

## Extra-pair copulations in a predominantly monogamous bird: observations of behaviour

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**Abstract.** The mating behaviour of indigo buntings, *Passerina cyanea* was studied. A total of 535 attempted matings in 3 years were observed. Of the 413 copulations that occurred within the female's presumed fertile period (from 12 days before to the day before the last egg was laid), 53 (12.8%) were extra-pair copulations (EPCs). The rate of within-pair copulations (WPCs) per pair-hour, EPCs per female-hour and territorial intrusions per h all peaked 3 days before the first egg was laid. Intruders were attracted to copulations, and males attempted to copulate with their mates more after an intrusion. Nearly all intruders and males attempting EPCs were territorial neighbours. More than half of the males attempting EPCs had one or more females nesting on their territories. Although males behaved as if they were guarding their mates from possible EPCs, they often left their females unguarded. Females resisted EPCs significantly more than WPCs, and attempted EPCs were less likely to make cloacal contact than attempted WPCs. However, some forced EPCs did make cloacal contact. The difficulties of estimating the rate of extra-pair fertilizations from observations of copulations are discussed. Finally, in the light of these results the possible role of nesting density, mate guarding, synchrony of breeding, male parental care and polygyny on the rate of EPCs is examined.

Theoretically, a male's reproductive success is limited primarily by his success at finding mates and not by his production of gametes (Trivers 1972). Males are thus selected to seek matings whenever possible and, in some situations, to seek copulations with the mates of other males. Such extra-pair copulations have now been reported in a large and steadily growing number of avian species (Ford 1983; McKinney et al. 1984). Most of these reports of extra-pair copulations (EPCs) have been anecdotal, so information about the frequency and circumstances of EPCs is not available for many species. Several studies have attempted to measure the frequency of EPCs quantitatively (MacRoberts 1973; Mineau & Cooke 1979; Fujioka & Yamagishi 1981; Werschkul 1982; Røskaft 1983; Fitch & Shugart 1984; Birkhead et al. 1985; Frederick, in press). However, all of these studies have focused on colonial species, so hypotheses generated by the authors about the occurrence of EPCs might be restricted to colonial species.

Several authors have suggested that EPCs should be more frequent in densely nesting populations (Birkhead 1978; Gladstone 1979). High density, they argue, creates more opportunities for EPCs. Birkhead (1978) found a correlation between density and the frequency of EPCs in guillemots, *Uria aalge*. In addition, colonial geese

have a higher rate of EPCs than that found in geese with dispersed nesting (McKinney et al. 1983). However, McKinney et al. (1984) and Frederick (in press) report no evidence of a similar relationship in ducks or in white ibis, *Eudocimus albus*, respectively. Since researchers have tended to focus on colonial species, more quantitative studies on dispersed nesters are needed to test the general role of density in the occurrence of EPCs.

Most researchers of EPCs have also focused on male behaviour and the advantages and disadvantages of EPCs for males. Fitch & Shugart (1984) argue that the costs and benefits of EPCs for females of species without an intromittent organ might determine the frequency of EPCs. Forced extra-pair copulations have been observed in many species with intromittent organs (McKinney et al. 1984), but in Fitch & Shugart's view cannot occur in species without such organs. They maintain that if EPCs are frequent in these species, then females of these species must be cooperating with, and presumably gaining from matings with extra-pair males. Frederick (in press) found that female white ibis cooperate during some EPCs, but can successfully resist the advances of extra-pair males. No study on non-colonial birds has examined the behaviour of females during EPCs.

Two types of males might pursue EPCs. Trivers

(1972) predicted that resident, paired males would pursue a mixed reproductive strategy by assisting their mates with the care of offspring and pursuing additional copulations when possible. Evidence from studies on colonial species tends to support this prediction (Mineau & Cooke 1979; Fujioka & Yamagishi 1981; McKinney et al. 1984). For example, Frederick (in press) found that nearly all EPCs in white ibis were performed by paired males from within a local part of the colony. Although these males were usually attacked when they intruded, they were not attacked by other neighbours as often as were non-resident intruders.

Such communal defence of the nest area does not occur in species with more dispersed nesting since individuals are too distant from each other. Non-resident individuals might have more success gaining EPCs in such species. Since in these species non-residents are usually unpaired, floating (i.e. non-territorial) males might seek EPCs as an alternative reproductive strategy to territory defence. To date, evidence from non-colonial species suggests that floating males do not gain many EPCs, whereas resident, paired males do (Ford 1983; McKinney et al. 1984; Afton 1985). However, quantitative studies of marked individuals are necessary to provide a definitive answer to this question.

If EPCs do occur, then resident males should evolve behaviour that protects their likelihood of paternity of their young (Trivers 1972). Mate guarding behaviour occurs in many species and has been taken as evidence that EPCs are at least occasionally successful in fertilizing some young (Erickson & Zenone 1976; Beecher & Beecher 1979; Birkhead 1979; Buitron 1983). Alternatively, Birkhead (1979) suggested that the male's ability to guard his mate might determine the frequency of EPCs. In several colonial species, ecological factors such as the distance to water (Mineau & Cooke 1979), nesting material (Werschkul 1982) and food (Frederick, in press) affect a male's ability to guard his mate and thus affect how often his mate received attempted EPCs. In non-colonial species, mate guarding is probably not affected by ecological factors since males of these species often defend territories that contain most of the resources they need. Little information on mate guarding and its relationship with EPCs is available for non-colonial species.

