

SHORT COMMUNICATIONS

Copulatory and other pre-incubation behaviors of Cooper's Hawks.—Data on pre-incubation behavior of falconiforms are scarce, and Brown and Amadon (1968) and Palmer (1988) give the only descriptions of pre-laying activities of the Cooper's Hawk (*Accipiter cooperii*). Their descriptions are based on Meng (1951), who provides an unquantified narrative summary of activities during this stage. Here we present a quantitative analysis of copulatory and related pre-incubation behaviors obtained over four breeding seasons.

Methods.—We observed pre-incubation behavior in 47 mated pairs of Cooper's Hawks at 28 nesting areas in Wisconsin during 24 March–19 April 1986 (9 pairs), 7–24 April 1987 (12 pairs), 26 March–5 May 1988 (16 pairs), and 23 March–12 May 1989 (10 pairs). Identification of nesting areas was based on an 11-year data set (Rosenfield and Bielefeldt, unpubl. data). Based on capture and re-capture data for marked birds, we believe a minimum of 46 different adults (28 males, 18 females) were involved. All observations were made after pair formation, and all mated pairs laid eggs. We watched Cooper's Hawks at partially constructed nests during 84 observation periods (20 in 1986, 18 in 1987, 27 in 1988, and 19 in 1989). Observations totaled 7325 min (\bar{x} = 87 min/episode, range = 16–326 min) mostly (N = 69 or 82%) beginning with the day's first arrival (04:30–05:15 h CST) of an adult near a nest. These are termed "early morning periods" (hereafter "early"), most (63 or 91%) of which ended at or before 08:30. Observations (N = 15) at other times of the day (hereafter "later") began after 08:30 (08:31–18:20). Early morning and later observations made up 73% (5327 min) and 27% (1998 min) of the total observation time, respectively. Our previous fieldwork (1980–1985) indicated that the hawks were predictably present on nesting areas at dawn. More time was spent on early morning observations when we expected greater frequency (and higher variance) for the behaviors considered here.

All components of behavior were not equally observable, and thus sample sizes vary. Unless the terms "separate" or "different" are explicitly applied to individuals, pairs, or nests, samples include multiple observations of the same individual birds. Birds in the same nesting area in different years are treated as separate cases. The hawks were sexed by size (males are markedly smaller) and vocalizations (females called more frequently and had larger repertoires [Rosenfield and Bielefeldt 1991]). We standardized the analyses of copulations, nest visits, and twig deliveries to partially constructed nests as number per hour.

Because it was impossible to determine whether sperm was transferred during copulation, we defined a copulation as occurring when a male mounted a female. Statistical analyses follow Cochran (1977) and Zar (1984). Significance was accepted at the 0.05 level. For a more detailed description of study area and methods see Rosenfield (1990).

Results and discussion.—Cooper's Hawks were not seen on nesting areas until mid-March, and eggs were laid in late April–early May. The pre-incubation period was thus at least 30 days. During the pre-incubation period, male Cooper's Hawks, like other raptor species (Newton 1979), leave the nesting area to hunt during some part of the day, while females remain near the nest. We never saw (1) either sex hunt near the nest, (2) females depart the nesting area and leave males unattended, or (3) females arrive at a nesting area with food. When we saw males depart the nesting area (N = 15) and leave females unattended, or at other times when unattended females were found on nesting areas (N = 4), returning males (N = 9 different birds) always arrived with prey. Females were present for 99% of 6200 min in which we could account for the presence of at least one bird on the nesting area, males for 80%. Males were more likely to be absent from nesting areas in later periods than in early morning periods. Pooled data for total observational time show males were absent for

458 of 1531 min (30%) in later periods and 782 of 4669 min (17%) in early periods, but both of these proportions are skewed by extended absences of a few individual males. Treating observation periods as independent, we found that mean proportion of time absent in 13 later periods was 21%, but only 9% in 64 early periods. Males are more likely to be present on nesting areas during the early morning hours and for a large proportion of the time at all hours of the day.

We observed 120 copulations: 23 among eight pairs of Cooper's Hawks in 1986, 24 among nine pairs in 1987, 42 among fourteen pairs in 1988, and 31 among six pairs in 1989. Copulations occurred throughout the pre-laying period with no apparent peaks in copulatory activity during this time (see Rosenfield 1990). During at least 45 (38%) copulations, both birds gave multi-noted "whaaa" calls (see spectrograph in Rosenfield and Bielefeldt 1991), and on at least 15 other occasions (12%), only the female called. At least one bird always called during all copulations. Fifty-seven copulations in our study averaged 4.5 sec in duration (range = 2–6 sec). All copulations, except one that occurred on the ground while a female was feeding, occurred in trees at distances of 20–80 m from the nest and at heights of 2–15 m. Males always ($N = 102$) flew toward females to copulate, never the reverse.

