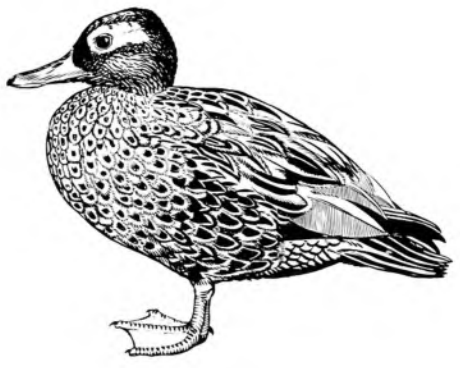
Comparative morphometrics of *Anas* ducks, with particular reference to the Hawaiian Duck *Anas wyvilliana*, Laysan Duck *A. laysanensis*, and Eaton's Pintail *A. eatoni*



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The Hawaiian Duck or Koloa, Laysan Duck, and Eaton's Pintail were compared morphometrically with their continental relatives, and the three insular endemics were found to be 19-59% less massive than their continental relatives. External dimensions showed similar decreases in insular species, whereas sexual dimorphism of most external measurements was similar in insular and continental groups. Relative wing size was slightly smaller in the Hawaiian Duck and moderately smaller in the Laysan Duck than in continental mallards; relative wing size of Eaton's Pintail was similar to that of the Northern Pintail. Canonical analyses of external measurements revealed that the Hawaiian Duck and Laysan Duck differed from the Common Mallard primarily in relative lengths of the bill and wing, whereas Eaton's Pintail had relatively shorter bills and longer tails than the Northern Pintail. Relative depth of the carina sterni was smaller in the Hawaiian Duck and the Laysan Duck than in continental mallards; relative carina depth was equal in the Northern and Eaton's Pintails. Wing elements of Hawaiian Ducks and Laysan Ducks were shorter (particularly distally) than those of continental relatives. Skeletal elements of the leg were shorter in the two insular mallards; in Hawaiian Ducks, the tibiotarsus is disproportionately short and distal elements long, whereas in the Laysan Duck the femur was disproportionately long and the tarsometatarsus and middle toe disproportionately short. Canonical analysis of complete skeletons of mallards confirmed that the Laysan Duck and (to a lesser extent) the Hawaiian Duck differed from continental species by their disproportionately small skulls, distally shortened wings, relatively small pectoral and pelvic girdles, and variably altered proportions within the leg. The morphological peculiarities of Hawaiian Duck, Laysan Duck, Eaton's Pintail, and other insular dabbling ducks (including subfossil species) are considered with respect to pectoral reduction, feeding ecology, parameters of reproduction, correlates of body mass, ontogeny, population size, and the extinction of dabbling ducks endemic to oceanic islands.

Dabbling ducks (Tribe Anatini, *sensu* Livezey 1986) comprise several genera of waterfowl, including *Anas*, one of the most speciose in the Class Aves (Bock & Farrand 1980). Some of the most aberrant and taxonomically controversial taxa of *Anas* are endemic to isolated oceanic islands (Delacour & Mayr 1945, Delacour 1956, Lack 1970, Weller 1980). These endemics include two mallards (subgenus *Anas*) and a pintail (subgenus *Dafila*) (Livezey 1991).

The Hawaiian Duck or Koloa *Anas wyvilliana* is a threatened species limited in distribution to the islands of Kauai (22°N, 159°30'W), rarely Niihau (22°N, 160°W), and (by reintroduction) Oahu (21°N, 158°W) and Hawaii (19°N, 155°W) (Fisher 1951, Berger 1981, Green 1992, Engilis & Pratt 1993); formerly, the Hawaiian Duck was found throughout the archipelago (Perkins 1903, Phillips 1923, Swedberg 1967, Olson & James 1982, 1991). The Hawaiian Duck is closely related to the Common Mallard *Anas platyrhynchos* (Livezey 1991, Browne *et al.* 1993), and currently is treated as a subspecies of *A. platyrhynchos* (Johnsgard 1978, 1979, Todd 1979) or as a closely related species (A.O.U. 1983, Livezey 1991).

The Laysan Duck *Anas laysanensis* is endemic to tiny Laysan Island (26°N, 172°W; 1463 km WNW of Honolulu) and also is close-

ly related to the Common Mallard (Moulton & Weller 1984, Livezey 1991, Browne *et al.* 1993). The Laysan Duck has been considered as a full species (e.g. Salvadori 1895, Fisher 1905, Peters 1931, Ripley 1960), a subspecies of *A. platyrhynchos* (e.g. Delacour & Mayr 1945, Delacour 1956, Johnsgard 1979), or a separate genus (Oberholser 1917); currently it is treated as a species (A.O.U. 1983). Through destruction of the native flora by introduced rabbits *Oryctolagus cuniculus* and over-hunting, the Laysan Duck almost was extirpated by 1910 (Warner 1963); only six birds were thought to remain in 1911 (Brock 1951). Intensive management has permitted the species to attain a stable, but threatened population (Berger 1981, Collar & Andrew 1988, Green 1992).

Eaton's Pintail *A. eatoni* is endemic to the Kerguelen (49°S, 69°E) and Crozet (46°S, 51°E) islands, southwestern Indian Ocean (Phillips 1923, Delacour & Mayr 1945, Delacour 1956). Eaton's Pintail is closely related to the Holarctic Northern Pintail *A. acuta* (Phillips 1923, Delacour & Mayr 1945, Delacour 1956, Johnsgard 1978, Todd 1979, Livezey 1991), and currently is treated as a full species by most taxonomists (Stahl *et al.* 1984, Weimerskirch *et al.* 1988, Livezey 1991).

During an ongoing study of flightlessness in carinate birds, including that of the Auckland Islands Teal *A. aucklandica* (Livezey 1990), I undertook comparisons between the Hawaiian Duck, Laysan Duck, and Eaton's Pintail, and their continental relatives (based on the methodology of Livezey 1991), to gain insights into the general morphological correlates of insularity in waterfowl. Limited mensural data also were collected on three extinct insular Anatini: the extinct Coues' Gadwall *Mareca (strepera) couesi* of Washington Island, Line Islands (6°N, 160°W), central Pacific Ocean; the recently extirpated Marianas Duck *A. oustaleti*, formerly of the Mariana Islands (13-15°N, 146°E) (Engbring & Pratt 1985), South Pacific, and the subject of substantial taxonomic controversy (Kuroda 1941, 1942, Yamashina 1948); and an unnamed, subfossil *Anas* from Amsterdam Island (38°S, 78°E), Indian Ocean (Martinez 1987). The morphological shifts undergone by these insular Anatini are compared to those of other insular Anseriformes (including several subfossil species), and interpreted with respect to phylogeny, ecogeographic circumstances (particularly parameters of reproduction), and possible predisposition toward flightlessness.

Methods

Taxonomy

I follow the classification given by Livezey (1991) to permit the simple labelling of plots displaying fine-scale morphometric differences; taxonomy of the North American species also conforms to that of Scott (1988) except for the rank of the genus *Mareca* and the rank of the allospecies of the mallard (*A. platyrhynchos*) complex. Two of the taxa currently considered subspecies of northern mallards (subgenus *Anas*) - the Greenland Mallard *A. (p) conboschas* and "Gulf Duck" *A. (fulvigula) maculosa* - were adequately represented in samples to be distinguished in analyses and plots. Within the brown pintails (subgenus *Dafila*, infragenus *Dafila*), Eaton's Pintail was compared with the Northern Pintail; specimens of the poorly differentiated Crozet population *A. eatoni drygalskii* were too few for separate analysis.

Specimens

I attempted to collect mensural data from at least 10-15 study skins of each sex of the following taxa: Common Mallard, Greenland Mallard, Mottled Duck *A. fulvigula*, "Gulf Duck", Mexican Duck *A. diazi*, American Black Duck *A. rubripes*, Marianas Duck, Hawaiian Duck, Laysan Duck, Northern Pintail, and Eaton's Pintail (Johnsgard 1961, 1978). The nominate subspecies of Eaton's Pintail comprised 35 of 38 study skins measured. Available skins of fledged, juvenile Common Mallards (3) and Hawaiian Ducks (2) were measured for ontogenetic inferences. I sought to measure 10-15 skeletons for each taxon-sex group, but several taxa lacked a single complete skeletal specimen. Samples of skeletons were: Common Mallard 28, Greenland Mallard 1, Mottled Duck 11, "Gulf Duck" 4, American Black Duck 32, Marianas Duck 2, Hawaiian Duck 13, and Laysan Duck 15. Seven partial (trunk) skeletons were available for the Mexican Duck. A single skeleton of a juvenile Hawaiian Duck also was measured. No complete skeletons of Eaton's Pintail were available, but a series of 15 sterna of the nominate subspecies was included

for study; a sample of 46 sterna of the Northern Pintail was measured for comparisons.

Mensural data

Six measurements were made on study skins (Livezey 1989a): culmen length, nail width, wing length, tail length, tarsus length, and middle-toe length. Wing areas were measured from tracings of an extended wing of freshly collected or thawed, fresh-frozen specimens using a compensating polar planimeter; these areas were doubled to estimate the total wing areas of individual birds (after Raikow 1973). Wing-loadings were calculated as the ratio of body mass (g) divided by total wing area (cm^2) (Clark 1971).

Five dimensions were recorded for sterna: lengths of the carina and basin, least and caudal widths of the basin, and depth of the carina. For complete skeletons, 33 measurements were made (including the five sternal dimensions), involving the skull, six wing elements, four elements of the pectoral girdle, all four major segments of the pelvic limb, and the pelvis. Possible bias stemming from slight appendicular asymmetry within individual specimens (Latimer & Wager 1941) was avoided through random selection of elements. Details of these measurements were given by Livezey (1988, 1989a,b, 1990). Abbreviations used in shaft widths of appendicular elements are: LWM, Least Width at Midpoint (most major limb elements) and LMW, Lateromedial Width Midpoint (tarsometatarsus only).

Supplementary data on external measurements, body masses, and wing areas of *Anas* were taken from published compilations (Müllenhoff 1885, Magnan 1913, 1922, Phillips 1923, Poole 1938, George & Nair 1952, Meunier 1959, Hartman 1961, Raikow 1973, Bellrose 1976, Palmer 1976, Cramp 1977, Weller 1975, 1980, Moulton & Weller 1984, Stahl *et al.* 1984, Madge & Burn 1988, Weimerskirch *et al.* 1988) and unpublished tabulations and wing tracings of R. Meinertzhagen (Snow 1987).

