

EXTRA-PAIR COURTSHIP AND COPULATION ATTEMPTS IN NORTHERN ORIOLES¹

BRUCE B. EDINGER²

*Bell Museum of Natural History, Department of Ecology and Behavioral Biology,
University of Minnesota, Minneapolis, MN 55455³*

Abstract. I observed 50 cases of male Northern Orioles (*Icterus galbula*) intruding on other males' territories. In 23 of 50 cases, the intrusion led to an extra-pair courtship or chase. Three of these intrusions resulted in extra-pair copulation. Intrusions were significantly more likely during the female's fertilizable period (during egg laying and up to 5 days before the first egg was laid). Intrusions occurred at the same time in the nesting cycle as pair copulations and both peaked during early morning hours. Both yearling and adult males intruded, but only adult males engaged in extra-pair copulation. In all cases where the intruding male was identified by color bands, he was a paired male from a territory 110 m to 280 m away from the target female's nest. Five unbanded intruders came from more than 200 m away. All but one female ignored or flew away from males performing extra-pair courtship. Most females gave loud calls when fleeing from intruders attempting extra-pair copulation; in two cases females were driven to the ground and mounted. Paired males showed three types of mate association when females were fertilizable: (1) "consorting," accompanying their mate when they left the territory to forage or gather nesting material; (2) "driving," when females moved close to neighboring males and were chased back into the territory; and (3) rapid pair copulation. The last behavior was observed only during song playback experiments that may have been perceived by resident males as territorial intrusions.

Key words: *Colorado; courtship; extra-pair copulation; extra-pair courtship; Northern Oriole; mate guarding; social behavior.*

INTRODUCTION

Trivers (1972) predicted that when absolute monogamy was not dictated by ecological limitations, males would be selected to seek extra-pair fertilizations without additional paternal investment. Extra-pair copulation (EPC) occurs in at least 104 bird species within 26 families (McKinney et al. 1984), and in several species EPC has been shown to result in fertilization (Red-winged Blackbirds, *Agelaius phoeniceus*, Bray et al. 1975; Mallards, *Anas platyrhynchos*, Burns et al. 1980, Everts and Williams 1987; swallows, Martin 1980; Pied Flycatchers, *Ficedula hypoleuca*, Alatalo et al. 1984; Acorn Woodpeckers, *Melanerpes formicivorus*, Joste et al. 1985, Mumme et al. 1985; Bobolinks, *Dolichonyx oryzivorus*, Gavin and Bollinger 1985; House Sparrows, *Passer domesticus*, Burke and Buford 1987, Wetton et al. 1987; and Indigo

Buntings, *Passerina cyanea*, Westneat 1987b). If territorial intrusions and extra-pair courtship also indicate some success in EPCs, estimates of the incidence of EPC will have to be increased (Ford 1983).

Most studies which have attempted to quantify the frequency of EPCs have been of colonial species (Mineau and Cooke 1979, Fujioka and Yamagishi 1981, Røskaft 1983, Birkhead et al. 1985). Reports of EPCs in species with dispersed nesting are relatively few (Ford 1983, McKinney et al. 1983, Afton 1985, Westneat 1987a), but this may reflect the greater difficulty of observing EPCs in dispersed nesting birds. Some authors have suggested that EPCs may be more frequent in colonially-nesting species (Gladstone 1979, McKinney et al. 1983) and two authors have found EPCs are more frequent in dense rather than dispersed populations of a single species (Birkhead 1979, Møller 1987). However, this relationship does not hold for interspecific comparisons. During 352 hr of observation Westneat (1987a) observed 53 EPCs (12.8% of all copulations) in the dispersed-nesting Indigo Bunting. Discovery of general trends between the frequency of EPCs and the dispersion of nest sites

¹ Received 13 August 1987. Final acceptance 7 March 1988.

² Present address: Department of Biology, Beloit College, Beloit, WI 53511.

³ Reprint requests.

will require more quantitative reports of EPCs in noncolonial birds.

If EPCs are common, mated males will be expected to guard their mates from intruding males (Trivers 1972). Mate guarding has been reported often in colonially nesting species (e.g., Beecher and Beecher 1979, Birkhead 1979, Buitron 1983, Møller 1987), but less often for noncolonial birds (e.g., Westneat 1987a). Mate guarding might be expected to be less common in noncolonial species which maintain territories if food, nesting material, and other resources required by females are found on the territory. Clearly there is little information on the relationship of EPC, mate guarding, and nest density.