The incidence of copulations is strongly associated with nest buildings by males. Among 102 copulations in which we clearly saw the male before mounting, he had visited the nest ≤ 1 min earlier on 82 occasions (80%). On 71 (70%) occasions, the male flew directly from the nest to the female without perching in the interim. On two of these 71 occasions, two different males gathered twigs and then attempted to copulate en route to the nest, but females seemed to reject copulation until after the males had visited the nests. In two other instances, two separate males that had unsuccessfully tried to break twigs flew immediately to their mates and copulated. Of the five times in which we saw females ($N = 4$ different birds) solicit copulations by tilting to a horizontal position when males were about 3–5 m away, all occurred while males were departing nests.

Copulations were also associated with courtship feeding. Copulations followed all but one of 10 cases in which different males provided prey to females. Eight different males each copulated once, and another male twice, while their mates were feeding. These copulations also immediately followed nest visits by males.

The total number of copulations per clutch is not known, but an estimate can be derived from the copulation rate. Copulations occurred throughout the day, but early morning rates were significantly higher than later rates (Mann-Whitney $U = 556.5$, $P = 0.003$). The copulation rates observed in our study were weighted according to available daylight hours in the pre-incubation period in stratified sampling of early and later strata (see Table 1), and the resulting estimate of number of copulations in the 30-day period prior to egg laying was 372 ± 184 (95% confidence interval).

In early morning observation periods ($N = 69$), the hawks vocalized at the nest site at dawn, 5–25 min before sunrise. On all but two occasions, both sexes called upon their arrival at dawn. We do not know where the hawks had roosted, but when visible to us ($N = 15$), 12 different males arrived from elsewhere before calling. Males' initial calling posts were 25–150 m from the nests ($N = 17$ separate individuals). Females' initial calling positions were difficult to determine because many called in flight while approaching the nesting area. We estimate, however, that the range of female-to-male distances at initial dawn calls was similar to that for male-to-nest distances. Median male-to-female distances at initial calls was 60 m ($N = 28$).

Females flew toward nests ($N = 15$) or male calling posts ($N = 20$) within 5–120 sec (median = 15 sec) of the initial calls by either bird, and male approach to female ($N = 1$) or mutual approach ($N = 1$) was rarer. Both sexes called frequently before and during these approaches, and this "exchange" of calls continued for 5–1050 sec (median = 120 sec).

TABLE 1
ESTIMATED NUMBER OF COPULATIONS PER CLUTCH^a FOR COOPER'S HAWKS IN WISCONSIN,
BASED ON STRATIFIED SAMPLING

Stratum	Total possible pair-year-h ^b	Total h ^c	Stratum mass	Mean copulations/h	Sample variance
Early obs.	22,560	65	29%	1.69	2.77
Later obs.	56,400	13	71%	0.56	0.99
Totals	78,960	78			
Stratified mean/h			0.89		
Stratified variance (of the mean)			4.19		
SE			0.20		

At the 95% confidence interval (14 df), estimated number copulations per clutch = 372 ± 184

^a Based on estimated 30 days of copulation prior to incubation.

^b Based on 14-h day \times 30 days per pair \times 47 pairs \times four seasons.

^c Standardized copulations/h based on variable-length observation periods, see text.

From 1.0–34.0 min (median = 8.4) after initial calls at dawn, visits to the nests began. We avoid the term “nest building” for the first nest visit of the day because birds carried no building material in at least nine instances. Males made 82% ($N = 56$) ($\chi^2 = 23.2$, $df = 1$, $P < 0.001$) of the initial morning nest visits.

At least one bird made a minimum of one visit to a partially constructed nest in 78 of 84 (93%) observation periods. On seven of these 78 observation periods, we could not determine the sex of a bird on a nest visit. We separated number of nest visits from number of twig deliveries because frequently we could not see whether a bird carried a twig on each visit. Both sexes built, and males made 69% of visits to partially constructed nests in early and later periods combined. This value is the mean of proportions of male nest visits at each nesting area in each year ($N = 43$), with a total of 542 nest visits by both sexes. Sign tests show that males made significantly more nest visits ($P < 0.001$, $N = 41$) and significantly more twig deliveries ($P < 0.01$, $N = 30$) than females in combined early and later periods (see Rosenfield [1990] for a breakdown of nest visits and twig deliveries by males and females for each nesting area).

In addition to absolute number of nest visits and twig deliveries, we evaluated rates of visits and deliveries (per h). Males exhibited a significantly higher nest visit rate (Mann-Whitney $U = 3474$, $P < 0.001$) and twig delivery rate ($U = 3159$, $P = 0.019$) than females for all observation periods combined.

Visits by male and female Cooper's Hawks to partially constructed nests occurred throughout the pre-laying period (see Rosenfield 1990). As with copulations, there was marked diurnal variation in nest building. Except for a marginally non-significant difference (Mann-Whitney $U = 484.5$, $P = 0.054$) in the diurnal variation in twig delivery rate for males, intrasexual nest visit rates to uncompleted nests were significantly higher during early observation periods than during later periods (Mann-Whitney $U = 568.0$, $P = 0.002$, and $U = 593.5$, $P = 0.01$, for male and female nest visit rates, respectively; and $U = 555.5$, $P = 0.002$ for twig delivery rate by females).