Statistical analyses

Linear measurements of study skins and skeletal elements were compared using two-way analysis of variance (ANOVA), with taxon and sex as fixed effects. Where main effects were significant, pairwise differences were assessed subsequently using Bonferroni adjusted levels of significance. Data on body mass were taken largely from the literature, and much of this information did not permit calculation of variances and statistical tests; consequently, interspecific differences in body mass (fortunately large) are presented without tests. Proportions composed by major skeletal elements within the wing and leg, as well as selected ratios of skeletal measurements, were compared using ANOVA of log-transformed data (base *e*); analyses based on proportions transformed to arcsines of square roots produced inferentially identical results. Two-way Levene's tests (T) and coefficients of variations ($SD/\bar{x}$, expressed as percentages) were used to compare the relative variability of measurements between groups.

Bivariate associations were quantified using Spearman correlation coefficients (r) for log-transformed data. Linear regressions (Type-I) based on log-transformed data were employed for estimates of mean wing areas based on mean wing lengths for selected taxa.

Canonical (variate) analysis (CA), a multivariate technique which derives mutually orthogonal axes that maximally discriminate predefined group means relative to pooled within-group variances (Pimentel 1979, Campbell & Atchley 1981, Gittins 1985), was used to investigate multivariate differences among taxon-sex groups. Discrimatory axes, termed canonical variates (CVs), were based on subsets of external or skeletal measurements (log-transformed to homogenize variances among variables) that were backstep-selected from the complete set of measurements based on partial F-statistics. Magnitude of total among-group variation represented by the set of canonical variates was assessed using the corresponding likelihood ratio (Wilks' lambda), and multivariate differences between specific groups were tested using associated pairwise F-statistics and Bonferroni P-values. Mahalanobis' distances (D) were calculated to summarize the multivariate distances between group centroids. Relative contributions of interspecific differences, sexual dimorphism, and species-sex interactions in multivariate distances among groups were assessed using stepwise multivariate analysis of variance (MANOVA) targeting these effects (on all canonical variates) and two-way ANOVA of scores of specimens on canonical variates. Methodological details of these techniques are described in previous papers (Livezey

1989a,b, 1990). Interpretation of canonical variates was based on partial correlation coefficients of log-transformed measurements with each CV, corrected for variance attributable to the first principal component of the pooled within-group covariance matrix (corresponds to the "shearing" of Bookstein *et al.* 1985). This approach permits the inclusion of all measurements in the interpretation of CVs (regardless of the subset of variables entered into the model), and provides measures of pattern that are independent of pooled within-group variance and comparatively stable with respect to magnitude of intergroup differences and multicolinearity of variables.

Jackknifed classifications (Lachenbruch & Mickey 1968), associated with the CAs, were used to cross-validate and determine the sexes of specimens lacking essential documentation. Two unsexed study skins of the Hawaiian Duck were classified based on placements with posterior probabilities greater than 0.90. The sexes of two unsexed skeletons also were assigned (posterior probabilities greater than 0.75), and the sex of a single, poorly documented skeleton was changed (posterior probability greater than 0.99).

Prior to multivariate analysis, data sets for external, sternal, and (complete) skeletal measurements were subjected to a procedure which provides estimates for missing data. Estimates were based on stepwise regressions of available measurements for the same taxon. A maximum of two, one, and five measurements were estimated for external, sternal, and (complete) skeletal records, respectively. This resulted in 19 estimates for 18 study skins (0.9% of data set for 337 specimens), eight estimates for eight sterna (0.9% of data set for 185 specimens), and 65 estimates for 22 complete skeletons (1.2% of data set for 112 specimens).

All statistical analyses were performed using the 1988 release of Biomedical Computer Programs (BMDP, Dixon 1990) on an IBM 3081 KX3 mainframe computer at the University of Kansas.

Results

Body mass

Within the mallards, insular endemics are substantially less massive than continental relatives (Table 1). Compared to the Common Mallard, the Hawaiian Duck (sex for sex) has undergone a 44% decrease in mean body mass; the Laysan Duck has undergone a 59% decrease in mass. Sex for sex, the mean body mass of the Laysan Duck is only 74% of that of

Table 1. Summary statistics ($\bar{x}$ ± SD) for body masses (g) and external measurements (mm) of selected species of mallard (subgenus *Anas*) and pintail (subgenus *Dafila*), by species and sex.

Species	Sex	Body mass[a]	n[b]	Culmen length	Wing length	Tail length	Tarsus length	Middle toe length
A. platyrhynchos[c]	M	1145 ± 139(268)	31	56.6 ± 2.1	282.5 ± 6.4	88.1 ± 5.5	47.8 ± 1.6	54.2 ± 2.6
	F	1001 ± 94(114)	28	51.9 ± 2.0	263.7 ± 9.8	82.2 ± 4.0	43.3 ± 1.7	49.9 ± 1.5
A. fulvigula[d]	M	1030 ± 107 (30)	10	55.5 ± 1.2	257.1 ± 8.1	85.8 ± 5.0	47.1 ± 2.3	54.9 ± 1.8
	F	968 ± 76 (11)	10	52.6 ± 2.1	240.0 ± 3.9	86.9 ± 3.2	44.6 ± 1.4	52.1 ± 1.9
A. rubripes	M	1400 (376)	15	54.3 ± 2.3	280.7 ± 9.4	82.9 ± 6.7	46.3 ± 2.0	54.4 ± 1.8
	F	1100 (176)	15	51.7 ± 1.9	266.5 ± 6.3	82.0 ± 6.2	44.3 ± 2.0	50.5 ± 1.9
A. oustaleti	M	919 (1)	6	51.5 ± 1.9	254.5 ± 6.1	77.5 ± 3.6	46.3 ± 2.2	52.2 ± 1.2
	F	816 (1)	3	50.0 ± 1.9	245.3 ± 6.5	72.3 ± 5.5	44.3 ± 1.5	51.7 ± 1.2
A. wyvilliana	M	628 (38) ± 105(10)	14	46.3 ± 1.6	233.2 ± 10.3	78.9 ± 5.9	41.7 ± 1.7	47.1 ± 1.5
	F	568 (22) ± 14 (3)	16	43.8 ± 1.7	220.8 ± 6.8	74.4 ± 4.4	39.9 ± 1.1	44.9 ± 2.1
A. laysanensis	M	448 (11) ± 36 (6)	11	39.4 ± 1.4	203.7 ± 10.9	74.5 ± 4.1	37.2 ± 1.4	41.7 ± 1.3
	F	434 (19) ± 38(14)	17	37.1 ± 2.0	192.3 ± 6.3	76.7 ± 5.9	35.5 ± 0.9	39.3 ± 1.6
A. acuta	M	854(260) ± 172(28)	15	52.5 ± 2.7	261.7 ± 8.0	106.9 ± 10.6	43.5 ± 1.6	49.7 ± 1.3
	F	735(120) ± 145(27)	15	47.3 ± 1.8	245.0 ±7.0	89.7 ± 5.9	41.6 ± 1.7	45.7 ± 1.0
A. eatoni[e]	M	495 (18) ± 30(18)	19	34.6 ± 1.5	223.8 ±6.2	96.3 ± 10.2	36.2 ± 1.6	40.1 ± 1.9
	F	441(7) ± 35 (7)	15	32.3 ± 1.7	204.9 ±8.8	80.9 ± 6.6	34.7 ± 1.5	38.4 ± 1.7

[a]Data taken from specimen labels and Palmer (1976), Cramp (1977), Weller (1980), Moulton & Weller (1984), and Stahl *et al.* (1984); sample sizes (parenthetical figures) are given separately for means and standard deviations (where different).
[b]Sample sizes for five linear measurements.
[c]Nominate subspecies.
[d]Excludes *A. (f.) maculosa*.
[e]Includes nominate subspecies and *A. e. drygalskii*.

the Hawaiian Duck. Based on single data for each sex, the mass of the Marianas Duck has decreased 19% relative to that of the Common Mallard. Within-sex coefficients of variation for body mass averaged 9.6% in the Hawaiian Duck and 8.4% in the Laysan Duck, figures comparable to the mean of 10.8% in the geographically widespread Common Mallard (Table 1).

Compared to the Northern Pintail, body mass of the insular Eaton's Pintail has undergone a mean within-sex decrease of 41%. The mean within-sex coefficient of variation for body mass was greater in the geographically widespread Northern Pintail (19.1%) than in Eaton's Pintail (7.0%).

External dimensions

In the mallards, differences among taxa were significant (ANOVA, $P<0.0001$) in all six measurements compared (Table 1). Sexual dimorphism was highly significant in lengths of the culmen, wing, tail, and middle toe (ANOVA, $P<0.0001$), and significant but of lesser magnitude in nail width ($P<0.01$); males tended to be larger than females in most comparisons (Table 1). Taxon-sex interaction effects, reflecting differences in sexual dimorphism across taxa, were significant ($P<0.005$) in lengths of the tail and tarsus. Summary statistics for the mallards show that the external dimensions of the three insular endemics followed body mass in intergroup rankings (Table 1); i.e. in order of decreasing size, the Marianas Duck, Hawaiian Duck, and Laysan Duck had the smallest external dimensions of the group.

The two species of pintail showed similar patterns in external dimensions (Table 1). Interspecific differences were highly significant in all six measurements (ANOVA, $P<0.0001$), and intersexual differences were of similar magnitude ($P<0.0001$) in all but the variable nail width. Species-sex interaction effects were significant ($P<0.0005$) only in middle-toe lengths, being more dimorphic in the Northern Pintail than in Eaton's Pintail (Table 1). As with body mass, external dimensions were substantially smaller in Eaton's Pintail than in its continental sister-species (Table 1). Stahl *et al.* (1984) documented that the nominate Kerguelen population and Crozet population (*drygalskii*) of Eaton's Pintail were very similar in external dimensions.