The role of females in EPC is poorly understood. Since passerine birds lack intromittent organs, Fitch and Shugart (1984) argue EPC in such species must involve some degree of female cooperation. The degree of female cooperation has not been well-studied in either colonially or noncolonially nesting birds. Westneat (1987a) found in Indigo Buntings that more EPCs than within-pair copulations (WPCs) were resisted (79% vs. 23%, respectively). Female Cattle Egrets (*Bubulcus ibis*) nesting in colonies successfully repulsed a significant portion of EPCs, and resisted a higher proportion of EPCs from less dominant males (Fujioka and Yamagishi 1981). Quantitative comparisons of pair and extra-pair courtship and copulation sequences are needed in many other species if the role of the female in EPCs is to be elucidated.

There has been only one published account of extra-pair behavior in Northern Orioles (*Icterus galbula*). Flood (1985) reported three "extra-pair" copulations by females after their mates were experimentally removed. This behavior might also be interpreted as re-pairing by a female to a bigamous male. Her usage of "extra-pair copulation" may be correct from the point of view of the already paired male, but not from the point of view of the widowed female.

Here I report a study of territorial intrusions and EPCs in Northern Orioles, a territorial, dispersed-nesting passerine. Most males pair with only one female, but a few males may attract more than one female (Williams 1982 and pers. comm.). Males feed offspring at approximately the same rate as females. This study addresses four major questions. (1) What are the similarities of within-pair and extra-pair courtship in this species? (2) When do within-pair copula-

tions, extra-pair intrusions and copulations, and defensive behavior by paired males occur with respect to the reproductive status of target females? (3) What is the breeding status and age of males performing intrusions? (4) What is the role of females in EPCs and EPC attempts?

METHODS

POPULATION AND STUDY AREA

The American Ornithologists' Union Check-list Committee (1973) currently recognizes Baltimore and Bullock's orioles as subspecies of the Northern Oriole (*Icterus galbula galbula* and *I. g. bullockii*). The subspecies differ conspicuously in plumage and vocalizations (Edinger 1985), but they did not differ noticeably in courtship behavior.

The study area was located in riparian floodplain woodland about 1.5 km SSW of Crook, Logan County, Colorado in the wooded portions of sections 14, 15, and 16, T10N, R49W, Crook Quadrangle. The vegetation consisted of groves of cottonwoods (*Populus deltoides*) interspersed with shrubby openings dominated by willow (*Salix amygdaloides*), snowberry (*Symphoricarpos occidentalis*), and currant (*Ribes cynosbati*). Baltimore Orioles were about twice as numerous in the study area as Bullock's Orioles (Corbin and Sibley 1977, Edinger 1985).

BEHAVIORAL OBSERVATION

Data presented here were recorded during 30-min monitor periods of 34 nesting pairs from 05:30 to 10:30 during May, June, and July of 1980 and 1981. Nests were monitored three to six times during construction and egg laying and four to 10 times after incubation began until fledging. Observations were made with binoculars or a 30× spotting scope from semiconcealed locations 8 to 20 m from the nest. General observations were made throughout daylight hours. For this paper, a total of 189 hr of timed observation and about 230 hr of general observation were included in the analysis.

Although some intrusions by foraging birds took place near the periphery of territories, usually 15 to 75 m from the nest, I concentrated on those which involved movement to within 7 m of the nest because they were more completely observed and there was less chance that they were coincidental (some males which intruded peripherally were foraging and did not appear to

be oriented to the female or nest). Intrusions are defined as movement of male orioles other than the paired male to within 7 m of the nest, with or without the presence of the female.

INDIVIDUAL IDENTIFICATION

Twenty-four percent (16 of 68) of the birds and 29% (10 of 34) of males included in this study were mist-netted, fitted with a U.S.F.W.S. aluminum band, and given a unique combination of three color bands. Considerable age, race, and individual variation in plumage allowed some intruders to be distinguished from local territorial birds with known plumage patterns. Only color-banded birds were included in data sets which depended upon individual identification.

STAGE OF NESTING

Every 2 or 3 days I determined the stage of nesting for 18 of 34 nests with a mirror pole to view the nest chamber. Egg-laying and hatching dates for 16 inaccessible nests were estimated on the basis of female behavior. In all accessible nests egg laying occurred only on days when females were observed lining their nests. This behavior was observed only twice outside of the laying period (once 1 day before the first egg date and once 1 day after the last egg date). Therefore, for inaccessible nests I estimated the first egg date by the onset of lining behavior. Day 0 represents the day the first egg was laid, day -1 represents the day previous to day 0, and day 1 represents the day after the first egg was laid.

In accessible nests, when the last or penultimate egg was laid, female visits to the nest increased in length from about 5 min to 20–45 min with the onset of incubation. For inaccessible nests I assumed clutch completion was coincident with the beginning of incubation. These behavioral cues agreed (to within 1 day) at all accessible nests.

Hatching dates for inaccessible nests were determined by the date parents first fed young. One- and 2-day-old nestlings are fed by regurgitation, which left moisture on the bills of the parents and was a reliable indication of recently hatched young. In this population Northern Orioles laid four to six eggs, incubated for 11 to 14 days, and fledged young 11 to 15 days after hatching. Females which nested on a male's territory were considered paired to that male.

