THE BEHAVIORAL ECOLOGY OF BREEDING AMERICAN COOTS IN RELATION TO AGE

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ABSTRACT.—Time-activity budgets were determined for breeding male and female American Coots (*Fulica americana*) of three age-classes. Time apportioned to foraging and courtship decreased with age, while time spent in defending territory and feeding young increased with age. We hypothesize that differences in time spent foraging, defending the territory and feeding young are the result of older coots occupying better-quality territories. Such a hypothesis is consistent with the generally assumed wide variability in spatial distribution of energy resources in marsh ecosystems. Such variability seems to be a primary proximate and ultimate factor affecting the reproductive success of American Coots.

Several recent theoretical papers predict that reproductive effort should increase with age or decrease with residual reproductive value (Williams 1966, Gadgil and Bossert 1970, Charlesworth and Leon 1976, Pianka 1976). Residual reproductive value is an animal's age-specific expectation of all present and future offspring, being discounted by the probability of adult mortality preceding the production of offspring (Fisher 1958). Younger birds have greater average residual reproductive value than do older birds. The theory predicts that younger birds should expend less effort than older ones on reproduction, thereby reducing risk and conserving energy, which will enhance survival and successful future reproduction.

Empirical studies have shown that clutch size, size of eggs, chronology of laying, and success in fledging young are related to age; older birds lay more and larger eggs earlier and are more successful in producing young (Coulson and White 1958, Brakhage 1965, Coulson et al. 1969, Mills 1973, Davis 1975, Ryder 1975, Coulson and Horobin 1976, Crawford 1977, Blus and Keahey 1978). Crawford (1975) found similar age-related phenomena in American Coots (*Fulica americana*).

An animal's apportionment of time, energy, and matter determines how it adjusts to its environment (Pianka 1974:201). Studies of age-related biology lead to the prediction of differences in the apportionment of time for various activities during the reproductive period. We wished to test this prediction by comparing quantitatively the behavior of three age-classes of breeding American Coots. We further attempted to re-

late environmental conditions to observed age-specific behavior, and to assess possible factors affecting reproductive success and adaptive behavior of coots.

STUDY AREA AND METHODS

Fieldwork was conducted in 1976 and 1977 at Smith's Slough, Dewey's Pasture, and Hottes Lake, wetlands in northwestern Iowa. Smith's Slough and Dewey's Pasture were described by Bennett (1938), Hayden (1943), and Low (1945). Conditions at the time of this study, and a description of Hottes Lake, are given by Ryan and Dinsmore (1979).

Time-activity budgets were determined for both sexes within three age-classes (one, two, and three years) during prelaying, laying-incubation, and brood-rearing periods. We made spot-observations of behaviors of known individuals every 30 s in one-hour time blocks distributed throughout the day (06:00–20:00). We used a metronome to time sampling 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, we used four four-m tower blinds in Smith's Slough and two water-level blinds at Dewey's Pasture. Coots were watched through a spotting scope or binoculars. Thirty males and 25 females were visible 77.3% (46.4 min/h) of 467 bird-hours of observation.

Coots were sexed in the field by voice (Gullion 1950) and assigned to age-classes by tarsal color (Crawford 1978). Some individuals were identified by coded nasal discs; others were identified by morphological characteristics, such as distinctive white feathering at various places 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 continued until we were no longer able to find the brood, or until feeding of the young by the parents was markedly reduced (approximately 20 days after the first egg hatched; Gullion 1954, Ryan and Dinsmore 1979).

We recognized 28 behavioral categories. To construct time-activity budgets, several categories were combined.

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 non-stereotyped 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 or walking; this included only those observations not obviously occurring simultaneously with other behaviors.

Loafing. Standing or floating while 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 the 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. 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 one bird-hour, made up of a maximum of 120 spot observations. Coots, although less secretive than many other rails, spent considerable time in dense vegetation and were not always visible. All percentages were calculated from the amount of time that birds were visible. We analyzed data from only sample hours in which birds were visible for more than 15 min (i.e., at least 30 spot observations).