In this paper I report a study of EPCs in a non-colonial passerine bird, the indigo bunting, *Passerina cyanea*. Most males pair with only a single

female, but a small proportion attract more than one female at a time. Most males also participate minimally in the care of offspring (Verner & Willson 1969; Carey & Nolan 1979). Several instances of EPCs in this species were previously described by Payne (1983a). This study addresses four major questions. (1) How frequent are EPCs in indigo buntings? (2) What is the role of the female in EPCs? (3) Who in the population pursues EPCs? (4) How well do males protect their females from EPCs?

## METHODS

### Population

I studied indigo buntings from May through August in 1983–1985, 5 km northeast of Niles in Cass County, Michigan. The habitat of the study area was composed of old and cultivated fields bordered by riparian woodland along an active railroad track. Woodcutters, off-road vehicles and periodic cuttings along the railroad kept the area in an early successional stage. In 1983 and 1984, none of the territories that I studied was affected by this disturbance, but in 1985, four–five territories along the railroad were unused because of cutting along the railroad right-of-way. This population has been under study by R. B. Payne since 1978 (Payne 1979, 1982, 1983a, b, 1984; Payne et al. 1981).

### Procedures

Individual birds were captured and banded with unique combinations of coiled plastic colour-bands and a U.S. Fish and Wildlife Service (FWS) aluminium band. Males were captured by setting a mist-net near a stuffed male bunting inside the resident's singing territory. Playbacks of a bunting's song attracted the male to the dummy. I avoided capturing males when their females might have been fertile (after the female arrived and before the last egg was laid). Females were netted near the nest, usually when the young were 3–7 days old.

R. B. Payne and his assistants banded and monitored breeding success and song for approximately 150 males and their mates each year. From this group I observed birds on 12–14 territories in 1983 and 15–20 territories in 1984 and 1985. This paper reports on observations made during the mating period on these territories.

In 1983 and 1984, I conducted focal observations on pairs. An observation session began as soon as I saw one member of the pair after I had entered the territory. In 1985, I switched my focus to females and so did not start the session until the female was seen. During all observations in all years I attempted to follow the female. If I lost sight of the female, I followed the male in the hope that he would lead me to the female. If I lost the male as well, I wandered the area (on and off the territory) until I located one of the pair. In 1983, observations lasted 45 min, and in 1984 and 1985 they usually lasted 90 min from the start of the session.

A running account of the birds' behaviour was recorded on cassette tape, and both the female's behaviour (foraging, nest-building, or other activity) and the male's behaviour (singing, foraging, on or off the territory, or other activity) were noted. I also recorded the approximate distance between the male and female, when the male could see the female, which member of the pair initiated movements and which followed the initiator. For all copulations the circumstances of, outcome of, and behaviour of the participants during the mating attempt were recorded. I also noted the presence of intruders, their identity if possible, their location relative to the female, their behaviour, and the outcome of their visit.

Copulations were categorized by outcome, female behaviour and partner. Often the outcome of an attempted copulation was unknown because the attempt occurred too quickly or was obscured. Similarly, the behaviour of the female during many copulations was difficult to see. I tried to record as much information as possible; for example, if a female did not solicit or overtly resist a copulation, but I could not tell if she cooperated, I scored her behaviour differently than if I knew whether or not she cooperated.

Through these focal observations and from information shared by R. B. Payne and his assistants I could locate most of the nests. Indigo buntings usually lay two–four eggs, incubate for 13 days, and fledge young 8–10 days after hatching. By either directly observing the pair or back-dating nests found after the eggs were laid, I could determine when a female began to lay the eggs. A female was considered paired to a male if she nested on his territory.

### Analysis

To analyse the results I took into account that I

often lost one or both of the birds I was watching. Therefore, most of the analyses are relative to the percentage of time the focal bird or pair was seen. Pair-hours refer to the total time at least one member of the pair was seen, female-hours to the time the female was seen, and observation-hours to the total time spent observing, regardless of whether or not the focal birds were seen.

## RESULTS

### Copulations

I witnessed 535 attempted copulations (within-pair and extra-pair) during 289 sessions totalling 352 h of observation. I knew or could infer the breeding status (relative to the date the first egg was laid) of the female in 194 sessions, totalling 243 h of observation. During this time, 413 attempted copulations were seen.

