MALE-DOMINATED INCUBATION IN OSPREYS

KARL E. GROVER

In mated pairs of Ospreys (*Pandion haliaetus*), incubation is primarily done by the female (Bent 1937, Garber and Koplin 1972, Green 1976, Levenson 1979, Jamieson et al. 1982). I report here a case in which it was done mostly by the male.

I studied incubation behavior of Ospreys nesting at two main-stream reservoirs, Canyon Ferry and Holter, approximately 39 km apart on the upper Missouri River in southwestern Montana. I monitored six nests, three at Canyon Ferry and three at Holter, for 131.7 h on 15 days between 16 May and 6 July 1982, to measure the duration of incubation duties by each sex. Of the observations, 48% were made between 05:30 and 13:30, and 52% were made between 13:30 and 21:30. Observation periods ranged from 2.8 to 13.5 h. In each pair I assumed the female to be the bird with the darker breast patch (Macnamara 1977), and was able to verify this at one nest by observing copulations.

Incubation began mostly during the second and third weeks of May and hatching occurred mostly during the last two weeks of June. At Canyon Ferry, the males at the three nests incubated 0 to 58% of the time on the days observed, only once incubating over 42%. At Holter, they incubated 43 to 71%, only once incubating less than 51%. Table 1 summarizes the results. The percent of time that males incubated differed significantly between the two localities (t = 3.80, df = 15, P < 0.005). I cannot explain this difference in incubation sharing. Stinson (pers. comm.) and my own investigation found weather to have little effect on incubation sharing. No significant difference was found in food habits (Grover 1984), productivity (t =0.93, df = 36, P = 0.18), or number of nests per 1,000 ha of reservoir surface area ($\chi^2 = 1.42$, df = 1, P = 0.24). My findings suggest, however, that the sharing of incubation duties should be measured in future studies of Osprey breeding habits; perhaps then an environmental variable could be identified that influences incubation behavior.

I thank R. L. Eng (Montana State University) for guidance and supervision of the study, J. E. Swenson (Montana Department of Fish, Wildlife and Parks) for critical review

The Condor 86:489-490 © The Cooper Ornithological Society 1984

VARIATION IN THE WEIGHT AND COMPOSITION OF MUTE SWAN (CYGNUS OLOR) EGGS

MIKE BIRKHEAD

Egg composition varies greatly among species (Romanoff and Romanoff 1949), yet eggs of species with precocial young generally have large yolks compared to those with altricial young (Ricklefs 1977). It has been suggested that the amount of yolk varies with the relative precocity of the young (Romanoff and Romanoff 1949, Ricklefs 1977, TABLE 1. Daytime incubation sharing by Ospreys, up-per Missouri River, 1982.

	Canyon Ferry	Holter
No. of nests observed	3	3
Total hours observed	90.4	41.3
Overall percent of incuba	ation by	
Female	74.0 ¹	41.4
Male	25.5	56.8
Neither ²	0.5	1.8

¹ Mean and standard deviation of observed percent male incubation at: Canyon Ferry; R = 23.8, SD = 16.2; Holter, R = 53.9, SD = 10.3. ² Does not include time taken by incubating bird to stand and "stretch" or time required to trade duties with its mate.

of the manuscript, and C. H. Stinson and an anonymous reviewer for helpful comments. During this portion of the study I was supported by the Montana Power Company. This paper is published as Journal Series 1547, Montana Agricultural Experiment Station.

