

A QUANTITATIVE STUDY OF THE BEHAVIOR OF BREEDING AMERICAN COOTS

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ABSTRACT.—Time-activity budgets of breeding male and female American Coots (*Fulica americana*) revealed that females spent more time than males feeding during prelaying. Both sexes contributed to territory establishment and maintenance, though males spent slightly more time at defensive activities than females. Swimming about the territory seems to be a form of territorial advertisement, and the high levels of territorial aggression seemingly are a function of the highly variable nature of food resources in marshes. Time spent by both sexes in intraspecific aggression and locomotion declined steadily throughout the reproductive period. Interspecific aggression peaked after the young hatched. Brood-platforms were built almost exclusively by males. Females spent more time foraging for and feeding young and fed young more frequently than did males. Both sexes reduced loafing to very low levels during brood-rearing. The large investment of time necessary for coots to care for their young successfully offers support for the hypothesis that clutch size has evolved in relation to adequacy of parental care. *Received 3 January 1979, accepted 22 May 1979.*

A FINITE amount of time, energy, and matter is available to any organism for foraging, growth, maintenance, and reproduction. The apportionment of time, as well as energy and matter, determines how an organism adjusts to the complexities of its environment, and therefore provides considerable information about its ecological niche (Pianka 1974: 201). Quantitative information provided by time-activity budgets can yield important information on the role of the sexes in reproduction and on aspects of a species' reproductive strategies.

Good qualitative information on the behavioral ecology of American Coots (*Fulica americana*) is available (Gullion 1953, 1954; Fredrickson 1970), but quantitative data are lacking. Such data would be valuable in helping to understand the adaptations of coots to their marsh environment. The purposes of this study were to collect quantitative data on the behavior of breeding American Coots, to relate the behavior of coots to environmental conditions, and to compare the role of the sexes in reproduction.

STUDY AREA AND METHODS

The study was conducted in 1976 and 1977 at Smith's Slough, Dewey's Pasture, and Hottes Lake, all state-owned wetlands in northwestern Iowa. In both years a severe drought caused reduced water levels and increased coverage of emergent vegetation at all three wetlands. Cattail (*Typha* spp.) was the dominant plant at Smith's Slough and Dewey's Pasture (in Clay County near Ruthven). Bennett (1938), Hayden (1943), and Low (1945) describe these areas in detail. In 1977 dense mats of filamentous algae at Smith's Slough made large areas unsuitable for coots. At the third wetland, 153-ha Hottes Lake (in Dickinson County near Spirit Lake), hardstem bulrush (*Scirpus acutus*) was the dominant emergent and was interspersed with open water. Open-water areas at Hottes supported dense stands of water milfoil (*Myriophyllum* sp.) and coontail (*Ceratophyllum demersum*). A heavily timbered glacial moraine dominates the upland east of Hottes, while pasture and grasslands border the marsh to the north, west, and south.

Time-activity budgets were determined for both sexes during prelaying, laying-incubation, and brood-rearing periods. Behavior was quantified by recording spot observations of behaviors of known individuals every 30 s in 1-h time blocks distributed throughout the day (0600–2000, local daylight time). We used a metronome to determine time intervals (Wiens et al. 1970). Usually both members of a pair of coots were watched simultaneously.

At Smith's Slough and Dewey's Pasture in 1976 and at Hottes Lake in 1977, coots were watched from an automobile or from locations far outside the marshes. In 1977 four 4-m tower blinds were used in Smith's Slough and two water-level blinds were used at Dewey's Pasture. Coots were watched through a 15-60 \times spotting scope or 7 \times 35 binoculars.

Coots were sexed in the field by voice (Gullion 1950). Some individuals were identified by alphanumerically coded nasal discs; others were identified by morphological characteristics such as distinct white feathering at various locations on the body or the unique shape of the callus (Gullion 1951).

