

## THE EFFECT OF FOOD ABUNDANCE ON THE REPRODUCTIVE PATTERNS OF COOTS<sup>1</sup>

WENDY L. HILL<sup>2</sup>

*Animal Behavior Program, Department of Psychology, University of Washington, Seattle, WA 98195*

**Abstract.** The effects of local resource abundance on the reproductive characteristics of American Coots (*Fulica americana*) were studied in eastern Washington. I examined the influences both of naturally occurring differences among habitats and of experimentally manipulated food resources. Females from lakes with high food abundance laid significantly heavier eggs than did females from lakes with low productivity. Similarly, eggs from experimentally enriched territories were significantly heavier than those from control territories. Clutch size did not vary systematically with resource abundance. These results suggest that when food is more abundant coots increased the quality, rather than quantity, of young produced. Nevertheless, a comparative analysis of the relationship between egg mass and body mass for 40 species of rails showed that the American Coot lays lighter eggs than would be predicted on the basis of body mass alone.

**Key words:** *Clutch size; egg mass; coots; food supply; reproductive patterns; avian ecology.*

### INTRODUCTION

The allocation of reproductive effort varies among species. In simplest terms, parents either produce many offspring and invest relatively little in each or they produce fewer and invest relatively more in each (MacArthur and Wilson 1967, Stearns 1976). Although investment patterns are typically discussed as a uniform characteristic of all members of a given species, individuals are able to alter these reproductive patterns in response to variations in conditions requisite for breeding, such as the physiological condition of the female (Lack 1968). For some animals, this plasticity may be the main component of their reproductive strategy (Geisel 1976).

The availability of food can affect how an individual allocates its reproductive effort (Lack 1968). For example, when food is abundant, either larger eggs or a larger clutch can potentially be laid. A larger clutch is beneficial only if increasing the quantity of young improves reproductive success. Under this condition, clutch size would be positively correlated with resource abundance. If the condition of the young produced is the crucial factor, however, parents should increase the energy invested in each egg.

Thus, as food availability increased, so would egg mass.

There are, however, obvious morphological and physiological limits to using egg size as an effective reproductive strategy. Rahn et al. (1975) showed that egg mass increases as a function of adult body mass. They regressed log egg mass on log body mass which results in a regression equation expressing egg mass ( $W$ ) as a function of body mass ( $B$ ) raised to a power:  $W = aB^b$ . They found that  $b$ , the slope of the log-log regression, was essentially constant among the 17 orders of birds analyzed and equal to 0.675. "Considering a common slope for all orders of birds is of considerable interest as it tells us that as a general rule egg weight increases in proportion to the surface of the female" (Rahn et al. 1975).

In this study I examined the relationship between food abundance and reproductive patterns in the American Coot (*Fulica americana*). Coots breed on marshes and feed aquatic insects and vegetation to their semiprecocial young (Fitzner and Schreckhise 1979). Marshes are ideal for studying the effects of local ecological variation because adjacent lakes may differ enormously in resource quality (Orians 1980). Furthermore, coots obtain most of their energy requirements for reproduction from their breeding territories (Alisauskas and Ankney 1985). Given the feeding habits of coots and the resource variation of marshes, the breeding efforts of coots present a model system in which to examine the effects of

<sup>1</sup> Received 8 April 1987. Final acceptance 14 October 1987.

<sup>2</sup> Present address: Department of Psychology, Busch Campus, Rutgers University, New Brunswick, NJ 08903.

food abundance on reproductive patterns. My main goal was to measure the effect of variation in resource density on the clutch size and egg mass of coots from the same population, breeding on different quality habitats. I examined the influence both of naturally occurring differences and of experimentally manipulated food resources. Because coots only feed within their own territories (Gullion 1954), experimental addition of food was easy to conduct and allowed me to examine proximate causes rather than just observe correlational associations. I then conducted a more complete analysis of egg and clutch size among the Rallidae, than did Rahn et al. (1975), to determine whether coots alter these reproductive parameters relative to the reproductive effort characteristic of their family.

## METHODS

The Turnbull National Wildlife Refuge, 30 km south of Spokane in eastern Washington, has lakes which vary in productivity and support large coot populations. For information regarding the ecology of my study site see Orians (1980). In 1981 four lakes were chosen for this study: Findley, McDowell, Isaacson, and East Tritt. Pine Lake was added in 1982 because only one pair of coots bred successfully on McDowell Lake that year.