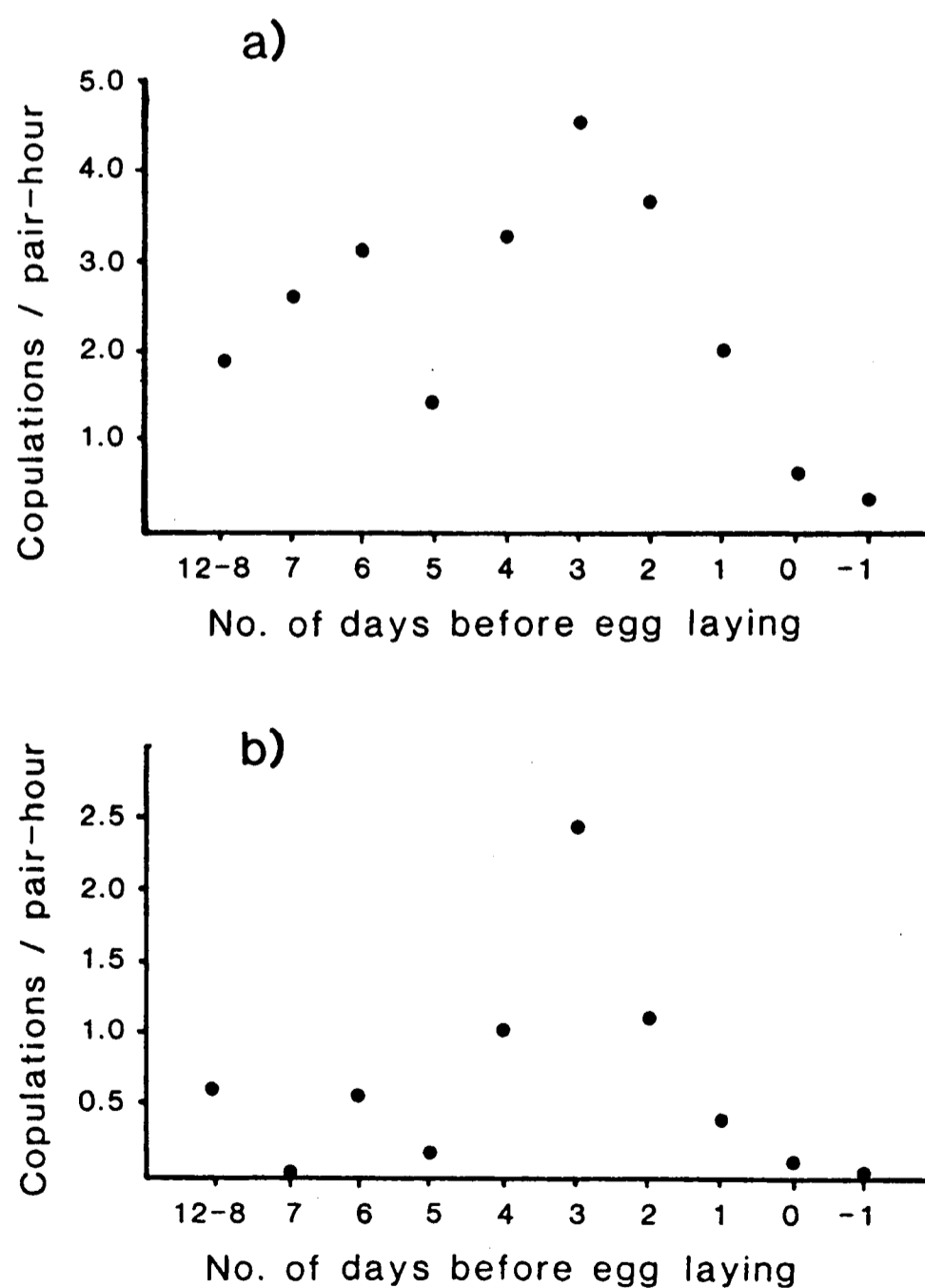


Figure 1. Temporal pattern of within-pair copulations (WPCs) relative to the day the first egg was laid (day egg was laid = 0). (a) Rate of total WPCs seen per pair-hour. (b) Rate of successful WPCs (male made cloacal contact with female) per pair-hour.

Because I could see within-pair copulations when I had sight of either member of the pair, I calculated the rate of WPCs per pair-hour. Over all years, I saw at least one member of the pair for 142.8 h out of the sessions where I knew the breeding status of the female. During this time, 360 WPCs (2.52 per pair-hour) were witnessed. A peak of mating activity occurred 3 days before the first egg was laid (Fig. 1a). The rate of WPCs dropped off rapidly after this time, and approached zero the day the first egg was laid.

Males' attempts to copulate varied in their success. Of the 413 attempts during the female's fertile period, the male appeared to make cloacal contact in only 120 (29.1%). Cloacal contact was said to have occurred when the male landed on the female's back and bent his tail below the female's body. The distribution of WPCs that made cloacal contact by the day before the first egg was laid (Fig. 1b) is similar to that of total WPCs, with a peak 3 days before the day the first egg was laid. In 70 additional attempts, males made some physical contact with the female but either did not bend their tails low enough to make obvious contact with the female's cloaca or it was not clear that they had made cloacal contact. In the rest of the attempts, the male either fluttered over the female or swooped at the female without making any physical contact (see section on female behaviour).

### Extra-pair Copulations

I witnessed a total of 61 attempted extra-pair copulations (EPCs) during 3 years. Of the attempted matings (within-pair and extra-pair) that I saw when I knew the female's breeding status, 53 (12.8%) were EPCs. Because EPCs could not be seen by following the resident male, the rate of EPCs is calculated per female-hour. I saw the female for a total of 72.9 h (30.0%) when I knew her breeding status, and thus the average rate of EPCs per female-hour was 0.73. The distribution of EPCs per female-hour (Fig. 2) is similar to that of WPCs, with a peak on the third day before the first egg was laid.