PLAYBACK EXPERIMENTS

I exposed 45 territorial males to a total of 65 tape-recorded playbacks of either a New York song sequence or a California Bullock's song sequence. These sequences are from the Cornell University Library of Natural Sounds housed in the Laboratory of Ornithology, Ithaca, New York. They are listed as Cornell Catalog cuts 3 and 11, respectively. I used a Uher 4400 tape recorder to play back the recording at a volume set to match natural song. Playbacks were conducted between 06:00 and 09:30 at nests where females had begun nest construction but had not yet started incubation. Although these playbacks were conducted to address questions not discussed in this paper, unusual male responses during the playbacks have significance here.

RESULTS

PAIR COURTSHIP

Arrival and initial courtship. During 1980 and 1981 males arrived on the study area an average of 5 days before the mean arrival date for females, although there was considerable variation. A few females arrived before some subadult males were first observed on the study area. After arrival, males immediately defended territories with song, border "face-offs," aerial chases, and occasional midair grappling.

When females arrived they were vigorously courted as they foraged within the territory, but they did not always remain on the territory where they were first observed. Males chased females that passed through their territories, sometimes driving them back within the boundaries, and displayed to females that lingered. This display consisted of the singing or chattering male hopping from branch to branch about 0.5 m in front of the female and, while facing her, bowing down and up about once a second with wings lowered and a fanned tail cocked at 45°. This bow display often exposed the contrasting orange and black coloration of the head, back, wings, and tail.

Females responded by either ignoring the male, singing or chattering in response, or by leaning forward and quivering their wings while uttering a trilling vocalization similar to that of begging nestling orioles ("crouch-quiver" display). Most females began nest building within 10 days of arrival. Only females constructed nests and wove the coarse outer shell in 4 to 5 days and com-

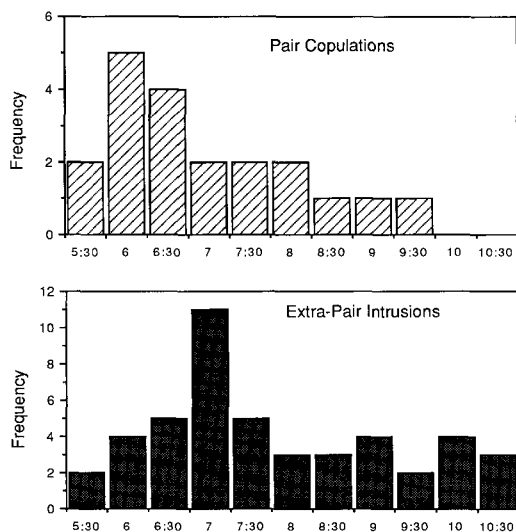
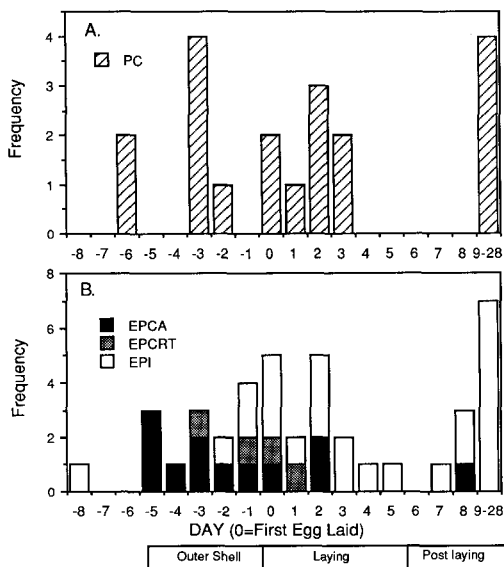


FIGURE 1. The reproductive stage of females in relation to timing of (A) 20 pair copulations (PC, hatched bars), and (B) 41 intrusions. Depicted are intrusions in which the intruder was chased before courtship (EPI, open bars); the intruder was not chased and courted the female, extra-pair courtship (EPCRT, stippled bars); and the intruder flew at and chased the female, extra-pair copulation attempts (EPCA, black bars).

FIGURE 2. The time of day pair copulations ($n = 20$) and intrusions ($n = 50$) occurred. The sampling effort was uniform from 05:30 to 10:30; observations after 10:30 were from ad libitum notes.

pleted the lining in another 4 to 6 days. Twice females started nest building on the boundary between two territories, and the neighboring males contended vigorously for the female with extended song bouts, chasing, and territorial face-off displays.

