MORPHOMETRIC CORRELATES OF AGE AND BREEDING STATUS IN AMERICAN COOTS

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ABSTRACT.—I studied morphometric variation in 13 linear measurements from 228 American Coots (*Fulica americana*) collected in southern Manitoba. Univariate and multivariate techniques revealed differences in size and shape among adult coots that were 1, 2, and >2 yr old. In addition to the obvious differences in size between males and females, the morphometry of older birds differed from that of younger birds in two ways. First, older coots were of larger body size than younger coots of the same sex. Second, older coots had proportionately larger feet and claws relative to the size of their tarsi, and proportionately wider bills and heads relative to other head measurements, than did younger birds. Multivariate dispersion matrices within age/sex cohorts were less variable for older coots. In an analysis of 1-yr-old males, breeders did not differ from nonbreeders in overall body size, but breeders had relatively longer claws and wings than nonbreeders. Age-related differences in morphology may have relevance to the social structure of nesting coots, which involves highly aggressive territorial behavior. Part of the age-related variation in nesting phenology that has been documented elsewhere for coots may be a consequence of covariation in body size and shape. *Received 15 September 1986, accepted 27 March 1987.*

INTRASPECIFIC morphological variation is related to several life-history traits of birds throughout their annual cycle. Variation in body size, or in the size of specific structures, has explained variability in mate choice (Petrie 1983), clutch size (Ankney and MacInnes 1978), egg size (Otto 1979), survival (Bumpus 1899), and differential migration (Ketterson and Nolan 1983). Often, these same traits are correlated with age, but in birds, where asymptotic growth of structural size is virtually complete before first reproduction (O'Connor 1984), systematic covariation between the size and age of adults has not been demonstrated, to my knowledge.

In American Coots (*Fulica americana*), female success at reproduction increases with age. Older females nest earlier, lay larger clutches, and pair with older males than do younger females (Crawford 1980). It is unknown, however, if some of this enhanced success also has a morphological basis. To date, studies of age-related morphological variation in coots have evaluated techniques for distinguishing hatching-year (HY) from after-hatching-year (AHY) birds, and males from females, on the basis of size (Gullion 1952a, Fredrickson 1968, Eddleman and Knopf 1985), and this can be done with limited success in the nonbreeding season. Coots are exceptional for studying age relationships among AHY birds during the nesting season because birds up to 4 yr old can be aged with 95% accuracy using tarsal color (Crawford 1978).

I used a sample of AHY coots collected during the nesting season to study the relationship between morphometric variation and age. In this paper I summarize sex- and age-related variation in body size, hypothesize that this variation may result from natural selection against smaller size morphs, and discuss some of the ecological implications of size variation to nesting coots.

METHODS

From 17 April to 9 July 1981, 242 American Coots were shot or caught in nest traps on the Delta Marsh in southern Manitoba (50°11'N, 98°19'W). This sample included 196 of the birds identified by Alisauskas and Ankney (1985) as *arriving*, *paired*, *laying*, or *incubating*, and 46 birds classified as non-nesters that could not be assigned with certainty to any of these categories. On the day of collection each bird was aged on the basis of tarsal color (Crawford 1978), its sex was determined by examining the gonads, and 13 morphological measurements were recorded: (1) *total length*, from the tip of the longest rectrix to the tip of the bill with the bird stretched on its back; (2) *wing chord*, with the wing flattened and flexed at the wrist, from the wrist to the tip of the wing; (3) *wing length*, with the flattened wing outstretched perpendicular to the body, measured from the body to the tip of the wing; (4) *tarsus length*, with the leg flexed, from the bottom of the crus to the top of the proximal edge of the web; (5) *middle toe length*, with the foot outstretched, from the insertion of the claw to the proximal junction of the first joint of the middle toe; (6) *hind toe length*, with the hind toe held perpendicular to the tarsus, from the insertion of the claw to the junction of the toe with the tarsus; (7) *middle claw length*, from insertion to tip; (8) *culmen*, from the posterior-dorsal extremity of the culmen shield to the tip of the upper mandible; (9) *bill height*, with mandibles closed, the greatest dorso-ventral distance at the nares; (10) *bill width*, with mandibles closed, the lateral distance between the posterior extremities of the upper mandible on each side; (11) *head length*, the maximum distance from the bill tip to the posterior extremity of the occipital process; (12) *head width*, the maximum distance along the dimension defined by the lateral extremities of the head; and (13) *keel length*, the distance between the notch at the furculum and the posteriormost point along the median of the sternum. Structures damaged during collection were not measured. All measurements were taken to the nearest 0.1 mm with calipers except total length and wing length, which were measured to the nearest 1 mm with a flat ruler.

