

on its back, and feathers around the elbow of either wing were swabbed with water to expose the brachial vein. This vein was punctured with a lancet, and blood was collected in one or two heparinized capillary tubes and a 10- μ l Unopette capillary pipette. The tubes were centrifuged at 16,580 G for 11 min and the PCV measured with a mm ruler. Capillary tubes were centrifuged within 6 hr of drawing the blood. Blood samples were kept at 10° to 15°C between collection and centrifugation. The Unopette capillary pipette was emptied into a previously opened Unopette reservoir containing 1.99 ml of diluent (Unopette Test 5850/5851; Unopette is a trademark of Becton, Dickinson and Co., Rutherford, NJ 07070). Erythrocyte numbers were determined with a hemocytometer from 2 to 3 samples of this mixture. Mean hematological values were compared by means of Student's *t*-tests.

RESULTS AND DISCUSSION

The mean hematocrits of Cooper's Hawks (49.2%) and Sharp-shinned Hawks (49.5%) were not significantly different (Table 1). For both species, hematocrits did not differ between the sexes or between immatures and adults.

Hunter and Powers (1980) reported a hematocrit of 45.0% for one Cooper's Hawk and $52.8 \pm 3.2\%$ for two Goshawks of unknown sex. Seal (cited in Elliott et al. 1974) measured an average hematocrit of 43.3% for four captive Goshawks of unknown sex and age.

Erythrocyte counts of Cooper's ($3.74 \times 10^6/\text{mm}^3$) and Sharp-shinned Hawks ($3.39 \times 10^6/\text{mm}^3$) were not significantly different (Table 2). The counts for immatures did

not differ significantly from those of adults, nor did males differ significantly from females for either species. Campbell and Dein (1984) indicate that in general the number of RBCs and hematocrit increase with age and are higher in male than female birds. Although our data on accipiters contain no statistically significant differences, they are consistent with this trend. Hematocrits and RBC counts in the literature are too few to make any meaningful comparisons between captive raptors and our sample of free-living raptors.

We thank EARTHWATCH, Belmont, Massachusetts, for providing part of the funding for this project and the Bureau of Land Management, Elko (Nevada) district, for logistical support. We appreciate the help of P. L. Kennedy in collecting and processing blood samples.

LITERATURE CITED

- CAMPBELL, T. W., AND F. J. DEIN. 1984. Avian hematology: the basics. *Vet. Clin. North Am. Prac.* 14: 223-248.
- ELLIOTT, R. H., E. SMITH, AND M. BUSH. 1974. Preliminary report on hematology of birds of prey. *J. Zool. Anim. Med.* 5:11-16.
- HART, J. S., AND M. BERGER. 1972. Energetics, water economy and temperature regulation during flight. *Proc. XV Int. Ornithol. Congr.*, 1970, p. 189-199.
- HUNTER, S. R., AND L. R. POWERS. 1980. Raptor hematocrit values. *Condor* 82:226-227.

The Condor 88:96-97
© The Cooper Ornithological Society 1986

CLUTCH OVERLAP IN AMERICAN COOTS¹

WENDY L. HILL²

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

Key words: Clutch overlap; reproduction; clutch size; parental care; coots.

It is unusual for parents to begin a second clutch while their first brood is still dependent upon them for parental care. However, by overlapping two clutches, which together may be more than a pair could rear as a single clutch during the most demanding investment period, parents may overcome the constraints that clutch size maintains over the total number of offspring produced (Burley 1980). Thus, in three reported cases of clutch overlap (Siegfried and Frost 1975, Burley 1980, Hays 1984), the period of simultaneous investment in two broods occurred during the least demanding phase of offspring development for the first clutch. The length of the breeding season relative to the developmental rate of the young may be an additional constraint which prevents parents from rearing two broods unless they overlap successive clutches. Accordingly, clutch overlap in Common Terns (*Sterna hi-*

rundo) occurred only among pairs breeding early in the season (Wiggins et al. 1984).

