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PROSPECTING FOR NEST SITES BY CAVITY-NESTING DUCKS OF THE GENUS *BUCEPHALA*

JOHN McA. EADIE

AND

GILLES GAUTHIER

ABSTRACT.—We studied the pattern of post-laying visitation of nest sites by non-nesting females in three species of cavity-nesting ducks, the Common and Barrow's goldeneyes (*Bucephala clangula* and *B. islandica*) and the Bufflehead (*B. albeola*). Nests were visited from mid-June to mid-July when most nesting females either had hatched their clutches or were finishing incubation. Females often visited more than one nest site and each nest site could be visited by several birds. Observations of marked individuals and body measurements of trapped birds show that most visiting females were either yearlings or failed breeders. These females always visited nest sites in intra- or inter-specific groups, and exhibited typical vocalizations and flight patterns. We propose that these females were "prospecting" for nest sites in preparation for the next breeding season. We could not find any detrimental effects of prospecting on incubating females. We also discuss the evolutionary significance of prospecting behavior and its relationship to delayed maturity and nest-site availability for both cavity- and ground-nesting North American ducks.

Selection of an appropriate nest site has an important influence on breeding success in waterfowl. In ground-nesting ducks, nest success and predation rates on nests have been related to both the location and the type of cover near the nest (Schrank 1972, Lokemoen et al. 1984). In cavity-nesting ducks, competition for nest sites can be intense (e.g., Jones and Leopold 1967), and nest-site location has been shown to influence reproductive success in the Common Goldeneye (*Bucephala clangula*; Dow and Fredga 1983). Although much quantitative information is available on nest-site characteristics for many species of ducks (e.g., Bengston 1972, Lokemoen et al. 1984), little is known about the behavioral mechanisms used in nest-site selection.

Most ducks search for nest sites immediately before nesting (Bengston 1972, Bellrose 1976, Palmer 1976). In the genus *Bucephala,* however, females have been reported to search for nest sites at the end of the summer, presumably in preparation for the next breeding season (Grenquist 1963, Bengston 1966, M. Jackson in Bellrose 1976, Cramp and Simmons 1977). This behavior has often been called "nest prospecting," to distinguish it from the more usual form of nest searching at the beginning of the breeding season.

The unusual timing of nest searching in *Bucephala* is interesting for three reasons. First, all three species of *Bucephala* nest in tree cavities, and nest sites are often limited (Erskine 1972, Savard 1982). It is possible that nest searching in advance of the next breeding season has evolved in response to the scarcity of suitable nest sites. Second, despite the above reports of "end of the season" nest searching in *Bucephala,* few data are available. We know of only one detailed study of nest searching in a hole-nesting duck (Patterson and Makepeace 1979, Patterson 1982, for the Common Shelduck, *Tadorna tadorna*). Third, Grenquist (1963) suggested that nest searching by female goldeneyes at the end of the breeding season might cause nest desertion by incubating females. This potential cost to incubating females has received little attention in previous studies.

The objectives of our study were, therefore: (1) to quantify and compare the late season nest visitation patterns of three species of cavity-nesting ducks, the Common and Barrow's goldeneyes (*Bucephala islandica*) and the Bufflehead (*B. albeola*), (2) to consider the hypothesis that females were "prospecting" for nest sites for the following year, and (3) to examine potential costs of this activity to both incubating and visiting females.

METHODS

Field work was conducted from April to August, 1984, near 100 Mile House in the Cariboo Parkland of British Columbia. Work on goldeneyes was conducted primarily by J.E. on Watson Lake, a shallow, 250-ha lake. There was a high density of nest boxes on the lake (42) and all but three were used in 1984. Only eight broods hatched from natural cavities, indicating that natural nest sites were rare relative to nest boxes.

Work on Buffleheads was carried out by G.G. on several small ponds (<8 ha) near Watson Lake. Although 160 nest boxes were available on these ponds, about two-thirds of the population nested in natural cavities. A large proportion of the Bufflehead and goldeneye population had been previously banded and marked with color-coded nasal saddles (Doty and Greenwood 1974) or colored leg bands, and nesting histories were known for many females.