Wing-loadings

Available data on wing-loadings (g cm^{-2}) of continental members of the subgenus *Anas* are comparatively few ($\bar{x} \pm SD$, n): Mallard (1.36 ± 0.15, 68) and American Black Duck (1.13 ± 0.15, 3). A flighted specimen of a domestic variety of the Common Mallard had a wing-loading of 1.45 (George & Nair 1952). Wing-loadings of six males and five females of the Laysan Duck averaged 0.99 and 0.96, respectively (Moulton & Weller 1984). Relative to the much smaller mass of the Laysan Duck, these wing-loadings are moderately high. A regression of wing area on body mass (log-transformed) for 63 Common Mallards was highly significant ($r = 0.69$, $P<0.001$). Projected wing areas (cm^2) corresponding to the mean masses of the Laysan Duck sampled by Moulton & Weller (1984) were 505 and 489 for males and females, respectively; these estimates are 1.15 times the areas actually measured for the Laysan Duck. The estimates based on the Common Mallard yield projected wing-loadings (0.86 and 0.83 g cm^{-2}) that are 0.13 g cm^{-2} lighter than those measured, figures which are comparable to those of continental dabbling ducks of similar body mass (Livezey 1990).

Information on wing-loadings of pintails is limited: Northern Pintail (1.06 (14) ± 0.19 (6)) and White-cheeked Pintail *A. bahamensis* (0.73 (1)). There are no data on wing areas of Eaton's Pintail, and none for the Hawaiian Duck or Marianas Duck. A linear regression of mean wing area on mean wing length (log-transformed data) for 16 flighted species of *Anas* was highly significant ($r = 0.90$, $P<0.01$), and yielded estimates of wing areas for these three species. Corresponding estimates of wing-loading (g cm^{-2}) are: Marianas Duck, 1.15; Hawaiian Duck, 0.95; and Eaton's Pintail, 0.82.

Canonical analyses of external measurements of mallards

A CA of the three insular species and six continental taxa of mallards significantly incorporated all six external dimensions (F-to-remove > 4.40; df = 17, 244; $P<0.001$) and provided significant discrimination among the 18 taxon-sex groups (Wilks' lambda = 0.0007; df = 6, 17, 249; $P<<0.001$). Stepwise MANOVAs documented significant inter-specific (Wilks' lambda = 0.199; df = 5, 1, 249;

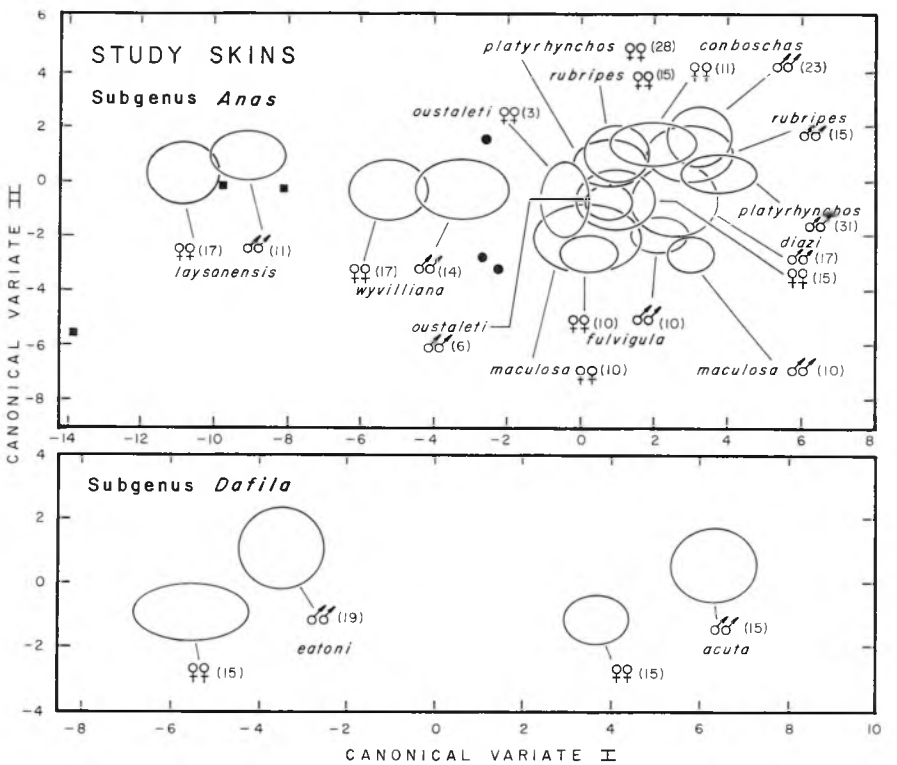

Figure 1. Top - plot of mean scores (± SD) of 18 taxon-sex groups (*n*) of mallards on the first two canonical variates of six external measurements (mm); also plotted are three immature Common Mallards (solid circles) and two immature Hawaiian Ducks (solid squares). Bottom - plot of mean scores (± SD) of four species-sex groups (n) of pintails on the first two canonical variates of four external measurements (mm).

$P<<0.0001$) and intersexual multivariate differences (Wilks' lambda = 0.549; df = 4, 1, 249; $P<<0.001$); multivariate species-sex interactions were not significant (Wilks' lambda = 0.990; df = 1, 1, 249; $P>0.10$).

The first canonical variate (CV-I) for mallards included significant interspecific and intersexual differences (ANOVA of scores, $P<0.0001$), and primarily separated the two Hawaiian endemics from continental taxa (Fig. 1); this axis accounted for 87% of the total dispersion among groups relative to pooled

Table 2. Partial correlation coefficients [a] and summary statistics for canonical variates of external measurements separating species and sexes of mallards (subgenus *Anas*) and pintails (subgenus *Dafila*).

	Anas		*Dafila*	
Character	CV-I	CV-II	CV-I	CV-II
Culmen length	0.24	-0.53	0.91	-0.85
Nail width	0.41	-0.56	0.03	-0.16
Wing length	0.60	0.95	-0.10	0.48
Tail length	-0.23	-0.08	-0.78	0.90
Tarsus length	-0.50	-0.26	0.03	-0.35
Middle-toe length	-0.24	-0.12	0.21	-0.19
Eigenvalue	18.8	1.6	24.5	1.0
Variance (%)	86.8	7.2	95.7	3.7
Canonical *R*	0.97	0.78	0.98	0.70

[a] Correlation coefficients between variables and canonical variates (based on backstep-selected subsets of variables), corrected for variance attributed to first eigenvector of pooled within-group covariance matrix for each subgenus.

within-group variation (Table 2). The Laysan Duck occupied an extreme position relative to continental forms, and the Marianas and Hawaiian Ducks had intermediate scores on CV-I. Juveniles of the Common Mallard approached adult Hawaiian Ducks on this axis, and juveniles of the Hawaiian Duck approximated or were more extreme in position than adult Laysan Ducks on CV-I (Fig. 1). Correlation coefficients indicate that CV-I largely contrasted size of the bill and wing with size of the tail, tarsus, and middle toe; mean scores on CV-I were correlated highly with mean body masses of groups (r = 0.96). In essence, CV-I reveals that the Hawaiian Duck and (especially) the Laysan Duck are smaller and have relatively shorter wings and bills than their continental relatives, and that these characteristics are more pronounced in juveniles.

The second canonical variate (CV-II) for skins of the mallard group contributed another 7.2% of the total differences among groups; CV-II included significant interspecific differences (ANOVA) of scores; F = 45.2; df = 8, 249; P<0.0001) but no significant intersexual or interaction effects (P>0.35). Correlation coefficients indicate that CV-II essentially reflects residual differences in relative wing length (Table 2), and primarily distinguished the nonmigratory Mottled Duck and "Gulf Duck" from other species (Fig. 1). Mean scores of groups on CV-II were not correlated with mean body masses (r = -0.23).

The remaining canonical variates, CV-III through CV-VI, together accounted for the remaining 6% of total intergroup dispersion. Although interspecific differences in scores were significant on CV-III, CV-IV, and CV-V (P<0.0001), the comparatively small differences provided no insights concerning insular differentiation and are not detailed.

Canonical analysis of external measurements of pintails

A CA for study skins of four species-sex groups of pintails retained lengths of the culmen, wing, tail, and middle toe significant-

Table 3. Summary statistics (x ± SD (n)) for five sternal measurements (mm) of selected species of mallard (subgenus *Anas*) and pintail subgenus *Dafila*), by species and sex.

		Carina		Basin		
Species	Sex	Length	Depth	Length	Least width	Caudal width
A. platyrhynchos[a]	M	105.9 ± 4.0 (15)	24.2 ± 0.8 (15)	90.2 ± 3.0 (15)	37.1 ± 1.4 (15)	54.5 ± 2.8 (14)
	F	98.6 ± 2.4 (14)	22.6 ± 1.0 (14)	85.5 ± 2.1 (14)	36.3 ± 1.5 (14)	51.4 ± 1.6 (13)
A. fulvigula[b]	M	103.3 ± 6.2 (7)	23.5 ± 1.7 (7)	87.0 ± 4.1 (7)	35.3 ± 0.9 (7)	48.8 ± 3.3 (6)
	F	92.8 ± 5.3 (7)	20.9 ± 0.7 (7)	79.6 ± 3.1 (7)	33.2 ± 1.1 (7)	46.2 ± 3.6 (7)
A. rubripes	M	105.4 ± 2.5 (17)	24.1 ± 1.2 (17)	90.8 ± 2.9 (17)	38.0 ± 1.1 (17)	55.5 ± 2.4 (16)
	F	99.1 ± 1.5 (16)	22.7 ± 0.9 (16)	86.0 ± 1.8 (16)	36.7 ± 1.4 (16)	53.9 ± 2.3 (16)
A. oustaleti	M	100.2 (1)	23.2 (1)	84.6 (1)	34.0 (1)	46.9 (1)
	F	91.0 (1)	20.1 (1)	79.0 (1)	30.5 (1)	41.5 (1)
A. wyvilliana	M	85.1 ± 3.5 (12)	20.4 ± 0.9 (12)	72.4 ± 3.0 (12)	29.7 ± 1.8 (12)	40.2 ± 3.0 (12)
	F	79.4 ± 1.1 (4)	17.7 ± 1.6 (4)	68.9 ± 1.1 (4)	28.2 ± 0.4 (4)	40.6 ± 3.9 (3)
A. laysanensis	M	72.4 ± 1.1 (3)	17.9 ± 0.7 (3)	62.1 ± 1.2 (3)	27.2 ± 0.7 (3)	38.8 ± 1.9 (3)
	F	73.0 ± 2.0 (14)	18.2 ± 0.5 (14)	62.3 ± 1.4 (14)	26.7 ± 0.5 (14)	36.6 ± 1.2 (13)
A. acuta	M	95.8 ± 3.1 (21)	23.9 ± 1.0 (21)	84.1 ± 2.3 (21)	34.9 ± 1.1 (21)	47.7 ± 2.5 (21)
	F	88.8 ± 3.9 (25)	22.3 ± 1.0 (25)	78.3 ± 2.8 (25)	33.4 ± 1.2 (25)	45.8 ± 2.2 (25)
A. eatoni[c]	M	73.5 ± 3.4 (9)	19.7 ± 1.0 (9)	63.5 ± 2.6 (10)	28.3 ± 1.5 (10)	37.5 ± 1.5 (9)
	F	70.7 ± 1.6 (5)	19.0 ± 0.4 (5)	61.3 ± 1.3 (5)	27.9 ± 1.2 (5)	36.8 ± 2.4 (4)