Pair courtship and copulations after nest initiation. Eighteen courtship sequences were observed from beginning to end. Ten of these ended in copulation. In 14 courtship sequences where males solicited copulation, they approached their mates with song nine times, bow displays four times, and a chase once. After four of 10 copulations males sang postcopulatory flight songs. These consisted of a rapid song uttered during a slow, ascending flight with exaggerated wing beats. Females initiated courtship during four of 18 sequences with crouch-quiver displays. In six of 10 sequences that led to copulation, females gave crouch-quiver displays before mating.

Timing of pair copulation. Sixteen of 20 (80%) copulations were performed when females were either constructing the outer shell of their nest or lining it (outer shell construction precedes nest

lining, and egg laying occurs during the nest-lining period, Fig. 1). The remaining four copulations took place during or within 1 day of laying. Pair copulations occurred most frequently between 06:00 and 07:30 hr (Fig. 2).

INTRUSIONS, EXTRA-PAIR COURTSHIP, AND EXTRA-PAIR COPULATION ATTEMPTS

Intruder's behavior and repulsed intrusions. I observed 50 intrusions by males into territories of paired males. Intruders either were immediately chased out by the resident male (repulsed intrusion), approached the female with singing or bow displays (extra-pair courtship), or flew at the female from concealed positions near the nest and drove her to the ground (extra-pair copulation attempt). In 23 of 27 repulsed intrusions, the intruder immediately left when chased by the female's mate, while in the other four cases the female ignored the intruder, who then left. Unlike conspicuous behavior when on their own territories, such as singing and preening on exposed perches, intruding males were silent during the approach, oriented toward the nest or female and remained hidden behind leaves.

Extra-pair courtship near the nest. Of nine intruders that bow-displayed to females near their nests, seven were ignored by the females and left, one was chased away by the female, and one

TABLE 1. Observed and expected frequencies of 41 intrusions (where reproductive stage of female was known) during 439 nest-monitor periods. Data for 1980 and 1981 are pooled.

Reproductive stage	No. hours observed	No. intrusions observed	No. intrusions expected
Nest construction and egg laying (13 days)	49.5	29	9.25
Incubation (13 days)	88	11	16.44
Nestlings (13 days)	82	1	15.31

copulated with the female after she fluttered to the ground. This female did not vocalize or fly away from the intruder, who sang a postcopulatory flight-song while leaving the territory.

Extra-pair courtship away from the nest. On five occasions females foraging or collecting nesting material away from their mate's territory were courted by neighboring males. Once, the earliest female to begin nest construction was chased by three unpaired males while collecting nesting material. During the other four occasions paired males bow-displayed in front of females. These displays may have been either an attempt to attract secondary females or to gain extra-pair copulations. In all five cases the females ignored the courting males and returned to their nests.

Extra-pair copulation attempts and female response. Of 14 males who intruded and chased females from their nests, eight were chased from the territory almost immediately by resident males, two intruders left the territory after the females fled, and one intruder left after being chased by the female. In the remaining three cases, two males each mounted the female after catching up with her, and each left the territory with a flight-song. A third intruder behaved similarly, except copulation, if it occurred, was obscured by vegetation. In all 14 extra-pair copulation attempts where the male flew directly at the female, the female flew away from the intruder. Eleven of 14 uttered loud, harsh vocalizations while being chased, while no females in 18 pair-courtship sequences uttered similar vocalizations. One female evaded her chaser when she flew into a river. In all three cases where copulation was observed or may have occurred, females fled and were chased to the ground from 30 to 70 m from the nest.

Timing of intrusions and female behavior. All three types of intrusion occurred most often when the target female was weaving or lining her nest (nest lining coincides with egg laying). Seventy percent (21 of 30) of intrusions that led to extra-pair courtship and copulation attempts occurred

when females had nesting material in their bills, although the exact egg dates of all of these females was not known. In the remaining nine cases, females were weaving or lining their nests within a day of the intrusion. Intrusions occurred from prenesting to the feeding of young, but a significantly higher proportion of intrusions than expected took place during nest construction and egg laying ($\chi^2 = 41.4$, $df = 2$, $P < 0.001$; Table 1). This peak in intrusions coincided with the peak occurrence of pair copulations (the cumulative frequency distribution of the timing of intrusions and pair copulations did not differ significantly; Kolmogorov-Smirnov two sample test, $T_1 = 0.02$, $P > 0.2$). Seven intrusions occurred during late incubation and brooding when females were no longer fertilizable. None of the later intrusions involved extra-pair courtship or extra-pair copulation attempts.

