

fledging of M1's second mate's clutch, F1 was again found incubating the third nest attempted by this pair. These eggs hatched at least 8 days after the M1-F2 clutch successfully fledged. Here then, for the first time, both mates' offspring required male parental care simultaneously.

We completed 5 h of observation spanning 8 days during which his first mate's nestlings and his second mate's fledglings both required care. During this time M1 fed F2's fledglings 24 times; he was, however, never observed to feed F1's nestlings. M1 appeared to have directed his feeding exclusively toward the older offspring of his new mate. The fledglings dispersed at approximately the same time as F1's nestlings disappeared. Shortly thereafter, M1 began construction of two nests, one in each mate's side of the territory. The bulk of his work was devoted to his first mate's nest. This nest was never completed, however, although the female remained in the territory. A third clutch of eggs hatched in F2's section of the territory on approximately 19 July 1980. The nestlings were fed by both M1 and F2, and all three fledged successfully on 31 July 1980.

We conclude that the above account represents opportunistic bigamy in the Mockingbird. In addition, the focus of the male's parental efforts seemed to switch from one female to another. After mating opportunistically with the second female, his parental care was redirected toward her offspring, even though he maintained a bond associated with decreased parental care with his first mate. The observations represent another example of the growing realization that individuals may enjoy greater reproductive success through the opportunistic adoption of mixed strategies [Trivers 1972, Pp. 136–179 in *Sexual selection and the descent of man* (B. Campbell, Ed.), Chicago, Aldine; Maynard-Smith 1974, *J. Theor. Biol.* 47: 209] that depart considerably from what has been regarded as the species-specific norm.

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### Male Starlings Delay Incubation to Avoid Being Cuckolded

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Sperm competition is an inevitable result of anisogamy (Bateman 1948, Trivers 1972). Cuckoldry is a form of sperm competition peculiar to organisms exhibiting extensive male parental care and can be defined as a male's involuntary rearing of another male's offspring as a result of the latter male (the "cuckolder") having inseminated the mate of the former male (the "cuckold"). "Cuckoldry" is not properly an anthropomorphic term, because its root ("cucu") and usage to describe human behavior go back at least to the 14<sup>th</sup> century, when the nest parasitism of cuckoos (*Cuculus* sp.) was used as an analogy for describing marital infidelity (Oxford English Dictionary 1933). Moreover, there is no replacement term for "cuckoldry," and it correctly describes a behavioral complex found in species exhibiting extensive male parental care. "Cuckoldry" as a technical term in evolutionary biology differs from the "nest parasitism" of the bird whose name provides the root word for "cuckoldry" in that in "cuckoldry" the sperm of a parasitic male is *substituted* for the sperm of a host male during fertilization, whereas in "nest parasitism" the egg of a parasitic female is *added* to (rarely substituted for) the egg of a host female during laying. Cuckolding another male should be generally favored, but being cuckolded should be always disfavored, because the cuckold (1) fails to reproduce his own genes or reproduces fewer of them, and (2) promotes the spread of a competitor's genes as though they were his own. Thus, behaviors preventing cuckoldry can be expected to evolve in tandem with male parental care (Trivers 1972, Alexander 1974). Here we present evidence of such behaviors in European Starlings (*Sturnus vulgaris*), including evidence that males avoid participation in incubation until after the end of laying in order to avoid being cuckolded.

Previously, it was known that (1) male Starlings provide extensive parental care, including participation in incubation with females (Kluijver 1933, Kessel 1957), (2) incubation begins before the end of laying in New Jersey (Crossner 1977), and (3) copulation continues throughout laying (Kessel 1957). Viewing these facts in the context of cuckoldry risk, we predicted that (a) only females would incubate before the end of laying, because males could not guard their females from insemination by other males if they themselves were incubating, and (b) males would monitor their mates more closely before the end of laying than after it.

We studied Starlings breeding in our trail of 120 nest boxes on the Livingston College campus of

Rutgers University in Piscataway, New Jersey during the nesting seasons of 1978–1980. Twenty-five nests were watched from parked automobiles by a team of 25 trained observers every day during the laying and incubation periods until 2 days after we had determined that both sexes incubated at each nest. Nesting phenology was determined by daily nest censuses.

One member of the pair at each of eight nests was marked, allowing ready identification of gender. At the other 17 nests, gender was determined by eye and mandible color. Females have light, yellowish eyes and pink patches at the bases of their mandibles, while males have dark, brownish eyes and blue patches (Witschi and Miller 1938, Bullough 1942). We found that we could use these characters to distinguish genders reliably when we positioned vehicles so that the birds were in good light. Sexing of birds was easiest when they poked their heads out of their entrance holes just before leaving their nests, because they nearly always paused at that time, affording a clear view of their faces.

