

## REPRODUCTIVE INVESTMENT AND ANTI-PREDATOR BEHAVIOR IN COOPER'S HAWKS DURING THE PRE-LAYING PERIOD

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**ABSTRACT.**—Based on marked intersexual behavioral differences during the pre-laying period in the Cooper's Hawk (*Accipiter cooperii*), and contrary to theory, we suggest that prior to fertilization male Cooper's Hawks, not females, make a greater investment in reproductive effort. Male Cooper's Hawks provided most of the food for the pair, they did most of the nest building, and males more frequently attacked potential predators.

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Esfuerzo reproductivo y conducta contra predadores del Gavilán Pechirrojo Mayor (*Accipiter cooperii*), durante el período anterior a la puesta de los huevos

**EXTRACTO.**—Basados en marcadas diferencias de conducta intersexual del Gavilán Pechirrojo Mayor (*Accipiter cooperii*), en el período anterior a la puesta de los huevos, y contrariando la teoría, sugerimos que antes de la fertilización son los Gavilanes Pechirrojos machos y no las hembras, los que contribuyen mayormente en los esfuerzos reproductivos. Los machos proveyeron la mayor parte de los alimentos para la pareja, son ellos también los que pusieron más trabajo en la construcción del nido, y fueron los que con más frecuencia atacaron a potenciales predadores.

[Traducción de Eudoxio Paredes-Ruiz]

Males and females make unequal energetic investments in gametes: females produce large (relative to male gametes) energy-rich eggs, while males only produce small sperm with negligible energy costs. This disparity ("anisogamy") has led to the prediction that reproductive effort up to the time of fertilization usually will be greater for females than males (Trivers 1972, 1985, Wilson 1975, Dawkins 1976). Beissinger (1987) claimed to have found the first empirical evidence of an exception to this prediction in his study of the pre-laying behavior of the Snail Kite (*Rostrhamus sociabilis*). Male Snail Kites did most of the nest building, chased predators and conspecifics more often than did females, and performed most of the foraging for their mates and themselves during the pre-laying period. Considering time and energy expenditures of these intersexual differences in pre-laying behavior, Beissinger

(1987) proposed that female Snail Kites had overcome the effects of anisogamy because males had made a greater investment in reproductive effort than females.

While recognizing that time and energy expenditures are not the only currency of reproductive investment, researchers have usually relied on such measures because these are readily quantified (Sordahl 1990). Antipredator behavior, for example, is a form of parental investment that often involves considerable risk, but such behavior is not readily observed and consumes only small amounts of energy, while the real costs of risk are difficult to measure (Sordahl 1990).

Here we summarize observations of intersexual behavioral differences in Cooper's Hawks (*Accipiter cooperii*) during the pre-laying stage (see Rosenfield et al. 1991) that parallel those reported by Beissinger (1987) and thus appear to represent another example of female raptors overcoming the effects of anisogamy. We also present data on anti-predator behavior of Cooper's Hawks in the pre-laying pe-

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riod, and suggest that intersexual differences in risk are likewise consistent with a pattern of greater male investment.

Our observations on pre-laying behavior of Cooper's Hawks come from an intensive study in Waukesha County, southeastern Wisconsin (42°53'N 88°29'W). We watched Cooper's Hawks from ground blinds erected within 5–70 m of uncompleted nests during late March to early May 1986–89. For a detailed description of the study area and observation techniques, see Rosenfield (1990) and Rosenfield et al. (1991).

There is marked asymmetry in the behavior of male and female Cooper's Hawks during the pre-laying period. Females exhibit reduced locomotor activity and remain near nests prior to egg laying (Rosenfield et al. 1991). Males are more active than females: they do twice as much nest building as females and most of the hunting for the pair (Rosenfield et al. 1991). That males are more active than females is accentuated by the fact that males must leave the vicinity of the nest to procure food (Rosenfield et al., 1991).