The coefficients of variation showed that this selection did not result in an unduly high degree of variability. The time-activity data showed no consistent diurnal rhythm for any of the behavioral categories (Ryan and Dinsmore 1979). Therefore, we pooled data over the entire diurnal observation period for our analyses.

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 were considered significant.

RESULTS

Time-activity data for three age-classes are presented for the prelaying (Table 1), laying-incubation (Table 2), and brood-rearing (Table 3) periods. Figure 1 summarizes the time budgets for each age class over the entire reproductive season.

For the entire reproductive season three-year-old coots spent less time feeding than younger birds. During prelaying, females showed an inverse, though non-significant, relationship between feeding time and age. Feeding time increased during brood-rear-

ing compared to laying-incubation for all sex and age groups. This increase reflects the greater effort required to feed the young. We could not differentiate quantitatively the time parents spent searching for food for chicks versus foraging for themselves. Three-year-old females spent less time feeding during brood-rearing than two- ($P = 0.02$) or one-year-old ($P = 0.09$) females. Three-year-old males also spent less time feeding than younger males.

Although feeding time for three-year-old coots was low, time spent feeding young was high. It is the combined effort of the parents that determines quality of care in rearing chicks. Because 96% of all pairs observed were of equal age, we could compare combined effort in feeding young. Three-year-olds spent more time feeding young than two- ($P = 0.08$) or one-year-old ($P = 0.001$) coots. The number of feedings of young (Table 4) closely parallel time budget data. One-year-old coots fed young at significantly lower rates than older birds. When sexes were combined, total feedings per hour were similar for two- and three-year-old coots. Data on three-year-old females were collected early in the brood-rearing stage (third and fifth day after hatching of the first egg) before feeding rates peak (approximately 10 days after hatching of the first egg; Ryan and Dinsmore 1979). Brood sizes (three to four young) of three-year-olds at this time were comparable to those of younger coots later in brood-rearing. Brood sizes for most pairs changed over time (due to asynchronous hatching and mortality), and not all brood members were fed simultaneously; therefore, precise information on feeding effort per young was not obtained.

Territorial integrity is maintained through direct aggression and advertisement. We (Ryan and Dinsmore 1979) have suggested that "locomotion" (visible presence on the territory) is a form of advertisement in coots. Three-year-old coots spent more time in intraspecific aggression and locomotion than younger coots (Fig. 1).

Three-year-olds began nesting shortly after their arrival on the breeding ground and, on the average, earlier than younger coots (Crawford 1980). Thus, it may be necessary for these older individuals to have firmly established pair-bonds upon arrival. Over the entire reproductive period three-year-olds courted less than two- ($P = 0.02$) or one-year-old ($P = 0.06$) coots.