The prelaying period commenced with the initiation of territorial aggression and ended with deposition of the first egg. The laying-incubation period ended with hatching of the first egg. Observations during the brood-rearing period were continued until we were no longer able to locate the brood or until feeding of the young by the parents was markedly reduced (approximately 20 days after the first egg hatched) (Gullion 1954, see Fig. 1).

Twenty-eight behavioral categories were recognized and recorded in the field. In order to construct time-activity budgets, several categories were combined and defined as follows:

Feeding.—Actively searching for or ingesting food.

Intraspecific aggression.—Stereotyped postures or movements as described by Gullion (1952) and Fredrickson (1967, 1970), as well as nonstereotyped behavior, such as resident birds supplanting territory intruders, usually by swimming directly toward the intruder.

Interspecific aggression.—Any attacks upon or attempts to supplant individuals of another species.

Locomotion.—Swimming (most observations in this category) or walking; only those observations not occurring simultaneously with other behaviors (e.g. feeding, aggression, carrying food to young).

Loafing.—Standing or floating idly, not engaged in any other behavior.

Maintenance.—Preening, bathing, or comfort movements.

Courtship.—Courtship preening, precopulatory chases (Gullion 1952, Fredrickson 1967), and mounting (copulation was not seen during time-activity budget observations).

Nest-building.—Obtaining, carrying, or manipulating material for construction of nests or brood platforms.

Feeding of young.—Carrying of food by a parent to an offspring and the actual transfer of food.

Miscellaneous.—Escape, aggression directed at young, or calling.

Out-of-sight.—Spot observations when coots were concealed by vegetation.

Time-activity budget data are expressed as percentages on a per-hour basis. The sample unit for statistical analysis is 1 bird-hour, made up of a maximum of 120 spot observations. Coots, though less secretive than many other rails, spend considerable time in dense vegetation and were not always visible. Thus, all percentages were calculated from the amount of time birds were visible. Statistical analyses were done using only sample hours in which birds were visible for more than 15 min (i.e. at least 30 spot observations). Examination of coefficients of variation showed that this selection did not result in an unduly high degree of variability. A three-way analysis of variance examining the effect of year and study area on sex comparisons showed no significant interactions for any behavioral category except feeding-of-young. We believe that this effect is a result of age differences in birds observed (Ryan 1978). Based on the seeming lack of influence of year and study area on sex comparisons, we pooled data for these classes for analysis.

Arcsine transformations of all percentage data were made (Sokal and Rohlf 1969), and statistical analyses were performed on the transformed data. Unless otherwise indicated, data were compared by using one-way analysis of variance. Calculated *F*- or Chi-square values with probabilities of less than 0.05 are considered significant.

RESULTS

The results are based upon 468 bird-hours of observation on 30 males and 25 females. Coots were visible an average of 77.3% (46.4 min/h) of the time watched. Visibility did not differ between the sexes (male \bar{x} = 75.9%, female \bar{x} = 78.8%, *F* = 1.75; *df* = 1, 466). The time-activity data showed no consistent diurnal rhythm for any of the behavioral categories (Table 1). During the laying-incubation period, both sexes loafed significantly more and females fed significantly less in the early morning than later in the day. This pattern was not observed in either the prelaying or brood-rearing periods. Based on these results, further analyses were made on data pooled over the entire diurnal observation period. Time-activity budgets for males and

TABLE 1. Significance levels resulting from ANOVA comparing four diurnal periods of time-activity percentages for American Coots.^a

	Prelaying		Laying-incubation		Brood-rearing	
	Male	Female	Male	Female	Male	Female
Behavior						
Feeding	NS ^b	NS	0.02	NS	NS	NS
Intraspecific aggression	0.02	NS	NS	NS	NS	0.01
Locomotion	NS	NS	NS	NS	NS	NS
Interspecific aggression	NS	NS	NS	NS	0.03	NS
Loafing	NS	NS	0.01	0.01	NS	NS
Maintenance	NS	NS	NS	NS	NS	NS
Nest-building	NS	—	0.01	NS	NS	0.05
Courtship	NS	NS	NS	NS	NS	NS
Feeding of young	—	—	—	—	NS	NS
Out-of-sight	NS	NS	NS	NS	NS	NS

^a Time periods = 0600–1000, 1000–1300, 1300–1600, 1600–2000.

