degree in its sister species *A. chlorotis*. Accordingly, the most parsimonious hypothesis holds that the initial (derived) shift toward flightlessness occurred in the common ancestor of *A. chlorotis* and *A. aucklandica*, and that these changes were further derived in the two insular populations (nominate *aucklandica* and *nesiotis*). Whether these subsequent modifications occurred in the common ancestor of the two flightless forms (i.e., are homologous) or were derived independently in each (i.e., are convergent) is not known. Given that the Auckland and Campbell islands are of volcanic origin and neither ever was connected to mainland New Zealand (Fleming 1975), it is most probable that both populations arose from colonizations by dispersing birds from northern source populations. Given the distances between the two island groups and the mainland, it seems reasonable to speculate that members of the founding population(s) retained at least limited capacity for

flight. Until additional anatomical material (particularly subfossil specimens from insular localities) and/or biochemical specimens (especially for *nesiotis*) are available, however, it remains most parsimonious to consider the flightless condition of the two insular endemics to be homologous.

Taxonomy and evolutionary inferences. Given a completely resolved phylogenetic hypothesis, the methodology for classifying included taxa is prescribed by existing taxonomic convention (cf. Wiley 1981) and depends partly on the species concept adopted. The topology given here (Fig. 1) confirms the monophyly of the Australasian teal, which are assignable to the subgenus *Nesonetta* Gray, 1844 (Livezey, unpubl.); *A. castanea-chlorotis-aucklandica* may be considered a superspecies including three allospecies (Haffer 1986). The designation of *nesiotis* as a subspecies, a rank not considered to be useful under the phylogenetic species concept (McKittick and Zink 1988), is provisionally retained only to reflect its uncertain diagnosability and undemonstrated reproductive status.

This treatment differs from the traditional classification in which *A. chlorotis* is considered to be conspecific with *A. aucklandica* (Delacour and Mayr 1945), although the traditional taxonomy has not been unanimously adopted by ornithologists (Dumbell 1986). Relegation of insular isolates with continental relatives to subspecific status is a tradition which is favored under the concept of “biological species” (Mayr 1963); this convention apparently derives from the impossibility of a “natural test” of interfertility, a prerequisite for assignment of species status within this conceptual framework. This practice has several fundamental drawbacks: (1) it is necessitated by the impossibility of testing “natural” reproductive isolation, a condition which reflects the (plesiomorphic) absence of an

isolating mechanism and therefore does not indicate close phylogenetic relationship (McKittrick and Zink 1988), and is a particularly problematic criterion for waterfowl in which interspecific hybridization (both in the wild and captivity) is widespread (Sibley 1957, Johnsgard 1960, Scherer and Hilsberg 1982); (2) it is inconsistently applied, being influenced by variously perceived phenetic differences between taxa; and (3) it relegates diagnosable, independently evolving, and genetically isolated populations to practical anonymity because trinomina are seldom considered by nontaxonomists in studies of ecological or evolutionary phenomena. For example, the global inventories of avian specimens (Wood et al. 1982, Wood and Schnell 1986) list only binomial taxa.

The classification of *A. aucklandica* provides a useful example of the impact of such taxonomic decisions on perceptions of evolutionary phenomena. During the era when *A. chlorotis* and *A. aucklandica* were placed in different genera, Newton (1896, p. 1006) observed that "... *Nesonetta [aucklandica]* . . . appears to be little else than a brevipennate form of the *Anas chlorotis* of New Zealand." In contrast, Buller and Hector (1896, p. 614) described the close relationship between the two taxa as "... a wonderful instance of evolution, for the brown duck [*A. chlorotis*] of New Zealand and the flightless duck of the Auckland Islands [*A. (a.) aucklandica*] were not merely distinct species, exhibiting entirely different habits, but represented different genera." The subsequent merging of the two taxa into a single species by Delacour and Mayr (1945) tended to obscure the magnitude and evolutionary importance of the differences between these populations, and effectively "... Buller and Hector's wonderful instance of evolution disappeared with the Delacour and Mayr (1945) review" (Dumbell 1986, p. 72).

Accordance of subspecific rank to the three New Zealand forms also carried important, but perhaps unintended evolutionary implications for some ornithologists. In a recent discussion of avian flightlessness, Diamond (1981, p. 508) reasoned: "How fast can flightlessness evolve? For flightless birds with no close relatives, we have no idea. But some flightless birds are exceedingly similar to flying relatives, implying that evolution of flightlessness has been rapid and recent. For example, the duck *Anas aucklandica* has flying subspecies on New Zealand and Campbell

Island [*sic*] and a flightless one on Auckland Island . . ." Diamond then cited the suspicion of S. L. Olson that flightlessness in rails can evolve in a matter of [presumably relatively few] generations (cf. Olson 1973a). First, based on the morphometric comparisons presented here (Figs. 3, 4, 8), the implication that *A. chlorotis* and *A. aucklandica* are "exceedingly similar" is debatable, with the exception of a similarity in plumage pattern. Second, whatever the plausibility of rapid, heterochrony-based loss of flight in some insular birds, the taxonomic rank accorded the populations concerned offers no empirical basis for an estimate of evolutionary rates, and when used in this fashion results in a logical circularity. Based on the phylogeny accepted here (Fig. 1), it can be inferred that flightlessness-related morphological changes (including those shared to a lesser degree by *A. chlorotis*) evolved subsequent to the divergence of the New Zealand clade from its common ancestor with *A. castanea*. Even within the context of a well-corroborated phylogenetic hypothesis, a resource not available for most groups including flightless members (e.g., the Rallidae), discussion of evolutionary rates must remain speculative in the absence of some method of calibrating absolute times of divergences. The Campbell and Auckland islands evidently are remnants of volcanic uplifts during the late Miocene or early Pliocene (Fleming 1975), and although the highlands of the austral islands of New Zealand evidently were significantly glaciated during the Pleistocene (Oliver 1955, Westerkov 1960, Fleming 1975), the littoral zone probably remained habitable and therefore provided no useful limit on the possible antiquity of the *aucklandica* lineage. The existence of several examples of species evidently "in transition" to flightlessness—the Falkland population of Rolland's Grebe (*R. r. rolland*) (Livezey 1989b), the Brown Teal (Fig. 3), and the Auckland Islands Merganser (Livezey 1989a)—suggests that the loss of flight may be a protracted evolutionary process in a number of avian lineages. Worthy (1988, p. 626) inferred, based on subfossil evidence, that the extinct duck *Euryanas finschi* underwent but a 10% reduction in skeletal wing length within 10,000 years, and evidently remained flighted; however, he went on to suggest that species may become flightless in "only a few thousand years."