Coot nests were located by wading or canoeing through the marsh area and were checked daily. Eggs were numbered using a waterproof marker as they were laid. All eggs were weighed with a Pesola 50-g scale and I used weight as my standard measure of mass. Chicks were weighed on the day of hatching and toe-clipped for individual recognition. During 1982, tarsus, wing, and culmen measurements were also recorded using vernier calipers.

Adults were caught at night using nest traps (Crawford 1977). Birds were weighed and body measurements were recorded. Individually color-coded wing tags and U.S. Fish and Wildlife Service aluminum leg bands were placed on the adults.

## FOOD ABUNDANCE

Adult coots are primarily vegetarians; 60% of their diet consists of algae and pondweed (Fitzner and Schreckhise 1979). Parents feed their semi-precocial young during their first 3 weeks of life. Animal foods, particularly emergent insects, are important for young coots (Fitzner and Schreckhise 1979). Evaluating food availability, there-

fore, required assessing the abundance of both vegetation and insects. Three measures of lake productivity were used to rank the study lakes according to the abundance of food: water conductivity, insect abundance, and the breeding distribution of blackbirds.

The conductivity of lake water is directly correlated with the concentrations of dissolved solids and the productivity of plankton (Rawson 1961, Weller 1981). Orians (1966, 1980) has shown that conductivity is a good indicator of lake quality in the Pacific Northwest; it estimates both plant and insect abundance. Every 2 weeks I collected a water sample from each lake. The conductivity of the samples was measured using a Hach conductivity meter and samples from all lakes were collected and analyzed on the same day.

Emerging insects were captured in 1-m<sup>2</sup>, wire-mesh insect traps (Cook and Horn 1968). One trap was placed on each lake during the third week of June. The location of the trap was changed daily to assess insect abundance over a variety of locations on each lake. The traps were checked in the early morning to collect insects caught the previous day.

The numbers of Red-winged (*Agelaius phoeniceus*) and Yellow-headed blackbird (*Xanthocephalus xanthocephalus*) nests on each lake were monitored during 1982. These birds are dependent upon emergent insects and sensitive to variations in their abundance (Orians 1980). Yellow-headed Blackbirds are competitively dominant over the smaller, Red-winged Blackbirds and thus breed on more productive lakes where their habitats overlap (Orians and Horn 1969). And, although the water level and vegetation structure of marshes can influence blackbird-nesting patterns these two variables did not have an appreciable effect on my study lakes. The ratio of Yellow-headed to Red-winged blackbird nests on a particular lake will therefore give an indication of insect abundance.

## ENRICHMENT PROCEDURE

During 1982 three randomly selected territories on Findley Lake (a low food abundance lake) were artificially enriched by adding 1 kg of Purina Hi-Protein Dog Meal to each three times a week. The remaining four unsupplemented territories on Findley Lake served as controls. Extensive behavioral observations for another aspect of this research (Hill 1984) enabled me to accurately

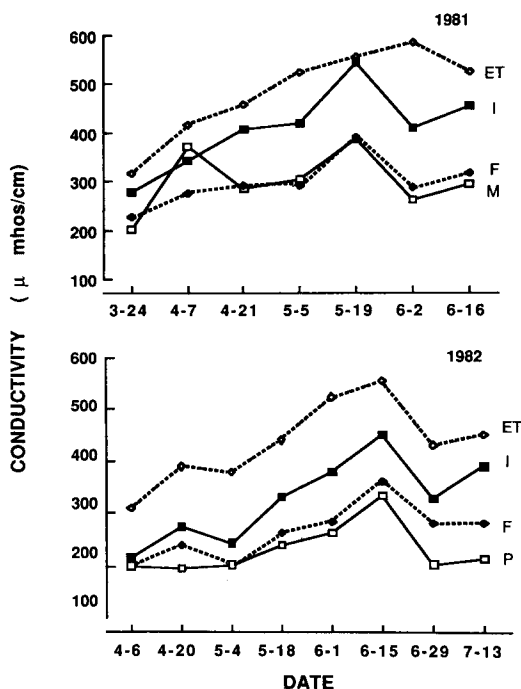


FIGURE 1. Semimonthly conductivity measures of the study lakes at the Turnbull National Wildlife Refuge during 1981 and 1982. F = Findley; M = McDowell; I = Isaacson; ET = East Tritt; P = Pine.

determine territory boundaries. The dog meal was distributed throughout the central confines of the enriched territories and remained available for consumption for at least 2 days. Because water flow was minimal, the dog food did not enter the control territories on the lake. In addition, during my behavioral observations, I saw pairs from the enriched territories eat the dog food, whereas I never saw pairs from the adjacent control territories use the supplemental food. The dog meal contained ground yellow corn, soybean meal, meat and bone meal, and corn gluten meal, and had a protein component of 26%. Food enrichment began the last week of March and continued until the end of June.