The onset of incubation was determined by noting the amount of time birds spent in their nest boxes and by touching eggs to determine whether they were warm or cold. At 14 nests, this "touch test" was performed during each nest census, and its results were compared to the results of behavioral observations. At 8 nests the touch test and behavioral observations indicated the same day of onset of incubation; at another 3 nests the touch test indicated the onset of incubation to be a day *earlier* than behavioral observations did, suggesting laying may have occurred just before the census; and at the remaining 3 nests the touch test indicated the onset of incubation a day *later* than behavioral observations did, suggesting that the birds at these nests may not have been incubating even though they were spending long periods in their nest boxes (Kenneth A. Crossner pers. comm.). Despite this variation, behavioral observations always indicated the onset of incubation within 1 day of the time indicated by the touch test.

Our results bearing on prediction (a) indicate that, in all cases, females began incubation before males (Sign Test,  $n = 25$ ,  $x = 0$ ,  $P < 0.0001$ ). Twenty of 25 females began incubation before clutch completion, 3 females began incubation the day of clutch completion itself, and 2 females began incubation the day following clutch completion. No male began incubation before clutch completion, and only one male began incubation on the day of clutch completion itself. These results corroborate prediction (a).

Males monitored the movements of their mates by (1) being at the nest box or in a position from which the box could be viewed when females entered or left their nests, and (2) guarding females from other males as they foraged. Guarding involved flying after and perching with females, waddling a few steps after or alongside females, and chasing away other birds that approached their mates or simply failed to move aside as a pair advanced. Males were at or within viewing distance of their nests on 169 out of 226 occasions (75%) when females entered or emerged from their nest boxes before the end of laying, but on only 76 out of 256 equivalent occasions (30%) afterward. This difference is significant ( $\chi^2 = 95.62$ ,  $df = 1$ ,  $P < 0.0001$ ). Moreover, 17 out of 18 males for which we had monitoring data from before as well as after clutch completion reduced their frequency of monitoring at the nest box following the end of laying (Sign Test,  $n = 18$ ,  $x = 1$ ,  $P < 0.0005$ ). Similarly, males guarded females on 81 out of 86 foraging trips (94%) before clutch completion, but on only 42 out of 73 foraging trips (58%) afterward. This difference is also significant ( $\chi^2 = 46.56$ ,  $df = 1$ ,  $P < 0.0001$ ). Of the 18 males for which we had monitoring data from before and after clutch completion, 12 decreased their guarding frequency after clutch completion, while the other 6 continued the same level of guarding (Sign Test,  $n = 12$ ,  $x = 0$ ,  $P < 0.001$ ). These results corroborate prediction (b).

At least two questions are raised by our findings: (1) how do they relate to other bird species? and (2) what costs do male Starlings incur by protecting themselves against cuckoldry?

(1) Because both predictions were derived from an hypothesis of cuckoldry risk, and their corroboration supports that hypothesis, Starlings can now be added to the growing list of species in which behaviors reducing cuckoldry risk have been found: Mallards (*Anas platyrhynchos*) (McKinney 1975, McKinney et al. 1978, Hailman 1978); Common Murres (*Uria aalge*) (Birkhead 1978); Ringed Turtle Doves (*Streptopelia risoria*) (Erickson and Zenone 1976, Zenone et al. 1979); Bank Swallows (*Riparia riparia*) (Hoogland and Sherman 1976, Beecher and Beecher 1979); Black-billed Magpies (*Pica pica*) (Birkhead 1979); Mountain Bluebirds (*Sialia currucoides*) (Power 1979, 1980; Power and Doner 1980); and Malachite Sunbirds (*Nectarinia famosa*) (Wolf and Wolf 1976).

Corroboration of prediction (a) is particularly interesting, because it demonstrates for the first time in any species that males providing extensive parental care will delay the onset of incubation until after the end of the period of cuckoldry risk. Because both sexes are known or suspected to incubate in at least some species in 118 (70%) of the 168 families of birds found over the globe (Van Tyne and Berger 1959) and in 116 (40%) of the 293 species of passerines found in North America (Verner and Willson 1969), we expect our results for Starlings to be repeated in many other species.

(2) Male Starlings incur several costs in order to assure their paternity. When males escort their mates rather than performing alternate bouts of incubation with them, they leave their nests unguarded and therefore subject to parasitism, usurpation, and predation. We have no quantitative estimates of the risks of nest usurpation by other Starlings or of predation of eggs, but both usurpation and predation have been recorded in Starling populations (Kluijver 1933, Kessel 1957).