Functional significance of flightlessness in Anas aucklandica. *Anas aucklandica* and, to a lesser

extent, *A. chlorotis* possess most of the morpho-ecological characters typical of insular waterfowl (Lack 1970, Weller 1980): reduced flying ability, small body size, reduced sexual dichromatism, white eye-rings, dark natal plumages (Buller 1891; Delacour 1956, 1964; Dumbell 1986), tameness toward humans (Scott 1971, Weller 1975a), and expansion of feeding niche to include more marine habitats (Weller 1975a, 1975b, 1980; Dumbell 1986). An empirical model for anatids presented by Rahn et al. (1975, p. 760) predicts clutch masses (products of clutch size and egg mass) of 368 g, 363 g, and 305 g for *A. castanea*, *A. chlorotis*, and *A. aucklandica*, respectively, figures which closely approximate observed parameters (Table 9). Based on predictions yielded by a model given by Rohwer (1988, p. 163) for the Anatini, the egg mass of *A. castanea* was typical for *Anas* of similar size, but those for *A. chlorotis* and *A. aucklandica*, however, were approximately 1.7 and 2.4 times as massive, respectively, as those predicted for dabbling ducks of equal body mass (Table 9). Clearly, the New Zealand teal conform to the typically insular pattern of increased per capita investment in a smaller number of progeny (Lack 1970, Weller 1980, Rohwer 1988). Also, at least *A. chlorotis* produces eggs with relatively high yolk content (44% of egg mass; Lack 1968). Comparable data on developmental periods of the Australasian teal are lacking, but the general model of Rahn and Ar (1974) permits estimates of incubation periods (days) based on mean egg masses: *A. castanea*, 27.3 (Frith [1967] reported a period of 28 days; Norman [1982] reported a mean of 26.6); *A. chlorotis*, 29.7 (Reid and Roderick [1973] reported a range of 27–30 days); and *A. aucklandica*, 30.4. Differences among these estimates are small, but a prolonged incubation period in *A. aucklandica* may shorten the period of relatively high mortality suffered by broods (see Shine 1989a, for review of the “safe harbor” hypothesis).

Relaxed seasonality of nesting schedules and relatively long-term pair-bonds, also characteristic of a number of insular anatids (Weller 1980), are weakly indicated in *A. aucklandica*, although relevant data are few (Kear 1970; Weller 1975a, 1980; Dumbell 1986). These characteristics, and the frequent attendance of broods by males in *A. aucklandica* (Weller 1975a), distinguish this species and a number of other insular waterfowl from the typical “duck model” of reproduction

(Maynard Smith 1977), in which there is minimal parental investment by males; there are, however, continental species of dabbling duck in which males participate in brood rearing (McKinney 1985).

The feeding habits of *A. aucklandica* are particularly diverse and modified, presumably to exploit more effectively the limited habitats and food diversity available within its limited distributional range. *Anas aucklandica* and *A. chlorotis* are comparatively terrestrial in foraging habit, frequently probing in vegetation and debris in uplands and along tide lines, although the former exploits marine shores more consistently than its sister species (Weller 1974, 1975a, 1975b; Dumbell 1986); both species also are partly nocturnal in feeding habit (Weller 1974, 1975a). Although *Anas* is included among the “dabbling” ducks (Tribe Anatini), *A. aucklandica* and, to a lesser extent, *A. chlorotis* employ dives during foraging (Kear and Johnsgard 1968; Weller 1974, 1975a). Bill lamellae and tomial flaps are well developed in both *A. chlorotis* and *A. aucklandica* (Delacour and Mayr 1945, Gravatt 1966), which presumably improve filter-feeding. Weller (1975a) noted that hardened commissural points were present in *A. aucklandica*, and hypothesized that these structures facilitate the swallowing of large, armored invertebrates. Finally, the relatively great sexual dimorphism in external dimensions of *A. aucklandica* provides a counterexample to the “rule,” albeit poorly documented (Reiss 1989), for sexual dimorphism to increase in lineages undergoing *increasing* size (Rensch 1950, 1960); however, the finding conforms with general expectations for niche expansion in birds in depauperate communities (Selander 1966, Shine 1989b).

Insularity and its concomitant ecological peculiarities, however, do not explain in toto the morphological changes evident in *A. aucklandica*, particularly its flightlessness. Among the surprisingly numerous evolutionary rationales proposed for avian flightlessness (cf. Livezey and Humphrey 1986), seven may apply to *A. aucklandica*: (1) flight, considered to be primarily an escape mechanism, was lost in the absence of (terrestrial) predators (Wiglesworth 1900, Lowe 1928, Snow 1966); (2) thermodynamic advantages of dwarfed extremities (sensu Allen’s Rule; Rensch 1960) selected for shortened wings and (indirectly) for reduced flying ability (Livezey and Humphrey 1986); (3) flight, as a mechanism per-

mitting long-distance, aerial dispersal, was lost because of the decreased need for or risks of departure from islands (MacArthur and Wilson 1967, Weller 1975a, Williamson 1981); (4) flight was lost to lessen vulnerability to aerial kleptoparasites (Snow 1966); (5) flight, essential for avian migration, was lost in response to constancy of local food supply (Wiglesworth 1900, Snow 1966); (6) flight was lost, in part, due to selection for shortened wings for terrestrial locomotion through heavy brush (Weller 1975a); and (7) flight, of negligible advantage for one or more of the reasons given above, was lost through a reallocation of somatic resources resulting from selection for "developmental economy" (Olson 1973a, Feduccia 1980, James and Olson 1983). Clearly, these alternative explanations could apply in combination, and the last rationale involving developmental savings provides a selective rationale for the foregoing suggestions concerning the loss of the advantages of flight. Even a modest shortening of primary remiges represents a significant caloric conservation; Pehrsson (1987) documented a significant decrease in lengths of primary remiges in Mallards on low-protein diets during wing molt.