#### COMPARATIVE ANALYSIS

From the literature I gathered data for 40 species, representing nine different genera of rails (Ridpath 1972, Siegfried and Frost 1975, Ripley 1977). Egg measurements for *Porzana carolina* and *F. americana* were from nests I examined in eastern Washington. When egg weights were not given in the primary sources, they were calculated using Hoyt's (1979) equation:  $W =$

$0.542LD^2$ , where L = length, D = maximum diameter or breadth, and 0.542 is a constant. Egg mass can be estimated within 2% using this equation (Hoyt 1979).

#### DATA ANALYSIS

For both egg mass and chick mass, interclutch variance was greater than intraclutch variance. To control for this among-female variation, I used a mean from each nest as the value for egg mass and chick mass. For planned comparisons I used ANOVA orthogonal comparisons (Sokal and Rohlf 1981). Scheffé's test was used for a posteriori comparisons ( $P < 0.05$ ).

#### RESULTS

##### RESOURCE ABUNDANCE

Lakes differed in conductivity during both years (two-way ANOVA without replication [Sokal and Rohlf 1981:344]: [1981:  $F = 29.3$ ,  $df = 3, 18$ ;  $P < 0.001$ ] [1982:  $F = 84.1$ ,  $df = 3, 21$ ;  $P < 0.001$ ]) and conductivity increased over time ([1981:  $F = 8.61$ ,  $df = 6, 18$ ;  $P < 0.001$ ] [1982:  $F = 27.36$ ,  $df = 6, 21$ ;  $P < 0.001$ ]). In 1981, Findley and McDowell lakes had significantly lower conductivities than Isaacson or East Tritt lakes (Fig. 1). In addition, the conductivities from East Tritt Lake were significantly greater than those collected from Isaacson Lake. Findley and McDowell lakes, however, did not differ in conductivity. These differences were replicated during 1982 except that Pine Lake substituted for McDowell Lake as a low conductivity lake (Fig. 1).

Insect emergence patterns were consistent with the conductivity data (Table 1). Significantly more insects were caught on Isaacson and East Tritt lakes than on the other three lakes during both years (two-way ANOVA without replication [1981:  $F = 35.6$ ,  $df = 3, 18$ ;  $P < 0.001$ ] [1982:  $F = 51.9$ ,  $df = 3, 18$ ;  $P < 0.001$ ]). In addition, East Tritt Lake yielded significantly more insects than Isaacson Lake whereas the lakes with lower insect abundance did not differ. Day of sampling had no significant effect on the number of insects caught.

Lastly, the breeding abundance of Yellow-headed Blackbirds relative to Red-winged Blackbirds for each lake, again supports a similar pattern of resource abundance (Table 2). Only Red-winged Blackbirds bred on Findley Lake whereas Pine Lake had near equal numbers of

TABLE 1. Total number and  $\bar{x} \pm SD$  of insects collected per day over a 1-week period in June during 1981 and 1982 at the Turnbull National Wildlife Refuge.

Lake	Total no. of insects	$\bar{x} \pm SD/day$
1981		
Findley	37	5.3 $\pm$ 1.5
McDowell	42	6.0 $\pm$ 3.3
Isaacson	86	12.3 $\pm$ 4.6
East Tritt	137	19.5 $\pm$ 7.6
1982		
Findley	51	7.3 $\pm$ 2.9
Pine	43	6.1 $\pm$ 4.1
Isaacson	105	15.0 $\pm$ 4.2
East Tritt	164	23.4 $\pm$ 10.2

the two species. Isaacson Lake had approximately three times as many Yellow-headed Blackbird as Red-winged Blackbird nests and East Tritt Lake supported about 50% more Yellow-headed Blackbirds.