Males attempting EPCs were much less likely to make either physical contact ( $\chi^2=17.9$ ,  $df=1$ ,  $P<0.001$ ) or cloacal contact ( $\chi^2=22.3$ ,  $df=1$ ,  $P<0.001$ ; Table I) with females than males attempting to copulate with their mates. In the 3 years of study I witnessed only two EPCs (1.6% of all successful copulations, 3.3% of all attempted

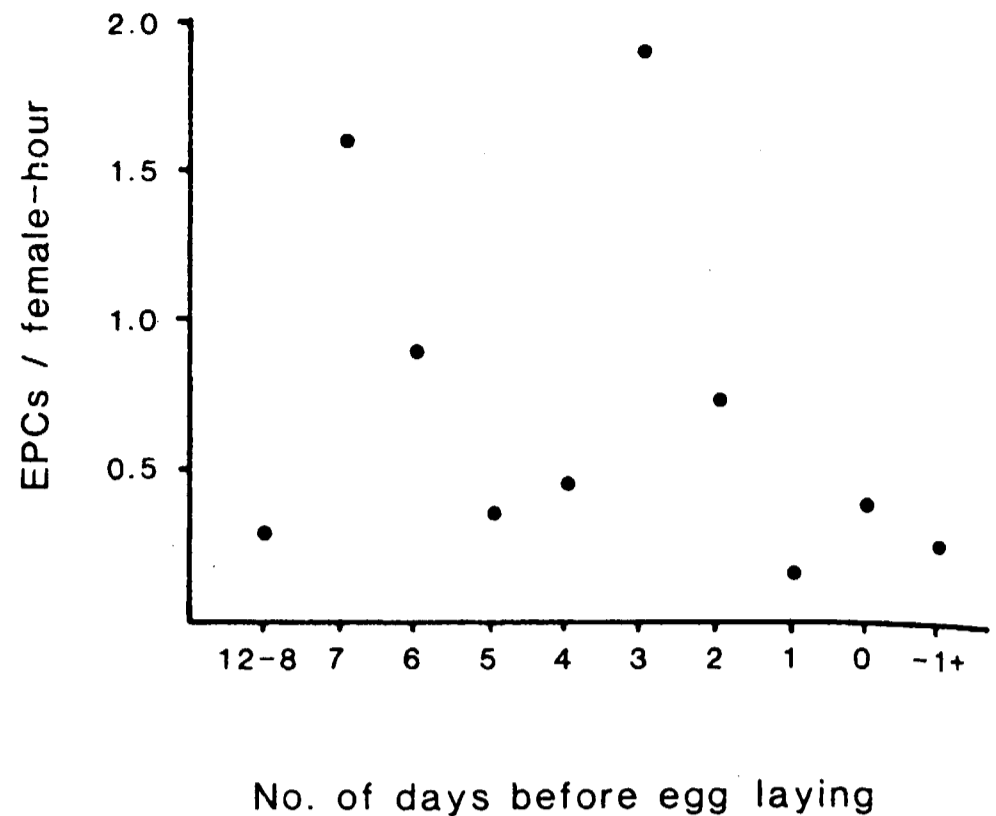


Figure 2. Temporal pattern of extra-pair copulations (EPCs) relative to the day the first egg was laid (day egg was laid = 0).

EPCs) during which I was certain that the male made cloacal contact with the female.

In some species, EPCs can occur when two or more males either contest for unprotected females (Frederick, in press), or chase and subdue females (Summers-Smith 1963; McKinney et al. 1984). All of the EPCs I saw in buntings were performed by solitary males entering the focal territory. Occasionally, two males were seen chasing a female. In all of these cases the resident male was following an intruder who was chasing the female. When the female stopped, the resident male attacked the intruder and not the female.

During one observation session in 1985, more than one male gained EPCs with one female. The male defending the territory at the time the female settled and began building a nest was an unbanded male (NOBA). Several days before the observation session, the male (XRGW) who had defended the territory in the previous year returned. On the day of the observation this male was still disputing with the NOBA male. Several times XRGW attacked the female who was carrying nesting material to a nest. The NOBA male continued to chase XRGW, and both often sang. In the middle of the session, a neighbour (RYXO) began intruding and attempted several times to mate with the unguarded female. Eventually, RYXO began to chase both the NOBA male and XRGW away from the female. All three males attempted matings with the female in the course of the session. At the end of the session, XRGW and NOBA were still disputing

**Table I.** Comparison of the number of extra-pair and within-pair copulations in which some physical contact or cloacal contact was made with the female (see text for definitions of types of contact)

	Outcome*			
	Cloacal contact	No cloacal contact	Any physical contact	No physical contact
EPCs	2	52	21	27
WPCs	118	212	169	57

\* In some copulations physical contact was made, but I could not tell if cloacal contact was made.

the territory while RYXO was escorting the female. Two days later I saw the NOBA male escorting the female. She began laying her eggs the next day. After she started incubating, the NOBA male disappeared and XRGW replaced him.

All the EPCs that I saw occurred on the focal male's territory or near the boundary of his territory and a neighbour's. I did occasionally see a female wander off her mate's territory and into a neighbour's territory alone. However, I never witnessed an EPC of any sort during these excursions.

### Female Behaviour

Buntings have very few pre- and post-copulatory displays. However, copulations did occur similarly across individuals. A typical WPC was preceded by movement of the female from one perch to another. The male followed and usually approached the female, whereupon the female either 'cooperated' with an attempted copulation, ignored an attempted copulation (uncooperative), or did nothing while the male landed nearby. Females 'cooperated' when they raised their tails and leaned forward after the males approached. Sometimes females solicited a mating by leaning forward, raising their tails, vibrating their wings and occasionally uttering a twitter vocalization, all before the males approached. I had difficulty interpreting the solicit posture when the male did not approach, because females occasionally behaved similarly in aggressive encounters. I defined as uncooperative the behaviour of females who did not solicit or cooperate with a male's attempted copulation.