[a]Nominate subspecies.
[b]Excludes *A. (f.) maculosa*.
[c]Nominate subspecies.

ly (F-to-remove > 3.50; df = 3, 57; P<0.05); discrimination of groups was significant (Wilks lambda = 0.017; df = 4, 3, 60; P<<0.001). Stepwise MANOVAs documented highly significant interspecific (Wilks' lambda = 0.044; df = 2, 1, 60; P<<0.001) and intersexual differences (Wilks' lambda = 0.315; df = 3, 1, 60; P<<0.001), and marginal species-sex interaction effects (Wilks' lambda = 0.925; df = 1, 1, 60; P<0.05). The interaction effects indicate that sexual dimorphism in the Northern Pintail (Mahalanobis' D = 3.3) was slightly greater than that in Eaton's Pintail (D = 2.9).

The first canonical variate (CV-I) displayed highly significantly interspecific and intersexual differences (ANOVA of scores; P<0.0001), and alone accounted for over 95% of the total within-group standardized variation among groups (Table 2). Separation of the Northern Pintail from Eaton's Pintail was the primary contribution of CV-I (Fig. 1), a discrimination that contrasted the lengths of the culmen and tail (Table 2). Mean scores of the four groups on CV-I were directly correlated with mean body mass (r = 1.00). Accordingly, the scores of the two species on CV-I indicate that Eaton's Pintail is smaller and has a relatively longer tail and shorter bill than the Northern Pintail. Although there are some similarities between the external correlates of insularity in mallards and pintails (including a decrease in size), the degree of overall convergence is small (vector product of sheared correlation coefficients for the two CV-Is was only 0.23).

The second canonical variate (CV-II) for skins of pintails contributed supplemental sexual dimorphism shared by both species (ANOVA of scores, P<0.0001), but included no interspecific differences (P>0.15). Scores on CV-II were not correlated with body mass (r = 0.06). CV-III (not shown) accounted for the remaining 0.6% of the intergroup dispersion of skins, but ANOVA of scores revealed significance only for species-sex interactions (P<0.005).

Sternal dimensions

Mean measurements of sterna of mallards and pintails tended to follow mean body mass in interspecific rankings (Table 3). Sternal dimensions of continental members of the mallard group did not differ (P>0.05; within-sex t-tests) but exceeded those of the Hawaiian Duck and (especially) the Laysan Duck. Similarly, sternal dimensions of the Northern Pintail exceeded those of Eaton's Pintail (P<0.0001; ANOVA). Sexual dimorphism was significant (P<0.05; ANOVA) but of smaller magnitude in all sternal dimensions but caudal basin widths of pintails (Table 3).

Canonical analysis of sternal dimensions of mallards

A CA of sternal measurements provided significant discrimination of the eight species-sex groups of mallards (Wilks' lambda = 0.014; df = 4, 13, 107; P<<0.001). The first canonical variate (CV-I) accounted for 94% of the total within-group standardized variation among groups (Table 4), and included significant interspecific (F = 275.36; df = 6, 107; df = 6, 107; P<0.0001) and intersexual differences (F = 44.85; df = 1, 107; P = 0.0001) in scores. Correlations between "sheared" data and CV-I indicate that the axis primarily contrasted dimensions of the carina (especially depth) with other sternal dimensions (Table 4). Positions of groups on CV-I indicated that differences between continental and insular spe-

Table 4. Partial correlation coefficients [a] and summary statistics for canonical variates of sternal measurements separating species and sexes (within subgenera) of mallards (subgenus *Anas*) and pintails (subgenus *Dafila*).

	Anas		*Dafila*	
Character	CV-I	CV-II	CV-I	CV-II
Carina length	-0.12	0.78	0.10	0.67
Depth	-0.62	0.28	0.01	0.46
Basin length	0.46	0.74	0.79	0.12
Least width	0.79	-0.43	0.26	-0.26
Caudal width	0.10	-0.83	0.32	-0.66
Eigenvalue	22.6	1.1	14.7	0.1
Variance (5)	93.6	4.4	99.3	0.7
Canonical R	0.98	0.72	0.97	0.31

[a]Correlation coefficients between variables and canonical variates (based on backstep-selected subsets of variables), corrected for variance accounted for by first eigenvector of pooled within-group covariance matrix for each subgenus.

cies dominated the axis (Fig. 1), and that insular mallards (especially immature birds) have relatively small carinae sterni. Mean scores of groups on CV-I were highly correlated with mean body mass (r = 0.97).

The second canonical variate (CV-II) for sterna contributed another 4.4% of the total variation among groups and largely reflected relative basin width (Table 4). Interspecific differences in scores on CV-II were significant (F = 12.80; df = 6, 107; P<000.1) whereas intersexual differences were not (F = 1.45; df =1, 107; P>0.20). CV-II primarily separated the "Gulf Duck" and the Hawaiian Duck from other species in the mallard group (Fig. 2), and was not correlated with body mass (r = 0.28).

Canonical analysis of sternal dimensions of pintails

Sterna of the four species-sex groups of pintails were discriminated significantly by a CA retaining three of the five measurements compared (Wilks' lambda = 0.058; df = 3, 3, 56; P<<0.001). The first canonical variate (CV-I) accounted for more than 99% of the total intergroup variation (Table 4), and included significant interspecific (F = 759.31; df = 1, 56; P<0.0001) and intersexual differences in scores (F = 23.78; df = 1, 56; P<0.0001). Correlations of measurements with CV-I indicate that the axis reflects size of the sternal basin (Table 4), an interpretation corroborated by the high correlation between mean scores on CV-I and mean body masses (r = 1.00). Interspecific differences in sternal conformation in pintails differed from those in mal-

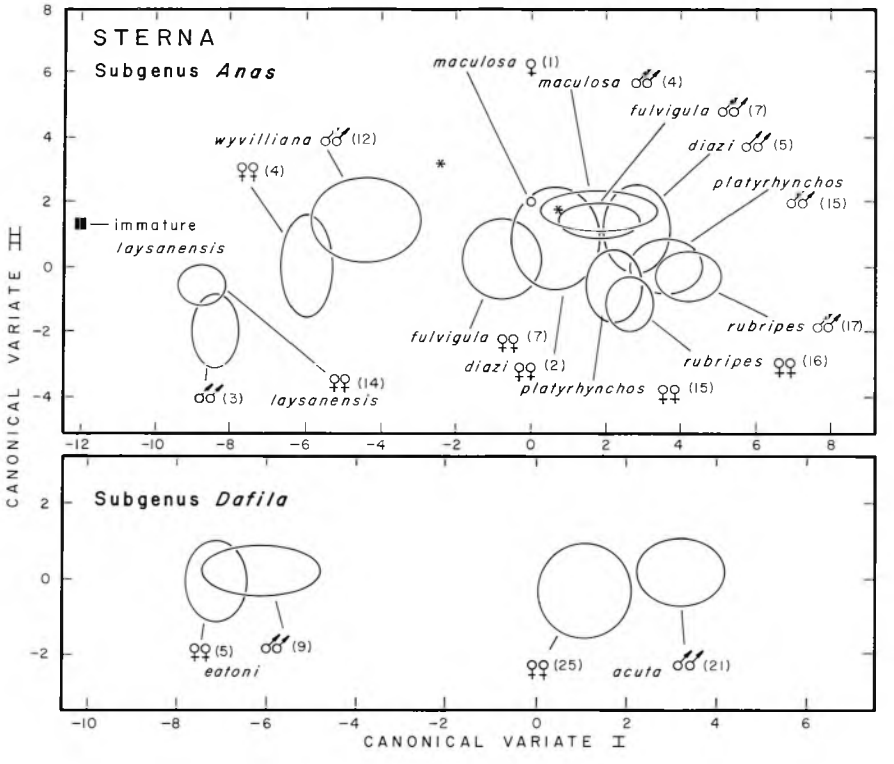

Figure 2. Top - plot of mean scores (± SD) of 14 taxon-sex groups (n) of mallards on the first two canonical variates of four sternal dimensions (mm); asterisks symbolize single specimens of the Marianas Duck, and a solid square symbolizes an immature specimen of the Laysan Duck. Bottom - plot of mean scores (± SD) of four species-sex groups (n) of pintails on the first two canonical variates for three sternal dimensions (mm).

lards (vector product of correlations for respective CV-Is was 0.61), and indicated that insular pintails are characterized by sterna having smaller basins but deep carinae (Table 4, Fig. 2).

The second canonical variate (CV-II) for sterna of pintails accounted for residual sexual dimorphism common to both species (F = 2.85; df 1, 56; P = 0.10). CV-II essentially discriminated the sexes by relative size of the carina sterni (Table 4), and was not correlated with mean body masses (r = 0.06).

Skeletal dimensions of mallards

Of the 33 skeletal measurements compared, all differed significantly among species (ANOVA; P<0.0001) and all but femur LWM differed between the sexes (ANOVA; P<0.05). Rankings among species in skeletal dimensions closely followed those for body masses, being largest in continental species, intermediate in the Hawaiian Duck, and least in the Laysan Duck (Table 5). The two specimens of the Marianas Duck were slightly larger than the Hawaiian Duck and substantially larger than the Laysan Duck. On average, skeletal measurements of the Hawaiian Duck and the Laysan Duck approximated 83% and 77%, respectively, of those of the Common Mallard.