The three productivity measures have significant agreement for ranking the lakes by resource abundance ([1981: Kendall's coefficient of rank correlation,  $r_s = 1.0$ ,  $P < 0.05$ ] [1982: Kendall's coefficient of concordance,  $r_s = 1.0$ ,  $P < 0.05$ ]). The ranking results, in conjunction with the significant differences found within each productivity measure, strongly suggest that East Tritt Lake had the greatest abundance of resources, followed by Isaacson Lake, and that both these lakes had significantly more food available than Findley, McDowell, and Pine lakes. Therefore, for convenience, the former lakes will be characterized as high abundance while the latter will be termed low abundance lakes.

#### NESTING PATTERNS

During the two breeding seasons 145 American Coot nests were located: 53 in 1981 and 92 in 1982. The temporal patterns of breeding were quite different between these years. Due to an early spring in 1981, coots initiated breeding by the end of March, more than a month before breeding was begun in 1982. The median hatch date for nests in 1981 was 24 May, whereas in 1982 it was 13 June.

The resource abundance of lakes did not influence the pattern of nest initiation during 1981 (Kruskal-Wallis rank order analysis:  $H = 5.7$ ,  $P > 0.10$ ). Nesting was equally represented among lakes across the breeding season. In 1982

TABLE 2. Frequency of Yellow-headed and Red-winged blackbird nests on lakes at the Turnbull National Wildlife Refuge during 1982.

Lake	Yellow-headed (Y)	Red-winged (R)	Y/R
Findley	0	18	0
Pine	26	22	1.2
Isaacson	28	10	2.8
East Tritt	38	27	1.5

the lakes differed significantly in the temporal pattern of breeding (Kruskal-Wallis test:  $H = 9.95$ ,  $P < 0.05$ ) but the nesting sequence was not consistent with the resource abundance of the lakes. Pine and East Tritt lakes had more nests hatching early in the breeding season than Findley and Isaacson lakes. In addition, the coots from enriched territories on Findley Lake did not breed earlier than those from the control territories (Fisher's exact probability median test:  $P = 0.11$ ). Thus, supplemental feeding and a greater abundance of resources did not affect the start of breeding in American Coots. Horsfall (1984) also found that supplemental feeding had no effect on the time of breeding in the Eurasian Coot (*F. atra*). These results contrast with research on other species demonstrating that pairs with supplemental food breed earlier (e.g., crows: Yom-Tov 1974; Great Tits: Kallander 1974; kestrels: Drent and Daan 1980).

#### CLUTCH SIZE

The modal clutch size during both years was eight. With more food potentially available one might predict larger clutches on the more productive lakes. Clutch size, however, did not vary systematically with lake quality. The sizes of completed clutches laid on the four lakes during 1981 did not differ (ANOVA:  $F = 0.35$ ,  $df = 3, 33$ ;  $P > 0.50$ ). The mean clutch size ranged from  $8.9 \pm 1.25$  (SD) on East Tritt Lake to  $10.0 \pm 2.76$  (SD) on Findley Lake. Similarly when only first clutches (i.e., not renests) were compared, again there were no significant differences during 1981 (ANOVA:  $F = 0.64$ ,  $df = 3, 23$ ;  $P > 0.50$ ).

Analyses of all clutches (ANOVA:  $F = 2.78$ ,  $df = 3, 61$ ;  $P < 0.05$ ) and of only first clutches ( $F = 3.58$ ,  $df = 3, 46$ ;  $P < 0.05$ ) showed significant differences among lakes in 1982. However, this was due to a difference between Findley and Pine lakes, two low abundance lakes, rather than between high and low abundance lakes. The mean clutch size for control territories on Findley Lake

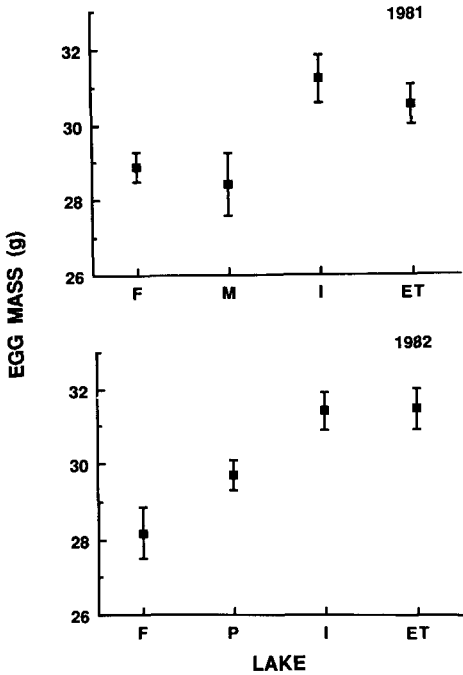


FIGURE 2. Egg mass (g) from coot nests at the Turnbull National Wildlife Refuge during 1981 and 1982. F = Findley; M = McDowell; I = Isaacson; ET = East Tritt; P = Pine. Bars indicate standard errors.