Our data indicate that males do at least twice as much building as do females. On some nest visits, as Meng (1951) suggests, females (or males) may only be “inspecting” the nest or “rearranging” twigs. We could not determine the frequency or sexual apportionment of non-building visits to the nest in all observation periods. However, in 39 periods where we saw birds clearly, males and females delivered twigs on 279 of 296 (94%) and 105 of 126

(83%) nest visits, respectively, while males (seven different birds) and females (minimum of five different birds) made at least seven and 16 visits without twigs, respectively. Thus a maximum of 6% of nest visits by males and 17% of visits by females could have been without twigs. We believe that these frequencies are representative of all observation periods.

Although nest building essentially occurred only when both members of a mated pair were present, only one bird built at a time while the other bird perched nearby. We never saw both birds gathering twigs at the same time. Of 542 visits to partially constructed nests, 534 (99%) occurred when both male and female were present. During one early observation period, an unattended male (the only instance in which a male was observed alone) made seven visits to a nest (all with twigs) during 25 min before we detected his mate. We saw only one nest visit (without a twig) among at least 12 different females during 20 h at 15 nests.

We watched Cooper's Hawks gather 331 twigs (235 by males and 96 by females), representing 77% of the 429 observed twig deliveries. All twigs (except two, one taken by a male from the ground, and one from a tree while in flight) were collected in trees by perched hawks using their beaks. Excluding alternate nest building (see below), all observed twig collections occurred within 20–80 m of the nest, most ($N = 214$ [65%]) within 30–40 m. Almost all (329 or >99%) twigs were taken from perches at heights of 2–15 m in nest-site habitat (Rosenfield and Bielefeldt, unpubl. data) where canopy trees were about 21 m tall. Hawks took twigs from white and red pine (*Pinus strobus*, *P. resinosa*), oaks (*Quercus* spp.), black cherry (*Prunus serotina*), black locust (*Robinia pseudoacacia*), box elder (*Acer negundo*), and probably other tree species. It seemed that the hawks were choosing convenient spots near the nest to collect twigs from an abundant supply of building materials.

Breeding Cooper's Hawks in Wisconsin typically build more than one nest during the same year prior to incubation. At least 14 of 16 (88%) and six of 10 (60%) pairs built at least two nests prior to egg laying during 1988 and 1989, respectively. One of these pairs built three nests, and one pair built four nests. Building probably occurred at more than one nest during the same day at five different nesting areas. After two males and one female (from three separate pairs) had collected a twig, they flew out of view instead of flying to the nest under observation. Their mates followed in the direction in which we subsequently found an alternate nest. In two other observation periods, birds left the original site with twigs and probably built on an alternate site, but then returned about 30 min later and resumed building on the original structure. Maximum distances between initial and alternate nests for the 20 pairs ranged from 27 to 335 m ($\bar{x} = 170$ m).

The need to assure paternity exists in Cooper's Hawks, as in other species with biparental care, because cuckolded males raising unrelated young would waste reproductive investment and lose individual fitness (Trivers 1972). Male Cooper's Hawks do most of the food-provisioning for their mates during the prezygotic period, hunt for prey away from the nest site, and thus must leave females unattended for parts of the day. Unattended females could be inseminated by other males. Moreover, females certainly do not know when, or if, resident males will return with food or return at all. Copulations are associated with prey deliveries. It might be advantageous for females to accept or even solicit extra-pair copulations (EPCs) in return for prey surrendered by non-resident males as a means of maximizing energy assimilation for egg production. Although no one has observed EPCs in Cooper's Hawks, several aspects of the males' behavior suggest that EPCs do occur. The copulation frequency of Cooper's Hawks was high, with an estimated average of 372 copulations in the 30-day period prior to egg laying; frequent copulations may help to assure paternity as suggested for other falconiforms (Birkhead et al. 1987). Among falconiforms, copulation rates are positively correlated with the extent of the male's provisioning of the mate (Moller 1987). Male Cooper's Hawks exhibit high paternal investment through courtship feeding, and as a result they should also invest heavily in paternity assurance (Birkhead and Lessells 1988).

Nest building—a related way to seek to assure paternity—and copulatory behavior are linked to each other by the timing of copulations, 70% of which immediately followed nest visits by males. It may be that nest visits by the male function as a pre-coital display that induces females to copulate and alternate nests may simply serve as another display site. Copulations occurred over a four week period prior to egg laying. It might be to the female's benefit to conceal her fertile period and solicit copulations before she is fertile to induce courtship feeding or nest building from the male (Birkhead and Lessells 1988). Cooper's Hawks may seek to assure paternity by remaining near the nest and the female (i.e., mate guarding; Parker 1974). Males need not leave the immediate vicinity of the nest for building materials because an abundant supply exists within 80 m of the nest. Although males did not hunt at the nest site they nevertheless were present at the nest for a large part of the day.

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