Skeletal proportions within limbs of mallards

Although skeletal wing lengths differed significantly among species (F = 268.77; df = 5, 93; P<0.0001) and between sexes (F = 54.35; df = 1, 93; P<0.0001), proportions of individual elements within the wing were virtually invariant within species; only ulnar proportions differed (marginally) between the sexes (F = 6.87; df = 1, 93; P<0.05). No significant species-sex interactions or differences in group variances in intra-alar proportions were detected.

Interspecific differences in proportions of skeletal wing length constituted by major elements, however, were substantial for all five skeletal segments: humerus (F = 32.59; df = 5, 93; P<0.0001), ulna (F = 91.08; df = 5, 93; P<0.0001), carpometacarpus (F = 90.58; df = 5, 93; P<0.0001), proximal phalanx (F = 31.73; df = 5, 93; P<0.0001), and distal phalanx (F = 43.36; df = 5, 93; P<0.0001). Interspecific heterogeneity in proportions was largely attributable to those of the two Hawaiian species (Fig. 3). Compared to the alar proportions of continental forms, the moderately short wing (83% as long as that of the Common Mallard) of the Hawaiian Duck had disproportionately short proximal elements (particularly the ulna) and disproportionately short distal elements (Fig. 3). Greater changes were evident in the wing skeleton of the Laysan Duck (Fig. 3); not only is skeletal wing length substantially reduced (73% of the length in the Common Mallard), the Laysan Duck has disproportionately long proximal elements (humerus and ulna) and disproportionately short distal elements (carpometacarpus and major digit).

Skeletal leg lengths differed among species (F = 165.84; df = 5, 90; P<0.0001) and between sexes (F = 43.73; df = 1, 90; P<0.0001). Proportions within the leg differed interspecifically in the femur (F = 22.18; df = 5, 90; P<0.0001), tibiotarsus (F = 2.88; df = 5, 90; P<0.05), tarsometatarsus (F = 9.69; df = 5, 90; P<0.0001), and digit III (F = 6.50; df = 5, 90; P<0001). Intersexual differences in leg proportions were slight; only the tibiotarsus (F = 6.91; df = 1, 90; P<0.05) and tarsometatarsus (F = 4.11; df = 1, 90; P<0.05) showed (marginally) significant sexual differences in proportions. No species-sex interactions were detected in

Table 5. Summary statistics (x ± SD (n)) for selected skeletal measurements (mm) of selected species of mallard (subgenus *Anas*), by species and sex.

Species	Sex	Humerus length	Ulna length	Carpometacarpus length	Femur length	Tibiotarsus length	Tarsometatarsus length	Coracoid length	Interacetabular width
A. platyrhynchos[a]	M	95.0±2.1(15)	80.8±2.0(15)	59.5±1.4(15)	51.5±1.2(15)	87.9±1.9(15)	46.3±1.0(15)	52.4±1.5(15)	28.7±1.6(15)
	F	91.4±2.1(14)	78.0±2.1(14)	56.7±1.5(14)	49.7±1.8(14)	85.1±1.9(13)	44.4±1.2(13)	48.9±1.2(14)	26.8±1.2(13)
A. fulvigula[b]	M	91.9±2.3 (7)	77.9±2.5 (7)	56.5±1.8 (7)	50.6±1.6 (7)	87.9±2.0 (7)	46.5±1.9 (7)	51.5±2.6 (7)	25.1±2.8 (6)
	F	85.2±4.1 (7)	72.6±3.4 (7)	51.1±1.6 (5)	46.7±2.7 (7)	80.9±4.3 (7)	42.7±2.1 (7)	45.3±1.9 (7)	24.6±1.2 (7)
A. rubripes	M	95.1±2.5(17)	81.3±2.7(17)	60.3±2.1(17)	52.2±2.2(17)	88.1±3.1(17)	46.7±1.4(17)	52.9±1.4(17)	29.2±1.6(17)
	F	90.8±2.0(16)	78.1±1.8(16)	56.9±1.0(16)	50.2±1.0(16)	85.6±1.8(16)	44.8±1.0(16)	49.3±1.3(16)	28.0±1.2(16)
A. oustaleti	M	95.3 (1)	81.3 (1)	58.2 (1)	52.0 (1)	89.1 (1)	47.4 (1)	50.1 (1)	26.1 (1)
	F	87.2 (1)	76.6 (1)	54.4 (1)	48.0 (1)	82.1 (1)	42.5 (1)	49.1 (1)	23.7 (1)
A. wyvilliana	M	79.0±2.8(10)	68.8±2.2(10)	48.7±1.2(10)	43.3±1.2(12)	74.5±2.2(10)	40.6±1.0(10)	41.2±1.4(12)	21.7±1.2(12)
	F	75.2±2.3 (4)	65.7±2.0 (4)	45.8±1.3 (4)	42.0±0.7 (4)	72.1±1.2 (4)	39.0±1.0 (4)	39.3±1.3 (3)	20.5±1.0 (4)
A. laysanensis	M	72.3±1.3 (3)	62.5±1.0 (3)	40.4±1.4 (3)	41.5±1.1 (3)	68.5±1.7 (3)	35.9±1.0 (3)	40.0±1.4 (3)	20.7±0.2 (3)
	F	70.8±0.8(14)	61.8±0.8(13)	39.4±0.6(13)	40.7±0.7(15)	67.1±1.2(13)	34.7±0.7(13)	36.2±0.6(13)	19.5±1.0(15)

[a]Nominate subspecies only.
[b]Excludes *A. (f.) maculosa*.

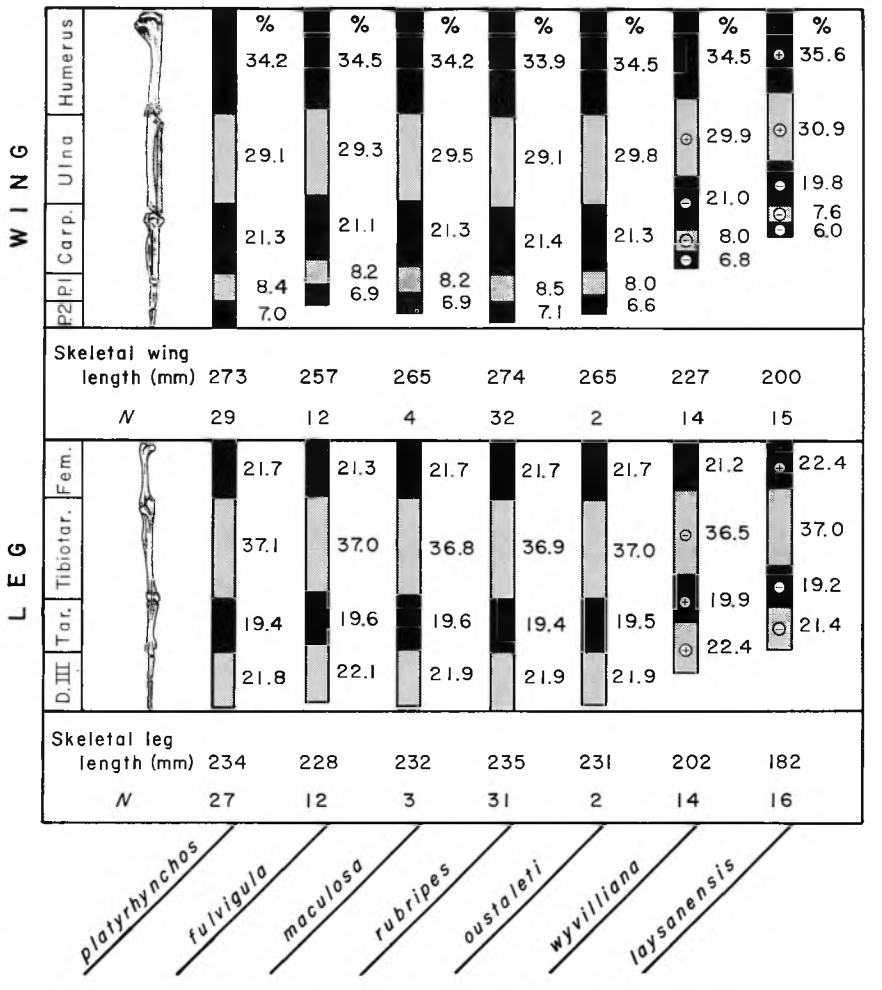

Figure 3. Diagrams of intra-appendicular skeletal proportions of insular and continental species of mallards: algebraic signs within segments indicate the direction of changes inferred. Elements shown in outline are those of the Common Mallard (KU 21814).

leg proportions ($P>0.30$). Only femoral proportions showed interspecific differences in variance (Levene's $T = 4.00$; df = 5, 90; $P<0.005$), being comparatively variable in two widespread continental species, the Common Mallard and the American Black Duck. As in alar proportions, interspecific heterogeneity in leg proportions largely reflected the aberrant proportions found in the Hawaiian endemics (Fig. 3). Within the moderately shortened leg of the Hawaiian Duck (mean skeletal length is 86% of that of the Common Mallard), the tibiotarsus is disproportionately short and the two distal elements are disproportionately long (Fig. 3). The leg skeleton of the Laysan Duck is even shorter (78% as long as the mean for the Common Mallard), wherein femoral proportions are uniquely high and tarsometatarsal and pedal proportions were disproportionately small (Fig. 3).