In rare instances, a female thwarted her mate's attempts to copulate by turning towards him as he approached. In 11 instances the female solicited

first and then thwarted the male's attempt to mate. I also witnessed 28 WPCs in which the male appeared to attack his female. These usually occurred when the female was flying and the male made contact with her in mid-air or immediately after she landed. The female never solicited or cooperated; often, she was knocked to the ground and she usually uttered rapid alarm calls. I considered a female that behaved in this manner as resisting the male's attempt to mate.

Apparent female cooperation increased the chance that an attempted copulation was successful. Cloacal contact was achieved significantly more often if the female solicited or cooperated (35 of 53 attempted copulations) than if she did not (3 of 74 attempted copulations) ( $\chi^2 = 56.3$ ,  $df = 1$ ,  $P < 0.001$ ). Similarly, males made physical contact less often if the female resisted or was uncooperative than if she cooperated ( $\chi^2 = 30.5$ ,  $df = 1$ ,  $P < 0.001$ ).

Females were less likely to accept and more likely to resist EPCs (resisted 34 of 43 attempts) than WPCs (resisted 72 of 320 attempts) ( $\chi^2 = 58.3$ ,  $df = 1$ ,  $P < 0.001$ ). However, some resisted EPCs were probably successful. For example, in one instance I observed a female (XRGO) carrying nesting material to a nest in male RYXR's territory. On one trip to the nest the female was hit by a male from above and they fluttered together to the ground. I saw that the male (XGGW) had the female's tail in his bill. The birds tugged for several seconds (I was not sure which bird was tugging) and I heard rapid alarm calls. The male hopped onto XRGO's back and mated with her. He then hopped off and walked around the female vibrating his wings. Soon thereafter she continued to the nest with her nesting material, and XGGW flew back to his territory 150 m away. Nearly all other EPCs

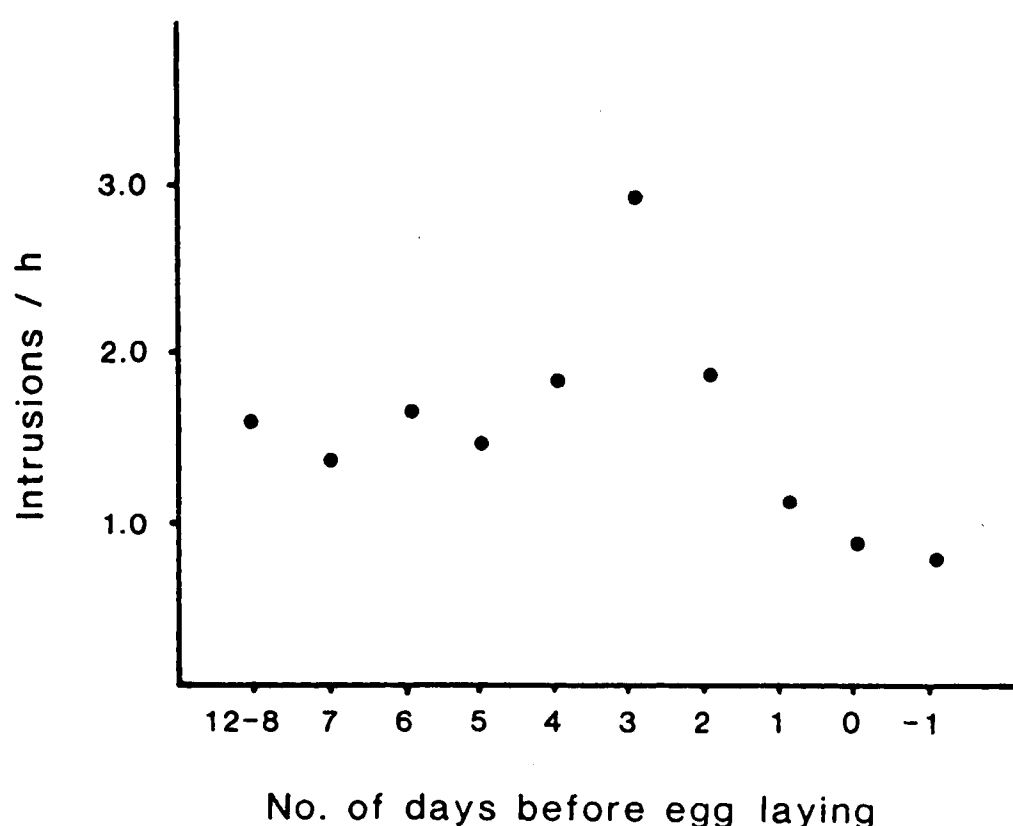
followed a similar pattern, but in most either the male did not contact the female or they fell into the brush where I could not see the outcome. I never saw a female solicit and receive an EPC.

### Intruders

I observed a total of 370 intrusions into the territories of males during the fertile period of the resident females. Intrusions peaked on the same day as WPCs and EPCs, 3 days before the first egg was laid (Fig. 3).