Analysis of frequencies was done using Chi-square or *G* tests of independence (Sokal and Rohlf 1981). Of the 242 coots that were collected, only 228 had complete morphological data, and so only this subset was used for morphometric analyses. All morphometric analyses were performed using $\log_{10}$-transformed data to more closely approximate multivariate normality (Pimentel 1979). Two-way analyses of variance (ANOVA) were used to test for equality of each of the 13 morphological variables with respect to sex and age (PROC GLM; SAS Inst. 1982). I used two-way multivariate analysis of variance (MANOVA) to determine if overall external morphology of coots varied with sex or age (PROC GLM; SAS Inst. 1982) and canonical variates analysis (CVA) to explore the nature of this variation (PROC CANDISC; SAS Inst. 1982). The null hypothesis of equal multivariate dispersion matrices among age and sex groups was used to test an a priori prediction of less variability in size or shape, or both, among older birds (PROC DISCRIM; SAS Inst. 1982). Rejection of the null hypothesis of equal dispersion matrices among groups did not preempt conclusions derived from MANOVA, because MANOVA is robust and insensitive to violations of the assumptions of homogeneity of variance if sample sizes between groups are large, or similar (see Pimentel 1979, Owen and Chmielewski 1985). I used formulae presented by Altman (1978) to construct 95% confidence ellipses for mean canonical scores of each group.

Morphometric variation within an age/sex cohort.—I compared the body size of 1-yr-old males, contrasting nonbreeders ($n = 21$) with breeders ($n = 35$) using MANOVA and CVA. Other sex/age cohorts were not investigated because such stratification resulted in very small samples of nonbreeders (Table 1).

TABLE 1. Age, sex, and breeding status of 242 American Coots collected on Delta Marsh, Manitoba, in summer 1981.

	Females		Males	
Age class (yr)	Breeder	Non-breeder	Breeder	Non-breeder
1	37	1	35	23
2	31	4	30	10
>2	26	0	37	8
Total	94	5	102	41

Geographic variation in culmen length.—I compared the culmen lengths of 1-yr-old coots collected in Manitoba with values reported from California (Gullion 1952a), and with values reported for coots that died as a result of severe spring weather in Iowa (Fredrickson 1969). This was the only measure common to all three studies, but culmen length covaried with other measurements of Manitoba coots (Table 4) such that culmen length may be considered at least as an index of body size when considered over a larger geographic area. Two sample comparisons of means were done according to procedures outlined by Steel and Torrie (1960: 73).

RESULTS

Population structure.—The sex ratio of coots from the entire sample (Table 1) was skewed (143:99) in favor of males ($\chi^2 = 8.0$, df = 1, $P < 0.005$), but there were equal numbers of males and females that bred (102:94, $\chi^2 = 0.33$, df = 1, $P > 0.50$), resulting in a large surplus of nonbreeding males. Over 95% of the female sample was involved in nesting, compared with only 71% of males ($G = 24.4$, df = 1, $P < 0.001$). The proportion of nonbreeders in each male age cohort declined with age ($G = 6.37$, df = 2, $P < 0.05$).

Morphometric variation among age/sex cohorts.—Based on univariate analyses, males were larger than females in all morphological characters ($P < 0.001$ in all cases), and older birds tended to be larger than younger birds ($P < 0.05$ for all characters except total length, keel length, middle toe length, culmen length, and bill height; Tables 2 and 3). There were no interactions between the effects of sex and age, indicating that age effects were similar for both sexes.