^b Not significant.

females during the three periods of the reproductive season are presented in Table 2, and unless otherwise indicated, all comparisons refer to that table.

Prelying period.—The prelying period was characterized by the establishment of territories and, seemingly, the accumulation of energy reserves for egg formation by the female. The time-activity budgets of the sexes reflect these primary tasks. Both sexes had the highest mean value for intraspecific aggression for the reproductive season during the prelying period. The mean percentage time engaged in intraspecific aggressive encounters for males was nearly three times that of females.

Gullion (1954) states that when coots were relieved of incubation duty by their mates, they swam about the territory seeking out any intruders that may have entered the territory while they were incubating. We found that such swimming about the territory occurred during all periods of the nesting season. We therefore believe that the percentage of time spent in “locomotion” may be an indirect measure of territorial aggressiveness. Locomotion and intraspecific aggression were higher for both sexes during the prelying period than in later stages of nesting. Locomotion was higher for males than females, although the difference was not significant.

Interspecific aggression during prelying was quite low for both sexes, although species such as the Pied-billed Grebe (*Podilymbus podiceps*), Redhead (*Aythya americana*), and Mallard (*Anas platyrhynchos*), which were repulsed frequently later in the season, were often present in or near coot territories.

Females spent more time foraging during the prelying period than did males (60% vs. 49%, $P < 0.001$). This difference probably reflects the females' needs for greater energy during the formation of eggs.

Maintenance behavior was at the lowest level for both sexes during prelying, although loafing time was moderate. Differences between the sexes for both behaviors were very small and not significant. We saw nest-building behavior during prelying too rarely to allow meaningful analysis and interpretation.

Gullion (1953, 1954) provides good evidence that courtship and pair-bond formation occur before territory establishment (i.e. before our “prelying” period). Sooter (1941), however, stated that courting peaked at the time of nest-building. We saw very little courtship behavior by coots during prelying. Coots breeding in northwest

TABLE 2. Comparison of mean time-activity percentages of male and female American Coots by nesting period.

Activity	Prelaying (male <i>n</i> = 41, female <i>n</i> = 31)	Laying-incubation (male <i>n</i> = 49, female <i>n</i> = 42)	Brood-rearing (male <i>n</i> = 151, female <i>n</i> = 153)	Significance level of <i>F</i> statistic ^a
Feeding				
Male	49.4 ± 17.6 ^b	48.7 ± 24.4	58.3 ± 17.8	B***C***
Female	60.4 ± 16.1 D** ^c	55.6 ± 24.9	68.7 ± 13.8 D***	B** C**
Intraspecific Aggression				
Male	6.8 ± 9.3	3.3 ± 7.3	1.8 ± 2.6	A** C***
Female	2.4 ± 4.4 D**	1.1 ± 2.3	0.9 ± 1.7 D**	C*
Locomotion				
Male	27.0 ± 14.4	18.6 ± 12.3	9.7 ± 7.7	A**B***C***
Female	21.6 ± 11.4	14.4 ± 11.9	5.0 ± 5.5 D***	A**B** C***
Interspecific aggression				
Male	0.1 ± 0.3	0.0 ± 1.0	0.6 ± 1.4	B* C**
Female	0.0 ± 0.2	0.2 ± 0.6	0.4 ± 1.3	C*
Loafing				
Male	6.6 ± 7.0	10.7 ± 18.8	1.1 ± 2.4	B***C***
Female	6.3 ± 7.5	8.9 ± 14.7	0.7 ± 1.2 D*	B***C***
Maintenance				
Male	8.9 ± 11.4	14.9 ± 15.2	14.3 ± 13.2	A* C**
Female	8.2 ± 10.3	17.6 ± 15.0	10.8 ± 12.9 D**	A**B**
Nest-building				
Male	0.4 ± 1.2	2.0 ± 4.3	5.4 ± 13.9 ^d	
Female	0.0 D*	1.2 ± 3.4	0.7 ± 3.1 D***	
Courtship				
Sexes combined	0.5 ± 1.0	0.8 ± 2.6	0.3 ± 1.3	B* C**
Feeding of young				
Male	—	—	8.7 ± 7.3	
Female	—	—	11.8 ± 7.9 D***	
Miscellaneous				
Male	0.3	1.1	0.0	
Female	0.6	0.3	0.8	