Females of the two species of goldeneyes are often difficult to distinguish in the field (e.g., Palmer 1976, Cramp and Simmons 1977). We found that we could reliably separate females of the two species by using measurements of culmen, tarsus, and wing length (Eadie, unpubl.). We tested this method with museum specimens of known identity and, in all cases ($n = 20$), our classification was correct. Our identifications were further corroborated for 38 females that returned to the study area in 1985 paired with a male. In all but one case, our classification based on bill and body measurements was correct.

In goldeneyes, patterns of nest-site visitation were determined by using nest traps to capture females. Traps were set on 12 of the 42 nest boxes on Watson Lake and were monitored several times between dawn and dusk (06:00–22:00). When a female was caught in a trap, she was marked, weighed, measured (culmen, tarsus, and wing length), and released. Nest trapping did not deter birds from visiting other nest boxes, and several birds were caught repeatedly at the same nest site. Buffleheads did not use the nest boxes on Watson Lake, and data obtained by nest trapping refer only to goldeneyes. Information on nest visitation by female Buffleheads was obtained during routine field work. Whenever we saw a female or a group of females flying to a nest box, or when we heard a female vocalizing (see results), we sat quietly on shore and observed their behavior at nest sites by using binoculars or a spotting scope.

Females caught or observed at nest sites after the egg-laying period are referred to as "nest visiting" females in our results.

RESULTS

CHRONOLOGY OF NEST VISITATION

Seventeen Common and 12 Barrow's goldeneye females were captured in nest boxes after the egg-laying period. These females were caught between 11 June and 16 July (Fig. 1), with a peak during the last week of June. Most captures occurred after the peak of hatching (Fig. 1), although some females were still incubating during the time that visits took place. All boxes on which females were trapped were empty, either because the brood had hatched out earlier, or because the nest had been deserted. These females were not, therefore, returning to their own nests. Common Goldeneyes tended to visit nest sites earlier in the season than Barrow's Goldeneyes (Fig. 1; Mann-Whitney U test, $0.1 > P > 0.05$), although hatching dates did not differ between the two species ($P > 0.1$). All observations of nest visitation by female Buffleheads occurred between 21 June and 5 July, indicating that the chronology of nest searching was similar to that for goldeneyes.

In all three species, ducks visited nests primarily in the morning, with a smaller peak of activity in the afternoon (Table 1A). The species did not differ significantly in the time of day of nest visits (pairwise G tests, all $P > 0.1$).

PATTERNS OF NEST BOX VISITATION

Most female goldeneyes were trapped in only one nest box, although some were caught in two boxes and one female visited three different boxes (Table 1B). Since nest traps were placed on only 12 of 42 nest boxes, the number of sites that were visited by a single female was undoubtedly higher. Nest visitation patterns were similar in Buffleheads, with most females being observed at a single nest site (Table 1B).

The number of female goldeneyes caught at each nest site varied considerably. For example, in three boxes, only a single female was captured, whereas in two other boxes, up to nine females were caught. Since boxes were open for different lengths of time, we calculated a daily rate of capture (total number of females caught/total number of days the trap was open). This measure (Fig. 2) clearly shows that some nest sites attracted more females than others.

Our observations on Buffleheads also suggest that some nest sites were visited more often than others. We saw up to four different females visiting the same site, while apparently suitable neighboring sites were ignored.