The results of MANOVA showed that the

TABLE 2. Means ± 1 SD of 13 linear measurements (mm) taken from 91 female American Coots of different age.

Measurement	Age (yr)		
	1 (n = 35)	2 (n = 33)	>2 (n = 23)
Total length	356.5 ± 11.1	358.6 ± 10.3	356.2 ± 12.5
Wing chord	178.5 ± 6.68	181.5 ± 4.83	182.7 ± 6.39
Wing length	280.1 ± 10.1	285.1 ± 8.69	285.4 ± 13.0
Keel length	54.2 ± 2.02	54.8 ± 2.09	54.5 ± 2.91
Tarsus length	60.1 ± 2.59	61.5 ± 1.62	61.7 ± 2.03
Middle toe length	67.2 ± 2.30	68.0 ± 4.21	68.1 ± 3.34
Hind toe length	21.4 ± 1.57	21.5 ± 1.63	22.2 ± 1.94
Middle claw length	12.3 ± 1.16	13.0 ± 0.91	13.1 ± 1.05
Culmen	46.2 ± 2.41	47.3 ± 2.20	46.5 ± 2.62
Bill height	11.9 ± 0.76	12.1 ± 0.54	11.9 ± 0.66
Bill width	8.4 ± 0.59	8.7 ± 0.62	8.9 ± 0.58
Head length	62.3 ± 1.57	63.2 ± 1.39	63.0 ± 1.71
Head width	21.6 ± 0.59	21.8 ± 0.55	21.9 ± 0.47

overall size or shape of coots varied with respect to sex ($F_{13,208} = 59.5$, $P < 0.001$) and age ($F_{26,416} = 2.34$, $P < 0.001$), with no interaction between sex and age ($F_{26,416} = 0.59$, $P = 0.95$).

Only two canonical axes were required to separate the 6 sex/age groups (Table 4). The sexes differed primarily along the first canonical axis (CV1), whereas both CV1 and CV2 were required to separate age groups within each sex (Fig. 1). CV1 separated males and females, and also age groups within each sex, on the basis of size, but CV2 indicated that the oldest coots were also different in shape from the youngest coots, independent of sex.

The within-group covariance matrices of each of the 6 sex/age groups were not homogeneous ($\chi^2 = 555.2$, $P < 0.001$). Log_{10} values of the determinants of each matrix for 1-, 2-, and >2-yr-old age groups were −47.48, −48.05, and −48.11, respectively, for females, and −46.50, −47.10, and −46.95, respectively, for males. This indicates that males were more variable than females in morphometry, but within each sex this variability was greatest in the youngest age groups.

Breeding and nonbreeding 1-yr-old males had mean CV1 scores of 0.50 and −0.84, respectively ($F_{13,42} = 2.18$, $P < 0.028$). Compared with nonbreeders, breeding males had longer wings and keels, larger heads, and, most noticeably, longer middle claws relative to the size of their feet (Table 5).

In both males and females, culmen lengths of 1-yr-old Manitoba coots were greater than

TABLE 3. Means ± 1 SD of 13 linear measurements (mm) taken from 137 male American Coots of different age.

Measurement	Age (yr)		
	1 (n = 56)	2 (n = 39)	>2 (n = 42)
Total length	382.4 ± 13.1	382.5 ± 12.4	386.6 ± 13.5
Wing chord	193.2 ± 5.72	195.9 ± 7.35	198.6 ± 5.65
Wing length	302.9 ± 17.8	306.0 ± 9.79	309.0 ± 9.69
Keel length	58.3 ± 2.57	60.0 ± 3.04	59.3 ± 3.04
Tarsus length	66.2 ± 2.76	66.8 ± 2.44	67.4 ± 2.34
Middle toe length	73.2 ± 4.33	73.4 ± 3.05	74.1 ± 4.04
Hind toe length	23.9 ± 1.93	23.8 ± 1.54	24.6 ± 1.79
Middle claw length	14.4 ± 1.16	14.5 ± 1.18	15.4 ± 1.22
Culmen	50.0 ± 2.39	50.6 ± 1.78	50.7 ± 1.95
Bill height	13.2 ± 0.73	13.2 ± 0.68	13.5 ± 0.51
Bill width	9.6 ± 0.73	9.5 ± 0.80	10.0 ± 0.75
Head length	66.8 ± 1.96	67.4 ± 1.76	67.5 ± 1.66
Head width	23.1 ± 0.86	23.2 ± 0.80	23.5 ± 0.68