STATUS OF INTRUDING MALES

Twelve intrusions by banded orioles were observed. These were performed by eight paired males with territories 110 to 280 m away from the intrusion site, although many banded males occurred on territories up to 1,200 m from where intrusions were recorded. One male intruded twice on one female and once on a different female. Five unbanded intruders could not have been from a territory within a 200-m radius of the target nest since their plumage did not match that of local territory holders, all of whose plumages were known. No known unpaired males were observed intruding, but there was no significant deviation from expected in rates of intrusion by unpaired males ($\chi^2 = 1.35$, $df = 1$, $P > 0.2$) because the ratio of resident unpaired to paired males over 2 years was only 11 to 64. No significant difference was found in the likelihood of yearling and adult males to intrude ($\chi^2 = 0.39$, $df = 1$, $P > 0.2$), and to engage in extra-pair courtship or copulation attempts ($\chi^2 = 0.89$, $df = 1$, $P > 0.2$) given their abundance in the population.

TABLE 2. Time (days) from first egg date of target females (first egg = day 0) and intruder's mates in nine cases where the intruder's identity and the nesting stages of both females were known.

Case	Target female's egg date	Target female fertile?	Intruder's mate's egg date	Intruder's mate fertile?
1. Courtship	-5	Maybe	-7	Maybe
2. Chase	-4	Yes	-3	Yes
3. Chase	-1	Yes	-4	Yes
4. Courtship	1	Yes	0	Yes
5. Chase	2	Yes	5	Maybe
6. Chase	2	Yes	6	No
7. Chase	3	Yes	0	Yes
8. Intrusion	8	No	3	Yes
9. Intrusion	10	No	8	No

Intruding males did not delay intrusions until after their mates were no longer fertilizable. In five of nine cases where intruding males were identified and breeding status of target female and the intruder's mate were known, their mates were either nest building or laying and therefore fertile (Table 2). On the day of the intrusion, intruder's mates were from 7 days before to 8 days after their first egg date. In cases 1, 2, 4, and 7 a fertilizable female was left for an intrusion on a female who was also fertile. In case 6 a male left a mate who had completed her clutch and attempted EPC with a female which had laid three eggs. In cases 8 and 9 males intruded on females who were already incubating; in case 8 the male left a fertile mate to intrude.

PAIRED MALE'S RESPONSE AND MATE ASSOCIATION BEHAVIOR

Paired males that discovered intruders invariably chased them from the territory. Often these chases were prolonged and once the intruder was struck in flight by the territorial male. While chasing intruders, territorial males often uttered low harsh notes that were not heard in other contexts. Chases were broken off from 75 to 170 m from the nests.

Males guarded their mates on some occasions with one of three behaviors: "consorting," "driving," and rapid pair copulation. During 18 of 99 monitor periods when the female was fertile (during nest building and egg laying) and in view at least 15 min of the 30-min period, males repeatedly followed (consorted) within 3 m of their mate when she flew 25 to 200 m from her nest. Consorting occurred significantly more often than

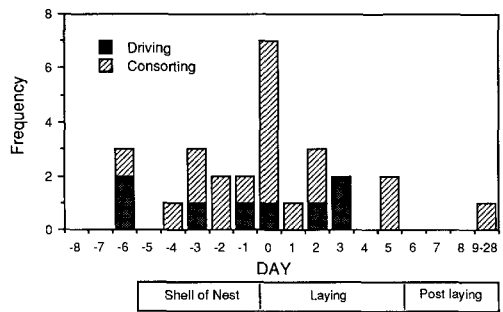


FIGURE 3. The reproductive stage of females in relation to the timing of mate consortng (open bars) and mate driving (hatched bars).

expected during nest construction than during incubation or provisioning (Fig. 3, $\chi^2 = 16.9$, $df = 1$, $P < 0.001$). Females were never observed to drive their mates away, therefore females are not preventing their mates from being close and it was up to the male to establish proximity. Interestingly, in eight of nine monitor periods that females were observed collecting nesting material from more than 120 m from the nests, they were seen with consorting mates. However, consortng was observed in only 10 of 90 periods when females ranged less than 120 m from the nest. Consortng is significantly more likely when females range more than 120 m from the nest ($\chi^2 = 34.1$, $df = 1$, $P < 0.001$).

I observed males driving or chasing their mates away from neighboring males on eight occasions. Naturally occurring driving was significantly more likely during nest construction and laying than after laying ($\chi^2 = 16.9$, $df = 1$, $P < 0.001$). Driving was also observed four times during 47 tape-recorded song playback experiments (conducted for other purposes, Edinger 1985) performed from within the territories.

During three playbacks, paired males chattered, mounted their mates, and rapidly copulated (rapid pair copulation). Females did not bow-quiver to their mates immediately beforehand, nor did males bow-display or sing before mounting. None of these copulations were followed by a postcopulatory song flight. In one case, the female approached the tape recorder's speaker 50 sec after the recording playback had begun and bow-quivered after a recorded song phrase was broadcast. Ninety seconds later the female's mate flew into her tree and a rapid pair copulation ensued. In one of the other two cases the female was within 15 m of the tape recorder

for at least a minute during the song playback before a rapid pair copulation was observed.