During the pre-laying period, male Cooper's Hawks also engaged in anti-predator behavior more frequently than females. On 14 occasions at 13 nests, when both male and female hawks were present, various intruders (including one or more American Crows (*Corvus brachyrhynchos*) on six occasions, one Red-tailed Hawk (*Buteo jamaicensis*), a Raccoon (*Procyon lotor*), and an Eastern Gray Squirrel (*Sciurus carolinensis*) on each of six occasions) were attacked and/or chased within 30 m of uncompleted nests, or, in two instances, when squirrels climbed onto the nests. Males chased these potential predators (and probably struck the Raccoon and at least two squirrels) significantly more often than did females (12 attacks by 12 individually-marked males and two by the same female;  $G = 10.9$ ,  $P < 0.001$ ; for statistical independence, only one of the attacks by the female is considered). In two of these instances, males also perched within 1–3 m of squirrels and exhibited threat postures (raised crests and outstretched wings). Gray Squirrels were only attacked when they were in trees, never while they were on the ground, even though at these and many other times we saw squirrels on the ground beneath nests and/or perched hawks. In all cases only one member of a mated pair of hawks attacked a potential nest predator; the other bird remained silently perched

nearby. One female eventually flew out of view toward the area where her mate had attacked some crows, while another female approached the Raccoon's location but did not attack it. Except for the Raccoon, which probably denned in the tree where it was attacked, all other intruders left the area of the hawk nest within 2 min after attacks began.

We suggest that the marked differences in behavior between the sexes during the pre-laying period, which are similar to the differences in activity exhibited by male and female Snail Kites (Beissinger 1987), make it likely that our results offer another example of females overcoming the effects of anisogamy. Moreover, it may be that the intersexual disparity in reproductive effort is accentuated in Cooper's Hawks because the pre-laying period is longer than that of Snail Kites (about 30 d; Rosenfield et al. 1991) versus 11–20 days.

By reducing activity (especially the energetically demanding activity of flight) and depending on males to provide most of their food during egg production, female Cooper's Hawks are presumably able to enhance energy assimilation and reduce the relative level of energy depletion during egg laying (Beissinger 1987). Female Cooper's Hawks are indeed heavier at the pre-laying stage than at the incubation or nestling stages (R.N. Rosenfield and J. Bielefeldt unpubl. data). Beissinger (1987) suggested that a female Snail Kite that withholds energy investments and builds endogenous reserves may be better able to replace clutches soon after nest failures, which were common in his study. He speculated that a high nest failure rate could have selected for male reproductive effort (through courtship feeding) to exceed female reproductive effort before laying. Reproductive failure, however, may not explain why female Cooper's Hawks have adopted a strategy so similar to that of female Snail Kites. Although many Cooper's Hawk nest failures occur during the egg stage and renesting typically occurs if nests fail early in incubation, in accord with Beissinger's (1987) hypothesis, only about 25% of all nests fail each year (R.N. Rosenfield and J. Bielefeldt unpubl. data) versus about 68% in the Snail Kite. Regardless of reproductive failure, egg production is energetically demanding (Walsberg 1983), and a complement of various strategies (e.g., increasing dietary intake, using stored nutrient reserves, reducing activity) could be used simultaneously to offset the energy demand of egg production (King and Murphy 1985). It also

may be that female Cooper's Hawks are inactive during the pre-laying period to protect developing eggs. Walter (1979:359) suggested that raptors, particularly those that hunt birds (as do Cooper's Hawks), encounter a considerable danger to developing eggs that could be damaged when a hawk chases and subdues prey.

Recent studies have investigated investment strategies of the sexes during the breeding season by dividing reproductive effort into mating effort (activities used to secure copulations) and parental effort (the sum of parental investments in each offspring) (Beissinger 1987, Brunton 1988). Females invest in offspring (eggs and young), whereas males are required to do likewise (through anti-predator behavior and courtship feeding, for example) and also to guard against cuckoldry (Trivers 1972). Under this categorization, investments by female Cooper's Hawks take the form of parental effort. During the pre-laying period, however, males must also invest much in mating effort, in an attempt to assure paternity through frequent copulations, building of the nest (perhaps a pre-coital display, Rosenfield et al., 1991) and courtship feeding (also associated with copulatory behavior in the Cooper's Hawk, Rosenfield et al., 1991). Burger (1981) suggested that because of the potential for cuckoldry, monogamous males must invest more rather than less in reproductive effort prior to egg laying, and her results on Black Skimmers (*Rynchops nigra*), and our own on Cooper's Hawks support this hypothesis. Also, the pre-laying behavior of many members of Falconiformes appears similar to that of the Cooper's Hawk and Snail Kite (Newton 1979:156-157); perhaps the behavior of numerous species in this order may be interpreted as overcoming the effects of anisogamy.

#### ACKNOWLEDGMENTS

We thank the Wisconsin Department of Natural Resources and the University of Wisconsin at Stevens Point for providing financial support of our work on Cooper's Hawks. K. Bildstein, L. and S. Garner, C. Morasky, and

J. Smallwood provided helpful comments on various drafts of this manuscript.

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Received 5 March 1991; accepted 26 June 1991