TABLE 4. Canonical variates analysis of 13 morphometric measurements from 228 American Coots with each of 6 age/sex cohorts considered as 1 of 6 groups.[a]

Measurement	Canonical variate 1		Canonical variate 2	
	Standardized canonical coefficient	Total canonical structure	Standardized canonical coefficient	Total canonical structure
Total length	**0.21**	0.81	**−0.26**	−0.25
Wing chord	**0.82**	0.88	0.33	0.08
Wing length	−0.10	0.85	−0.22	−0.07
Keel length	0.15	0.71	−0.28	−0.18
Tarsus length	0.09	0.85	0.36	−0.10
Middle toe length	0.17	0.66	0.26	−0.11
Hind toe length	0.05	0.66	**0.56**	0.19
Middle claw length	**0.46**	0.76	**0.74**	0.30
Culmen	−0.07	0.71	**−0.23**	−0.23
Bill height	**0.44**	0.80	**−0.70**	−0.22
Bill width	0.05	0.70	**0.75**	0.34
Head length	0.11	0.87	**−0.39**	−0.19
Head width	**0.32**	0.81	−0.11	−0.05

[a] Boldface coefficients correspond to variables important in separating groups.

those of Iowa coots, which in turn were greater than those of California coots (Table 6).

DISCUSSION

Older coots could be larger because growth continues after the first year of life, because smaller adults experience greater mortality than larger adults, or because of a combination of both effects. Continued growth of coots beyond the first year of life may enhance age-related differences in size, and documentation of this effect would require that marked coots of known age be measured repeatedly over a series of years (Smith et al. 1986). Continued growth after attainment of sexual maturity is unlikely, however, because there is no conclusive evidence for it in other wild birds.

If mortality is greater for smaller individuals, then as cohorts age, they would have a larger average body size with a corresponding reduction in variance. Variability in the overall morphology of coots was greatest in the youngest age cohorts of each sex, suggesting that the hypothesis of differential mortality is tenable. Such short-term selection on body size has been demonstrated in passerines (e.g. Schluter and Smith 1986).

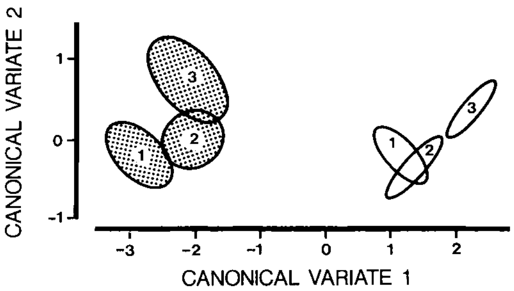

Fig. 1. Ninety-five percent confidence ellipses for bivariate plots of canonical variate scores resulting from the canonical variates analysis summarized in Table 4. Numbers (1, 2, and 3) correspond to age cohorts of 1-, 2-, and >2-yr-old coots for females (stippled) and males (open).

Variation in migration distance may result in chronic selection for larger body size in coots. Male coots winter at higher latitudes than do smaller-bodied females (Brisbin et al. 1973). Ketterson and Nolan (1983: 362) hypothesized that if "smaller bodied individuals were less likely than larger bodied conspecifics to survive winter at higher latitudes, then sex-age classes (or races) having smaller bodies might be expected to evolve toward longer migrations that would take them into milder climates." Thus, a correlation between risk of mortality and migration distance could result in size-specific mortality rates between age and sex classes, and may contribute to the highly skewed sex ratio in favor of males (Table 1).