DISCUSSION

Except for 11 intrusions during incubation and nestling periods, 78% (39 of 50) of intrusions took place 5 days before to 5 days after the first egg date. This period is probably the most fertile period for oriole females. The same cues of nest construction and carrying of nesting material by females seem to be used by intruding males to time intrusions and by paired males to initiate pair copulation. This pattern has also been found in Bank Swallows (*Riparia riparia*) where extra-pair chases are most common during the period of mud collection (Beecher and Beecher 1979). The temporal pattern of extra-pair intrusion coinciding with female fertility is similar to that reported in other species (e.g., Yellow-billed Magpies, *Pica nuttalli*, Verbeek 1972; Cattle Egrets, *Bubulcus ibis*, Fujioka and Yamagishi 1981; Yellow Warblers, *Dendroica petechia*, Ford 1983; and several waterfowl, McKinney et al. 1983). Unlike Black-billed Magpies, *Pica pica* (Buitron 1983), intruding male orioles did not delay intrusions until after their females were no longer fertile. The high degree of nest synchrony in orioles (Edinger 1985) may reduce the possibility that intruding males can limit the risk of leaving fertile mates when intruding.

The timing and context of mate consorting, mate driving, and rapid pair copulations by male orioles suggest these are tactics of paired males to avoid cuckoldry. Male consorting occurred more often than expected by chance during peak female fertility as has been reported for several other passerines (Black-billed Magpies, Birkhead 1979, 1982 and Buitron 1983; starlings, Power et al. 1981; and Mountain Bluebirds, *Sialia currucoides*, Power and Donner 1980). The relatively low incidence of mate consorting in orioles is puzzling when compared with the nearly continuous mate guarding reported in magpies (Buitron 1983) and Bank Swallows (Beecher and Beecher 1979). If females do not range very far, their mates may be in visual or auditory contact without close association. In fact, during nest construction females often sang or chattered in response to male chatters or when leaving the nest. In a different habitat in California, Williams (pers. comm.) radio-collared four female orioles and found their home range to be 2 to 4 ha, well

beyond such contact. She rarely observed close association in mated pairs.

Mate driving was observed only during the period of fertility and when the female was close to another male. Mate driving in response to song playbacks also suggests that the male is attempting to sequester his mate from other males. Driving behavior has also been reported in magpies (Buitron 1983), Rock Doves, *Columba livia* (Goodwin 1967), and the Red-cheeked Cordonbleu, *Uraeginthus bengalus* (Goodwin 1982). It was only in the context of song playbacks that I observed rapid pair copulation, which is probably a rarely used tactic by a paired male to increase the probability his sperm will fertilize his mate's ova in situations where his female may have copulated with another male. Rapid pair copulation in similar contexts has been reported in Mallards (Barrett 1973, Barash 1977) and in Green-winged Teal, *Anas crecca* (McKinney and Stolen 1982). In captive teal, 65% (9 of 14) of rapid pair copulation attempts occurred within 11 min of a forced copulation attempt on the female, and all occurred during the period when forced extra-pair copulations were going on.

Extra-pair copulation, extra-pair courtship, and polygyny in Northern Orioles demonstrates a mixed strategy within the extra-pair reproductive behavior of male orioles and changes the traditional view of mate fidelity within this species. Ford (1983) has suggested that polygynous deviation from monogamy may be expected among species in which the males play a minor role during incubation. If the male plays a major role in feeding the young, females should mate preferentially with unpaired males, and potential polygynists will be selected to hide their paired status. This may explain the "polyterritoriality" (sensu Alatalo et al. 1981) reported by Williams (1982) and my observations on two males attempting polygyny by advertising and courting additional females well away from the primary female's nest.

The conditions under which paired females are the target of or tolerate extra-pair copulation (EPC) are poorly known. Females may react with less resistance to extra-pair courtship or copulation attempts if they have lost a mate (Flood 1985) or if courted by a dominant male. Dominant Cattle Egrets attempted more EPCs and completed a higher proportion of EPC attempts than lower ranked males (Fujioka and Yamagishi 1981). Since 87% of female egrets who responded

aggressively to EPC were successful in dislodging the males, and overall 41% of all EPC attempts were repulsed by females, female egrets exercise some choice over which males copulate with them. In the Brown-headed Cowbird (*Molothrus ater*), dominant males in captive flocks sang songs that elicited greater copulatory response than subordinate male songs (West et al. 1981). There is some evidence that dominance interactions are important in Northern Orioles. Yearling males defend territories adjacent to those of adult males. In four cases yearling males with territories adjacent to adult males switched their songs during early June to match those of the neighboring adult males. In three interactions between adult and yearling neighbors, when chased by the adults, the yearlings gave female-like bow-quiver displays that defused further aggression. How male dominance interactions in male orioles are perceived by females is uncertain.

