

Wildl. Mgmt. 34: 756) data showing that incubation commences approximately 2 weeks earlier in southern Ontario than in Minnesota (Brander 1967, Wilson Bull. 79: 28; Gullion 1967, The Ruffed Grouse in northern Minnesota, Univ. Minnesota, Forest Wildl. Relations Project (multilith); Schladweiler 1968, J. Wildl. Mgmt. 32: 246). Thus, our data not only support Wenstrom et al.'s (op. cit.) findings, but suggest that molt in conjunction with other aspects of the annual cycle of Ruffed Grouse may occur earlier in southern Ontario than in the Cloquet area of Minnesota.—ALLAN GARBUTT and A. L. A. MIDDLETON, *Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada*. Accepted 5 Jun. 73.

Flight speed and wingflapping rate of Sacred Ibis.—Meinertzhagen (1955, Ibis 97: 81) gives flight speeds for several species of birds but none for ibises. I calculated flight speeds for adult Sacred Ibis (*Threskiornis aethiopica*) at the breeding colonies at Lake Shala, Ethiopia (7° 30' N, 38° 30' E, elevation 1,570 m). On 9 March 1969 at midday with little to no wind, 34 Sacred Ibis, flying 2–3 m above the water, took 150 seconds to fly 1.6 km from Pelican Island to Abdim Island (see Brown and Urban 1969, Ibis 111: 206 for map of Shala). These adults traveled at a speed of 38.4 kph (23.9 mph).

Meinertzhagen (loc. cit.), Blake (1947, Auk 64: 619; 1948, Condor 50: 148), and Kahl (1971, Auk 88: 428) also give wingflapping rates of several species of birds, but again none for ibises. I recorded wingflapping rates of Sacred Ibis breeding at Abdim Island on 4–10 April 1967; the birds averaged 4.2 flaps per second (range 3.6–4.8; 19 counts varying from 4.3–12.9 seconds in duration). Charles H. Blake (pers. comm.) reports mean wingflapping rates in the White Ibis (*Eudocimus albus*) of 3.3 ± 0.3 per second (range 2.9–3.6; 9 observations) and in the Glossy Ibis (*Plegadis falcinellus*) of 3.2 per second (range 2.8–3.8; 4 observations).

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Site attachment in the Northern Shoveler.—Territory typically refers to “any defended area” (Mayr 1935, Noble 1939, Tinbergen 1939, Nice 1941) that is thought to arise as the outcome of two distinct tendencies, site attachment and hostility (Tinbergen 1957). Although the concept has been considered to be generally valid for ducks (McKinney 1965), controversy exists over the use and validity of the concept in some species (Dzubin 1955, Bezzel 1959, Lebret 1961, Hori 1963). Although hostility of male ducks towards conspecifics has been shown to occur in several species, the question of the male's attachment to a site has remained unresolved and largely uninvestigated. The present study was designed to assess the possibility that such site attachment does occur in a manner consistent with the territory concept.

Demonstration of site attachment in ducks is rendered difficult under natural conditions because, as McKinney (1965) pointed out, the possibility cannot nor-

mally be excluded that a male is defending the female rather than a site to which he is attached. To separate these two variables, I tried an experimental approach that involved moving a female away from the defended area. I chose as the study bird the Northern Shoveler (*Anas clypeata*), which appears to be territorial in the classical sense (McKinney 1967, Seymour MS).

The experiment was conducted between 27 May and 10 June 1970 on the Delta Marsh, Manitoba, Canada. The birds under test were watched for a total of 27 hours and, in addition, hourly checks of the study area from 05:00 to 22:00 (darkness prevented earlier and later observation) were made on 10 days. The study area was a flooded grass meadow of approximately 20 ha that never exceeded 0.5 m in depth. Prior to the experiment, I had counted from two to seven unmated male shovelers on the meadow feeding and courting females of transient pairs. Seven males, including those referred to below as males 1 and 2, were caught on the meadow in a clover trap described by Lincoln and Baldwin (1929), marked with nasal markers (Bartonek and Dane 1964), and released where captured.