was  $9.3 \pm 2.5$  (SD) whereas the mean for Pine Lake was  $6.4 \pm 2.1$  (SD). The difference in clutch sizes between these two lakes was statistically significant (Scheffé's test:  $P < 0.05$ ).

The mean clutch size for first nests on enriched ( $7.6 \pm 0.58$  [SD]) and on control ( $9.3 \pm 2.5$  [SD]) territories at Findley Lake were statistically different (Fisher's exact probability median test:  $P < 0.05$ ). This result is the opposite of what would be predicted, given a greater abundance of resources. However, each group had one pair which re-nested due to predation: when these two re-nests are included, the mean for the enriched territories was  $8.75 \pm 1.26$  (SD) and for the control territories was  $9.0 \pm 2.7$  (SD), and these were not significantly different (Fisher's exact probability median test:  $P = 0.23$ ). Thus, greater food supplies did not result in larger clutches among coots: clutch size seemed to be resistant to food changes.

#### EGG MASS

Egg mass increased significantly with the productivity of the lake during both breeding seasons (Fig. 2). Heavier eggs were laid on lakes with

greater food abundance (ANOVA [1981:  $F = 3.74$ ,  $df = 3, 49$ ;  $P < 0.05$ ] [1982:  $F = 4.49$ ,  $df = 3, 78$ ;  $P < 0.005$ ]). Nests from Isaacson and East Tritt lakes had consistently heavier eggs than did nests from the lower quality lakes (Fig. 2). There were no differences between egg masses from Isaacson and East Tritt lakes during either 1981 or 1982, whereas these differed significantly from the other lakes.

Eggs from enriched territories on Findley Lake were significantly heavier than those from unenriched territories (Mann-Whitney  $U$ -test,  $U = 12$ ;  $P < 0.05$ ). The mean for eggs laid on the three enriched territories was  $29.7 \pm 0.38$  (SD) g which was 5% greater than the mean for the control territories ( $\bar{x} = 28.1 \pm 0.08$  g). Thus, supplemental feeding appeared to influence proximate mechanisms controlling egg size.

To determine if there were trade-offs between clutch size and egg size, the mean within-nest egg mass was regressed on clutch size. In neither year were these reproductive parameters significantly related. Similarly, the lack of a significant association persisted when clutch size was regressed on egg mass.

#### CHICK MASS

During the 2 years, the egg mass from which 38 chicks had hatched was known. Egg mass explained 67% of the variation in chick mass at hatching ( $Y = 0.58x^{1.06}$ ;  $r^2 = 0.66$ ,  $P < 0.001$ ). Because the slope of the log-log regression was not significantly different from one, chick hatching mass represented a constant proportion of egg mass. However, because on some of the lakes we were only able to catch chicks from a small number of nests (e.g., only two nests at Findley in 1981), analyses of variance did not reveal an overall significant difference in chick mass among lakes. Nevertheless, the means were positively related to habitat differences. For example, chicks from East Tritt Lake averaged 14% more mass than those from McDowell Lake during 1981.

Wing length was also significantly related to egg mass ( $Y = 5.73x^{0.44}$ ;  $P < 0.001$ ) although tarsus length and bill measurements were not. Tarsus length was significantly related to chick mass ( $Y = 7.6x^{0.25}$ ;  $P < 0.005$ ), as was wing length ( $Y = 11.0x^{0.27}$ ;  $P < 0.005$ ).

#### COMPARATIVE ANALYSIS

The allometric equation of egg mass on body mass for the 40 species of rails was  $W = 0.632B^{0.63}$

( $P < 0.001$ ). This relation is similar to that found by Rahn et al. (1975) for nine members of the Gruiformes. Body mass explained 91% of the variation in egg mass. As shown in Figure 3, *F. americana* fell 1 SD below the regression equation. Thus, American Coots lay lighter eggs than would be predicted on the basis of body mass alone. For example, *F. americana* is comparable to *F. atra* in size and yet the eggs of American Coots are 24% lighter.