IDENTITY OF VISITING FEMALES

Two lines of evidence suggest that most of the visiting females were either yearlings or unsuccessful breeders. First, three Bufflehead and two goldeneye yearlings were trapped or observed visiting nest sites. These five females had been individually marked as ducklings the previous summer, within 1.5 km of the nest

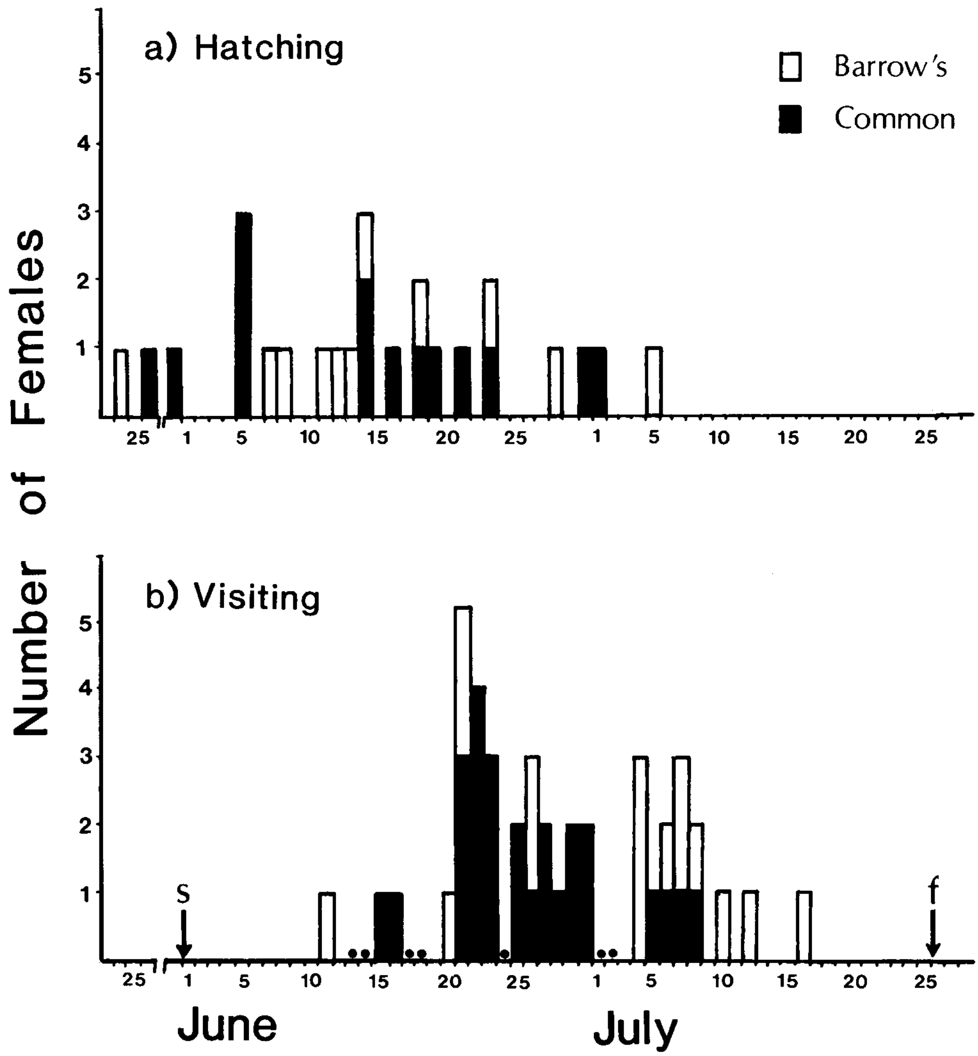


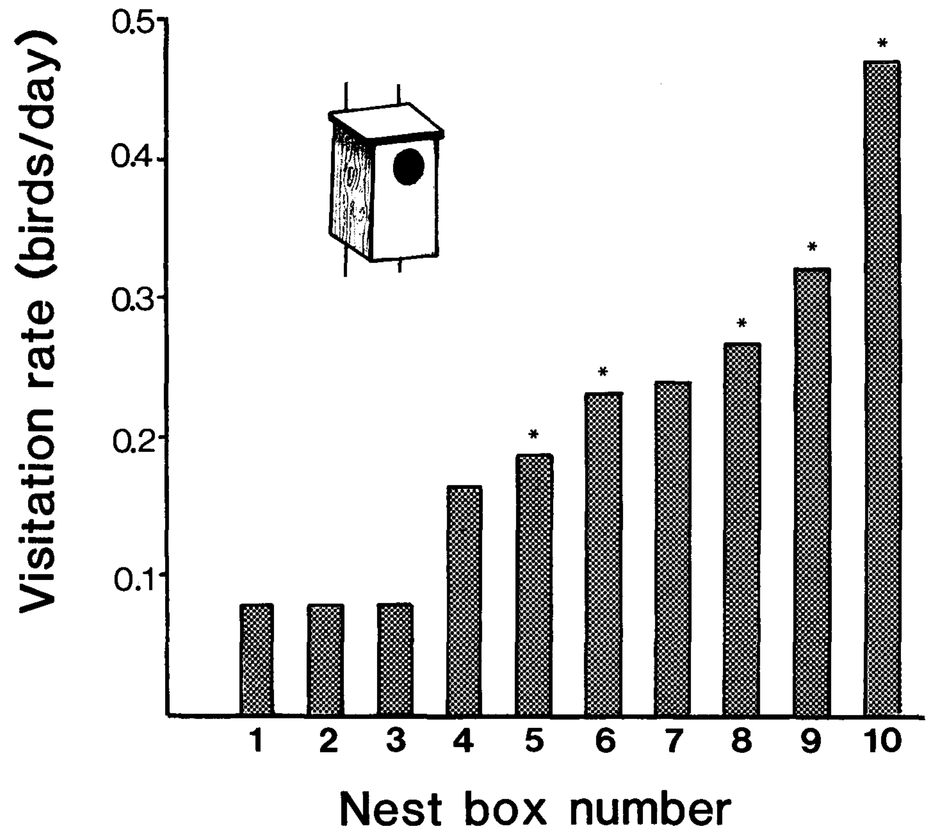
FIGURE 1. Seasonal chronology of (a) hatching and (b) nest visiting in Common Goldeneyes (closed bars) and Barrow's Goldeneyes (open bars). Arrows in (b) indicate the date when nest trapping was started (s) and finished (f). Solid dots indicate days when nest traps were closed.

TABLE 1. Frequency of post-laying nest visitation in Common and Barrow's goldeneyes and Buffleheads according to the time of day and the number of nest sites that were visited by each female. Data were obtained by nest trapping for goldeneyes and by distant observation for Buffleheads.

	Common Goldeneye	Barrow's Goldeneye	Bufflehead	Total
A) Time of day				
06:00–10:00	18	10	13	41
10:00–14:00	3	2	1	6
14:00–18:00	0	0	3	3
18:00–22:00	5	4	0	9
Total	26	16	17	59
B) Number of nest sites visited per female				
1 site	10	10	9	29
2 sites	7	1	4	12
3 sites	0	1	0	1
Total	17	12	13	42

site where they were seen. In addition, one female Bufflehead and one female Barrow's Goldeneye that had been marked and were known to have nested unsuccessfully in 1984 were later caught or seen at other nest boxes.

Second, female goldeneyes that were caught on nest traps were significantly lighter and slightly smaller than nesting females (Table 2). In both Common and Barrow's goldeneyes, nesting females were 50 to 100 g heavier than visiting females. Culmen and tarsus length also tended to be smaller in visiting females (significantly so in Common Goldeneye for tarsus length, Table 2). Some visiting females were trapped after the end of the hatching period, and they were consequently weighed later in the season. To control for this factor, we repeated the analyses by using only birds that were caught during the same time period (11–



No. ♀'s	1	1	1	3	3	3	6	4	9	9
No. Days	13	13	13	18	16	13	25	15	28	19

FIGURE 2. Nest visitation rates by female Common and Barrow's goldeneyes in 10 nest boxes on Watson Lake (two boxes that were open for less than two days were excluded). Sample sizes, in terms of total number of females caught and total days that the trap was open, are shown below for each nest box. Asterisks above bars indicate nest boxes that contained a parasitized nest earlier in the season.