Time spent loafing or in maintenance activities probably was determined by how
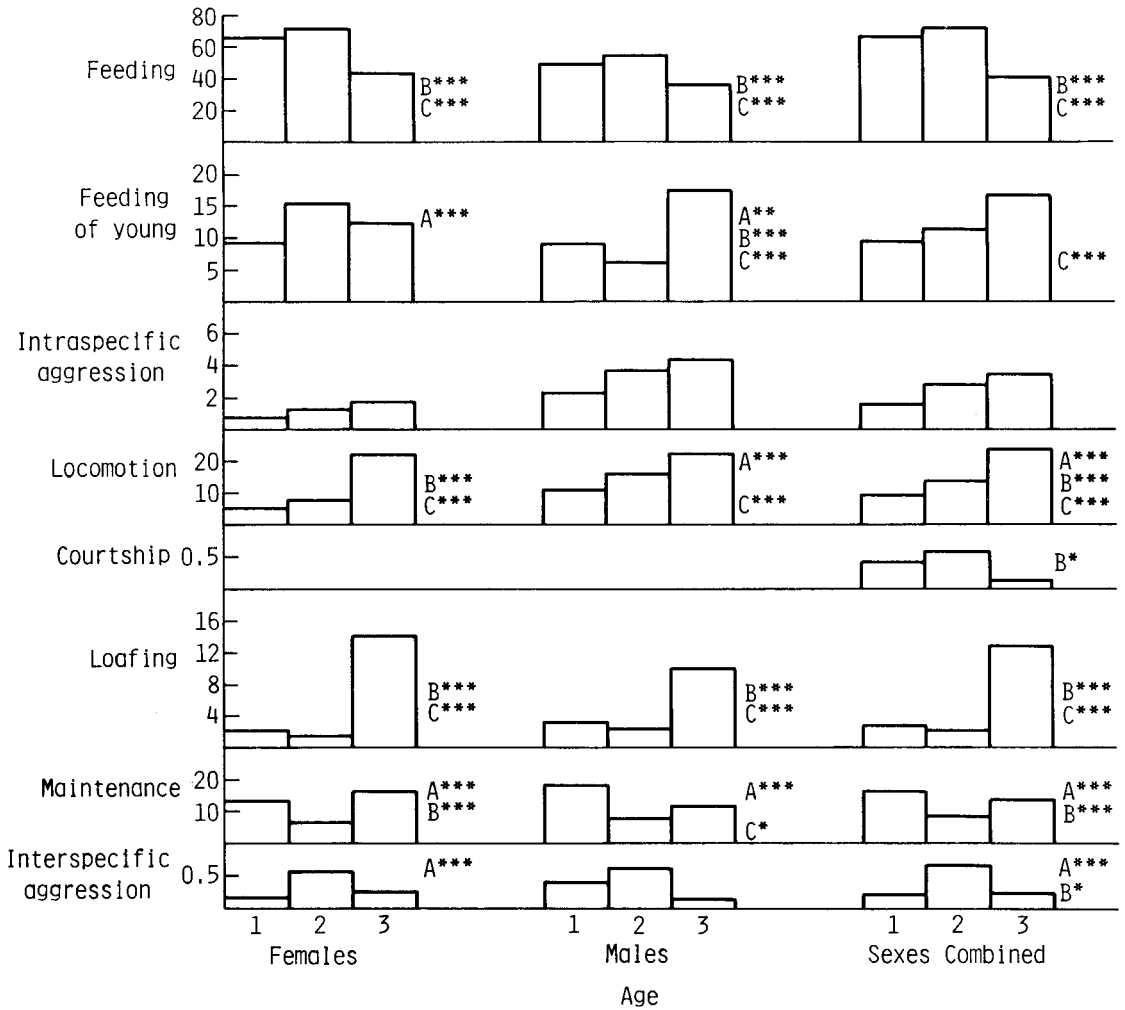
FIGURE 1. Comparison of mean time-activity percentages for male and female American Coots, by age class, over the entire reproductive season. Feeding of young includes data only from the brood-rearing period. Symbols as in Table 1.

much time was left after other, more essential activities were completed. Age-class differences probably resulted from age-specific time investment in other activities (e.g., feeding, territory defense, care of young).

No age-specific patterns in interspecific aggression were apparent. One-year-olds were seen building nests more frequently than older birds, but differences were not significant (Tables 1 and 2). Time spent building brood platforms increased dramatically with age for males (Table 3).

DISCUSSION

The reproductive success (number of young fledged) of American Coots has been related directly to age (Crawford 1980). Therefore, it was not surprising that we found numerous differences in time-activity budgets among the age-classes.

Time expenditure by breeding coots should be determined largely by the energy requirements of the individuals and the temporal and spatial distribution and abundance of resources. We assume that basal metabolic rates are equal and that food selectivity is similar among age-classes. Physiologically, energy requirements should not differ among males of different age-classes. This is not the case with females; because clutch size increases with age (Crawford 1980), older females need more energy. These demands might be met by increased daily energy intake, by equivalent energy consumption per day but over a longer period (i.e., into the laying phase), or by some combination of the two methods.

Adult coots are primarily vegetarians (Jones 1940, Fredrickson 1977). The biomass of annual, submerged, freshwater

TABLE 1.   Comparison of mean time-activity percentages (±1 S.D.) for male and female American Coots, by age class, during the prelaying period.