Synchrony of breeding and benefits of male parental care may limit the intensity of selection for EPC behavior (Westneat 1987a). Northern Orioles in northeastern Colorado bred synchronously; 84 of 92 (91%) successful nesting attempts monitored during 1979 to 1981 fledged young during the period 5 days before to 5 days after the mean fledging date (Edinger 1985). This synchrony appears to be food-based since during all 3 years one species of leaf-rolling moth caterpillar (Lepidoptera: Tortricidae) was most available during 2 weeks which coincided with the oriole nestling period. Larvae of this moth accounted for 73% of provisioning trips to fledglings (Edinger, unpubl. data). Nests with emaciated young or reduced broods were observed most often in nests fledging later in the season. Since nesting attempts are highly synchronized there may be fewer opportunities for EPC without leaving mates unguarded. Since both male and female Northern Orioles provision young about equally (although there is considerable variation among pairs, Edinger, unpubl. data), EPC attempts by mated males during the fledging period may increase the chance the young will starve.

Study of individually identified Northern Orioles demonstrates that this species may be added to the growing list of apparently monogamous bird species which show several kinds of extra-pair courtship and mating behavior. The timing of extra-pair courtship and copulation attempts coincides with apparent peak fertility in target

females. The behaviors by mated males of courting, driving, and rapid pair copulation appear to be adaptations to reduce the risk of cuckoldry.

ACKNOWLEDGMENTS

I thank D. N. Alstad, K. W. Corbin, P. Gowaty, N. Ford, K. Oberhauser, F. McKinney, D. Westneat, P. Williams, and an anonymous reviewer for reading and improving earlier drafts. Marvin Gardner and Ronald Desilite of the Colorado Game and Fish Commission permitted the research on the Tamarack Ranch Wildlife Refuge. Darryl and Stephanie Crawford extended warm hospitality to the oriole team during both field seasons. I thank Diana Hildreth, Timothy Lamey, and Kathryn Smith for able help with fieldwork. Financial support was provided by the Dept. of Ecology and Behavioral Biology Ecology Fund, the Dayton and Wilkie Natural History Funds of the James Ford Bell Museum of Natural History, the F. M. Chapman Fund of the American Museum of Natural History, an Alexander Wetmore Award from the American Ornithologists' Union, a Paul Stewart Award from the Wilson Ornithological Society, and a Grant-In-Aid of Research from Sigma-Xi.

LITERATURE CITED

- AFTON, A. D. 1985. Forced copulation as a reproductive strategy of male lesser scaup: a field test of some predictions. *Behaviour* 92:146-167.
- ALATALO, R. V., A. CARLSON, A. LUNDBERG, AND S. ULFSTRAND. 1981. The conflict between male polygyny and female monogamy: the case of the pied flycatcher, *Ficedula hypoleuca*. *Am. Nat.* 117: 738-753.
- ALATALO, R. V., L. GUSTAFSSON, AND A. LUNDBERG. 1984. High frequency of cuckoldry in Pied and Collared flycatchers. *Oikos* 42:41-47.
- AMERICAN ORNITHOLOGISTS' UNION. 1973. Thirty-second supplement to the American Ornithologists' Union check-list of North American birds. *Auk* 80:411-419.
- BARASH, D. P. 1977. Sociobiology of rape in Mallards (*Anas platyrhynchos*): response of the mated male. *Science* 197:788-789.
- BARRETT, J. 1973. Breeding behavior of captive Mallards. M.S.thesis, Univ. of Minnesota, Minneapolis.
- BEECHER, M. D., AND I. M. BEECHER. 1979. Sociobiology of bank swallows: reproductive strategies of the male. *Science* 205:1282-1285.
- BIRKHEAD, T. R. 1979. Mate guarding in the magpie, *Pica pica*. *Anim. Behav.* 27:866-874.
- BIRKHEAD, T. R. 1982. Timing and duration of mate guarding in magpies, *Pica pica*. *Anim. Behav.* 30: 277-283.
- BIRKHEAD, T. R., S. D. JOHNSON, AND D. N. NETTLESHIP. 1985. Extra-pair matings and mate guarding in the common murre *Uria aalge*. *Anim. Behav.* 33:608-619.
- BRAY, O. E., J. J. KENNELLY, AND J. L. GUARINO. 1975. Fertility of eggs produced on territories of vasec-