^a A = statistical comparison of prelaying and laying-incubation periods; B = statistical comparison of laying-incubation and brood-rearing periods; C = statistical comparison of prelaying and brood-rearing periods; if a letter does not appear, the comparison is not significant. Significance levels: * = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001.

^b Standard deviation.

^c D = statistical comparison of males and females; if the letter does not appear, the comparison is not significant.

^d Percent time building brood platforms.

Iowa, especially older birds, may be paired when they arrive on the breeding ground (Ryan 1978).

Laying-incubation period.—Time spent in active behavior (those categories other than loafing and maintenance) was at a minimum during the laying-incubation period. Maintenance behavior increased significantly from prelaying for both sexes. Loafing time, although increased, was not significantly different from prelaying for either sex. These increases resulted from reductions in time spent in intraspecific aggressive encounters and locomotion for both sexes and a reduction in feeding time by females.

TABLE 3. Comparison of rates of feeding offspring by male and female American Coots.

Sex	Hours of observation	Number of feedings	Feedings/h ^a
Male	114.2	2,602	22.8
Female	116.1	4,338	37.4

^a $\chi^2 = 403.1$, $df = 1$, $P < 0.005$.

Intraspecific aggression during laying-incubation decreased by half for both sexes from the prelaying period. This decrease was significant for males. The ratio of aggressiveness of males to females remained constant from the prelaying period (2.8:1), but the between-sex difference was no longer significant ($P = 0.07$). The ratio of male to female locomotion percentages also remained constant from the prelaying period (1.3:1). Both sexes showed a significant decrease in mean percentage time in locomotion, but no difference could be shown statistically between the sexes. This parallel trend of locomotion and intraspecific aggression supports the concept of a territorial function for locomotory behavior. Interspecific aggression remained very low in the laying-incubation period, with females showing a small but nonsignificant increase. No significant difference was found between the sexes.

Coots continued to add material to their nests after the first egg was laid. Fredrickson (1970) indicates that both sexes build the nest. Our data support his findings, with males averaging slightly more nest building than females, but the difference was not significant. Courtship activities increased slightly but not significantly from the prelaying period.

Brood-rearing period.—Care of the young resulted in significant changes in nearly all behavioral categories for both sexes. Feeding time increased significantly over both prior time periods for both sexes, rising most sharply in females. This increase clearly reflects the greater effort required to feed the young. It was not possible to differentiate quantitatively the time spent by parents searching for food for chicks from that spent foraging for themselves. Females spent significantly more time feeding young than did males, contributing 63% of all feedings of young (Table 3). Females fed young at a greater rate than did males throughout the brood-rearing period (Fig. 1). Feeding of young reached a peak approximately 10 days after the first egg hatched. All young from most clutches had hatched (eggs within clutches hatch asynchronously) by this time, but older chicks had not yet begun to feed themselves to any large extent (Gullion 1954). After this time, the feeding rate dropped quickly as older chicks began to increase their own foraging effort.