These ideas differ in plausibility relative to *A. aucklandica*, however. Terrestrial predators, at least mammalian examples, were absent on the Auckland Islands prior to the arrival of humans (Weller 1975a); the extinction of teal on the main island since the introduction of domestic cats (*Felis catus*) and pigs (*Sus scrofa*) demonstrates the vulnerability of flightless teal to mammalian predators (Weller 1975a, Dumbell 1986). Turbott (1967) considered the introduced brown rat (*Rattus norvegicus*) to be the main predator of Campbell Island Teal. Weller (1975a) pointed out, however, that Brown or Southern Skuas (*Catharacta lonnbergi*) pose a substantial threat to ducklings of *A. aucklandica*, and Robertson (1976) found remains of *A. (a.) nesiotis* in skua "middens" on Campbell Island; the skeletal elements of *A. (a.) nesiotis* measured herein were collected from such middens. Weller (1975a, 1980) reported that skuas primarily hunt the teal from the ground and often at night, effectively acting as nocturnal terrestrial predators. Weller (1975a) reasonably associated the stealthful movements and cryptic coloration of adults and young of *A. aucklandica* with avoidance of predators. These observations render doubtful the suggestion by Worthy (1988) that cover effec-

tively eliminated the threat of aerial predation for *A. aucklandica*, thereby permitting the loss of flight. Other possible avian predators of flightless teal (especially young; see Weller 1975a) include the New Zealand Falcon (*Falco novaeseelandiae*), Northern Giant-Petrel (*Macronectes halli*), and Kelp Gull (*Larus dominicanus*); in addition, the southern sea lion (*Phocarctos hookeri*) may pose a submarine threat (Weller 1975a). The documented vulnerability of continental *Anas* to predation during wing molt, including attacks by aerial predators (Oring 1964, Sjöberg 1988), supports the probable importance of aerial predation for flightless ducks. Consequently, the habitat of *A. aucklandica* cannot be described as effectively predator-free, although neither *A. chlorotis* nor *A. aucklandica* historically have been exposed to the diversity of predators characteristic of most continental regions.

The possible thermodynamic advantages of shortened wings in cold climates also seems an improbable explanation for flightlessness in *A. aucklandica*. Although there have been substantial reductions in skeleto-muscular bulk in the pectoral limb of *A. aucklandica* (Figs. 5, 9–11), the diminutive wings of the species largely reflect a shortening of the primary remiges. Once fully grown (and no longer vascularized), the remiges are insulative structures rather than radiators of body heat, and therefore a shortening of these feathers cannot contribute to the thermodynamic conservation of energy.

Of the remaining explanations, one involving selection for developmental savings from reduced pectoral appendages, structures rendered of negligible utility for escape, migration, or dispersal, seems the most likely. However, not all of the derived characters of *A. aucklandica* need be interpreted as individually adaptive. Assuming that the pectoral reduction of this flightless species represents a selectively advantageous, heterochronically produced modification, several other characters of *A. aucklandica* may be interpreted simply as selectively neutral by-products (cf. Gould 1977, Gould and Lewontin 1979). For example, reduced body size, traditionally considered to represent an ecological optimum for feeding and/or terrestrial locomotion on islands (Lack 1970; Weller 1975a, 1980), may simply be a correlate of the generally arrested development of adults. Similarly, the sexually monochromatic, juvenal-like plumage of *A. aucklandica* may represent a developmentally

constrained by-product of a generalized paedomorphosis which selectively "targeted" the pectoral limb, instead of being a separate adaptation for crypsis, especially of brood-attendant males (Weller 1975a). Another interpretation (e.g., Lack 1970) holds that the drab plumages of males of some insular waterfowl reflect a relaxation of selection for precopulatory "isolating mechanisms" in the comparatively depauperate avifaunal communities of islands. There are many counterexamples to this second explanation, however, and other, perhaps more general hypotheses have been proposed (Butcher and Rohwer 1989).

The evolutionary context of paedomorphosis in *A. aucklandica* differs fundamentally from those characteristic of the more dramatic examples in some amphibians (reviewed by Gould 1977), in which paedomorphic lineages reach sexual maturity as somatic larvae under conditions favoring early reproduction with minimal parental care. The latter reproductive traits traditionally have been considered to be "r-selected," and contrast with the "K-selected" traits of delayed age of reproduction, low fecundity, and maximal per capita parental investment (reviewed by Stearns 1976, 1977). The latter "K-selected" reproductive traits, which clearly characterize *A. aucklandica* (Table 9) and are typical of insular populations of birds, are particularly pronounced in birds at high latitudes (Cody 1966, 1971). The evident progenesis of *A. aucklandica*, in that it evolved under a regime of stable population densities and relatively constant (but harsh) environmental conditions, is an exception to the typical correspondence (Gould 1988) between neoteny and circumstances associated with "K-selection."