Intruders might be using the mating activity in neighbours' territories as a cue for the presence of fertile females. If so, intrusions ought to be associated with within-pair copulations. To analyse the relationship between intrusions and copulations, I assumed that matings that occurred more than 5 min apart were independent. Otherwise, copulations were lumped into mating bouts. In 63 of 208 mating bouts, intruders arrived in the 5 min subsequent to the last copulation in the bout. In only 48 of a random pick of 5-min intervals (paired within the observation session) was at least one intruder present. This difference is significant (normal approximation of binomial;  $z = 2.47$ ,  $r = 0.23$ ,  $N = 208$ ,  $P < 0.02$ ) and suggests that intruders were attracted by copulations.

I could identify (by either seeing the bands or following the intruder back to its territory) 227 of the intruders and 213 (93.8%) were males from territories within 200 m of the focal pair. Five of the



**Figure 3.** Temporal pattern of intrusions into the focal territory relative to the day the focal female laid the first egg (day egg was laid = 0).

others were territorial owners from territories more distant than 200 m. The nine remaining individuals were unbanded and did not have territories in the immediate study area. Similarly, of the 61 total EPCs I witnessed, I saw the male's bands in 39; 35 of these EPCs were by neighbours from within 200 m. For 25 of these attempted EPCs I knew the breeding status of the male; nine already had a female nesting on their territories, four had a female laying eggs, two had nest-building females, and 10 were apparently unpaired at the time of the mating attempt. Four attempted EPCs were performed early in 1984 by an unbanded male, probably a young floater. All occurred on the same female within a span of 15 min. The resident male chased the intruder, and none of the four attempts made cloacal contact.

### Mate Guarding

If some EPCs were successful in fertilizing an egg, then some males must have been cuckolded. Thus, males ought to protect their paternity by guarding their females from the advances of other males. In buntings, males nearly always chased intruders out of their territories. However, males also chase intruders before they have females and when their females are incubating eggs. The time a male spends close to the female could be another measure of mate guarding. I considered that male buntings within 30 m of their females were capable of seeing and responding to intruders near the female. In the buntings, the time a male spent within 30 m of the female was constant throughout the fertile period of the female until 2 days before the first egg was laid (Fig. 4). After this point the male spent less time within 30 m of the female.

The time the male spent close to the female is not necessarily a good indicator that males are indeed guarding their mates. For example, the female might gain from the proximity of the male if (1) males feed their mates (Krebs 1970; Nisbet 1977), (2) multiple copulations are necessary to ensure fertilizations, or (3) males protect females from predators (Lumpkin 1981). Male buntings do not feed their mates, but females might gain from the proximity of the male for these other reasons. Stronger evidence of mate guarding would be a difference in the responsibility for maintaining the proximity of the pair (Bjorklund & Westman 1983; Davies 1985), such as if males followed females more than females followed males.

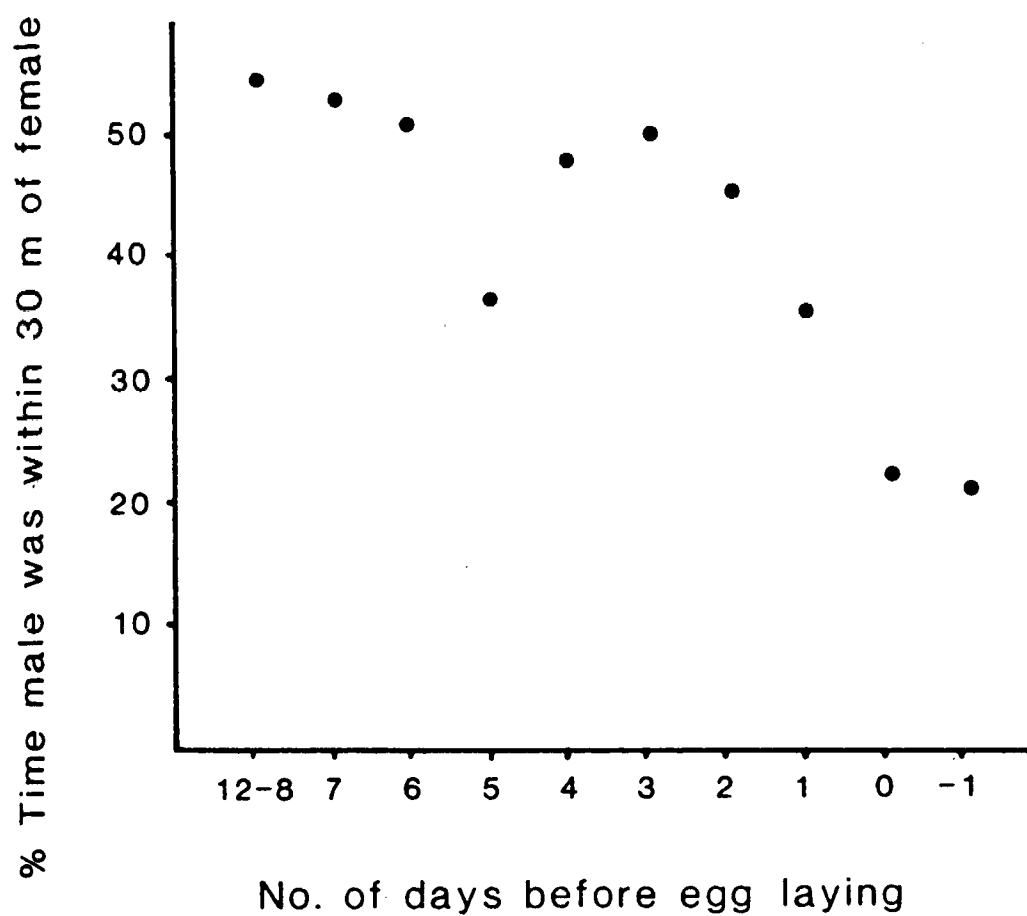


Figure 4. Amount of time (percentage of pair-hours observed) the male spent within 30 m of the female relative to the day the female laid her first egg (day egg was laid = 0).