We do have a preliminary estimate of the magnitude of nest parasitism. Intraspecific nest parasitism occurs in the form of dumping of eggs by females into the nests of other Starlings. Egg dumping is common in our study population. At 24 nests not included in our natural experiment, we made daily censuses and marked all newly laid eggs in order to detect dumping. We found dumping in 11 (46%) of these 24 nests. Clearly, intraspecific nest parasitism is a serious threat to Starlings. It is not as great a threat to males as cuckoldry, however, because egg dumping merely adds to the burden of parental care without reducing the actual number of offspring a male sires and rears. Only cuckoldry has the potential to divert all of a male's parental care onto young he has not sired. Even cuckoldry involving only one egg in a clutch is genetically more expensive to a male than the addition of a foreign egg to his nest by a dumper, because the price in terms of lost paternity is  $1/n$  for the act of cuckoldry but  $1/(n + 1)$  for the act of dumping (where  $n$  = the clutch size of the male's mate).

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### Importance of Structural Stability to Success of Mourning Dove Nests

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Studies of nest-site selection and nesting habitats often involve a "characterization" of nests and of habitats in which nests are found. Our objective in the present work is to identify nest-site characteristics that are associated with variation in components of Mourning Dove (*Zenaida macroura*) fitness (e.g. the probability of a nest succeeding), as opposed to simply "characterizing" dove nest sites. If certain nest-site characteristics affect the probability that a nest will succeed, then we suspect that these characteristics will be associated with either concealment (the probability of detection by certain predators) or structural stability (the probability of eggs or entire nests falling to the ground as a result of wind, rain storms, parental activity, etc.). Although other workers agree that structural stability is an important determinant of Mourning Dove nesting success (e.g. McClure 1944: 384; Woolfenden and Rohwer 1969: 59), we are aware of no actual tests of this hypothesis.

Here we report results of an investigation designed to determine whether or not structural stability is associated with the probability of nesting success in Mourning Doves. First, we monitored a sample of dove nests and recorded whether they succeeded or failed. We then obtained an independent measure of structural stability and classified each nest into one of two groups based on this measure. Finally, we estimated daily survival probabilities for nests in each group and used these estimates to test the null hypothesis that nest success was independent of the structural stability measure.

Dove nests were located on the grounds of the Patuxent Wildlife Research Center ( $n = 56$  nesting attempts) and in residential areas of Bowie and Laurel, Maryland ( $n = 6$ ). Nests were located from 17 March to 3 August 1979; the majority (77%) were found during 15 April to 15 June. After their initial location, all nests were visited at intervals of 1 to 8 days until either success (fledging) or failure occurred. "Success" is difficult to determine when nestlings reach an age at which they are known to be capable of fledging (e.g.  $\geq 10$  days). For example, if a nest contains 11-day-old nestlings one day and is empty the next, determination of fledging or predation is often impossible. For this reason, we operationally defined a successful nest as one in which a single nestling was known to attain an age of 10 days. In many instances, nests were visited on the day of hatching and nestling ages were known exactly. In the remaining instances, we aged nestlings using the key and photographs of Hanson and Kossack (1963). All nests were visited on day 10 after hatching to determine success or failure.

We can envision two approaches to obtaining a "measure" of the structural stability of a nest: (1) obtain sets of actual measurements believed to be associated with structural stability, (2) obtain measures of a single integrated variable believed to reflect structural stability. We chose the second approach and used a nest persistence index (NPI). All nests monitored in 1979 were revisited in 1980 and given the following NPI ratings: (1) nest absent, (2) nest remnant present but incapable of holding eggs, (3) nest present and capable of holding eggs. NPI is thus a variable that, in effect, integrates the various components affecting structural stability of nests (see also McClure 1944: 389). A value of "1" or "2" indicates that a nest did not survive the winter intact and is assumed to reflect poor construction or site location, or both. Conversely, a value of "3" is indicative of a nest that did survive the winter and reflects good construction or site location.

Between 26 March and 5 May 1980, we assigned a NPI to 47 of 54 nests located during the previous breeding season. The remaining 7 nests were discarded for various reasons (e.g. incomplete nesting record, human disturbance of nest site, uncertainty of exact nest location). In considering the relation between nest fate and NPI, nests were separated into two groups (Table 1): (1) nests that were used only once ( $n = 40$ ), plus final nesting efforts in nests that were used more than once during 1979 ( $n = 7$ ); and (2) nesting efforts for nests used more than once, but not including the final effort ( $n = 8$ ). If there are