Intraspecific aggression continued to decrease for both sexes, the mean percentage being significantly less than that for the prelaying but not the laying-incubation period. Males were again significantly more aggressive than females. Locomotion also declined significantly for both sexes. The mean locomotion percentage for males was significantly greater than that of females. Gullion (1953) reported a sharp increase in "territorial" aggressiveness by coots with the hatching of the clutch. He included both intra- and interspecific aggression in this consideration. Our data show that intraspecific encounters decreased as the nesting season progressed, but a significant increase in interspecific aggression occurred in both sexes after the clutch hatched.

Both sexes reduced loafing time severely from earlier periods. Although their mean percentage was quite low, males did loaf significantly more than females. These extremely low levels reflect the effort required to feed the brood. Time spent in

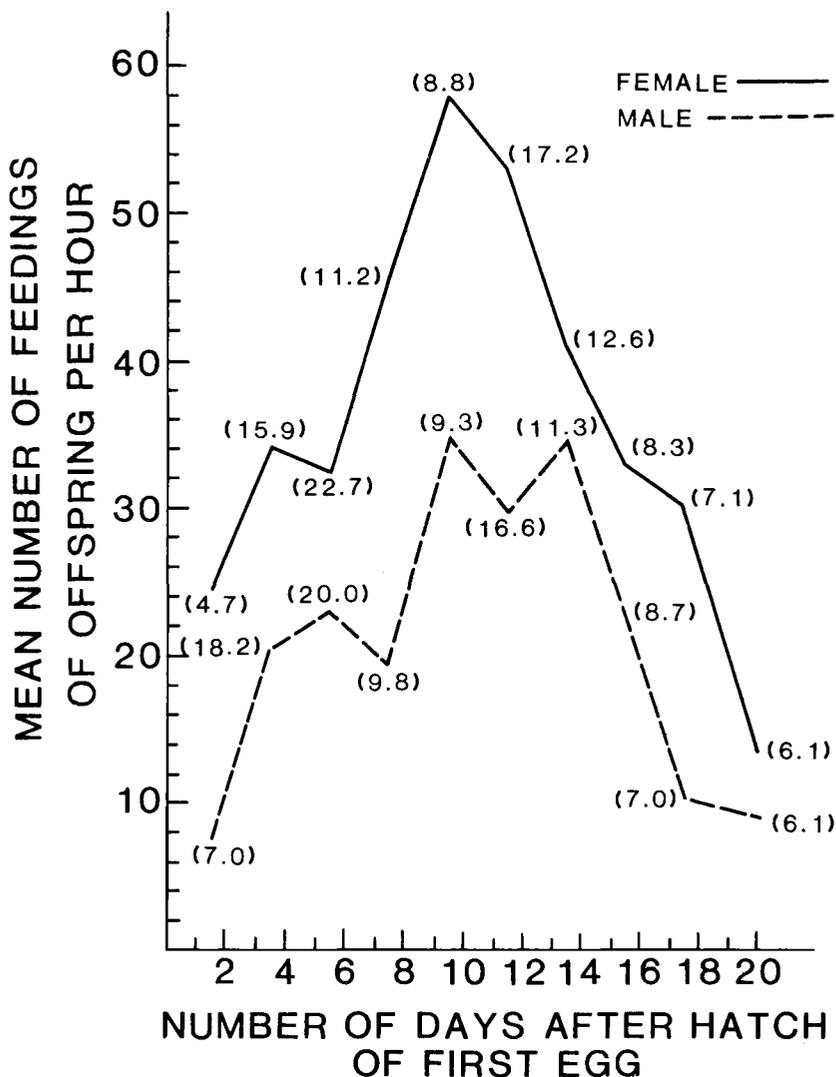


Fig. 1. Relation of mean rates of feeding young by male and female American Coots and time after hatching of first egg. Mean values are for 2-day (3-day for "day" 20) intervals. Numbers in parentheses are number of hours from which mean is calculated.

maintenance behavior by males remained at the same level seen during laying-incubation. Females, however, reduced their maintenance activity significantly from the laying-incubation period. The resulting difference between the sexes was highly significant. The decrease in female maintenance time probably also is related to demands of brood care. We suggest that, in an effort to provide adequate care for their young, coots first reduce loafing activities. When this increase in time for brood care is insufficient, then maintenance time is reduced.