Canonical analysis of skeletons of mallards

A stepwise CA of 33 skeletal dimensions retained ten variables significantly (F-to-remove > 3.10, df = 11, 88; $P<0.005$), and effec-

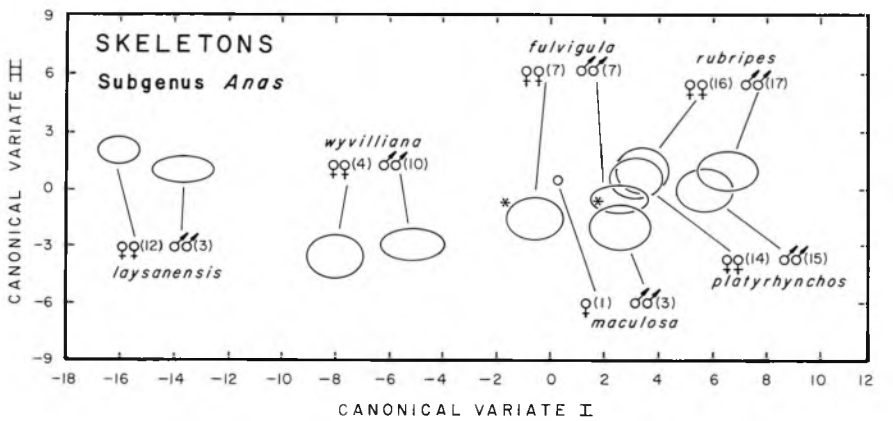

Figure 4. Plot of mean scores (± SD) of 12 taxon-sex groups (*n*) of mallards on the first two canonical variates of 10 of 33 skeletal measurements (mm) retained in the backstep-selected model; asterisks symbolise single specimens of the Marianas Duck.

tively separated the 12 species-sex groups of mallards contrasted (Wilks' lambda = 0.0005; df = 10, 11, 97; $P<<0.001$). Stepwise MANOVAs confirmed significant effects attributable to interspecific differences (Wilks' lambda = 0.043; df = 8, 1, 97; $P<<0.001$), sexual dimorphism (Wilks' lambda = 0.379; df = 5, 1, 97; $P<<0.0001$), and species-sex interactions (Wilks' lambda = 0.951; df = 1, 1, 97; $P<0.05$).

The first canonical variate for complete skeletons (CV-I) alone accounted for over 90% of the total within-group standardized variation among groups (Table 6), reflected significant interspecific (F = 791.45; df = 5, 97; $P<0.0001$) and intersexual differences (F = 104.15; df = 1, 97; $P<0.0001$), and was correlated strongly with mean body masses of groups (r = 0.98; excluding the inadequately sampled Marianas Duck). Correlation coefficients for CV-I indicate that the axis primarily contrasted lengths of the proximal wing elements, depth of the carina sterni, and widths of leg elements with dimensions of the skull, lengths of distal wing elements, and most dimensions of the pectoral and pelvic girdle (Table 6). Scores of groups on CV-I indicate that the Laysan Duck and (to a lesser extent) the Hawaiian Duck are distinguished from continental forms by the disproportionately small skulls, distally shortened wings, relatively small pectoral and pelvic girdles, relatively long femora, and disproportionately short distal leg elements of the insular species (Fig. 4).

The second canonical variate (CV-II) included significant interspecific differences (F = 41.33; df = 5, 97; $P<000.1$) and species-sex interactions (F = 3.36; df = 5, 97; $P<0.01$), was not correlated with mean body mass (r = 0.06), and primarily separated the Hawaiian Duck from the Laysan Duck and continental species (Fig. 4). Correlation coefficients for CV-II revealed that the axis contrasted cranial dimensions, lengths of distal wing elements, and dimensions of the coracoid, sternal basin, and distal leg elements with widths of proximal wing elements, leg elements, sternal basin, and pelvis (Table 6); scores for the Hawaiian Duck on CV-II (Fig. 4) indicated that the species is relatively large in the former dimensions and relatively small in the latter.

The third canonical variate (CV-III) contributed additional separation of species (F = 23.17; df = 5, 97; $P<0.0001$) and sexes (F = 20.58; df = 1, 97; $P<0.0001$), and primarily distinguished the Mottled Duck and "Gulf Duck" from the other species; sexual dimorphism displayed on CV-III varied interspecifically (interaction effects; F = 9.83; df = 5, 97; $P<0.0001$). This discrimination was based largely on the relatively large bills, large feet, and narrow pelves of the Mottled Duck and "Gulf Duck" (Table 6), and was not correlated strongly with body mass (r = 0.33).

Of the remaining canonical variates, only CV-IV included significant interspecific differences (F = 4.12; df = 5, 97; $P<0.005$). CV-IV provided further discrimination of the Common Mallard from other species and displayed supplemental sexual dimorphism in the "Gulf Duck" and the Hawaiian Duck.

Table 6. Partial correlation coefficients [a] and summary statistics for the first three canonical variates of 33 skeletal measurements separating species and sexes of mallards (subgenus *Anas*).

Character[b]	CV-I	CV-II	CV-III
Bill length*	0.52	-0.61	-0.55
Cranium length	0.61	-0.55	0.12
Height	0.24	-0.01	0.24
Width*	0.63	-0.61	-0.00
Humerus length	-0.09	-0.09	-0.01
Head width*	0.18	-0.06	0.21
LWM	-0.20	0.41	0.11
Radius length	-0.04	-0.16	0.27
LWM	-0.12	0.22	0.22
Ulna length*	-0.18	-0.13	0.16
LWM	-0.04	0.21	0.13
Carpometacarpus length*	0.74	-0.79	0.26
Major digit, phalanx 1 length	0.51	-0.46	0.30
Phalanx 2 length	0.51	-0.60	0.03
Femur length	-0.36	0.22	-0.08
Head width	-0.19	0.24	0.12
LWM*	-0.68	0.78	-0.17
Tibiotarsus length	0.02	-0.15	-0.13
LWM	-0.43	0.41	-0.13
Tarsometatarsus length	0.31	-0.57	-0.19
LWM	-0.28	0.30	-0.21
Digit-III length*	0.24	-0.60	-0.38
Scapula length	-0.08	0.19	-0.13
Coracoid length*	0.20	0.01	-0.36
Basal width	0.30	-0.48	0.18
Sternum carina length*	0.16	-0.35	-0.23
Carina depth	-0.18	0.05	-0.24
Basin length	0.26	-0.40	-0.05
Basin least width	0.15	0.11	0.21
Basin caudal width*	-0.11	0.21	0.30
Furcula height	0.13	-0.17	-0.20
Synsacrum length	0.27	0.09	-0.16
Interacetabular width	0.10	0.34	0.48
Eigenvalue	59.8	2.9	2.4
Variance (%)	90.5	4.4	3.6
Canonical *R*	0.99	0.86	0.84

[a]Correlation coefficients between variables and canonical variates (based on backstep-selected subsets of variables), corrected for variance attributable to the first eigenvector of pooled within-group covariance matrix.
[b]Asterisks mark variables included in canonical analysis by stepwise selection procedure.

Discussion

Appendicular characteristics of typical Anas

Members of the genus *Anas*, and most other Anatini (*sensu* Livezey 1986, 1991), are capable of leaping directly into the air and maintaining swift, manoeuverable flight (Raikow 1973). Comparatively low body masses, large wing areas, deeply emarginated distal-most primary remiges, relatively massive hearts (approximately 1.1% of body mass), large breast muscles (approximately 22.5% of body mass), and a capacity for rapid wing beats (roughly 5 sec^{-1}) also characterize flighted Anatini (Meinertzhagen 1955, Hartman 1961, Greenewalt 1962, Raikow 1973, Livezey 1990). The underlying pectoral girdle and alar skeleton reflect these dimensions and muscles (Hoerschelmann 1971, Raikow 1985), and are characteristic of Anatini and, to variable extents, functionally convergent members of other tribes of Anseriformes (Faith 1989). The pelvic limbs of typical *Anas* are typified by skeletal proportions and musculature permitting sustained surface swimming, shallow dives, and adequately swift terrestrial locomotion (Raikow 1985).

Pectoral changes in insular Anas

Relative size of the pectoral limb of both the Hawaiian and Laysan Ducks, as indicated by external (Tables 1, 2, Fig. 1) and skeletal dimensions (Tables 3, 6, Figs 2-4), has undergone reduction. Strongest evidence of this is provided by disproportionately short distal wing elements and shallow carinae sterni

(Figs 2-4), structures in the Laysan Duck which have undergone moderate reduction. The pectoral changes manifest in the Laysan Duck, in combination with a tameness shared with a number of insular species (Humphrey *et al.* 1987), presumably underlie its "weak" and "reluctant" flight (Rothschild 1893, Fisher 1906, Munro 1944, Carlquist 1970, Ely & Clapp 1973). Truncation of the distal portion of the wing and relatively shallow carinae are characteristic of flightless or flight-impaired waterfowl, including steamer-ducks *Tachyeres* spp. (Livezey & Humphrey 1986, 1992), Auckland Islands Teal (Livezey 1990), Auckland Islands Merganser *Mergus australis* (Livezey 1989a), and the extinct seaduck *Chendytes* (Livezey 1993). Pectoral changes evident in the Laysan Duck exceed those of the Hawaiian Duck (Figs 1-4). Further evidence of alar reduction in the Laysan Duck is the frequent loss of one primary remex (229 [74%] of single wings examined in 310 birds; J. Kear *fide* Moulton & Weller 1984); a more extreme variation in number of primary remiges occurs in the Auckland Islands Teal (Livezey 1990).

Similar tendencies toward reduction are indicated in several recently extinct or subfossil insular *Anas* (Howard 1964). Ratios of mean wing lengths divided by tarsus lengths revealed that the dwarfed Coues' Gadwall (ratio = 5.43) had much smaller relative wing lengths than the Common Gadwall (ratio = 6.46). Ratios of mean humerus lengths divided by mean tarsometatarsus lengths indicated that *A. theodori* of Mauritius Island (Newton & Gadow 1893) and *Euryanas finschi* of New Zealand (Worthy 1988) had "relative humerus lengths" (ratios of both approximated 1.70) that are exceeded by that of the Common Mallard (ratio = 2.05); the ratios of the former species are similar to the ratio of 1.76 for the Brown Teal *A. chlorotis*, a weakly flighted species showing moderate pectoral reduction (Livezey 1990). Two insular *Anas* known only from subfossil remains - *A. pachyscelus* from Bermuda (Wetmore 1960) and an unnamed "teal" from Amsterdam Island, Indian Ocean (Martinez 1987) - had humerus:tarsometatarsus ratios of 1.91 and 1.38, respectively. These figures indicate only a slight reduction in relative wing length in *A. pachyscelus*, but a substantial shortening in the endemic *Anas* of Amsterdam Island; the latter was almost certainly flightless, having scores of -28.2 and -11.5, respectively, on the first canonical variates of sternal dimensions for mallards (Fig. 2) and Australasian teal (Livezey 1990, Fig. 7).