- tomized Red-winged Blackbirds. *Wilson Bull.* 87: 187-195.
- BUITRON, D. 1983. Extra-pair courtship in black-billed magpies. *Anim. Behav.* 31:211-220.
- BURKE, T., AND M. W. BUFORD. 1987. DNA fingerprinting in birds. *Nature* 327:149-152.
- BURNS, J. T., K. M. CHENG, AND F. MCKINNEY. 1980. Forced copulation in captive Mallards I.: fertilization of eggs. *Auk* 97:875-879.
- CORBIN, K. W., AND G. C. SIBLEY. 1977. Rapid evolution in orioles of the genus *Icterus*. *Condor* 79: 335-352.
- EDINGER, B. B. 1985. Limited hybridization and behavioral differences among sympatric Baltimore and Bullock's orioles. M.Sc. thesis, Univ. of Minnesota, Minneapolis.
- EVARTS, S., AND C. J. WILLIAMS. 1987. Multiple paternity in a wild population of Mallards. *Auk* 104: 597-602.
- FITCH, M. A., AND G. W. SHUGART. 1984. Requirements for a mixed reproductive strategy in avian species. *Am. Nat.* 124:116-126.
- FLOOD, N. J. 1985. Incidences of polygyny and extra-pair copulation in the Northern Oriole. *Auk* 102: 410-413.
- FORD, N. L. 1983. Variation in mate fidelity in monogamous birds, p. 329-356. *In* R. F. Johnston [ed.], *Current ornithology*. Vol. 1. Plenum Press, New York.
- FUJIOKA, M., AND S. YAMAGISHI. 1981. Extramarital and pair copulations in the Cattle Egret. *Auk* 98: 134-144.
- GAVIN, T. A., AND E. K. BOLLINGER. 1985. Multiple paternity in a territorial passerine: the Bobolink. *Auk* 102:550-555.
- GLADSTONE, D. E. 1979. Promiscuity in monogamous colonial birds. *Am. Nat.* 114:545-577.
- GOODWIN, D. 1967. Pigeons and doves of the world. The British Museum (Natural History), London.
- GOODWIN, D. 1982. Estrilid finches of the world. The British Museum (Natural History), London.
- JOSTE, N., J. D. LIGON, AND P. B. STACEY. 1985. Shared paternity in the acorn woodpecker (*Melanerpes formicivorus*). *Behav. Ecol. Sociobiol.* 17:39-41.
- MARTIN, R. F. 1980. Analysis of hybridization between hirundinid genera *Hirundo* and *Petrochelidon* in Texas. *Auk* 97:148-159.
- MCKINNEY, F., AND P. STOLEN. 1982. Extra-pair-bond courtship and forced copulation among green-winged teal (*Anas crecca carolinensis*). *Anim. Behav.* 30:461-474.
- MCKINNEY, F., K. M. CHENG, AND D. J. BRUGGERS. 1984. Sperm competition in apparently monogamous birds, p. 523-545. *In* R. L. Smith [ed.], *Sperm competition and the evolution of animal mating systems*. Academic Press, New York.
- MCKINNEY, F., S. R. DERRICKSON, AND P. MINEAU. 1983. Forced copulation in waterfowl. *Behaviour* 86:250-294.
- MINEAU, P., AND F. COOKE. 1979. Rape in the lesser snow goose. *Behaviour* 70:280-291.
- MØLLER, A. P. 1987. Advantages and disadvantages of coloniality in the swallow, *Hirundo rustica*. *Anim. Behav.* 35:819-832.
- MUMME, R. L., W. D. KOENIG, R. M. ZINK, AND J. A. MARTEN. 1985. Genetic variation in a California population of Acorn Woodpeckers. *Auk* 102:305-312.
- POWER, H. W., AND C.G.P. DONNER. 1980. Experiments on cuckoldry in the mountain bluebird. *Am. Nat.* 116:689-704.
- POWER, H. W., E. LITOVICH, AND M. P. LOMBARDO. 1981. Male Starlings delay incubation to avoid being cuckolded. *Auk* 98:386-389.
- RØSKAFT, E. 1983. Male promiscuity and female adultery by the Rook (*Corvus frugilegus*). *Ornis Scand.* 14:174-179.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 139-179. *In* B. Cambell [ed.], *Sexual selection and the descent of man*. Aldine, Chicago.
- VERBEEK, N.A.M. 1972. The exploitation system of the yellow-billed magpie. *Univ. Calif. Publ. Zool.* 76:1-58.
- WEST, M. J., A. P. KING, AND D. H. EASTER. 1981. The cowbird: reflections on development from an unlikely source. *Am. Sci.* 69:56-66.
- WESTNEAT, D. F. 1987a. Extra-pair copulations in a predominantly monogamous bird: observations of behaviour. *Anim. Behav.* 35:865-876.
- WESTNEAT, D. F. 1987b. Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. *Anim. Behav.* 35:877-886.
- WETTON, J. H., R. E. CARTER, D. T. PARKIN, AND D. WALTERS. 1987. Demographic study of a wild House Sparrow population by DNA fingerprinting. *Nature* 327:147-149.
- WILLIAMS, P. L. 1982. A comparison of colonial and non-colonial nesting by Northern Orioles in central coastal California. M.S. thesis, Univ. of California, Berkeley.