Although breeding males differed most from nonbreeding males in claw length relative to middle toe length, they also had larger wings, keels, and heads. Coots paired after arrival onto breeding areas, but before they settled onto breeding territories (Gullion 1954, Alisauskas and Ankney 1985). In addition, females were the rarer sex (Table 1). These facts suggest that in coots, females choose males during pair formation, and they do this on the basis of morphological cues, or behaviors correlated with that morphology, and not on the basis of territory quality. In Common Moorhens (*Gallinula chloropus*), females compete for males and apparently prefer smaller males, which are also fatter, to larger males (Petrie 1983). Depending on the heritabilities of morphological traits in coots, fitness differences of different-size males

TABLE 5. Canonical variates analysis of 13 morphological measurements on 35 breeding and 21 nonbreeding male coots 1 yr old.[a]

Measurement	Canonical variate 1 Standardized canonical coefficients	Total canonical structure
Total length	0.00	0.17
Wing chord	−0.53	0.11
Wing length	**0.87**	0.49
Keel length	**0.37**	0.37
Tarsus length	−0.03	−0.16
Middle toe length	**−0.57**	−0.40
Hind toe length	−0.43	−0.14
Middle claw length	**0.27**	0.55
Culmen	**−0.46**	−0.34
Bill height	0.24	0.07
Bill width	−0.21	0.12
Head length	**0.22**	0.22
Head width	**0.39**	0.36

[a] Boldface coefficients correspond to variables important in separating groups.

TABLE 6. Comparison of culmen lengths of 1-yr-old male and female American Coots from different geographical areas. Values are means ± 1 SD (n). Asterisks indicate statistically different ($P < 0.001$) values between areas.

	Females	Males
California[a]	41.4 ± 1.9 (18)	45.7 ± 1.6 (28)
	*	*
Iowa[b]	44.0 ± 1.5 (140)	47.0 ± 1.5 (150)
	*	*
Manitoba[c]	46.2 ± 2.4 (35)	50.0 ± 2.4 (56)

[a] Gullion 1952a.

[b] Fredrickson 1969.

[c] This study.

in Manitoba that result from differential success at mate acquisition may compound any effects of disproportionate mortality against smaller size morphs.

How could selection against small body size be balanced by selection against large body size? Large-scale die-offs as a result of inclement weather have been documented for prebreeding American Coots in spring (Fredrickson 1969) and in wintering Eurasian Coots (*Fulica atra*; Visser 1978). When ambient temperatures are low, larger body size is presumably advantageous because of an improved thermoregulatory ability (Calder and King 1974). Body size can evolve to covary clinally with average winter temperatures (e.g. Lefebvre and Raveling 1967). But if food limitation accompanies such conditions, then large body size is not necessarily advantageous. Based on 16 years of data, Cavé and Visser (1985) found that annual survival of Eurasian Coots was inversely related to the number of "ice days" during the previous winter. They assumed winter mortality was a result of starvation due to food limitation, and not of an inability to thermoregulate properly (see Visser 1978). In other species, food limitation is thought to result in proportionately greater mortality among large compared with small individuals. In a large winter roost of Brown-headed Cowbirds (*Molothrus ater*) and Red-winged Blackbirds (*Agelaius phoeniceus*), adult males experienced proportionately greater mortality than females, and within sex cohorts dead birds had longer wings than live birds (Johnson et al. 1980). Similarly, large coots that eventually arrive in Manitoba may have difficulty maintaining energy reserves under conditions of food limitation. When coots arrive on breeding areas in spring, large individuals have more protein, but there is no relationship between fat reserves and body size in either males or females (Alisauskas and Ankney in press). Therefore, faced with severe food limitation in spring (Fredrickson 1969), large coots with a higher metabolic rate, but not necessarily with more energy reserves, may be more predisposed to starvation mortality than smaller individuals (but see Visser 1978). Females may have an advantage over males under such conditions, because although they are smaller, they contain proportionately more fat than do males at arrival (Alisauskas and Ankney 1985). Furthermore, the timing of such environmental inclemency may compound mortality against large, relative to small, females because older (larger) females arrived before younger (smaller) females (Alisauskas and Ankney 1985). Thus, older females run a greater risk of exposure to such conditions than do younger females. Such selection against larger body size would be sporadic, and may not be detectable in most years.