ACKNOWLEDGMENTS

This research was supported by National Science Foundation grant BSR-8516623, and by visitation grants from the American Museum of Natural History and U.S. National Museum of Natural History. I am grateful to W. Boles, B. Gillies, A. Isles, G. Mack, B. and M. Cameron, and H. Levenson for their hospitality, and to P. S. Humphrey for sharing his insights and unpublished data. M. W. Weller generously provided wing loadings for *A. aucklandica*, and R. L. Zusi provided invaluable instruction on myological techniques. Curatorial personnel of the following institutions granted access to specimens or provided loans of requested material: Department of Ornithology, American Museum of Natural History, New York (abbreviated in text and figure legends as AMNH); Subdepartment of Ornithology, British Museum (Natural

History), Tring, Hertfordshire (BMNH); Division of Birds, National Museum of Natural History, Washington, DC (USNM); Museum of Vertebrate Zoology, University of California, Berkeley; Peabody Museum, Yale University, New Haven (YAPM); New Zealand National Museum (Natural History), Wellington (NZNM); Otago Museum, Dunedin, New Zealand; Canterbury Museum, Christchurch, New Zealand; Auckland Institute and Museum, Auckland, New Zealand (AIM); Department of Ornithology, Australian Museum, Sydney; Department of Ornithology, National Museum of Victoria, Melbourne, Australia; CSIRO Division of Wildlife Research, Canberra, Australia; South Australian Museum, Adelaide; Queensland Museum, Brisbane, Queensland, Australia; Royal Ontario Museum, Toronto, Ontario, Canada; Department of Biology, University of South Florida, Tampa; Department of Zoology, University of Florida, Gainesville; Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; Philadelphia Academy of Sciences, Philadelphia, Pennsylvania; Museum of Natural Science, Louisiana State University, Baton Rouge (LSU); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; Museum of Natural History, University of Kansas, Lawrence (KUMNH); Division of Birds, Field Museum of Natural History, Chicago, Illinois; Division of Birds, Museum of Zoology, University of Michigan, Ann Arbor; and the Los Angeles County Museum of Natural History, Los Angeles, California. A. H. Bledsoe, J. Craft, and P. S. Humphrey made helpful comments on the manuscript, and M. Schmalz typed its several drafts.

LITERATURE CITED

- BAILEY, A. M., AND J. H. SORENSEN. 1962. Subantarctic Campbell Island. Denver Museum Natural History, Denver, CO.
- BETHKE, R. W., AND V. G. THOMAS. 1988. Differences in flight muscle mass among geese, dabbling ducks, and diving ducks relative to habitat use. *Can. J. Zool.* 66:2024-2028.
- BOUBIER, M. 1934. Les oiseaux qui ne volent pas. *Bull. Ornithol. Romand (Geneve)* 1:77-89.
- BULLER, W. L. 1888. A history of the birds of New Zealand, 2nd ed. Vol. II. Published privately (by the author), London.
- BULLER, W. L. 1891. Further notes and observations on certain species of New Zealand birds. *Trans. Proc. N.Z. Inst.* 24:75-91.
- BULLER, W. L. 1894. Notes on the flightless duck of the Auckland Islands (*Nesonetta aucklandica*). *Trans. Proc. N.Z. Inst.* 27:128-129.
- BULLER, W. L. 1905. Supplement to the birds of New Zealand. Vol. II. Published privately (by the author), London.
- BULLER, W. L., AND J. HECTOR. 1896. [Commentary on] Notes on the ornithology of New Zealand. *Trans. Proc. N.Z. Inst.* 29:614.
- BUTCHER, G. S., AND S. ROHWER. 1989. The evolution of conspicuous and distinctive coloration for communication in birds, p. 51-108. *In* D. M. Power [ed.], *Current ornithology*. Vol. 6. Plenum Press, New York.