Clutch weight (CW; mean clutch size multiplied by mean egg mass) was significantly related to body mass ( $CW = 3.93M^{0.61}$ ;  $P < 0.001$ ). Similarly, the percent of body mass represented by clutch weight was a decreasing function of body size ( $Y = 391.9x^{-0.39}$ ;  $r^2 = 0.51$ ,  $P < 0.01$ ). This is accomplished by relatively smaller eggs rather than smaller clutches because clutch size (CS), itself, was *not* a function of body size ( $CS = 6.22M^{0.01}$ ;  $P > 0.05$ ). This is in contrast with many other birds in which clutch size is strongly related to body mass. Ar and Yom-Tov (1978) suggest that among precocial birds clutch size is inversely related to body mass, whereas among altricial species the relationship is positive. In semiprecocial birds, clutch size appears to be constant across body size and in rails is equal to about six. The clutch size of American Coots ( $\bar{x} = 8.5$ ) is therefore 40% greater than the average clutch size for the family. In fact, only five species of rails laid larger clutches than American Coots. Thus, coots tend to lay smaller eggs but larger clutches.

## DISCUSSION

Studying both natural correlations and experimental manipulations of resources is crucial if we are to understand the effect that variations in food abundance have over ultimate breeding success (Drent and Daan 1980). Using these two methods, my results suggest that increased food supplies affect the reproductive effort of coots by increasing the condition of young produced. Coot egg mass was positively related to the naturally occurring resource differences among breeding lakes. Moreover, supplemental food increased egg size relative to controls from the same habitat. Clutch size did not vary systematically with either resource variable.

Variations in food abundance may influence different reproductive parameters, depending upon the species (Lack 1968, Miller et al. 1970, Bengston 1971, Drent and Daan 1980, Hogstedt

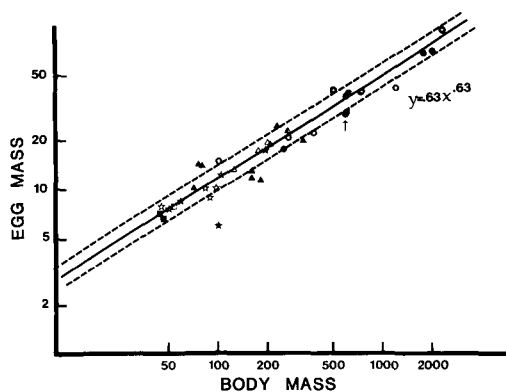


FIGURE 3. Allometric (log-log) regression for egg mass (g) on body mass (g) for 40 species of the Rallidae. Arrow indicates coordinates for *Fulica americana*. Symbols correspond to different genera: closed circles—*Fulica*; open circles—*Gallinula*; closed circles with stars—*Phorphyrio*; closed stars—*Rallina*; open stars—*Porzana*; closed triangles—*Rallus*; open triangles—*Amaurornis*; closed squares—*Coturnicops*; open squares—*Laterallus*. Broken lines indicate  $\pm 1$  SD.

1981, Winkler and Walters 1983). Horsfall (1984), for example, did not find significantly heavier eggs among the Eurasian Coot breeding on grain-enriched territories, although there was lower within-clutch variation in egg mass. This decreased variation resulted from the first eggs laid in nests on experimental territories being larger than those from control territories. The causes for these species differences remain to be determined. My comparative analysis of the reproductive effort of rails suggests an explanation for the characteristic pattern of coots. American Coots lay smaller eggs than would be predicted on the basis of their size and family group. Consequently, they have the capacity, anatomically, to lay larger eggs than they do typically. If they laid relatively large eggs for their size they would not have the ability to respond to variations in food abundance by increasing egg size but might respond by laying a larger clutch. However, their clutches are already among the largest for rails. The lack of a strong correlation between increased food supply and a generalized increase in egg mass in the closely related Eurasian Coot may be due to the fact that they typically lay relatively large eggs for their size. This is not to suggest that American Coots evolved the characteristic of laying small eggs so that they could respond to environmental conditions by varying egg size. Rather, the option of increasing egg size

is a by-product of American Coots laying characteristically small eggs.