Activity	Age class 1 (Male N = 11) (Female N = 7)	Age class 2 (Male N = 24) (Female N = 16)	Age class 3 (Male N = 7) (Female N = 8)	Significance[a] level of F statistic
Feeding				
Male	53.2 ± 17.8	46.4 ± 18.8	53.6 ± 12.6	
Female	65.3 ± 17.9	61.4 ± 17.2	54.1 ± 11.5	
Intraspecific aggression				
Male	3.8 ± 3.2	8.8 ± 11.6	4.6 ± 4.3	
Female	2.4 ± 2.2	2.6 ± 5.8	2.1 ± 2.5	
Sexes combined	3.2 ± 2.9	6.3 ± 10.1	3.2 ± 3.6	
Locomotion				
Male	22.0 ± 7.0	30.2 ± 16.8	24.0 ± 12.5	
Female	17.9 ± 13.4	23.4 ± 12.1	21.3 ± 8.3	
Interspecific aggression				
Male	0.0	0.1 ± 0.4	0.0	
Female	0.0	0.0	0.2 ± 0.5	
Loafing				
Male	10.0 ± 9.1	4.8 ± 5.6	7.2 ± 6.6	
Female	4.9 ± 6.0	3.3 ± 6.0	13.4 ± 7.4	B***C*
Maintenance				
Male	9.3 ± 11.8	8.4 ± 11.4	10.0 ± 12.4	
Female	8.5 ± 5.1	7.7 ± 9.7	8.1 ± 15.2	
Nest-building				
Male	1.0 ± 2.0	0.2 ± 0.5	0.4 ± 1.0	
Female	0.0	0.0	0.0	
Courtship				
Sexes combined	0.5 ± 0.9	0.7 ± 1.1	0.1 ± 0.5	B*
Miscellaneous				
Male	0.2	0.5	0.1	
Female	0.4	1.1	0.7	

[a] A = Statistical comparison of age classes 1 and 2; B = statistical comparison of age classes 2 and 3; C = statistical comparison of age classes 1 and 3; if a letter does not appear the comparison is not significant.
* Significant at <0.05, ** significant at <0.01, *** significant at <0.001.

plants generally increases from early spring to midsummer (Wetzel 1975:376–377). This increase should enhance foraging efficiency (energy consumed per unit time). Mean nest initiation dates for three years on some of the same areas we studied were 20 May, 1 June, and 12 June for three-, two- and one-year-old coots, respectively (Crawford 1975, 1980). During the prelaying period, older coots should spend more time foraging than younger coots, since they establish territories earlier, when food is scarcer. Furthermore, because of egg production costs of females, time spent foraging should increase more with age for females than for males. Our results are not consistent with these predictions (Table 1).

Overlying the temporal effect on feeding time is the spatial distribution of food, which is extremely variable in marsh environments (Verner and Willson 1966, Orians 1969a, Verner and Engelson 1970). Older coots might be expected to occupy better sites as a result of earlier nesting, greater experience (i.e., better ability to distinguish potentially high quality areas), and/or more aggressiveness (see below). The effect of variability in food distribution on age-specific feeding time therefore should be opposite to that of the temporal factors outlined above. The time necessary to acquire energy is reduced by the increased food density. The results (Tables 1 and 2) from prelaying and laying-incubation suggest strong differences in habitat quality among territories of different-aged birds, particularly between three-year-old and younger coots. Males showed no significant differences in feeding time during the prelaying period, but females spent slightly less time feeding with increasing age. During laying-incubation, three-year-old males and females fed only half as much as all younger coots.

The data on feeding time may be explained by the possibility that older birds

TABLE 2. Comparison of mean time-activity percentages (±1 standard deviation) for male and female American Coots by age class, during the laying-incubation period.