- CALDER, W. A., III. 1974. Consequences of body size for avian energetics. *Publ. Nuttall Ornithol. Club* 15:86-144.
- CLARK, R. J. 1971. Wing-loading—a plea for consistency in usage. *Auk* 88:927-928.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20:174-184.
- CODY, M. L. 1971. Ecological aspects of reproduction, p. 461-512. *In* D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. I. Academic Press, New York.
- DELACOUR, J. 1956. The waterfowl of the world. Vol. 2. *Country Life*, London.
- DELACOUR, J. 1964. Corrections and additions. *In* J. Delacour [ed.], *The waterfowl of the world*. Vol. 4. *Country Life*, London.
- DELACOUR, J., AND E. MAYR. 1945. The family Anatidae. *Wilson Bull.* 57:3-55.
- DEMENT'EV, G. P., AND N. A. GLADKOV. 1967. Birds of the Soviet Union. Vol. IV. *Israel Progr. Sci. Trans.*, Jerusalem.
- DIAMOND, J. M. 1981. Flightlessness and fear of flying in island species. *Nature* 293:507-508.
- DIXON, W. J. (CHIEF ED.). 1985. BMDP statistical software. Univ. of California Press, Berkeley.
- DUMBELL, G. 1986. The New Zealand Brown Teal: 1845-1985. *Wildfowl* 37:71-87.
- FALLA, R. A. 1953. The Australian element in the avifauna of New Zealand. *Emu* 53:36-46.
- FALLA, R. A., AND E. F. STEAD. 1938. The plumages of *Nesonetta aucklandica* Gray. *Trans. Proc. N.Z. Inst.* 68:37-39.
- FEDUCCIA, A. 1980. The age of birds. Harvard Univ. Press., Cambridge, MA.
- FEDUCCIA, A., AND H. B. TORDOFF. 1979. Feathers of *Archaeopteryx*: asymmetrical vanes indicate aerodynamic function. *Science* 203:1021-1022.
- FIELDS, J. 1977. Sex and age variation in wing-length in the Coot *Fulica atra*. *Ardea* 65:115-125.
- FLEMING, C. A. 1975. The geological history of New Zealand and its biota, p. 1-86. *In* G. Kuschel [ed.], *Biogeography and ecology in New Zealand*. Dr. W. Junk, The Hague.
- FLEMING, J. H. 1935. A new genus and species of flightless duck. *Occas. Pap. R. Ont. Mus. Zool.* 1: 1-3.
- FRITH, H. J. 1967. Waterfowl in Australia. East-West Center Press, Honolulu, HI.
- FUJIOKA, T. 1955. Time and order of ossification centres in the chicken skeleton. *Acta Anat. Nippon.* 30:140-150.
- GADOW, H. 1902. The wings and the skeleton of *Phalacrocorax harrisi*. *Novit. Zool. London* 9:169-176.
- GEORGE, J. C., AND A. J. BERGER. 1966. *Avian myology*. Academic Press, New York.
- GEORGE, J. C., AND K. K. NAIR. 1952. The wing-spread and its significance in the flight of some common Indian birds. *J. Univ. Bombay* 20:1-5.
- GOULD, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biol. Rev.* 41:587-640.
- GOULD, S. J. 1977. *Ontogeny and phylogeny*. Belknap, Cambridge, MA.
- GOULD, S. J. 1988. The uses of heterochrony, p. 1-13. *In* M. L. McKinney [ed.], *Heterochrony in evolution: a multidisciplinary approach*. Plenum Press, New York.
- GRAVATT, D. J. 1966. Ecological studies of the New Zealand Brown Teal Duck (*Anas chlorotis*) on Great Barrier Island. IIBB Zoology Project, Univ. of Auckland, New Zealand.
- GRAY, G. R. 1844. *Genera of birds*. Vol. III. Longmans, London.
- GRAY, G. R. 1845. Birds, p. 21-39. *In* J. Richardson and J. E. Gray [eds.], *The zoology of the voyage of HMS Erebus and Terror, under the command of Captain Sir James Clark Ross, R. N., F. R. S., during the years 1839 to 1843*. E. W. Janson, London.
- GREENEWALT, C. H. 1962. Dimensional relationships for flying animals. *Smithson. Misc. Coll.* 144:1-46.
- HAFER, J. 1986. Superspecies and species limits in vertebrates. *Z. Zool. Syst. Evolutionsforsch.* 24: 169-190.
- HARTMAN, F. A. 1961. Locomotor mechanisms of birds. *Smithson. Misc. Coll.* 143:1-91.
- HECTOR, J. 1873. On *Cnemidornis calcitrans*, showing its affinity to the *Natatores*. *Proc. Zool. Soc. (Lond.)* 1873:763-771.
- HOWARD, H. 1955. New records and a new species of *Chendytes*, an extinct genus of diving geese. *Condor* 57:135-143.
- HOWARD, H. 1964. Fossil Anseriformes, p. 233-326. *In* J. Delacour [ed.], *The waterfowl of the world*. Vol. 4. *Country Life*, London.
- HUDSON, G. E., AND P. J. LANZILLOTTI. 1964. Muscles of the pectoral limb in galliform birds. *Am. Midl. Nat.* 71:1-113.
- HUDSON, G. E., D. O. SCHREIWEIS, AND S. Y. C. WANG. 1972. A numerical study of the wing and leg muscles of tinamous (Tinamidae). *Northwest Sci.* 46: 207-255.
- HUMPHREY, P. S., AND G. A. CLARK, JR. 1961. Pterylosis of the Mallard duck. *Condor* 63:365-385.
- HUMPHREY, P. S., AND B. C. LIVEZEY. 1982. Flightlessness in Flying Steamer-Ducks. *Auk* 99:369-372.
- HUMPHREY, P. S., AND K. C. PARKES. 1959. An approach to the study of molts and plumages. *Auk* 76:1-31.
- JAMES, H. F., AND S. L. OLSON. 1983. Flightless birds. *Nat. Hist.* 92:30-40.
- JOHNSGARD, P. A. 1960. Hybridization in the Anatidae and its taxonomic implications. *Condor* 62: 25-33.
- JOHNSGARD, P. A. 1965. *Handbook of waterfowl behavior*. Constable, London.
- JOHNSGARD, P. A. 1978. *Ducks, geese, and swans of the world*. Univ. of Nebraska Press, Lincoln.
- KEAR, J. 1970. The adaptive radiation of parental care in waterfowl, p. 357-392. *In* J. H. Crook [ed.], *Social behaviour in birds and mammals*. Academic Press, New York.
- KEAR, J., AND P. A. JOHNSGARD. 1968. Foraging dives by surface-feeding ducks. *Wilson Bull.* 80:231.
- KEAR, J., AND R. J. SCARLETT. 1970. The Auckland Islands Merganser. *Wildfowl* 21:78-86.
- KLIMA, M. 1962. The morphogenesis of the avian