A possible evolutionary explanation for the typical pattern of laying relatively small eggs in coots is that it is the result of selection for high reproductive rates in response to unpredictable breeding conditions. Grant (1982) has proposed this hypothesis to explain the small eggs of Darwin's finches (however, upon further analysis it appears that Darwin's finches lay relatively large eggs for their body size [Scott and Ankney 1983, Grant 1983]). Coots breed in unpredictable environments (Orians 1980, Weller 1981) and rapid breeding may be an important response for coping with uncertain environmental variations.

Another important consequence of small eggs is a shorter incubation period, which also contributes to rapid breeding. Incubation length can be predicted from a bird's body mass (Rahn et al. 1975). Examining this relationship for coots gives an estimate of 27 days incubation, whereas the actual value is between 21 and 23 days (Gullion 1954, Fredrickson 1970, Hill 1986). Thus, smaller eggs allow chicks to hatch sooner and possibly benefit from favorable conditions. In addition, it may also shorten the exposure of eggs to predators. Predation can be extensive among coots (Errington 1967); as many as two thirds of the nests on a lake may be lost to predators (Hill, unpubl. data). Following predation, renesting is common. I have observed pairs which laid as many as four clutches because their earlier nests were taken by predators. Coots are quick reneesters and laying small eggs may be a way to decrease the investment in each clutch given that there is a high probability of the nest failing.

Nevertheless, when conditions appear favorable for breeding (e.g., a great abundance of food) coots increase the size of their young. In a wide variety of species, chicks hatching from larger eggs have a higher probability of survival to fledging (Parsons 1970, Schifferli 1973, Davis 1975, Nisbet 1978, Boersma and Wheelwright 1979, Williams 1980). Increased survival may be due to (1) larger eggs providing the chicks with more food reserves at hatching, an advantage if food is scarce, or (2) larger eggs giving rise to chicks whose bigger size better enables them to compete with siblings, or be more adept at foraging. My evidence is consistent with the latter situation: body proportions of chicks at hatching were significantly correlated with egg size differences. There would be no relationship between

chick mass and body proportions, such as wing length, if increased egg size was due solely to increased food reserves (yolk). Heavier chicks would be fatter due to yolk retention, rather than larger. An analysis of the yolk and albumen components of coot eggs supports the conclusion that chicks were not heavier because of increased amounts of yolk: larger eggs contained significantly greater amounts of albumen whereas the percent of yolk decreased (Hill 1984). Given that large chicks grow to be large adults (Widdowson 1964), chicks raised on high productivity lakes may always be at a competitive advantage over their conspecifics from low productivity lakes.

In summary, the observed reproductive patterns of coots are the result of the interaction between ultimate and proximate factors determining egg size. Evolutionary pressures, possibly high predation rates, influenced the species-typical pattern of laying relatively small eggs whereas proximate factors, like food availability, affect the individual's reproductive effort within a given season. And, in turn, these individual responses can have evolutionary ramifications.

#### ACKNOWLEDGMENTS

I thank T. J. Jackson and B. J. Higgins for their assistance in the field. D. P. Barash, P. D. Boersma, W. J. Erckmann, R. B. Huey, P. J. Morin, and R. D. Stevenson provided helpful comments on the manuscript. The research was supported by the American Ornithologists' Union through a Josselyn van Tyne Research Award and a Herbert and Betty Carnes Research Award. Additional support was provided by the American Museum of Natural History and Sigma Xi. Eastern Washington University allowed me to use the excellent facilities at the Turnbull Laboratory for Ecological Studies. I gratefully acknowledge the help of the biologists and staff at the Turnbull National Wildlife Refuge.

#### LITERATURE CITED

- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1985. Nutrient reserves and the energetics of reproduction in American Coots. *Auk* 102:133-144.
- AR, A., AND Y. YOM-TOV. 1978. The evolution of parental care in birds. *Evolution* 32:655-669.
- BENGSTON, S. A. 1971. Variations in clutch-size in ducks in relation to the food supply. *Ibis* 113:523-526.
- BOERSMA, P. D., AND N. T. WHEELWRIGHT. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the Fork-tailed Storm-Petrel. *Condor* 81:157-165.
- COOK, P. P., AND H. S. HORN. 1968. A sturdy trap for sampling emergent *Odonata*. *Ann. Entomol. Soc. Am.* 61:1506-1507.
- CRAWFORD, R. D. 1977. Comparison of trapping