Activity	Age class 1 (Male N = 26) (Female N = 26)	Age class 2 (Male N = 11) (Female N = 5)	Age class 3 (Male N = 12) (Female N = 11)	Significance[a] level of F statistic
Feeding				
Male	52.4 ± 30.1	59.3 ± 13.9	32.7 ± 12.1	B***C***
Female	64.4 ± 23.5	63.7 ± 17.2	31.0 ± 12.2	B***C***
Intraspecific aggression				
Male	3.0 ± 4.7	0.5 ± 1.0	6.4 ± 12.8	
Female	0.9 ± 2.1	0.5 ± 1.1	2.0 ± 2.9	
Sexes combined	1.9 ± 3.7	0.5 ± 1.0	4.3 ± 9.5	
Locomotion				
Male	13.5 ± 10.1	22.5 ± 9.7	26.0 ± 14.5	A* C**
Female	9.7 ± 6.4	16.9 ± 12.3	24.4 ± 15.6	
Interspecific aggression				
Male	0.0	0.8 ± 1.9	0.2 ± 0.6	
Female	0.1 ± 0.3	0.0	0.5 ± 1.0	
Loafing				
Male	8.6 ± 19.2	7.1 ± 7.0	18.8 ± 24.9	C*
Female	5.7 ± 14.0	3.8 ± 2.5	18.6 ± 15.7	B* C***
Maintenance				
Male	18.5 ± 17.0	7.7 ± 8.8	13.7 ± 14.1	
Female	15.7 ± 15.4	14.4 ± 15.8	23.5 ± 13.1	
Nest-building				
Male	3.7 ± 5.3	0.0	0.0	
Female	1.9 ± 4.2	0.0	0.0	
Courtship				
Sexes combined	1.1 ± 3.4	0.5 ± 0.8	0.0	B** C*
Miscellaneous				
Male	0.0	1.6	2.2	
Female	0.4	0.2	0.0	

[a] Symbols as in Table 1.

possess, on the average, territories with more food. Birds holding better sites should expend more time on territory defense than those on inferior sites. The pooled data on territory defense (Fig. 1) show intraspecific aggression and locomotion time (an indirect measure of territorial aggression; Ryan and Dinsmore 1979) increasing with age, as predicted. When the data are examined by stage of the nesting season, however, the results are ambiguous. Particularly confusing are the high expenditures for territorial defense during prelaying by two-year-olds and the increase in defense time by three-year-olds during laying-incubation. These departures from expected results may be explained by the chronology of territory establishment. Three-year-old coots, by nesting early, do not have to contend with many established territory owners when acquiring sites. Territorial defense for older coots is most intense when younger birds begin attempting to claim territories among the mosaic of claimed sites (i.e., during laying-incubation of older birds). For two-year-olds, aggression is probably strongest at the time of territory establishment (prelaying) because they must contend with already established birds as well as many nonterritorial floaters.

Three-year-old coots spent less time foraging, but equal or greater amounts of time feeding young than do younger birds. Coot chicks are fed aquatic invertebrates for the first few weeks after hatching (Fredrickson 1977). The proportions of feeding-of-young time to feeding time are 0.15, 0.17, and 0.45 for one-, two-, and three-year-old coots, respectively (feeding and feeding-of-young time combined for sexes, Table 3). Two plausible explanations for the increase in proportions with age are: 1) better prey-capturing ability of older birds and 2) higher densities (availability) of food organisms in territories of older birds. The two factors are not mutually exclusive. Lower foraging efficiencies by younger birds have been shown for the Brown Pelican (*Pelecanus*

TABLE 3.   Comparison of mean time-activity percentages (±1 standard deviation) for male and female American Coots, by age class, during the brood-rearing period.

