

other times of the year, Scrub Jays are usually tolerant of mockingbirds in their territories, and individuals of the two species often perch on adjacent branches of a single tree. Most aggressive interactions between the species are brief, do not result in injury of either bird, and seem to involve conflict over exposed perches used on both jays and mockingbirds when scanning for aerial predators, or territorial intruders, or both (pers. observ.).

Though extraordinary, the observation described above suggests that aggression from Scrub Jays poses a risk to adult mockingbirds and other small passerines. In this regard it is notable that few mockingbirds nest in recently burned scrubby flatwoods at Archbold Biological Station (Woolfenden 1969); many hold winter territories there during the nonbreeding season (Woolfenden 1970), but most leave to breed in other nearby habitats (Halkin 1983) rarely used by Scrub Jays (Woolfenden and Fitzpatrick 1984). Scrub Jays approaching mockingbird nests are actively mobbed and are therefore likely nest predators, but mockingbirds face other potential nest predators in forest and edge habitats (e.g., Blue Jays, *Cyanocitta cristata*). I speculate that the risk of injury or death from Scrub Jay attacks could help to explain why so few mockingbirds nest in open scrub habitats at Archbold Biological Station.

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## CUCKOLDRY IN AN AMERICAN KESTREL TRIAD<sup>1</sup>

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*Key words:* American Kestrel; desertion; dominance; extra-pair copulation; *Falco sparverius*; sex ratio; sperm competition.

The American Kestrel (*Falco sparverius*) is a small, monogamous, sexually dimorphic falcon which ranges throughout North and South America. Several studies have reported promiscuous behavior in kestrels early in the breeding season (Fast and Barnes 1950, Cade 1955, Balgooyen 1976). Balgooyen (1976) observed promiscuity in female kestrels prior to the formation of site tenacity and pair-bonding. He suggested that early copulations may act as a mechanism for bringing female kestrels into sexual readiness, and stated that promiscuous behavior by females apparently does not elicit "jealousy" in male kestrels that witness these acts.

During spring 1985, I observed two instances of cuckoldry involving a paired female, her mate, and an unpaired neighboring male. Both episodes of extra-pair copulations (EPCs) occurred more than a month after the female had paired with her mate, as determined by her exclusive use of his territory, and within 12 days of the onset of egg laying. The EPCs occurred as the mated male was foraging in an agricultural field at distances >100 m from the female. On both occasions, the unpaired male approached the female while she perched at a favored promontory. The female immediately exhibited solicitation behavior which included drooping her wings, leaning forward, and lifting her tail feathers (see Willoughby and Cade 1964). The unpaired male responded each time by mounting the female, and both EPCs proceeded to presumed cloacal contact and ejaculation. The female's mate apparently witnessed both EPCs; each time he gave *klee* vocalizations as he flew to the preening, postcopulatory birds, driving the unpaired male away. After the first EPC, the female then solicited mounting by her mate and

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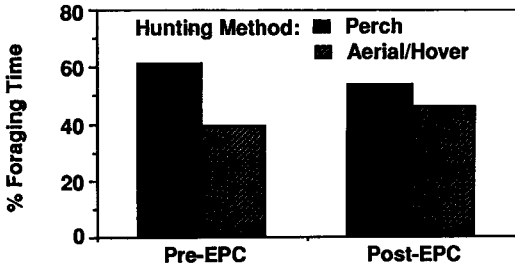


FIGURE 1. Percentage of foraging time the paired male American Kestrel spent perch hunting <60 m from his mate vs. hovering and aerial hunting over a tilled field >100 m from his mate. Post-EPC = foraging time following the first observed EPC.

proceeded to copulate with him. Following the second EPC, she flew away at his approach and disappeared into the tree where their nest box was located. Observation of these birds was limited to 6 hr per week throughout the breeding season; it is possible that unobserved EPCs occurred.

I did not detect a change in the mated male's behavior in response to the EPCs. He stayed with the female and provisioned through the fledging of her young (although it is possible that his provisioning rates were lower than they would have been without EPCs). He did not display an increase in aggression toward the female or toward the unpaired male, who continued to live adjacent to the mated pair throughout the breeding season. Both before and after the EPCs were observed, he chased the unpaired male only in reaction to the EPCs and during attempts by the unpaired male to forage on his territory. Further, he did not increase female-directed vigilance (e.g., Beecher and Beecher 1979, Morton 1987); he neither reduced the distance between the female and himself while foraging, nor increased the frequency of perch hunting close to the female (Fig. 1; see Rudolph 1982 for possible energetic constraints on the latter strategy).

There are several possible explanations for the apparent tolerance (vis-à-vis desertion) exhibited by the cuckolded male. (1) Since female kestrels are larger than males, it is possible that they are dominant in reproductive dyads, and that males are deferential to females. Although there is evidence that male kestrels are cautious toward females, they do harass females that intrude on winter territories (Smallwood 1988), and Willoughby and Cade (1964) found no evidence of dominance-subordinance relationships in captive pairs of breeding kestrels. Further, desertion by the male would have left the larger female with no opportunity to retaliate. (2) The paired male may have been copulating with his mate often enough to greatly reduce the risk that she would be fertilized by EPCs. This appeal to the sperm competition hypothesis (Birkhead et al. 1987) is supported by Balgooyen's (1976) data that show high copulation rates by mated kestrels. However, I witnessed more copulations by the unpaired male than by the mated male while the female probably was fertile. (3) The adult sex ratio was male-biased in this population of kestrels (31 males : 25 fe-

males); the paired male could have been making the best of a bad deal. Desertion might have left the male without the opportunity to pair with a second female (Smith 1988).

Trivers (1985, p. 268) suggested that the decision to desert should depend only on future mating opportunities. He noted that most monogamous male birds are attached to their territories, and that pairing with another female would necessitate driving the original female mate off the territory. Bowman and Bird (1987) used a mate-removal experiment to show that kestrel males were entirely unsuccessful at replacing lost mates and breeding again. Thus, a male kestrel appears to have little to gain by driving his mate away. For the cuckolded male that I observed, attachment to his territory, the poor prospects for pairing with an alternative female, and perhaps his small size relative to his mate, may have collectively set strong constraints against responding to his mate's EPCs. For the female kestrel, these same factors may have afforded the chance to increase the genetic diversity within her clutch by breeding with more than one male.

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