Brood platforms were built almost exclusively by males. They spent over 5% of their time engaged in this activity. Courtship was at its lowest point during brood-rearing, being significantly less than in either of the prior reproductive periods.

DISCUSSION

Striking differences in time-activity budgets of male and female coots occurred during the reproductive season, particularly in the prelaying and brood-rearing periods (Table 2). Trivers (1972) suggested that in monogamous species, such as coots, males should invest less parental care than females, although probably more than half as much. The most likely factor influencing the between-sex differences is the initial parental investment (i.e. the energy cost of the gametes). Growth of the ovary and oviduct and production of eggs require a great deal more energy than testicular growth and synthesis of spermatozoa. In large birds rapid synthesis of yolk in the ovum begins 7–10 days before ovulation (King 1973). For coots, which lay 1 egg a day and have normal clutches of 4–12 eggs (Fredrickson 1977), this major energy demand occurs during the prelaying period. For birds approximately coot size, the peak energy demand for egg formation is at least 25% of the daily energy budget (King 1973). Female coots spent 22% more time feeding than males during prelaying (Table 2). Assuming no difference between the sexes in metabolic maintenance costs or food selection, the difference in feeding time accounts for nearly all the additional energy required by females for egg production. Coots are primarily vegetarians (Jones 1940, Fredrickson 1977). Additional energy gains might accrue to females if they shifted dietary emphasis from plants to more readily assimilated invertebrate material, as do females of several species of ducks (Krapu 1974a, 1974b; Swanson et al. 1974; Serie and Swanson 1976). We collected no data on this aspect of coot feeding ecology. The lack of significant differences between the sexes in feeding time during laying-incubation further substantiates the relation between egg-laying costs and increased feeding time by females during prelaying (Table 2).

Before the role of the sexes in territorial defense can be evaluated, a discussion of the potential function of "locomotion" is necessary. Advertisement, usually through vocalization or stereotyped display, is one of several ways in which territorial integrity is maintained in birds (Wilson 1975: 262). We suggest that locomotion is a form of advertisement in coots. Coots, by swimming about the territory, may by their mere presence there indicate that the territory is occupied and will be defended. Early in territory formation, groups of up to 30 nonterritorial coots commonly were present on the study areas. When territory residents were hidden in the dense emergent vegetation, trespass by these "floaters," usually to feed, was common. When territory owners were visible, such trespass was reduced. No quantitative measures of this phenomenon were recorded.

If our conclusion that locomotion functions in territory defense is correct, then both sexes make a considerable contribution to territory maintenance (Table 2). Female contribution, although lower than that of males, seems greater than has been previously acknowledged (Gullion 1953, Crawford 1975).

Brown and Orians (1970) suggest that the most important factor determining space-related agonistic behavior is the distribution of food resources in time and space. The spatial and temporal distribution of resources for breeding birds is extremely variable in marsh environments (Verner and Willson 1966, Orians 1969, Verner and Engelson 1970). Such variability should make competition for better areas keen. The large investments of time and energy in territory defense by coots suggest that severe competition is occurring for resources. Considering the high levels of expenditure on territory defense, it is not unreasonable to suggest that resources within some territories approach the limit of economic defendability

(Brown 1964). Indeed, several times we were surprised to see territorial pairs allow nonterritorial birds to feed just inside the boundaries of the territory. Coots were most tolerant when groups of invaders were large (>5), and thus the cost of defense was high. Indirect evidence that competition for territories among coots is sometimes high is found in Crawford's (1975) data on nonbreeding coots on some of the same sites we studied; 25% of the resident population over a 2-yr period was nonbreeding. The high variability of resource distribution and abundance in marsh environments and the resulting competition have probably been strong factors selecting for high female aggressiveness.