- sternum. Prace Brnenske Zakladny Ceskoslovenske Akademie Ved 34:151-194.
- LACK, D. 1967. The significance of clutch-size in waterfowl. *Wildfowl* 18:125-128.
- LACK, D. 1968. The proportion of yolk in the eggs of waterfowl. *Wildfowl* 19:67-69.
- LACK, D. 1970. The endemic ducks of remote islands. *Wildfowl* 21:5-10.
- LATIMER, H. B. 1927. Postnatal growth of the chicken skeleton. *Am. J. Anat.* 40:1-57.
- LIVEZEY, B. C. 1986a. Geographic variation in skeletons of Flying Steamer-Ducks (Anatidae: *Tachyeres patachonicus*). *J. Biogeogr.* 13:511-525.
- LIVEZEY, B. C. 1986b. A phylogenetic analysis of Recent anseriform genera using morphological characters. *Auk* 103:737-754.
- LIVEZEY, B. C. 1988. Morphometrics of flightlessness in the Alcidae. *Auk* 105:681-698.
- LIVEZEY, B. C. 1989a. Phylogenetic relationships and incipient flightlessness of the extinct Auckland Islands Merganser. *Wilson Bull.* 101:410-435.
- LIVEZEY, B. C. 1989b. Flightlessness in grebes (Aves, Podicipedidae): its independent evolution in three genera. *Evolution* 43:29-54.
- LIVEZEY, B. C. 1989c. Morphometric patterns in Recent and fossil penguins (Aves, Sphenisciformes). *J. Zool. (Lond.)* 219:269-307.
- LIVEZEY, B. C. 1989d. Phylogenetic relationships of several subfossil Anseriformes of New Zealand. *Univ. Kansas Mus. Nat. Hist. Occas. Pap.* 128:1-25.
- LIVEZEY, B. C., AND P. S. HUMPHREY. 1984. Sexual dimorphism in continental steamer-ducks. *Condor* 86:368-377.
- LIVEZEY, B. C., AND P. S. HUMPHREY. 1986. Flightlessness in steamer-ducks (Anatidae: *Tachyeres*): its morphological bases and probable evolution. *Evolution* 40:540-558.
- LOWE, P. R. 1928. A description of *Atlantisia rogersi*, the diminutive and flightless rail of Inaccessible Island (southern Atlantic), with some notes on flightless rails. *Ibis* 70:99-131.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, NJ.
- MADGE, S., AND H. BURN. 1988. Waterfowl: an identification guide to the ducks, geese and swans of the world. Houghton Mifflin, Boston, MA.
- MAGNAN, M. A. 1913a. Rapport de la surface alaire avec le poids du corps chez les oiseaux. *Bull. Mus. Hist. Nat. Paris* 19:45-52.
- MAGNAN, M. A. 1913b. Variations de la surface alaire chez les oiseaux. *Bull. Mus. Hist. Nat. Paris* 19:119-125.
- MAGNAN, M. A. 1922. Les caractéristiques des oiseaux suivant le mode de vol. *Ann. Sci. Nat. (Ser. 10)* 5:125-334.
- MAILLARD, J. 1948. Recherches embryologiques sur *Catharacta skua* Brunn. *Rev. Suisse Zool.* 55 (Suppl.):1-114.
- MARPLES, B. J. 1930. The proportions of birds' wings and their changes during development. *Proc. Zool. Soc. (Lond.)* 1930:997-1008.
- MARTINEZ, J. 1987. Un nouveau cas probable d'endémisme insulaire: le canard de l'île Amsterdam, p. 211-218. *In* C. Mourer-Chauvire [Coord.], L'évolution des oiseaux d'après le témoignage des fossiles. *Docum. Lab. Géol. Lyon.* No. 99.
- MAYNARD SMITH, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25:1-9.
- MAYR, E. 1963. Animal species and evolution. Belknap, Cambridge, MA.
- MCKINNEY, F. 1985. Primary and secondary male reproductive strategies of dabbling ducks, p. 68-82. *In* P. A. Gowaty and D. W. Mock [eds.], Avian monogamy. *Ornithol. Monogr.* No. 37. American Ornithologists' Union, Washington, DC.
- MCKITRICK, M. C., AND R. M. ZINK. 1988. Species concepts in ornithology. *Condor* 90:1-14.
- MCMANARA, K. J. 1986. A guide to the nomenclature of heterochrony. *J. Paleontol.* 59:4-13.
- MEINERTZHAGEN, R. 1955. The speed and altitude of bird flight (with notes on other animals). *Ibis* 97:81-117.
- MEUNIER, K. 1951. Korrelation und Umkonstruktion in den Grössenbeziehungen Zwischen Vogel-flügel und Vogelkörper. *Biologia Generalis* 19:403-443.
- MEUNIER, K. 1959. Die Grössenabhängigkeit der Körperform bei Vögeln. *Zeit. Wissen. Zool.* 162:328-355.
- MILLER, L. 1925. *Chendytes*, a diving goose from the California Pleistocene. *Condor* 27:145-149.
- MONTAGNA, W. 1945. A re-investigation of the development of the wing of the fowl. *J. Morphol.* 76:87-113.
- MOULTON, D. W., AND M. W. WELLER. 1984. Biology and conservation of the Laysan Duck (*Anas laysanensis*). *Condor* 86:105-117.
- MÜLLENHOFF, K. 1885. Die Grosse der Flugflächen. *Pflueger's Arch. Ges. Physiol.* 35:407-453.
- NEWTON, A. 1896. A dictionary of birds. Adam and Charles Black, London.
- NITZSCH, C. L. 1840. System der Pterylographie. Edward Anton, Halle.
- NORMAN, F. I. 1982. Eggs, egg-laying and incubation in the Chestnut Teal. *Emu* 81:195-198.
- NORMAN, F. I., AND V. G. HURLEY. 1984. Gonad measurements and other parameters from Chestnut Teal *Anas castanea* collected in the Gippsland Lakes region, Victoria. *Emu* 84:52-55.
- NORMAN, F. I., AND F. MCKINNEY. 1987. Clutches, broods, and brood care behaviour in Chestnut Teal. *Wildfowl* 38:117-126.
- OLIVER, W. R. B. 1955. New Zealand birds. 2nd ed. A. H. and A. W. Reed, Wellington, New Zealand.
- OLSON, S. L. 1973a. Evolution of the rails of the South Atlantic islands (Aves: Rallidae). *Smithson. Contrib. Zool.* 152:1-53.
- OLSON, S. L. 1973b. A classification of the Rallidae. *Wilson Bull.* 85:381-416.
- OLSON, S. L., AND H. F. JAMES. 1982. Prodomus of the fossil avifauna of the Hawaiian Islands. *Smithson. Contrib. Zool.* 365:1-59.
- OLSON, S. L., AND A. WETMORE. 1976. Preliminary diagnoses of two extraordinary new genera of birds from Pleistocene deposits in the Hawaiian Islands. *Proc. Biol. Soc. Wash.* 89:247-258.