The general success of overlapping clutches remains to be determined, and an examination of this uncommon behavior may suggest specific factors which constrain parents from rearing more young. During a four-year study of the American Coot (*Fulica americana*), I noted seven cases in which pairs overlapped two clutches and attempted to rear both broods. The period of overlap was greater than that reported for any other birds. I discuss here the characteristics of clutch overlap in coots and the potential environmental factors and parental investment patterns which influence this reproductive behavior.

I studied the breeding biology of coots along the northwest shore of Lake Washington (LW), Seattle, Washington during 1980 and 1983 and at the Turnbull National Wildlife Refuge (TNWR), Spokane County, Washington, during 1981 and 1982. Coots from these areas typically rear one brood per season. Nests were located by wading or canoeing through the marshes and were checked daily. After eggs were laid, I numbered them with a waterproof marker. All eggs were weighed with a Pesola 50-g scale to the nearest 0.1 g and measured with vernier calipers. U.S. Fish and Wildlife aluminum leg bands and individually color-coded wing tags or neck collars were placed on adult birds caught at night with nest traps (Crawford 1977).

¹ Received 30 November 1984. Final acceptance 23 September 1985.

² Present address: Department of Psychology, Rutgers University, New Brunswick, New Jersey 08903.

During the four breeding seasons, I found seven cases of clutch overlap among 88 successful nests. Five occurred at TNWR during 1981 and two at LW during 1980. In all instances the second clutch of eggs was laid in the same nest a few days before the first clutch hatched, or as it hatched. This laying sequence resulted in the simultaneous incubation of the first and second clutches. I considered the two groups of eggs as separate clutches because the embryos were in different developmental phases. Incubation lasts between 21 and 23 days in coots (Gullion 1954, Fredrickson 1977). The average period between the initiation of the first and second clutches in the same nest was 21 days (range: 19 to 23).

In two cases, either the second clutch or both clutches were taken by predators. A third set of parents failed to hatch their second clutch because they deserted the nest after I banded one of the pair. Thus, only four pairs successfully hatched their second clutches.

Several lines of evidence suggest that in each case the overlapping clutches were laid by the same female. The eggs of the first and second clutches were of similar size. The population variances for egg weight, length, and width were not equal to the mean variance for these measurements within clutch-overlap nests ($F_{\max} = \text{test}$ [Sokal and Rohlf 1981]; egg weight [$F = 5.43, P < 0.01$]; length [$F = 4.26, P < 0.01$] and width [$F = 5.66, P < 0.01$]). In addition, the pigmentation and speckling patterns of the two groups of eggs within a nest were indistinguishable; females typically lay eggs with individually distinctive markings (Yom-Tov 1980). Lastly, I observed all pairs daily and found that they consistently and vigorously defended their territories against intruders (Hill 1984). These observations together suggest that the second clutch in each case was laid by the female that owned the nest.

Females in pairs with overlapping clutches laid more total eggs than the average number laid by females in pairs with a single clutch. In 1980 the mean clutch size for females with a single clutch was 8.0 ± 1.5 (SD), whereas the first clutches for the pairs with two clutches each numbered seven and nine eggs, respectively. The totals for both clutches of each pair were 10 and 12 eggs. Similarly, the mean size for single clutches in 1981 was 9.2 ± 2.5 (SD); however, the mean for the first clutch in the overlapped nests was 9.6 ± 1.7 (SD) and the mean total number of eggs laid in both clutches was 14.0 ± 1.2 (SD).

The years in which females laid two clutches were characterized by early breeding. In 1981, 10 of 38 nests (26%) were begun earlier in the season than the first nest was started in 1982. All four cases of clutch overlap in 1981 occurred earlier than the median period of nesting in 1982. Similarly, nearly twice as many nests (seven) were initiated during the first two weeks of the breeding season in 1980 than in a similar period in 1983 (four). The females which laid two clutches initiated nesting during this period. Clutch overlap in Common Terns has also been related to early breeding (Wiggins et al. 1984).