An unmated female, hatched from a wild-procured egg and held in captivity for a year, was placed in the trap to decoy the unmated males. Three trapping sites referred to as sites A, B and C were chosen. Site B was 65 m from site A, site C was 150 m from site B and 185 m from site A. Laths located at 5-m intervals from the trap, which I refer to as the trap site, allowed me to determine where interactions occurred relative to the trap site. Specific objectives, details of procedures, and observations are reported below in five parts that correspond to shifts in the location of the decoy female.

(1) The female was placed at site A for 4 days, then removed from the meadow for 2 days, to determine (a) whether unmated males would be attracted to her, (b) whether one male would become dominant over the others and establish a territory, and (c) to assess the behavior of the male(s) after removal of the female.

Within one day of placing the female at site A, a male (male 1) became dominant in the area and chased and pecked other males with which he had previously shown no apparent hostility. After the first day, the other males tended to avoid him. By the second day male 1, who had learned how to pass freely into and out of the trap, could approach the female and not be threatened or pecked by her. The female reacted to other males by adopting an inciting posture and by an avoidance response as they approached the trap. Thus, an association suggesting a typical pair bond appeared to have been established between male 1 and the female. Male 1 remained with the female until she was removed from the study area 4 days later.

After the female was removed, male 1 remained at site A. During hourly checks he was typically seen within 5 m of a lath that marked the former location of the female. This male threatened, chased, and made pursuit flights after virtually all shoveler males that flew or swam within approximately 30 m of site A. He invariably returned to site A after each pursuit flight. During this time the unmated males, who formerly had been attracted to site A by the female, fed together elsewhere on the meadow and showed little of the hostility among themselves that they had exhibited previously when in association with the female.

(2) Two days after I had removed the decoy female I returned her to the meadow at site B for 2 days to determine if male 1 would desert site A to follow her to site B. The female in the trap at site B was readily visible from site A where male 1 was located.

Male 1 deserted site A and joined the female within 2 hours after she was placed at site B. On arrival at site B he immediately chased several unmated males, most of which had also been at site A, from near the trap and quickly assumed dominance in the area. I did not see him return to site A while the female was at site B.

(3) Two days after putting the female at site B, I shifted her for 2 days to site C, which was visually isolated from Site B. This made it possible for me to test further whether male 1 would locate and follow the female even though she was not directly visible to him so long as he stayed at site B.

Male 1 remained at site B in the absence of the female and continued to chase conspecifics that flew or swam within approximately 30 m of the site. At site C another male (male 2) became dominant over other males, although the female threatened and avoided him. The female, in apparent agitation, swam almost continuously around the trap at site C.

After 36 hours, male 1 found the female at site C, but was prevented from approaching closer than approximately 15 m of the trap by male 2, who maintained his dominance over all males, including male 1. While the female was at site C male 1 typically remained 5 to 30 minutes at the site and then returned to site B where he remained within 1 or 2 m of the site. Male 1 also chased male shovellers at site C when he was there, but was never seen trying to chase male 2 after what I believe was their initial encounter, in which male 2 forced male 1 to retreat.

(4) After the female had been 2 days at site C, I shifted her back to site B for 3 days to determine whether male 2 would follow the female or remain at site C, and to determine the behavior of males.

Male 1 joined the female within 30 minutes after she was placed back at site B. Male 2 deserted site C the next day and also flew to site B. This time male 2 was prevented from approaching close to the female by male 1, who remained dominant over all males at site B. Male 1 was obviously more aggressive towards other males at site B than he had been at site C. Male 2 showed a corresponding lack of hostility at site B.

(5) I removed the female from the study area to determine how long males 1 and 2 would remain in the area in the absence of the female. Male 1 remained at site B for at least 2 days after removal, but male 2 left the study area on the day of removal. This final move terminated the experiment.

In agreement with the literature, the behavior of males 1 and 2 demonstrated the initial importance of the female in determining where the defensive behavior of the male occurs. Certainly it was the female and not the particular topographic site that attracted the males to the trap site. Additional evidence was provided for this view by the fact that both males deserted their former areas of dominance to follow the translocated female. Attachment of the male to the female prior to the establishment of the territory, which occurs naturally, presumably ensures that the male will follow the female until her activity becomes localized in an area that the male could then begin to defend (see Hochbaum 1944). The behavior of both males 1 and 2 showed that unmated males can undergo a rapid change to courtship and defensive behavior, as required by the above interpretations.