LITERATURE CITED

- BENT, A. C. 1937. Life histories of North American birds of prey. U. S. Natl. Mus. Bull. 167.
- GARBER, D. P., AND J. R. KOPLIN. 1972. Prolonged and bisexual incubation by California Ospreys. Condor 74:201-202.
- GREEN, R. 1976. Breeding behaviour of Ospreys Pandion haliaetus in Scotland. Ibis 118:475-490.
- GROVER, K. E. 1984. Nesting distribution and reproductive status of Osprey along the upper Missouri River, Montana. Wilson Bull. 96:496–498.
- JAMIESON, I., N. SEYMOUR, AND R. P. BANCROFT. 1982. Time and activity budgets of Ospreys nesting in northeastern Nova Scotia. Condor 84:439-441.
- LEVENSON, H. 1979. Time and activity budgets of Ospreys nesting in northern California. Condor 81:364– 369.
- MACNAMARA, M. 1977. Sexing the American Osprey using secondary sexual characteristics, p. 43-45. *In* J. C. Ogden [ed], Transactions of the North American Osprey research conference. U. S. Natl. Park Serv. Trans. Proc. Ser. 2.

6670 Amsterdam Road, Manhattan, Montana 59741. Received 30 January 1984. Final acceptance 5 July 1984.

Carey et al. 1980). The relationship between composition and egg size has been examined in detail for few anseriform eggs. Basic data are available for the domestic duck (Anas sp.), goose (Anser sp.) and Mallard (Anas platyrhynchos) (Romanoff and Romanoff 1949, Carey et al. 1980, Ricklefs 1977). Examining the proportion of yolk in the eggs of many wildfowl species, Lack (1968) concluded that it did not vary significantly with egg size. He discarded the idea that chicks of species with proportionately large eggs might hatch with proportionately large yolk reserves but gave no intraspecific analyses. I studied the eggs of Mute Swan (Cygnus olor) in order to learn their general characteristics and to determine the relationship between egg size and yolk reserves. I wanted to see if larger eggs had disproportionately larger yolk reserves since such eggs may give a survival advantage to newly hatched young.

Ten swan eggs were collected (under license from the Nature Conservancy Council) within 24 h of laying from

ten nests on the River Thames and its tributaries, the Thame and Windrush, near Oxford, England. Nests were selected purely on the basis of availability, that is, as annual nest rounds were made, freshly laid eggs were collected from the first 10 nests visited. Any egg was taken except the first or last laid, as these may be slightly smaller than the others (Bacon 1979). On the same day as collection, the eggs were weighed, measured and hard-boiled so that the yolk and white could be separated easily. The eggs were reweighed after boiling to check that they had not lost weight. Two samples of each egg were dried at 60°C and the lipids extracted in chloroform using the Soxhlet extraction method. Such extraction techniques produce results comparable to those used in other studies. (See Grodzinski et al. 1975, Jones 1979.) Egg volumes were determined using length \times breadth² \times constant (0.512; see Bacon 1979 for details). All values are presented as means with standard errors in parentheses, unless otherwise stated.

The mean egg weight was 364 g (± 9.7 SE, range = 293.7– 396.6 g) and the mean egg volume was 336.6 (10.1 SE). The average egg volume was within the range of a much larger series of samples collected over a five-year period (range of means 328.2-336.7; Birkhead et al. 1983). The wet weight of yolk averaged 135.7 g (4.7 SE) and comprised 37.2% of the wet weight of the fresh egg. This was within a previously quoted range (34-40%) for Mute Swans (see Lack 1968) and is similar to that of other precocial species (Ricklefs 1977). The lipid content of dry yolk was 69.8% (0.3 SE), which was high compared with other precocial species (Ricklefs 1977). In addition, the ratio of yolk to albumen (0.75) was high even compared to that of other wildfowl. Variation in the lipid fraction of dry yolk (range = 68-71%) was positively correlated with wet weight of yolk (r = 0.61, P < 0.05). The water fraction of yolk was 43.4% (0.3 SE), which was similar to that found in other anseriforms (43-48%; Ricklefs 1977) and the wet weight of the yolk increased with fresh egg weight (r =0.90, P < 0.001).

The wet weight of albumen was correlated with fresh egg weight (r = 0.91, P < 0.001). The fraction of water in albumen was 82% (0.54 SE), which was slightly lower than the range quoted for other species (85–90%; Ricklefs 1977).