30 June). These results were identical to the previous analysis, with body weight being again the only measure that differed significantly between nesting and visiting females.

BEHAVIOR OF VISITING FEMALES

Female hole-nesting ducks have been reported to fly rapidly around potential sites in groups while prospecting for nest sites. (Bengston 1966, M. Jackson in Bellrose 1976, Cramp and Simmons 1977). We also observed groups of two to seven females of all three species flying repeatedly around a single nest cavity or nest box, occasionally entering the cavity, or hovering and perching at the entrance. These "bouts" could last for up to 30 min and generally involved the same group of birds for the whole bout. We often saw two females perched on a cavity or even entering the cavity together. In one instance, three females of two species (two Barrow's Goldeneyes and one Bufflehead) were perched on an open-top cavity together. On several occasions, females of more than one species visited a cavity simultaneously, although mixed species "prospecting" has not been previously reported.

Aggressive interactions among females at a nest site were also observed. In one case, a marked female Bufflehead repeatedly chased two other female Buffleheads from a nest box, and further attacked these birds when they landed on the water in front of the nest site. In a second case, a female Barrow's Goldeneye perched at the entrance of a cavity and prevented two other female goldeneyes from landing at the cavity. On most occasions, however, aggressive interactions were absent.

Vocalizations by prospecting females have been reported in the Common Goldeneye (see Cramp and Simmons 1977:664 for a description of the call). We observed that females of all three species always emitted the same rapid *cuk-cuk-cuk* call while flying around nest cavities. This call was so characteristic that the

TABLE 2. Body weight and measurements of Common and Barrow's goldeneyes that were caught while nesting (late incubation) or visiting nest sites. Mean ± SE (n). Nesting and visiting females were compared by means of a two-tailed t-test.

Breeding stage	Culmen (mm)	Tarsus (mm)	Wing (mm)	Weight (g)
Common Goldeneye				
Nesting	34.7 ± 0.3 (15)	46.5 ± 0.5 (15)	213 ± 1 (14)	635 ± 10 (14)
	NS	*	NS	***
Visiting	34.0 ± 0.3 (17)	45.0 ± 0.4 (17)	212 ± 1 (17)	575 ± 7 (17)
Barrow's Goldeneye				
Nesting	31.7 ± 0.3 (14)	46.9 ± 0.5 (14)	221 ± 1 (14)	736 ± 10 (13)
	NS	NS	NS	***
Visiting	31.4 ± 0.4 (10)	47.0 ± 0.2 (11)	223 ± 1 (10)	628 ± 6 (11)

NS: $P > 0.05$.
* $P < 0.05$.
*** $P < 0.001$.

vocalization alone enabled us to find visiting females.

DOES PROSPECTING CAUSE DESERTION?

Nineteen of 41 goldeneye nests and 14 of 38 Bufflehead nests were deserted in 1984 (excluding a few nests that were depredated). Of these, only three goldeneye and four Bufflehead nests were deserted during the period of nest visitation by females (i.e., after 10 June, Fig. 1). When the number of nests that were active before and during nest visitation are considered, significantly more nests were deserted *before* nest visitation began in goldeneyes (G test with Yates correction, G = 5.01, $P < 0.05$), whereas in Buffleheads there was no significant difference (G = 2.16, $P > 0.1$). Considering only nests that were deserted when females were incubating, three of five goldeneye nests and four of seven Bufflehead nests were deserted after 10 June. Therefore, we found no evidence that more incubating females deserted their nests during the period of nest visitation.

DISCUSSION

Several lines of evidence indicate that the birds we observed were inspecting nest cavities for the next breeding season. First, none of these females laid eggs during their nest visits. Second, nest visits occurred primarily from the third week of June until mid-July. This is at least one week after the latest egg-laying noted for these species in this area (5 June for goldeneyes, and 16 June for Buffleheads). Finally, Buffleheads and goldeneyes have never been reported to nest in their first year (Erskine 1972, Palmer 1976), yet some of the visiting females were known yearlings.