I analysed the movements of males and females to determine which member of the pair was responsible for keeping the distance between the pair to a minimum. When the female moved a distance of at least 10 m, the male nearly always followed within 2 min (258 of 306 female movements), whereas if the male moved a similar distance, the female rarely followed within 2 min (45 of 168 male movements). The male also left the female less often than the female left the male (168 to 306 movements). If the pair was separated, the male rejoined the female more often than she rejoined the male (normal approximation of binomial,  $z = 9.3$ ,  $r = 0.5$ ,  $N = 158$ ,  $P < 0.001$ ; Table II).

Males did, however, spend time away from the females during their fertile periods. Males averaged only 41.4% of the time I could see them within 30 m of their females. Also, over a third of all movements separating the pair were initiated by the male.

Table II. Test of male mate guarding; the member of the pair responsible for movement that re-established contact between the pair (within 10 m)

Year	Male to female	Female to male
1983	33	3
1984	39	5
1985	66	12

Although in some of these movements males left to chase an intruder, in most they flew off to sing elsewhere on their territories.

Extra-pair copulations could also induce selection for other mechanisms besides mate guarding that reduce sperm competition. Morphological tactics such as ejaculatory plugs (Rothschild 1955; Parker 1970; Abele & Gilchrist 1977) and organs that can remove sperm (Waage 1979) are not known in birds. Males could respond to the possible presence of foreign sperm by mating repeatedly and swamping other males' sperm with their own. Bunting males in this study appeared to do this. Intruders were present in 75 of the 189 possible 5-min intervals immediately preceding the first copulation of a mating bout. This is significantly more than expected based on a random pick of 5-min intervals (paired within observation session; normal approximation of binomial;  $z = 4.70$ ,  $r = 0.25$ ,  $N = 189$ ,  $P < 0.001$ ).

## DISCUSSION

### Extra-pair Copulations and Fertilizations

Extra-pair copulations comprised 11.4% of all attempted copulations seen and were a regular feature of the mating behaviour of indigo buntings. Because the rates of intrusions and attempted EPCs mirror closely the rate of WPCs during the female's fertile period, EPCs probably fertilize some young. How many young result from EPCs is critical to understanding the adaptiveness of this behaviour. However, any estimate of the number of extra-pair fertilizations based on observations of copulations will be inaccurate because of biases in counting copulations and biases in the success of different types of copulations in inseminating the female.

One major bias in counting copulations occurs because in most species the observer will rarely see all copulations between individuals. In buntings, in contrast to some colonial species (Birkhead et al. 1985; Frederick, in press), females can and probably do copulate when they are out of sight of the observer or off their males' territories. If the observation of the males' behaviour affects the observation of females, estimates of the frequency of EPCs relative to WPCs will be difficult to calculate, and therefore so will the relative proportion of young resulting from EPCs. For example, in the buntings, 12.8% of all copulations during the

fertile period of the female were EPCs. However, since I frequently followed the male when I had lost the female, I witnessed some WPCs by watching the male rather than the female. Thus the numbers of copulations of each type cannot be compared directly but the rates can. The best estimate of the rate of WPCs is the number of WPCs per pair-hour, whereas the best estimate of the rate of EPCs is the number of EPCs per female-hour. Therefore, the best estimate for the total number of copulations a female receives per h is the sum of the number of EPCs per female-hour and the number of WPCs per pair-hour. Extra-pair copulations were 22.5% of the copulations a female received per h.

This estimate might also be biased because of differences in the visibility of EPCs and WPCs. The behaviour of the individuals involved in an EPC was qualitatively different from that during a WPC; EPCs were quicker, were more likely to occur behind vegetation, and the partners were associated for a shorter time than during WPCs. In addition, although I never witnessed females actively seeking EPCs, some females might have sought surreptitious copulations. Both of these factors would have reduced by an unknown amount the proportion of EPCs that I saw.

Estimates of extra-pair fertilizations based on observations might also be biased because of differences between WPCs and EPCs in the chances of insemination. For example, differences in the female's behaviour between EPCs and WPCs affect the estimated frequency of EPCs. Female buntings appeared to resist EPCs, which probably caused the lowered likelihood of success of EPCs. EPCs were probably less likely to inseminate the female than WPCs.

Finally, the effects of sperm competition, sperm precedence and the timing of fertilization are poorly known for most species, so inferences from observations are weak. Fresh sperm (Payne & Kahrs 1961; Compton et al. 1978; Cheng et al. 1983) and repeated inseminations (Martin et al. 1974) generally increase the probability of fertilization. The egg is probably fertilized just after ovulation, which occurs in some species soon after the previous egg is laid (Sturkie & Mueller 1976; Welty 1982). However, Sturkie & Mueller (1976) report that the highest fertility of a mating occurs 2–3 days after the copulation. Storage of sperm is known in many species of birds (Sturkie & Mueller 1976), and so the optimal time of insemination in buntings might be when the peak of matings (WPC

and EPC) occurs, 3 days before the first egg is laid. In this study the frequency of EPCs on that day, computed by dividing the rate of EPCs per female-hour by the sum of rate of EPCs per female-hour plus the rate of WPCs per pair-hour, was 28.6% of all copulations.