In contrast to the general trend of pectoral reduction in insular waterfowl (Lack 1970, Weller 1980), neither Eaton's Pintail nor the Marianas Duck show significant changes in relative wing length (Tables 1, 3, 5, Figs 1, 3, 4) or sternal size (Table 3, Figs 2, 4). Comparisons of ratios of lengths of wings and tarsi indicate that a number of other insular *Anas* have undergone no reduction in relative wing size (compared to continental conspecifics or closely related species), including the Andaman Teal *A. albogularis*, Galápagos Pintail *Anas bahamensis galapagensis*, and South Georgia Pintail *A. g. georgica* (Weller 1975, 1980). Evidently, as in Eaton's Pintail (Stahl *et al.* 1984), aerial mobility remained selectively advantageous for these insular species.

Effects of "disuse" on pectoral robustness

Compared to the pectoral reductions observed in flightless anatids (Livezey & Humphrey 1986, Livezey 1990, Olson & James 1991), those evident in Hawaiian *Anas* (Tables 1-6, Figs 1-4) are minor. Relative sizes of the breast muscles (Mm. pectoralis and supracoracoideus) are reflected, to a large extent, by the depth of the carina sterni; this proportionally indicates moderate reductions in relative bulk of breast muscle in the Hawaiian Duck and (especially) the Laysan Duck (Table 3, Fig. 2), although direct myological measurements are lacking. For birds generally, M. pectoralis constitutes approximately 15.5% of total body mass (Hartman 1961). Even in domesticated Muscovy Ducks *Cairina moschata*, in which mean body mass approximated 3 kg and 2 kg for males and females, respectively, M. pectoralis averaged 14.2% of total body mass (Hartman 1961). Comparable data from wild-taken Laysan Duck would be most informative, although seasonal atrophy of pectoral muscles, like that documented in grebes (Piersma 1988, Gaunt *et al.* 1990), may complicate interspecific comparisons.

Among domestic varieties of the Common Mallard, a continuum of pectoral reduction occurs (Darwin 1868, Timmann 1919), involving characters of the integument, musculature, and skeleton. Darwin (1868: 286-287) speculated that "... during the earlier stages of the process of reduction [of the pectoral apparatus of insular species], such birds

might be expected to resemble in the state of their organs of flight our domesticated ducks." Although confusion between the appendicular changes of insular endemics and domesticated forms seems unlikely, assessments of modifications in pectoral musculature could be improved through comparisons of ultrastructural changes (Rosser & George 1986, 1988, George *et al.* 1987). For example, Kaplan (1964) found that concentrations of lactase dehydrogenase in the breast muscle of the Laysan Duck was substantially less than that of a wild Common Mallard but exceeded that of a domestic Common Mallard.

Pelvic changes in insular Anas

Leg elements of Hawaiian mallards not only have undergone shortening (in rough concordance with decreases in body mass, Table 1), but have assumed different proportions among constituent elements (Fig. 3). The Common Mallard typifies dabbling ducks in its pelvic limb, and is capable of swift surface swimming but only limited terrestrial locomotion and dives (Verheyen 1955, Weidmann 1956, Raikow 1970, 1973). Compared to the Common Mallard, the leg of the Hawaiian Duck differs in its disproportionately short tibiotarsus and long tarsometatarsus and middle toe (Fig. 3). The short tibiotarsus indicates a sacrifice of aquatic propulsive power, and in combination with the disproportionately elongate tarsometatarsus suggests enhanced ability for terrestrial locomotion (Stolpe 1932, Storer 1971, Raikow 1985); the slight increase in digital proportion may represent a compensatory improvement in aquatic propulsion (Raikow 1973). The leg skeleton of the Laysan Duck is distinguished by a disproportionately long femur and short middle toe, both of which probably represent a loss of propulsive capacity in aquatic locomotion (Stolpe 1932, Raikow 1970) but enhanced ambulatory ability (Raikow 1971). Evidently, both the Hawaiian Duck and Laysan Duck have undergone functionally comparable but morphologically different shifts within the pelvic limb that improve terrestrial mobility; observational confirmation of this functional refinement is lacking, however.

Sexual dimorphism

Magnitude of sexual dimorphism in the insular endemics did not differ from those inferred for continental relatives (Tables 1, 3, 5, Figs 1, 2, 4), in contrast to the comparatively great "size" dimorphism documented in some insular species (Selander 1966, Wallace 1978). Increased morphometric dimorphism sometimes accompanies the evolution of flightlessness (Livezey 1989b, 1990, 1992a); therefore, given the limited pectoral reduction of Hawaiian mallards, a modest increase in sexual dimorphism might be predicted. Plausible reasons for differences in sexual size dimorphism among species of *Anas* include competitive or independent refinements for foraging (Shine 1989), differential optima for reproduction (Downhower 1976), or possible differences in intensity of sexual selection (Selander 1972, Trivers 1972, Bradbury & Davies 1987). The last hypothesis interprets the reduced sexual dichromatism of insular ducks as the adaptive loss of "isolating mechanisms", a "defense" against the interspecific hybridization that is virtually universal among Anseriformes (Scherer & Hilsberg 1982), in communities with fewer congeners (Sibley 1957, Johnsgard 1963, Lack 1970, Weller 1980). However, the importance of "isolating mechanisms" in waterfowl has been questioned (Livezey 1991), and insular reductions in dichromatism may be interpreted alternatively as a correlate of increased involvement by males of insular endemics in brood-rearing (West-Eberhard 1983); biparental attendance of broods is typical of insular *Anas* (Weller 1980) and is associated in most anatines with reduced sexual dichromatism (Kear 1970).

Oceanic islands generally are thought of as free of predators (human-related introductions aside), but most insular waterbirds are vulnerable to both submarine and aerial predators (Livezey & Humphrey 1986, Livezey 1990, 1992a). Cryptic coloration can be important in the avoidance of detection by predators (Endler 1978, Baker & Parker 1979). The obsolete sexual dichromatism and subdued plumage coloration of insular waterfowl (Lack 1970, Weller 1980) - shared by the Hawaiian Duck (Swedberg 1967), Laysan Duck (Warner 1963, Moulton & Weller 1984), and Eaton's Pintail (Stahl *et al.* 1984) - probably improves concealment from aerial predators (especially during nesting and biparental attendance of broods).

Ontogenetic patterns

Heterochrony, the genetic alteration of ontogenetic schedules, has been recognized increasingly as an important mechanism of evolutionary change (Gould 1977, Goodwin 1982, McKinney 1988a, b). Heterochrony offers an alternative perspective on evolutionary change leading to reduction in size (e.g. pectoral reduction in the Laysan Duck), traditionally envisioned as "degeneration" or genetically stochastic "wasting" of structures of diminished functional utility (Brace 1963, Peters & Peters 1968, Peters 1988). The evolutionary importance of development is twofold: a potential mechanism for rapid evolution of novel phenotypes (Bonner & Horn 1982, Müller 1990, Raff *et al.* 1990), and, seemingly paradoxically, a conservative *Bauplan* that constrains the possible directions of evolutionary change (Alberch 1982, Maynard Smith 1985).

Positions of immature specimens of insular *Anas* on canonical plots (Figs 1, 2) indicate that the disproportionately shortened wing elements and shallow carina sterni of the Laysan Duck (Figs 2, 3) are interpretable as "underdeveloped" or paedomorphic, an inference supported by the relatively late development of pectoral elements in birds (Kulczycki 1901, Marples 1930, Klima 1962); these features are more obvious in the flightless Auckland Islands Teal (Livezey 1990). As in the Auckland Islands Teal, the small body size of other insular dabbling ducks makes "progenesis" (somatically early sexual maturation, McNamara 1986) a possible heterochronic mechanism (Livezey 1990). The drab alternate plumages of adult (particularly male) Hawaiian Ducks, Laysan Ducks, Eaton's Pintails, and a number of other insular waterfowl (Lack 1970, Weller 1980, Livezey 1990), closely resemble the juvenal plumages of their continental relatives. Streets (1876: 46-47) commented on the "immature" plumage of the two specimens of Coues' Gadwall. Unfortunately, no independent documentation of age was recorded, and the subsequent extinction of Coues' Gadwall precludes the study of what may be the most extreme example of plumage paedomorphosis among insular Anatidae.

Feeding ecology

A change in diet characterizes the Hawaiian Duck, Laysan Duck, and Eaton's Pintail (Weller 1980, Moulton & Weller 1984, Stahl *et al.* 1984), all of which consume greater proportions of animal matter than their continental relatives (Martin & Uhler 1939, Bellrose 1986). The diet of the Hawaiian Duck includes substantial numbers of earthworms (*Lumbricus*), larvae of dragonflies (*Anisoptera*), and molluscs from freshwater and brackish environments (*Melania*, *Hydrobia*), as well as variable amounts of plant material, especially seeds (Perkins 1903, Schwartz & Schwartz 1953, Swedberg 1967). The Laysan Duck heavily exploits insects, especially the larvae and adults of a brine fly (*Agrotis dislocata*) that is abundant in the single inland lake on Laysan Island (Fisher 1906, Warner 1963, Caspers 1981, Moulton & Weller 1984). Both the Hawaiian Duck and Laysan Duck differ from their continental relatives in the frequent terrestrial pursuit of insects and their largely crepuscular (sometimes nocturnal) foraging schedules (Warner 1963, Moulton & Weller 1984). The diet of Eaton's Pintail consists primarily of insects, nematodes, oligochetes, isopods, and amphipods, most taken by probing on tide flats or along small streams, as well as some vegetable material (Kidder 1875, Sharpe 1879, Hall 1900, Paulian 1953). Likewise, the diet of the South Georgia Pintail consists of more animal items, most taken terrestrially, than that of the continental Brown Pintail *A. g. spinicauda* (Lack 1970, Weller 1975a, 1980). The Auckland Islands Teal consumes more animal prey and more frequently forages on land and at night than its continental relatives (Weller 1975b). Weller (1980) reasoned that the finer bill lamellae of insular waterfowl enable improved capture of invertebrates; a similar rationale may apply to the comparatively spatulate bill of the Laysan Duck (Ripley 1960, Delacour 1964). Whether these convergent dietary shifts result from "competitive release" (Lack 1970, Wallace 1978, Weller 1980), are closely related to decreased body size, or simply reflect similar food resources of oceanic islands is not clear. The peculiar pelvic proportions of the Hawaiian Duck and Laysan Duck (Fig. 3), however, are undoubtedly related to terrestrial foraging.