One additional line of evidence supports the hypothesis that visiting females were prospecting for nest sites in preparation for the next breeding season. Of the 28 visiting female goldeneyes that were marked in 1984, 14 returned to the same lake in 1985, 10 of them paired with males. Five of these females nested within 100 m of the nest site where they were trapped in 1984. The other five apparently did not nest successfully. Previous studies of nest prospecting in *Bucephala* have only suggested that females return to nest in sites they have visited the previous summer. Our study therefore offers the first conclusive evidence that some prospecting females return to nest near sites visited in the preceding year.

Except for the few marked females, we could not reliably distinguish age classes in any of the three species by using plumage or other external characters. Visiting female goldeneyes, however, were slightly smaller and significantly lighter than nesting females. It is reasonable to suppose that many of these females were either young birds or birds in poor condition. Seven female Common Goldeneyes that were caught in nest traps had wing lengths of less than 210 mm and weights of less than 590 g, and, therefore, can tentatively be classified as yearlings according to Palmer's (1976) and Cramp and Simmons's (1977) criteria.

Some of the prospecting females were also known to be failed breeders. Since most females that hatched young successfully were marked, we are confident that few, if any, of the visiting females were successful breeders. The apparent absence of successful breeders in our sample of visiting females is not surprising since Eriksson (1979) and Dow and Fredga (1983) showed that female Common Goldeneyes changed nest sites if they were unsuccessful in the previous year, whereas successful females did not.

Nest searching behavior during the pre-laying period has been reported in most species of ducks, including goldeneyes and Buffleheads (Bellrose 1976, Palmer 1976). We have also seen some flights that were followed by nest site visits during the pre-laying and laying stages. This nest searching behavior, however, differs from the post-laying nest prospecting behavior in two ways. First, pre-laying nest searching always involved lone females or females followed by a male. Second, these females never vocalized. This contrasts with the prospecting females, who always visited nests in groups and who vocalized constantly. We therefore suggest that most of the pre-laying nest searching in *Bucephala* is re-inspection of nest sites that were visited the previous summer. Because of this difference between the two behaviors, we further propose to limit the use of the term "prospecting" to the post-laying nest searching behavior in cavity-nesting ducks.

Locating a suitable nest site is clearly an important prerequisite for breeding in hole-nesting birds. Searching for nest sites well before the next breeding season could be advantageous, or even necessary, if nest cavities are limited (e.g., Savard 1982). The timing of this behavior at the end of the incubation period of most nesting females (Fig. 1) suggests that prospecting females could learn about the suitability or availability of nest sites either by visiting nests that are still incubated or by following incubating females (Bellrose 1976: 434). The presence of egg shells or membranes in recently hatched nests could also indicate that a nest has been successfully used.

This idea is consistent with Dow and Fredga's (1985) finding that female Common Goldeneyes showed a significant preference for nest boxes that had been recently occupied. They argued that evidence of recent use of a nest site would indicate that such a site was safe from predators. Our observations on the timing of nest prospecting relative to that of hatching offers a mechanism by which females could learn the previous history of a nest site.

We did not find any evidence to support Grenquist's (1963) suggestion that interference by visiting females caused desertion by incubating females. Some costs may be indirectly incurred, however, by the prospecting females themselves. Nest parasitism is common in both species of goldeneyes on our study area (Eadie, unpubl. data), and boxes with the highest visitation rates also tended to have contained parasitized nests earlier in the season (Fig. 2). Therefore, females that prospect in groups and thereby inspect (and possibly select) the same nest site may be more likely to be parasitized in the following year.