- methods for American Coots. *Bird-Banding* 49: 209-213.
- DAVIS, J.W.F. 1975. Age, egg-size and breeding success in the Herring Gull *Larus argentatus*. *Ibis* 117:460-473.
- DRENT, R. H., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225-252.
- ERRINGTON, P. 1967. Of predation and life. Iowa State Univ. Press, Ames.
- FITZNER, R. E., AND R. G. SCHRECKHISE. 1979. The American Coot on the Hanford site. Battelle Memorial Institute Document #PNL-2462, Richland, WA.
- FREDRICKSON, L. 1970. Breeding biology of American Coots in Iowa. *Wilson Bull.* 64:83-97.
- GEISEL, J. T. 1976. Reproductive strategies as adaptations to life in temporarily heterogeneous environments. *Annu. Rev. Ecol. Syst.* 7:57-79.
- GRANT, P. R. 1982. Variation in the size and shape of Darwin's finch eggs. *Auk* 99:15-23.
- GRANT, P. R. 1983. The relative size of Darwin's finch eggs. *Auk* 100:228-230.
- GULLION, G. W. 1954. The reproductive cycle of American Coots in California. *Auk* 71:366-412.
- HILL, W. L. 1984. The reproductive ecology of the American Coot (*Fulica americana*). Ph.D.diss., Univ. of Washington, Seattle.
- HILL, W. L. 1986. Clutch overlap in American Coots. *Condor* 88:96-97.
- HOGSTEDT, G. 1981. Effect of additional food on reproductive success in the magpie (*Pica pica*). *J. Anim. Ecol.* 50:219-229.
- HORSFALL, J. A. 1984. Food supply and egg mass variation in the European coot. *Ecology* 65:89-95.
- HOYT, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73-77.
- KALLANDER, H. 1974. Advancement of laying of Great Tits by the provision of food. *Ibis* 116:365-367.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, NJ.
- MILLER, G. R., A. WATSON, AND D. JENKINS. 1970. Responses of red grouse populations to experimental improvement of their food, p. 323-335. In A. Watson [ed.], *Animal populations in relation to their food resources*. Blackwell Press, Oxford.
- NISBET, I.C.T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate terns, *Sterna hirundo* and *S. dougallii*. *Ibis* 120:207-215.
- ORIAN, G. H. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. *Condor* 68:321-337.
- ORIAN, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton University Press, NJ.
- ORIAN, G. H., AND H. S. HORN. 1969. Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. *Ecology* 50: 930-937.
- PARSONS, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). *Nature* 228:1221-1222.
- RAHN, H. C., C. V. PAGANELLI, AND A. AR. 1975. Relation of avian eggs to body weight. *Auk* 92: 750-765.
- RAWSON, D. S. 1961. A critical analysis of the limnological variables used in assessing the productivity of northern Saskatchewan lakes. *J. Limnol.* 14:160-166.
- RIDPATH, M. G. 1972. The Tasmanian Native Hen, *Tribonyx mortierii*, III. *Ecology*. CSIRO Wildl. Res. 17:91-118.
- RIPLEY, S.D. 1977. *Rails of the world*. Godine, Boston.
- SCHIFFERLI, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits *Parus major*. *Ibis* 115:549-558.
- SCOTT, D. M., AND C. D. ANKNEY. 1983. Do Darwin's finches lay small eggs? *Auk* 100:226-267.
- SIEGFRIED, W. R., AND P.G.H. FROST. 1975. Continuous breeding and associated behavior in the Moorhen *Gallinula chloropus*. *Ibis* 117:102-109.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. Freeman and Co., San Francisco.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51:3-47.
- WELLER, M. W. 1981. *Freshwater marshes*. Ecology and wildlife management. Univ. of Minnesota Press, Minneapolis.
- WIDDOWSON, E. M. 1964. Early nutrition and later development. In G.E.W. Wolstenholme and M. O'Connor [eds.], *Diet and bodily constitution*. Little, Brown and Co., Boston.
- WILLIAMS, A. J. 1980. Variation in weight of eggs and its effect on the breeding biology of the Great Skua. *Emu* 80:198-202.
- WINKLER, D. W., AND J. R. WALTERS. 1983. The determination of clutch size in precocial birds, p. 33-68. In R. F. Johnston [ed.], *Current ornithology*. Vol. 1. Plenum Press, New York.
- YOM-TOV, Y. 1974. The effect of food and predation on breeding density and success, clutch size and laying date of the Crow (*Corvus corone* L.). *J. Anim. Ecol.* 43:479-498.