Parameters of reproduction

An anomaly of insular waterfowl is the unusually large size of their eggs and their small clutch sizes (Lack 1970, Weller 1980, Rohwer

Table 7. Mean dimensions (mm) and estimated masses (g) of eggs, mean clutch sizes, and estimated clutch masses (g) of selected mallards and pintails.

Species	Egg length x width (*n*)	Egg mass[a]	Clutch size (*n*)	Clutch mass[b]	Sources[c]
A. platyrhynchos[d]	58.1 x 41.7 (20)	56.6 (6.4%)	8.7 (7131)	492 (49%)	15, 16
A. oustaleti	61.6 x 38.9 (7)	52.2 (6.4%)	7.0 (1)	365 (45%)	7
A. wyvilliana[e]	49.8 x 35.9 (3+)	35.9 (6.3%)	7.1 (4+)	255 (45%)	8, 11, 13, 17
A. laysanensis	56.6 x 39.1 (2)	48.5 (11.2%)	4.7 (10)	228 (53%)	4, 9, 10, 12, 14, 18
A. acuta	54.7 x 38.8 (95)	46.1 (6.3%)	7.8 (1553)	360 (49%)	15, 16, 19
A. eatoni[f]	52.2 x 36.8 (61)	39.6 (9.0%)	4.3 (22)	170 (39%)	1, 2, 3, 5, 6, 20

[a]Estimated by method of Hoyt (1979) using K_w for *A. platyrhynchos*. Values in parentheses are percentage of mean body mass of females.

[b]Products of estimated egg mass and mean clutch size. Values in parentheses are percentages of mean body mass of females.

[c]References: (1) Kidder & Coues (1876); (2) Sclater & Salvin (1878); (3) Verrill (1895); (4) Fisher (1903); (5) Loranchet (1916); (6) Falla (1937); (7) Kuroda (1941-42); (8) Munro (1944); (9) Ripley (1960); (10) Warner (1963); (11) Richards & Bowles (1964); (12) Ripley *in* Delacour (1964); (13) Swedberg (1967); (14) Ely & Clapp (1973); (15) Bellrose (1976); (16) Palmer (1976); (17) Weller (1980); (18) Moulton & Weller (1984); (19) Stahl *et al.* (1984); (20) Weimerskirch *et al.* (1988).

[d]Nominate subspecies.

[e]Indeterminate *n* result from unspecified sample sizes for means given by Munro (1944) and here counted as a single datum.

[f]Includes both nominate subspecies and *drygalskii*.

1988), both of which are characteristic of the Hawaiian Duck, Laysan Duck, and Eaton's Pintail (Table 7). Similar characteristics are indicated in the Brown Pintail (Phillips 1923, Schönwetter 1961, Weller 1975a): South Georgia Pintail (estimated egg mass = 38 g, 8.1% of mean body mass of females) *vs.* continental Brown Pintail (41 g, 5.9%). The massive eggs and small clutches of the Auckland Islands Teal represent an extreme example of increased *per capita* reproductive investment (Livezey 1990). Reduced clutches of enlarged eggs also are indicated in the Andaman Teal and Madagascan Teal *A. bernieri* compared to those of the Gray Teal *A. gibberifrons* (Schönwetter 1960). Essential reproductive data are lacking for Coues' Gadwall, Galápagos Pintail, and the extinct Rennell Island Teal *A. gibberifrons remissa* (Schönwetter 1960, Lack 1970, Weller 1980, Rohwer 1989).

Reiss (1985, 1989) found that larger species tend to invest relatively less in their offspring because of the increased energy requirements for somatic maintenance. Size-related decreases in relative reproductive investment, however, do not appear to characterize dabbling ducks, in which clutch mass averages about 50% of that of females in both insular and continental populations (Table 7). Differences in the energy invested by females per unit mass of eggs may differ among populations, however, especially in the relative amounts of yolk and albumen (Lack 1968). Differences in neither *per capita* nor total parental care by females were evident between continental and insular *Anas* (except the Auckland Islands Teal, Livezey 1990), although data are few (Weller 1980). With few exceptions, little or no parental care is contributed by males of most species of *Anas* (Maynard Smith 1977, Weller 1980, Livezey 1991); once again the flightless Auckland Islands Teal is exceptional (Weller 1975b). However, a trade-off between number of offspring and *per capita* investment in offspring is evident in insular *Anas* (Table 7, Livezey 1991), a pattern attributed to the competitive advantages of rapid development and large size in "*K*-selected" environmental regimes of islands (Lack 1970, Williamson 1981, Rohwer 1988).

One possible advantage for large eggs in precocial birds (including waterfowl) is large size and greater energy stores of hatchlings, particularly if the enlarged eggs contain appreciably more yolk (Lack 1967, 1968, Ar & Yom-Tov 1978). However, large eggs also require longer incubation periods (Rahn & Ar 1974) and are at higher risk of breakage (Ar *et al.* 1979, Rahn & Paganelli 1989). If the comparatively great longevity of the Laysan Duck (Moulton & Weller 1984) is representative of other insular *Anas*, then the group conforms with a general inverse correlation between life span and clutch size among "*K*-selected" avian species (Haukioja & Hakala 1979). Also, the association between brood amalgamation and "*K*-type" traits inferred by Eadie *et al.* (1988) for North American Anatidae suggests that intraspecific parasitism of nests and (post-hatch) brood amalgamation may be relatively frequent in insular *Anas*.

Body size and its correlates

Insularity commonly is associated with a change in body size (Carlquist 1966, 1974, Case 1978, Abbott 1980, Williamson 1981). Among insular *Anas*, small body size is characteristic (including insular populations of Pacific Gray Duck *A. superciliosa pelewensis* and *A. s. rogersi*, and the Galápagos Pintail); the single exception is the Greenland Mallard (Weller 1980), which is also unique among mallards in the delaying of breeding until two years of age (Salomonsen 1972). In contrast, among Anseriformes exclusive of Anatini, only four of eight taxa that are permanent residents of islands are smaller than their continental relatives (Weller 1980). Three of the latter that are larger than their mainland relatives are tadornines endemic to the high-latitude Falkland Islands: Falkland Upland Sheldgoose *Chloephaga picta leucoptera*, Falkland Kelp Sheldgoose *C. hybrida malvinarum*, and Falkland Flightless Steamer-Duck *Tachyeres brachypterus*.

The reasons for the decrease in body size of insular *Anas* are not clear. The importance of island size or antiquity of insular isolation to morphological characteristics (Rotondo *et al.* 1981) is suggested by the difference in body size between the Hawaiian Duck (inhabiting the larger, younger islands of the southeast) and the Laysan Duck (endemic to the smaller, older Laysan atoll of the northwest). A comprehensive assessment of this trend, however, must await a morphometric analysis of skeletal elements of modern and prehistoric populations of the Hawaiian Duck by island; James (1987) found that skeletal elements of an extinct *Anas* on Oahu, provisionally referred to the Hawaiian Duck, were smaller than those of modern Hawaiian Ducks. Regrettably, no specimen of the evidently extinct *Anas* reported from tiny Lisianski Island (northwest of Laysan) was collected (C. Isenbeck *fide* Kittlitz 1834, Rothschild 1893, Warner 1963, Clapp & Wirtz 1975). Lack (1970, 1974) assumed that a medium-sized *Anas* reflected an adaptive optimum on remote islands, but suggested no specific selective advantage for decreased body size. Given the important correlates of body size, it may be that small body size (and, to a lesser extent, pectoral reduction) of the Hawaiian mallards and several extinct insular *Anas* reflects the advantages of reduced "costs" of development and maintenance of anatomical structures of lessened utility, lessened selection for a capacity for fasting and thermodynamic efficiency in temperate and tropical environments, and the intensified advantages of high *per capita* reproductive investment in the confined, possibly highly competitive ecological circumstances of oceanic islands.

Insularity, deme size, and extinction

The isolation of remote islands imposes several important genetic characteristics on endemic populations - founder effects (limited genetic variation in colonists), genetic drift (stochastic loss of genetic variation within small demes), and inbreeding depression (increased phenotypic expression of recessive, often disadvantageous alleles in homozygous progeny of closely related individuals) - the importances of which are related inversely to population size (Carlquist 1966, 1974, Boag 1988). At least one of these characteristics, founder effects, can increase the likelihood of rapid, innovative evolutionary change in isolated populations (Carson & Templeton 1984, Provine 1989, but see Barton & Charlesworth 1984); possible examples among insular *Anas* include reduction of the pectoral apparatus and the loss of sexual dichromatism. Grant (1965) suggested that the drab plumages of insular passerines may be selectively neutral by-products of the unusual genetics of founding populations.

Deme size of insular *Anas* is not only limited by the areas of islands inhabited, but also by the proportion of the islands that are habitable. Both aspects were severely limiting for the recently extirpated Marianas Duck (Fosberg 1960) and the nearly extirpated Laysan Duck (Brock 1951, Warner 1963, Moulton & Weller 1984). The subsequent, human-imposed, genetic bottleneck suffered by the Laysan Duck undoubtedly further reduced genetic diversity in the surviving remnant (Moulton & Weller 1984, Collar & Andrew 1988). Introgression with introduced congeners also poses a threat to insular *Anas*, as evidenced by the widespread hybridization of Pacific Gray Ducks with the introduced Common Mallard in New Zealand (Gillespie 1985). Elevated frequencies of leucisticism in the Laysan Duck (Weller 1980, Moulton & Weller 1984) and some domestic varieties of the Common Mallard (Kagelmann 1951), as well as in the Andaman Teal (Weller 1980), provide additional evidence of reduced genetic diversity of insular

populations. These genetic characteristics, in combination with small population sizes, demographic fluctuations, destruction of habitat, illegal hunting, and introduced predators and disease continue to jeopardize the remaining insular species of *Anas* (Diamond 1984, Ralph & van Riper 1985, Simberloff 1986, Loope & Mueller-Dombois 1989).

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