Why, then, do females prospect in groups? In shelducks, Patterson and Makepeace (1979) suggested that either group prospecting is an anti-predator adaptation, or females may follow other birds in order to find nest sites. The anti-predator hypothesis is unlikely to apply here because the risk of predation for visiting females is probably low. The nest location hypothesis may be more tenable, although if most prospecting females are yearlings or failed breeders, as our data suggest, one may wonder whether any reliable information could be gained by following other inexperienced or unsuccessful birds.

The role of vocalizations during prospecting also remains obscure, although vocalizations are given by prospecting females in most species of waterfowl (Grice and Rogers 1965, Palmer 1976). McKinney (1975) suggested that vocalizations during nest searching in dabbling ducks might lure nest predators and thus inform a female of their presence in the area. In cavity-nesting ducks, this call could perhaps also lure potential competitors or conspecifics that may be present inside the cavity.

Finally, we suggest that prospecting behavior is linked to other life-history traits in these species. All three species of *Bucephala* do not breed until their second year, and it is possible that both delayed maturity and nest prospecting as yearlings have evolved in relation to scarcity of suitable nest sites. As a preliminary test of this hypothesis, we asked if the type of nest site (ground or cavity nest) is related to age at maturity. We found that, among 29 species of North American ducks (data from Bellrose 1976), cavity-nesting ducks tend to mature at a later age; eight of 23 ground-nesters (35%) mature at two or more years of age, whereas five of six (83%) cavity-nesters do so, a significant difference (G test with Yates correction, $G = 5.5$, $P < 0.05$). Prospecting behavior has been reported in four of the latter five species, which suggests an association between nest-site limitation, delayed maturity, and prospecting behavior.

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Institute of Animal Resource Ecology and Department of Zoology, University of British Columbia, 2204 Main Mall, Vancouver, British Columbia V6T 1W5, Canada. Received 29 October 1984. Final acceptance 29 June 1985.

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RECENT PUBLICATIONS

Avian biology, Volume VIII.—Edited by Donald S. Farner, James R. King, and Kenneth C. Parkes. 1985. Academic Press, Orlando, FL. 256 p. $49.50. This volume, unlike its predecessors, consists of two long, diverse chapters: "The adaptive significance of coloniality in birds," by James F. Wittenberger and George L. Hunt, Jr., and "The fossil record of birds," by Storrs L. Olson. Both demonstrate the enormous advances in conceptualization and knowledge that have been made in their fields since the original chapters that were published in Volume I (1971). Wittenberger and Hunt "examine advantages and disadvantages potentially accruing to individuals who join breeding or roosting colonies .... [They] focus on selective factors that have been suggested to explain why individuals should form colonies rather than dispersing within the available foraging space." Olson has not attempted to treat the entire fossil record of birds but instead concentrated on the Mesozoic and Tertiary history. Taking a fresh systematic approach, his aim has been to use paleontological data in tracing the first appearance and evolution of the major avian taxa. Both chapters are excellent and important syntheses of their subjects. They are likely to stimulate new research, just as their antecedent articles doubtless engendered some of the work that led to them. Considering the disparate nature of the chapters and the high cost of the book, however, it is questionable whether many individuals will be willing to buy it. Perhaps sociobiologists and paleontologists will want to pair up so as to purchase and divide copies. Illustrations, lists of references, indices.

Experimental behavioral ecology and sociobiology.—Edited by B. Hölldobler and M. Lindauer. 1985. Sinauer Associates, Inc., Sunderland, MA. 488 p. $55 cloth, $30 paper. This volume presents the papers which were read at a 1983 memorial symposium held in honor of Karl von Frisch. "His way of asking questions and obtaining answers from the animals by ingenious experimentation, has been and will continue to be a major inspiration for experimental behavioral ecologists and sociobiologists." Reflecting his research interests, the 28 papers deal with orientation, learning, and foraging; the analysis of communication signals; communication and reproductive behavior; social organization; and physiology and societies. Only three papers explicitly concern birds—most of them having to do with social insects—yet teachers of animal behavior will find the papers valuable for their demonstrations of an experimental approach. Illustrations, references, indices.