A further complication of evaluating the importance of selection on morphological traits in coots is that the intensity of selection may differ geographically. If covariance of body size and culmen length (Table 4) is geographically homogeneous, then it can be inferred that larger coots nest farther north (Table 6).

While there is more than one explanation for increasing body size with age in this sample of coots, the benefits of large body size to breeding coots are clearer. Larger size could indirectly confer an advantage on older females by allowing them to winter closer to prospective breeding areas than younger, smaller females. This would explain the earlier migration of older coots on spring staging areas (Eddleman et al. 1985), their earlier arrival on nesting areas (Alisauskas and Ankney 1985), their earlier nesting (Crawford 1980), and their more advanced ovarian recrudescence (Alisauskas and Ankney 1985) compared with younger, smaller females.

Some of the age-related variation in the reproductive success of coots may result directly from differences in body size. Crawford (1980) showed that older females laid larger clutches, and although most of the protein requirements for clutch formation are obtained exogenously, protein reserves are also important (Alisauskas and Ankney 1985). Moreover, much of the variation in protein reserves of nesting coots is related to their structural size (Alisauskas and Ankney in press). The size and mass of Lesser Snow Geese (*Chen caerulescens*) about to nest were similarly correlated, and heavier geese had larger potential clutches (Ankney and MacInnes 1978). Thus, larger body size in female coots can influence the number or size of eggs laid by increasing the upper limit on the amount of protein reserves that they can store.

Secondarily important variables for discriminating age classes of coots included relative claw length (Table 3). This character appears to play an important role in the general territorial behavior of nesting coots, which is typified by extreme aggression (Gullion 1952b). Displays associated with high levels of aggression (e.g. splattering, fighting, churning; Gullion 1952b) involve postures that bring the tarsi above the waterline so that they are visible to an antagonist. Claws are important weapons, because fighting involves grabbing the adversary "with the long claws of one foot, leaving the other foot free to slap the opponent" (Gullion 1952b: 88). Such encounters are violent and can result in the death of one of the opponents (Henshaw 1918).

Crawford (1978) suggested that tarsal color in coots is influenced by testosterone levels, and androgens can result in territorial expansion and increased aggression (Watson and Parr 1981). Thus, visibility of tarsal color, covarying with body size, and proportionately larger feet and claws, may signal the social dominance of older males (Ryan and Dinsmore 1980) and perhaps their greater physical strength (Alisauskas and Ankney in press). If this is true, then mismatched (i.e. different-age) coots are not predicted to reach the high levels of aggression that are predicted for similarly aged opponents. Instead, I suspect that younger coots are deterred from opposing larger, older birds.

The covariation of large body size, reduced size variance, and age I describe suggests that small coots may be predisposed to greater mortality than large coots. Among the youngest males, mate acquisition was correlated with secondarily important characters for discriminating ages, and also on characters that seem to be important for territorial defense (Table 5). Selection for large body size can result from fecundity differences or through differential mortality, but the size distribution of characters showing allometry to body size (claw length) may be altered by sexual selection. The intensity of selection may vary stochastically (due to harsh weather) and partly deterministically (due to density dependence). Selection on body size may be relaxed when the ratio of coots to breeding resources declines, or when sex ratios are such that there are fewer surplus males. Such density dependence seems reasonable because the availability of breeding habitat for prairie-nesting coots shows considerable annual variability (Pospahala et al. 1974). Information on heritabilities of continuously varying characters and long-term studies of marked age cohorts would increase understanding of the agents that alter intraspecific variation in morphological characters such as those of American Coots.

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