Activity	Age class 1 (Male N = 92) (Female N = 95)	Age class 2 (Male N = 50) (Female N = 56)	Age class 3 (Male N = 9) (Female N = 2)	Significance[a] level of F statistic
Feeding				
Male	56.8 ± 16.3	64.1 ± 17.7	34.3 ± 19.0	A* B***C***
Female	67.8 ± 14.7	70.9 ± 11.2	49.8 ± 27.7	B*
Feeding of young				
Male	9.1 ± 6.3	6.6 ± 6.4	17.1 ± 13.8	A** B***C***
Female	9.6 ± 6.3	15.4 ± 9.1	13.6 ± 0.5	A***
Sexes combined	9.4 ± 6.3	11.3 ± 9.1	16.5 ± 12.5	C***
Intraspecific aggression				
Male	1.7 ± 2.2	2.1 ± 3.3	0.6 ± 1.4	
Female	0.9 ± 1.2	1.1 ± 2.4	0.0	
Sexes combined	1.3 ± 1.9	1.6 ± 2.9	0.5 ± 1.3	
Locomotion				
Male	8.8 ± 7.3	10.3 ± 7.1	15.6 ± 11.5	C*
Female	5.3 ± 5.5	3.8 ± 3.8	23.9 ± 22.2	A* B***C***
Interspecific aggression				
Male	0.5 ± 1.3	0.7 ± 1.7	0.1 ± 0.3	
Female	0.1 ± 0.4	0.9 ± 2.0	0.0	
Sexes combined	0.3 ± 0.9	0.8 ± 1.9	0.1 ± 0.3	A***
Loafing				
Male	1.0 ± 2.2	1.4 ± 2.7	1.0 ± 1.5	
Female	0.7 ± 1.2	0.5 ± 1.2	0.0	
Maintenance				
Male	17.7 ± 13.3	8.5 ± 10.6	11.6 ± 15.0	A*** C*
Female	14.8 ± 13.8	5.8 ± 9.3	9.3 ± 13.2	A***
Nest-building[b]				
Male	2.7 ± 6.9	7.5 ± 16.0	21.6 ± 33.5	A* C***
Female	0.7 ± 3.4	0.7 ± 2.7	0.5 ± 0.7	
Courtship				
Sexes combined	0.2 ± 0.9	0.4 ± 2.0	0.0	
Miscellaneous				
Male	1.5	0.0	0.0	
Female	0.0	0.5	2.8	

[a] Symbols as in Table 1.
[b] Building of brood-platforms.

occidentalis; Orians 1969b), Little Blue Heron (*Florida caerulea*; Recher and Recher 1969), Forster's Tern (*Sterna forsteri*; Salt and Willard 1971), Sandwich Tern (*Sterna sandvicensis*; Dunn 1972), and Royal Tern (*Sterna maxima*; Buckley and Buckley 1974). All these species, however, feed primarily on fish, which are considerably more mobile than the invertebrates preyed upon by coots for their young. Ryan (1978) has noted that, because of substantial amounts of cover, finding and capturing invertebrate prey is very time-costly for coots. The lack of experience probably accounts

TABLE 4.   Comparison of rates of feeding offspring by sex and age-classes of American Coots.

Sex	Age class 1			Age class 2			Age class 3			Significance of χ² tests[a]
	Hours of observ.	No. of feedings	No./h	Hours of observ.	No. of feedings	No./h	Hours of observ.	No. of feedings	No./h	
Male	78.9	1,916	24.3	30.2	531	17.6	5.1	155	30.3	A***B***C***
Female	77.6	2,476	31.9	37.3	1,804	48.4	1.2	58	49.4	A*** C***
Sexes combined	156.5	4,392	28.1	67.5	2,335	34.6	6.3	213	33.9	A*** C***

[a] For explanation of symbols see Table 1.

for some of the inefficiency of one-year-old birds, but we doubt that the difference between two- and three-year-old coots can be totally accounted for by this factor. Sharp differences in habitat quality, however, might easily explain the observed results. Again, the hypothesis of greater food resources being available to older coots is consistent with the results.

In addition to the proximate factors discussed, time-activity budgets of breeding birds should, at least in theory, be affected by the reproductive effort. Because older birds have lower residual reproductive value than younger ones, they should invest more energy (and presumably time) in reproductive activities (Williams 1966, Gadgil and Bossert 1970, Charlesworth and Leon 1976, Pianka 1976, but see Fagen 1972 and Schaffer 1974). Differences in reproductive success, such as those documented for coots (Crawford 1975), are not necessarily indicative of reproductive effort (Pianka and Parker 1975). A bird may produce a smaller clutch and fledge fewer young and still expend equal effort, differences resulting from degrees of efficiency of time-energy utilization or availability of resources. The differences in time expenditures among age-classes of breeding coots may be explained by the hypothesis that older birds occupy better territories. Investigations of the nature and extent of territory quality are required before age-specific reproductive efforts of coots can be evaluated.