The total number of eggs produced by indeterminate layers is influenced by tactile stimulation (Klomp 1970). Given that coots are indeterminate layers, the second clutch might have resulted from decreased stimulation to the female from the "missing" hatched eggs. In only one case, however, was the second clutch laid after the first clutch had started hatching. In all other cases the second clutch was initiated before the first had begun hatching. Moreover, the lessened stimulation does not account for the seasonal influence of the laying pattern.

I could not determine fledgling success rates for any of the pairs, because it was difficult to count broods accurately when young birds hid in vegetation (Gullion 1954).

Parents feed the young during the first few weeks after hatching (Gullion 1954) and because eggs hatch asynchronously, males and females must continue to incubate eggs while they feed the newly-hatched young. Thus, even when rearing one brood, coots typically divide their time between conflicting parental behaviors: incubation of eggs and the feeding of young, mobile chicks. Parental feeding peaks approximately ten days after the first egg has hatched (Ryan and Dinsmore 1979); nestling starvation during this time can be as high as 40% (Hill 1984). I did not find any nestlings dead from starvation in the territories of pairs that overlapped clutches, which suggests that overlapped clutches may sometimes be successful. For the coots I observed, rearing two overlapping clutches appeared to be similar to the parental activities needed to rear one brood, albeit stretched over a longer time period. Given that pairs attempted to rear two clutches only during early breeding seasons, the crucial factor permitting the production of two broods may have been that there was enough time for the second clutch to reach independence before the breeding season ended.

My research was supported by the American Ornithologists' Union through a Josselyn van Tyne Research Award and a Herbert and Betty Carnes Research Award, by the American Museum of Natural History through a Frank M. Chapman Memorial Research Award, and by the Sigma Xi Research Society. Additional support was provided by a grant to P. D. Boersma from the National Institute of Mental Health. I thank T. J. Jackson and B. J. Higgins for help with the field work. D. Barash and D. Johnson provided useful discussions. Comments by L. Fredrickson, J. Dinsmore and an anonymous reviewer improved the manuscript.

LITERATURE CITED

- BURLEY, N. 1980. Clutch overlap and clutch size: alternative and complementary reproductive tactics. *Am. Nat.* 115:223-246.
- CRAWFORD, R. D. 1977. Comparisons of trapping methods for American Coots. *Bird-Banding* 49:209-213.
- FREDRICKSON, L. 1977. American Coot (*Fulica americana*), p. 123-147. In G. C. Sanderson [ed.], Management of migratory shore and upland game birds in North America. Int. Assoc. Fish and Wildlife Agencies, Washington, DC.
- GULLION, G. 1954. The reproductive cycle of American Coots in California. *Auk* 71:366-412.
- HAYS, H. 1984. Common Terns raise young from successive broods. *Auk* 101:274-280.
- HILL, W. L. 1984. The reproductive ecology of the American Coot (*Fulica americana*). Ph.D. diss., Univ. of Washington, Seattle.
- KLOMP, H. 1970. The determination of clutch size in birds. *Ardea* 58:1-124.
- RYAN, M. R., AND J. J. DINSMORE. 1979. A quantitative study of the behavior of breeding American Coots. *Auk* 96:704-713.
- SIEGFRIED, W. R., AND P. G. H. FROST. 1975. Continuous breeding and associated behavior in the moorhen *Gallinula chloropus*. *Ibis* 115:102-109.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. Freeman and Co., San Francisco.
- WIGGINS, D. A., R. D. MORRIS, I. C. T. NISBET, AND T. W. CUSTER. 1984. Occurrence and timing of second clutches in Common Terns. *Auk* 101:281-287.
- YOM-TOV, Y. 1980. Intraspecific nest parasitism in birds. *Biol. Rev.* 55:93-108.