- ORING, L. W. 1964. Predation upon flightless ducks. *Wilson Bull.* 76:190.
- OWEN, R. 1866. On *Dinornis* (Part X): containing a description of part of the skeleton of a flightless bird indicative of a new genus and species (*Cnemiornis calcitrans*, Ow.). *Trans. Zool. Soc. (Lond.)* 5:395-404.
- OWEN, R. 1875. On *Dinornis* (Part XX): containing a restoration of the skeleton of *Cnemiornis calcitrans*, Ow., with remarks on its affinities in the lamellirostral group. *Trans. Zool. Soc. (Lond.)* 9:253-272.
- PALMER, R. S. 1976. *Handbook of North American birds*. Vols. 2 and 3. Yale Univ. Press, New Haven, CT.
- PEHRSSON, O. 1987. Effects of body condition on molting in Mallards. *Condor* 89:329-339.
- PENNYCUICK, C. J. 1975. Mechanics of flight, p. 1-75. In D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. 5. Academic Press, New York.
- PHILLIPS, J. C. 1925. *A natural history of the ducks*. Vol. 3. Houghton Mifflin, Boston, MA.
- PIMENTEL, R. A. 1979. *Morphometrics: the multivariate analysis of biological data*. Kendall/Hunt, Dubuque, IA.
- POOLE, E. L. 1938. Weights and wing areas in North American birds. *Auk* 55:511-517.
- PROVINE, R. R. 1981. Wing-flapping develops in chickens made flightless by feather mutations. *Develop. Psychobiol.* 14:481-486.
- RAHN, H., AND A. AR. 1974. The avian egg: incubation time and water loss. *Condor* 76:147-152.
- RAHN, H., C. V. PAGANELLI, AND A. AR. 1975. Relation of avian egg weight to body weight. *Auk* 92:750-765.
- RAIKOW, R. J. 1973. Locomotor mechanisms in North American ducks. *Wilson Bull.* 85:295-307.
- RAIKOW, R. J. 1985. Locomotor system, p. 57-147. In A. S. King and J. McLelland [eds.], *Form and function in birds*. Vol. 3. Academic Press, London.
- REID, B., AND C. RODERICK. 1973. New Zealand Scaup *Aythya novaeseelandiae* and Brown Teal *Anas aucklandica chlorotis* in captivity. *Int. Zoo Yearbook* 13:12-15.
- REISS, M. J. 1989. *The allometry of growth and reproduction*. Cambridge Univ. Press, Cambridge, United Kingdom.
- RENSCH, B. 1950. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergrösse. *Bonn. Zool. Beitr.* 1:58-69.
- RENSCH, B. 1960. *Evolution above the species level*. Columbia Univ. Press, New York.
- RICKER, W. E. 1984. Computation and uses of central trend lines. *Can. J. Zool.* 62:1897-1905.
- RIPLEY, S. D. 1942. A review of the species *Anas castanea*. *Auk* 59:90-99.
- ROBERTSON, C.J.R. 1976. The Campbell Island Teal. *Wildlife—A Review* 7:45-46.
- ROHWER, F. C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. *Auk* 105:161-176.
- SALVADORI, T. 1895. *Catalogue of the birds in the British Museum*. London.
- SAVILE, D.B.O. 1957. Adaptive evolution in the avian wing. *Evolution* 11:212-224.
- SCHERER, S., AND T. HILSBURG. 1982. Hybridisierung und Verwandtschaftsgrade innerhalb der Anatidae—eine systematische und evolutionstheoretische Betrachtung. *J. Ornithol.* 123:357-380.
- SCHINZ, H. R., AND R. ZANGERL. 1937. Beiträge zur Osteogenese des Knochensystems beim Haushuhn, bei der Haustaube und beim Hanbenseissfuss. *Denkschr. Schweiz. Naturforsch. Ges.* 77:117-164.
- SCOTT, D. 1971. The Auckland Islands Flightless Teal. *Wildfowl* 22:44-45.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151.
- SHINE, R. 1989a. Alternative models for the evolution of offspring size. *Am. Nat.* 134:311-317.
- SHINE, R. 1989b. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* 64:419-461.
- SIBLEY, C. G. 1957. The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. *Condor* 59:166-191.
- SJÖBERG, K. 1988. The flightless period of free-living male Teal *Anas crecca* in northern Sweden. *Ibis* 130:164-171.
- SNOW, B. K. 1966. Observations on the behaviour and ecology of the Flightless Cormorant *Nannopterum harrisi*. *Ibis* 108:265-280.
- STEAD, E. F. 1938. The supposed flightless duck from Campbell Island. *Trans. Proc. N.Z. Inst.* 68:100-101.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51:3-47.
- STEARNS, S. C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* 8:147-171.
- TODD, F. S. 1979. *Waterfowl: ducks, geese, and swans of the world*. Sea World, San Diego, CA.
- TURBOTT, E. G. 1967. *Buller's birds of New Zealand*. MacDonald, London.
- VANDEN BERGE, J. C. 1979. Myologia, p. 175-219. In J. J. Baumel, A. S. King, A. M. Lucas, J. E. Breazile, and H. E. Evans [eds.], *Nomina anatomica avium*. Academic Press, London.
- WAITE, E. R. 1909. Vertebrates of the subantarctic islands of New Zealand, p. 542-600. In C. Chilton [ed.], *The subantarctic islands of New Zealand*. Vol. II. Philos. Inst. Canterbury, Wellington, NZ.
- WEIMERSKIRCH, H., R. ZOTIER, AND P. JOUVENTIN. 1988. The avifauna of the Kerguelen Islands. *Emu* 89:15-29.
- WELLER, M. W. 1974. Habitat selection and feeding patterns of Brown Teal (*Anas castanea chlorotis*) on Great Barrier Island. *Notornis* 21:25-35.
- WELLER, M. W. 1975a. Ecological studies of the Auckland Islands Flightless Teal. *Auk* 92:280-297.
- WELLER, M. W. 1975b. Seasonal variation in estuary use by Brown Teal (*Anas castanea chlorotis*) on Great Barrier Island. *Notornis* 22:246-247.
- WELLER, M. W. 1980. *The island waterfowl*. Iowa State Univ. Press, Ames.
- WELSH, A. H., A. T. PETERSON, AND S. A. ALTMANN.