Our quantitative data on incubation behavior are insufficient to analyze for sex-related differences, but Gullion (1954) and Fredrickson (1970) indicate that coots share incubation and that males may actually do more of it. Time spent feeding young and rates of feeding young also show cooperative efforts by the sexes. If the increase in feeding time from laying-incubation to brood-rearing is assumed to be directly related to foraging for young and is added to time spent feeding young, the resulting figures (24.9% = female, 18.4% = male) yield an effort ratio (1.4:1, females to males) approximating that of feedings of the young by the sexes (1.7:1) (Table 3). The summed values of foraging for and feeding young are probably conservative, because in our judgement a preponderance of time spent "feeding" during brood-rearing was devoted to securing food for young, and ingestion of food by adults was incidental to this searching. The greater investment in time and energy by females in feeding young is probably a function of their greater initial parental investment (Trivers 1972).

Without energetics data, exact comparisons of effort by the sexes are not possible. Examinations of the time-activity budgets, however, provide support for Triver's (1972) suggestion on the relative efforts of the sexes, as stated above. Males spend slightly more time on territorial functions and possibly on incubation. Females invest more energy through their gametes and spend more time feeding young.

Lack (1947, 1948, 1954: 31, 1968: 5) suggested that, in birds that feed their young, clutch size is ultimately determined by the ability of parents to feed their young. In an experimental study of clutch size, Fredrickson (1969) showed that coots could successfully hatch more eggs than were normally laid. Mortality in these artificially large broods (12 to 16 young vs. normal brood sizes at hatching of 2 to 11) was high, and Fredrickson (1969) suggested that inadequacies in the brooding or feeding ability of the parents were responsible. Our data show that, during brood-rearing, males spent 67% and females 80% of their time foraging for themselves and young and feeding young. Loafing time averaged less than 1% for the sexes combined. This suggests that coots do not have sufficient time and energy available to rear more young than are normally produced. Additional data on energy resources available to coots are needed to elucidate more fully the relation between clutch size and feeding ability.

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The American Ornithologists' Union solicits applications for research grants from its **Josselyn Van Tyne and Alexander Wetmore Memorial Funds**. The Van Tyne awards will consider any aspect of avian biology; the Wetmore awards are limited to taxonomy/systematics. Grants are usually in amounts of a few hundred dollars. Preference is given to students and other persons without other sources of funds. Applicants should send three copies of the following: (1) a 3–5 page description of research goals and procedures; (2) an itemized budget, with a justification of major items and the total amount requested; and (3) a brief résumé of academic/ornithological experience. In addition, all applicants should request two or three letters of recommendation from recognized ornithologists, to be sent directly by the writers. If possible, recommendations also should be submitted in triplicate. All application materials, including letters, *must* be received before **1 March 1980**. Awards will be announced on or before 1 May 1980. Send all materials to **Dr. A. S. Gaunt, A.O.U. Committee on Research Awards, Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210**.

The **98th Stated Meeting of the AOU** will be held at Colorado State University, Fort Collins, Colorado during the week of 11–15 August 1980.

Fellows and Elective Members of the AOU are reminded that nominations for Elective Members are to be submitted to the Secretary on the prescribed form 5 months prior to the opening of the 1980 annual meeting. Nominations for Fellows must also be received by that date, which is **11 March 1980**. Nominations for President-elect, Vice-President, and Elective Councilors (3) may be sent to the Secretary any time prior to the annual meeting.

Student membership awards are made available in limited number each year by the A.O.U. Students at any stage of academic training who are not and have not been A.O.U. members are eligible. Application forms will be mailed in November to ornithologists who normally have contact with students. Forms are also available from Frank Heppner, Department of Zoology, University of Rhode Island, Kingston, R.I. 02881, or from the chairman of the Student Awards Committee, Kenneth P. Able, Department of Biology, S.U.N.Y. at Albany, Albany, New York 12222. The deadline for receipt of applications is **10 December 1979**.