The behavior of males 1 and 2 also demonstrated that once they were established on a physical site, it then held special significance for them in the absence of the female. Both males, but particularly male 1, remained at the trap sites for

periods of up to 2 days after the female was removed, and both males exhibited typical territorial defense and dominance at this time. These results therefore provide definite evidence that a site *per se*, and not just the female, may provide a basis for attachment and apparent defensive behavior in this species. The fact that at site C male 1 could see and presumably hear the female with whom he had formed a definite bond, yet was unable to dominate male 2, suggests further that the mere presence of the mate does not ensure that the male will be dominant at a given site. Unrestrained paired females would be expected to flee with the mate from a site which the mate does not control. At both sites B and C, prior ownership apparently gave one male the advantage over the other, further demonstrating the importance of site attachment.

The survival value of territorial behavior and site attachment has been the subject of controversy (see Hinde 1956, Tinbergen 1957). In the shoveler, localization of the male's activities on the territory presumably enables the female to return there to seek her mate's protection from not infrequent harassment by territorial and unmated male shovelers that she may encounter while off the nest (Seymour MS). Perhaps of equal importance Tinbergen suggested that site attachment allows males to advertise their presence in a territory. Although I have not presented here proof of territorial advertisement in the shoveler, the conspicuous coloration of the male suggests that this occurs. If so, then site attachment that localizes the male on the territory presumably functions to allow conspecifics to identify and associate the territory with the hostile male, thereby reducing encroachment and harassment, and possibly limiting breeding pair density.

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Morphology of the bony stapes in New and Old World suboscines: New evidence for common ancestry.—Owing to the tremendous degree of morphological uniformity within the class Aves, presumably because of the restrictive physical demands of flight, the relationships of the higher taxa of birds are perhaps the most poorly understood of all the vertebrate groups. Particularly enigmatic have been the relationships of the major groups of the massive order Passeriformes.

The order Passeriformes has been subdivided classically on the basis of syrinx morphology into two major groups, the "oscine" passerines (suborder Passeres), which possess a complex syrinx with more than three pairs of intrinsic syringeal muscles, and a heterogeneous group known as the "suboscines," which have been thought to be the more primitive because they have an anatomically simpler syrinx than that found within the oscines (Ames 1970, Peabody Mus. Nat. Hist. Bull. 37). The "suboscines" comprise several groups, presently given subordinal rank by most authors

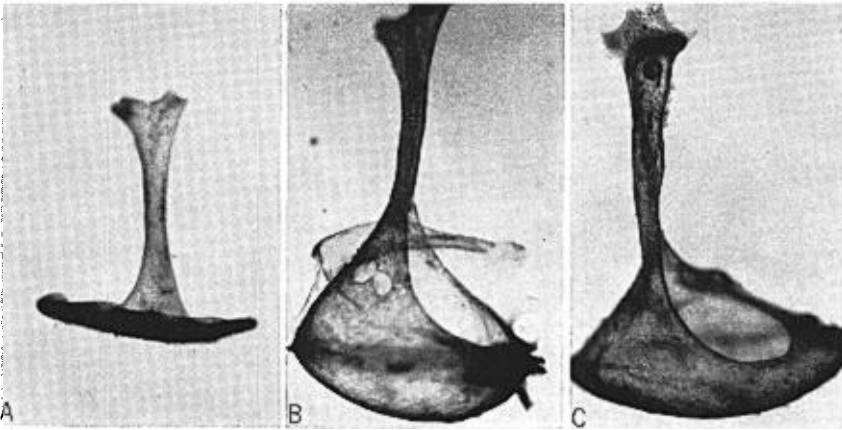


Figure 1. Alizarin-stained stapes of A, *Spreo superbus* (oscine: Starling); B, *Xiphocolaptes promeropirhynchus* (New World suboscine: Woodhewer); and C, *Pitta angolensis* (Old World suboscine: Pitta). All approximately $\times 40$. Stapes may be prepared after extraction from the ear either by coating them with a conductive substance such as gold for scanning electron microscopy, or by staining with Alizarin Red S, and placing them in vials containing glycerine. Alizarin-stained specimens are more easily studied with conventional light microscopy, and are easily photographed under any normal scope; all specimens in Figure 1 were prepared in this manner.