In sum, the spatial distribution of food is a primary proximate factor affecting reproductive success and is probably an important ultimate factor affecting the adaptive habits of coots.

ACKNOWLEDGMENTS

LITERATURE CITED

BENNETT, L. J. 1938. The Blue-winged Teal. Iowa State University Press, Ames.
BLUS, L. J., AND J. A. KEAHEY. 1978. Variation in re-
productivity with age in the Brown Pelican. Auk 95:128–134.
BRAKHAGE, G. K. 1965. Biology and behavior of tub-nesting Canada Geese. J. Wildl. Manage. 29:751–771.
BUCKLEY, F. G., AND P. A. BUCKLEY. 1974. Comparative feeding ecology of wintering adult and juvenile Royal Terns (Aves: Laridae, Sterninae). Ecology 55:1053–1063.
CHARLESWORTH, B., AND J. A. LEON. 1976. The relation of reproductive effort to age. Am. Nat. 110:449–459.
COULSON, J. C., AND J. HOROBIN. 1976. The influence of age on the breeding biology and survival of the Arctic Tern Sterna paradisaea. J. Zool. 178:247–260.
COULSON, J. C., G. R. POTTS, AND J. HOROBIN. 1969. Variation in the eggs of the Shag (Phalacrocorax aristotelis). Auk 86:232–245.
COULSON, J. C., AND E. WHITE. 1958. The effect of age on the breeding biology of the Kittiwake Rissa tridactyla. Ibis 100:40–51.
CRAWFORD, R. D. 1975. Breeding biology of American Coots in relation to age. Unpubl. Ph.D. thesis, Iowa State University, Ames.
CRAWFORD, R. D. 1977. Breeding biology of year-old and older female Red-winged and Yellow-headed blackbirds. Wilson Bull. 89:73–80.
CRAWFORD, R. D. 1978. Tarsal color of American Coots in relation to age. Wilson Bull. 90:536–543.
CRAWFORD, R. D. 1980. Effects of age on reproduction in American Coots. J. Wildl. Manage. 44:183–189.
DAVIS, J. W. F. 1975. Age, egg-size and breeding success in the Herring Gull, Larus argentatus. Ibis 117:460–473.
DUNN, E. K. 1972. Effect of age on the fishing ability of Sandwich Terns Sterna sandvicensis. Ibis 114:360–366.
FAGEN, R. M. 1972. An optimal life-history strategy in which reproductive effort decreases with age. Am. Nat. 106:258–261.
FISHER, R. A. 1958. The genetical theory of natural selection. Second ed. Dover Publication Inc., New York.
FREDRICKSON, L. H. 1967. Some aspects of reproductive behavior of American Coots (Fulica americana). Unpubl. Ph.D. thesis, Iowa State University, Ames.
FREDRICKSON, L. H. 1970. Breeding biology of American Coots in Iowa. Wilson Bull. 82:445–457.
FREDRICKSON, L. H. 1977. American Coot (Fulica americana), p. 123–147. In G. C. Sanderson [ed.], Management of migratory shore and upland game birds in North America. International Association of Fish and Wildlife Agencies, Washington, DC.
GADGIL, M., AND W. H. BOSSERT. 1970. Life historical consequences of natural selection. Am. Nat. 104:1–24.
GULLION, G. W. 1950. Voice differences between sexes in the American Coot. Condor 52:272–273.
GULLION, G. W. 1951. The frontal shield of the American Coot. Wilson Bull. 63:157–166.
GULLION, G. W. 1952. The displays and calls of the American Coot. Wilson Bull. 64:83–97.
GULLION, G. W. 1954. The reproductive cycle of American Coots in California. Auk 71:366–412.
HAYDEN, A. 1943. A botanical survey in the Iowa lake region of Clay and Palo Alto counties. Iowa State Coll. J. Sci. 17:277–415.
JONES, J. C. 1940. Food habits of the American Coot with notes on distribution. U.S. Dep. Inter. Wildl. Res. Bull. 2.