The relative size of yolk in eggs of various species can best be compared by normalizing the data on yolk weight. This is done by multiplying the slopes of the relationships (of the proportion of yolk on egg weight) by the standard deviations of egg weight (Ricklefs 1977). In the European Starling (Sturnus vulgaris; Ricklefs 1979), Great White Pelican (Pelecanus onocrotalus; Jones 1979) and domestic fowl (Gallus gallus, var. domesticus; Ricklefs 1977), the relationship was negative, indicating a decrease in the amount of yolk with respect to egg size. Interspecific comparisons may be furthered by examining the regression coefficients of the logarithm of fresh weights of the egg components on the logarithm of fresh egg weights (Jones 1979). If the slope of the regression is significantly greater or less than unity, then the proportional contribution of the component increases or decreases respectively with egg weight. If the slopes are not significantly different from unity, then the variables are increasing in proportion with egg weight.

The regression coefficient for the logarithm of wet weight of yolk on the logarithm of fresh egg weight was 1.13 (0.003 SE, r = 0.92, t = 43; testing the slope from a hypothetical value of 1), P < 0.001; log wet weight of albumen on log fresh egg weight was 0.85 (0.002 SE), r = 0.90, t = 75, P < 1000.001 and log yolk lipid on log fresh egg weight 1.21 (0.004 SE), r = 0.91, t = 53, P < 0.001. When I compared the same relationships against log fresh egg weight minus eggshell, I found no significant differences from the above results. In the Mute Swan it appears that as egg weight increases, there is also a relative increase in the total amount of yolk and the lipid in the yolk. To my knowledge, this has not been recorded in any other species. Such a result contradicts Lack's (1968) suggestion that larger eggs will not have proportionately larger yolk reserves. My results indicate that larger Mute Swan eggs may produce hatchlings with proportionately larger yolk reserves. Such cygnets presumably may in turn survive better than those with smaller yolks. Closer intraspecific examination of other precocial species eggs may demonstrate a similar relationshin.

Recent studies on the Mute Swan have demonstrated variation in egg volume and clutch size for different genotypes (Bacon 1979, Birkhead et al. 1983). The dominant homozygote is known to lay larger clutches of smaller eggs; the recessive homozygote lays the smallest clutch with the largest eggs while the heterozygote is intermediate. Consequently, it appears that there might be a trade-off between egg size and clutch size in the Mute Swan.

I am grateful to Jayne Pellat for doing the analyses and to John Horsfall and Tim Birkhead for reading and improving an earlier version of the manuscript.

LITERATURE CITED

- BACON, P. J. 1979. Population genetics of the Mute Swan Cygnus olor. Unpubl. Ph.D. diss. Oxford Univ., Oxford.
- BIRKHEAD, M. E., P. J. BACON, AND P. WALTER. 1983. Factors affecting the breeding success of the Mute Swan. J. Anim. Ecol. 52:727-741.
- CAREY, C., H. RAHN AND P. PARIS. 1980. Calories, water, lipid and yolk in avian eggs. Condor 82:335-343.
- GRODZINSKI, W., R. Z. KLELOWSKI AND A. DUNCAN. 1975. Methods for ecological bioenergetics. I.B.P. Handbook. No. 24. Blackwell Scientific Publications, Oxford.
- JONES, P. J. 1979. Variability of egg size and composition in the Great White Pelican *Pelecanus onocrotalus*. Auk 96:407-408.
- LACK, D. 1968. The proportion of yolk in the eggs of waterfowl. Wildfowl 19:67-69.
- RICKLEFS, R. E. 1977. Composition of eggs of several bird species. Auk 94:350–356.
- RICKLEFS, R. E. 1979. Variation in size and quality of the starling egg. Auk 96:167–168.
- ROMANOFF, A. L. AND A. J. ROMANOFF. 1949. The avian egg. Wiley, New York.

Edward Grey Institute of Field Ornithology, South Parks Road, Oxford OX1 3PS, England. Received 18 October 1983. Final acceptance 7 April 1984.