1988. The fallacy of averages. *Am. Nat.* 132:277-288.
- WESTERKOV, K. 1960. Birds of Campbell Island. New Zealand Department Internal Affairs (Wildlife Service), Wellington, New Zealand.
- WIGLESWORTH, J. 1900. Inaugural address on flightless birds. *Trans. Liverpool Biol. Soc.* 14:1-33.
- WILEY, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley and Sons, New York.
- WILLIAMS, G. R. 1964. Extinction and the Anatidae of New Zealand. *Wildfowl* 15:140-146.
- WILLIAMS, M. J. 1985. Brown Teal, p. 146-147. In C.J.R. Robertson [ed.], Complete book of New Zealand birds. Reader's Digest, Sydney, Australia.
- WILLIAMS, M. J. 1986. The numbers of Auckland Island Teal. *Wildfowl* 37:63-70.
- WILLIAMSON, M. 1981. Island populations. Oxford Univ. Press, Oxford.
- WOOD, D. S., AND G. D. SCHNELL. 1986. Revised world inventory of avian skeletal specimens, 1986. American Ornithologists' Union and Oklahoma Biological Survey, Norman, OK.
- WOOD, D. S., R. L. ZUSI, AND M. A. JENKINSON. 1982. World inventory of avian spirit specimens, 1982. American Ornithologists' Union and Oklahoma Biological Survey, Norman, OK.
- WORTHY, T. H. 1988. Loss of flight ability in the extinct New Zealand duck *Euryanas finschi*. *J. Zool. (Lond.)* 215:619-628.
- ZINK, R. M., AND J. V. REMSEN, JR. 1986. Evolutionary processes and patterns of geographic variation in birds, p. 1-69. In R. F. Johnston [ed.], Current ornithology. Vol. 4. Plenum Press, New York.
- ZUSI, R. L., AND G. D. BENTZ. 1978. The appendicular myology of the Labrador Duck (*Camptorhynchus labradorius*). *Condor* 80:407-418.
- | | |
|-------------------|----------------------------------|
| M. lat. dors. | M. latissimus dorsi caudalis |
| M. corbra. cran. | M. coracobrachialis cranialis |
| M. corbra. caud. | M. coracobrachialis caudalis |
| M. delt. maj. | M. deltoideus major |
| M. delt. min. | M. deltoideus minor |
| M. scaphum. cran. | M. scapulohumeralis cranialis |
| M. scaphum. caud. | M. scapulohumeralis caudalis |
| M. subscap. | M. subscapularis |
| M. subcor. vent. | M. subcoracoideus pars ventralis |
| M. subcor. dors. | M. subcoracoideus pars dorsalis |
- ANTEBRACHIUM
- | | |
|----------------|---------------------------|
| M. humtric. | M. humerotriceps |
| M. scaptric. | M. scapulotriceps |
| M. bic. bra. | M. biceps brachii |
| M. brac. | M. brachialis |
| M. pron. sup. | M. pronator superficialis |
| M. pron. prof. | M. pronator profundus |
| M. ect.-uln. | M. ectepicondylo-ulnaris |
| M. ent.-uln. | M. entepicondylo-ulnaris |
| M. sup. | M. supinator. |
- CARPOMETACARPUS
- | | |
|-------------------------------|---|
| M. flx. carp. uln. cran. | M. flexor carpi ulnaris pars cranialis |
| M. flx. carp. uln. caud. | M. flexor carpi ulnaris pars caudalis |
| M. flx. dig. sup. | M. flexor digitorum superficialis |
| M. flx. dig. prof. | M. flexor digitorum profundus |
| L. elas. m. f. c. u. | Ligamentum elasticum m. flexoris carpi ulnaris |
| L. hum. carp. | Ligamentum humerocarpale |
| M. ext. met. rad. dors. | M. extensor metacarpi radialis caput dorsale |
| M. ext. met. rad. vent. | M. extensor metacarpi radialis caput ventrale |
| M. ext. dig. com. | M. extensor digitorum communis |
| M. ext. met. uln. | M. extensor metacarpi ulnaris |
| M. ext. long. alu. | M. extensor longus alulae |
| M. ext. long. dig. maj. prox. | M. extensor longus digiti majoris pars proximalis |

APPENDIX

Listed below are the abbreviations for muscles used in Figures 9-16, grouped by primary skeletal elements acted upon (based on Raikow 1985). Nomenclature follows Vanden Berge (1979).

SCAPULA

- | | |
|---------------------|--|
| M. rhom. sup. | M. rhomboideus superficialis |
| M. rhom. prof. | M. rhomboideus profundus |
| M. serr. sup. cran. | M. serratus superficialis pars cranialis |
| M. serr. sup. caud. | M. serratus superficialis pars caudalis |
| M. serr. prof. | M. serratus profundus |

HUMERUS

- | | |
|---------------------|-------------------------------|
| M. pect. | M. pectoralis |
| M. supracor. | M. supracoracoideus |
| M. lat. dors. cran. | M. latissimus dorsi cranialis |

M. ext. long. M. extensor longus digiti majoris pars distalis
 dig. maj. dist.
 M. ulnmet. M. ulnometacarpalis dorsalis dors.
 M. ulnmet. M. ulnometacarpalis ventralis vent.

DIGITS

M. int. dors. M. interosseus dorsalis
 M. int. vent. M. interosseus ventralis
 M. ext. brev. M. extensor brevis alulae alu.
 M. abd. alu. M. abductor alulae
 M. flx. alu. M. flexor alulae
 M. add. alu. M. adductor alulae
 M. abd. dig. M. abductor digiti majoris maj.
 M. flx. dig. M. flexor digiti minoris min.

PATAGIUM AND REMIGES

M. serr. sup. M. serratus superficialis pars metap.
 M. tens. pro- M. tensor proapatagialis pat.

T. long. M. tensor proapatagialis pars longa, tendo longa
 T. brev. M. tensor proapatagialis pars brevis, tendo brevis
 L. elas. proapat. Ligamentum elasticum proapatagiale
 M. lat. dors. M. latissimus dorsi metapatagialis metap.
 M. bic. proapat. M. biceps proapatagialis
 M. exp. sec. M. expansor secundariorum
 M. cucul. cap. M. cucullaris capitis pars proapatagialis proapat.
 M. cucul. cap. M. cucullaris capitis pars interscapularis interscap.
 M. cucul. cap. M. cucullaris capitis pars clavic. clavic.

MISCELLANEOUS

M. sternocor. M. sternocoracoideus
 D. alu. Digitalis alulae
 D. maj. Digitalis majoris
 D. min. Digitalis minoris
 P. I-III Phalanges I-III