Low, J. B. 1945. Ecology and management of the Red-head, *Nyroca americana,* in Iowa. Ecol. Monogr. 15:35–69.

Mills, J. A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull *Larus novaehollandiae scopulinus.* J. Anim. Ecol. 42:147–162.

Orians, G. H. 1969a. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589–603.

Orians, G. H. 1969b. Age and hunting success in the Brown Pelican (*Pelecanus occidentalis*). Anim. Behav. 17:316–319.

Pianka, E. R. 1974. Evolutionary ecology. Harper and Row, New York.

Pianka, E. R. 1976. Natural selection of optimal reproductive tactics. Am. Zool. 16:775–784.

Pianka, E. R., and W. S. Parker. 1975. Age-specific reproductive tactics. Am. Nat. 109:453–464.

Recher, H. F., and J. A. Recher. 1969. Comparative foraging efficiency of adult and immature Little Blue Herons (*Florida caerulea*). Anim. Behav. 17:320–322.

Ryan, M. R. 1978. A quantitative study of the behavior of breeding American Coots in relation to sex and age. Unpubl. M.S. thesis, Iowa State University, Ames.

Ryan, M. R., and J. J. Dinsmore. 1979. A quantitative study of the behavior of breeding American Coots. Auk 96:704–713.

Ryder, J. P. 1975. Egg-laying, egg size, and success in relation to immature-mature plumage of Ring-billed Gulls. Wilson Bull. 87:534–542.

Salt, G. W., and D. E. Willard. 1971. The hunting behavior and success of Forster's Tern. Ecology 52:989–998.

Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age structure. Ecology 55:291–303.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco.

Verner, J., and G. H. Engelson. 1970. Territories, multiple nest building, and polygyny in the Long-billed Marsh Wren. Auk 87:557–567.

Verner, J., and M. F. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47:143–147.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Co., Philadelphia, PA.

Wiens, J. A., S. G. Martin, W. R. Holthaus, and F. A. Iwen. 1970. Metronome timing in behavioral ecology studies. Ecology 51:350–352.

Williams, G. C. 1966. Adaptations and natural selection. Princeton University Press, Princeton, NJ.

Department of Animal Ecology, Iowa State University, Ames, Iowa 50011. Accepted for publication 14 February 1980.

RECENT PUBLICATIONS

Birds.—[Various authors] with introductions by Barry W. Wilson. 1980. W. H. Freeman and Co., San Francisco. 276 p. Paper cover. "This book contains 25 of the more than 40 *Scientific American* articles about birds published since 1948." The articles are grouped into seven sections: diversity of birds, flight, migration and navigation, evolution, behavior, physiology and song, birds and people. Introductions to each section by Wilson provide essential background information. The quality of the writing and illustrations is familiar to those who know the magazine. This collection can serve as supplementary reading for a variety of college courses, and teachers, themselves, will find it a convenient source of lecture material.

Form and Function in Birds, Volume 1.—Edited by A. S. King and J. McLelland. 1979. Academic Press Inc., London. 459 p. $64.50. This is the first in a projected series of three volumes on the functional morphology of birds. "The overriding objective has been to show why birds are built as they are, and to assemble this information into a reference work for all biologists who research or teach with avian material." The general principles of avian morphology are set forth in the opening chapter by A. S. King and D. Z. King. Following are chapters on the coelomic cavities (H.-R. Duncker), digestive system (McLelland), urinary organs (O. W. Johnson), female genital organs (A. B. Gilbert), blood cells (R. D. Hodges), and the autonomic nervous system (A. R. Akester). The treatment is at an advanced level and is largely descriptive, despite the editors' aims. As compared with the equivalent chapters in King and Farner's *Avian Biology* (1971–1975, Academic Press)—except for that on the coelomic cavities, which has no predecessor in that series—the present chapters are longer, more detailed, more fully illustrated, and of course, more up-to-date. For the topics included, this volume is the most comprehensive reference available. Those who need information on the anatomy of birds will continue to be indebted to Academic Press. Photographs, drawings, diagrams, lists of references, index.