It is clear that estimates based on observations vary considerably, depending on the method of calculation. The actual number of young resulting from extra-pair copulations must be estimated by the use of genetic paternity analysis. In an electrophoretic study on this same population, described in the following paper (Westneat 1987) I found that at least 14.4% of the offspring in 1983 and 1984 were not the offspring of the resident male. Because electrophoresis underestimates the number of cases of extra-pair fertilizations in the buntings by approximately 60% (Westneat, Frederick & Wiley, unpublished data), 27% and 42% of all young were estimated to result from extra-pair fertilizations in 1983 and 1984 respectively.

These estimates from electrophoresis are higher than the estimate from observations of copulations if the low chance of success per attempt for EPCs is taken into account. One possible explanation for this difference is that females are mating inconspicuously with extra-pair males. The observations showed no evidence that females were behaving in this way. Another possibility for the difference between the estimates from electrophoresis and those from observations is that extra-pair copulations are more potent. Unfortunately, as yet this has not been shown in any species, and the data presented here are not sufficient to evaluate this hypothesis. Because the number of copulations witnessed was probably a small proportion of the total that occurred, the most likely explanation for the disagreement in the two estimates is chance. Even if the two estimates had agreed, it would not mean that the correct biases in the observations had been corrected. Ultimately, observations of copulations cannot be used reliably to estimate reproduction gained. I advocate the use of genetic analyses such as electrophoresis to measure the frequency of extra-pair fertilizations, and observations of behaviour to understand how those fertilizations occur. In the case of indigo buntings, both methods have provided valuable information.

#### **Correlates of EPC Behaviour: Interspecific Comparisons**

Indigo buntings show one of the highest frequen-



cies of extra-pair fertilizations of any species yet examined. Certainly coloniality is neither necessary nor sufficient for EPCs to occur (see also McKinney et al. 1984; Frederick, in press). Furthermore, nesting density cannot be a general correlate of EPCs across species. Density might have an effect within a species, but the evidence for this hypothesis is also mixed (McKinney et al. 1984; Birkhead et al. 1985; Frederick, in press). In densely populated areas, the proximity of individuals might favour more EPCs, because information on the breeding status of neighbours might be easier to obtain. However, since birds can move large distances quickly, inter-neighbour distance is probably less important in this regard. Male buntings appear to know the breeding status of females in neighbouring territories, since EPC attempts and intrusions peak on the same day as within-pair matings. Males often leave their territories even when no neighbouring female is mating (Westneat, unpublished data). On these forays males might gain information on the breeding status of neighbours.

Most of the EPCs were apparently resisted by the female. Fitch & Shugart (1984) have argued that in species without intromittent organs, females control the outcome of all copulations. Buntings have no intromittent organs, yet many EPCs in the buntings were forced, and during at least one of these the male made cloacal contact with the female. Data from electrophoresis of muscle tissue shows that many offspring came from matings with neighbouring males (Westneat 1987). If the copulations observed were representative of the copulations that gave rise to these young, then females are not controlling copulations in this species. Unfortunately, I do not have genetic evidence of extra-pair fertilizations in those cases where I witnessed EPCs.

The possibilities for the response of females to EPC attempts are complex. Resistance could be a tactic that incites male-male conflict (Cox & LeBoeuf 1977) or weeds out weak, less persistent males. Females did occasionally solicit, then refuse, copulations from their mates in the presence of intruders. However, females did not resist WPCs very often. Frequently they cooperated with their mates' attempts to copulate, only to resist an EPC soon after. Females ought to test males when they need information about which male would be the best to mate with. Therefore, I would expect females to behave similarly regardless of the identity of the male. That females do behave differently

depending on the identity of the male suggests that the outcome of EPCs has a different payoff for females than the outcome of WPCs.

In indigo buntings, EPCs are usually performed by resident, paired males from neighbouring territories. This result supports Trivers' (1972) prediction that males should pursue a mixed reproductive strategy whenever possible. Unpaired and non-resident males do not gain many EPCs, as might be predicted by theories of alternative strategies. These males probably gain more by seeking a territory and attracting a mate (Birkhead et al. 1985). In buntings, males neither gain a territory nor attract a mate by pursuing EPCs (Westneat, unpublished data).

There has been a general consensus among researchers that mate guarding is inferential evidence for the occurrence of EPCs (Birkhead et al. 1985) and that it has evolved in response to occasional cuckoldry (Trivers 1972; Erickson & Zenone 1976). Male buntings do guard their mates as predicted, but not as effectively as one would expect.

Poor mate guarding has an ecological basis in little blue herons, *Egretta caerulea* (Werschkul 1982) and white ibis (Frederick, in press). However, male buntings probably obtain nearly all the resources they require on their territories, so there does not seem to be a major ecological reason for their poor mate guarding. Female buntings are cryptic and shy, and might be as difficult for male buntings to follow as for human observers. This is possible in those cases when the female moved and the male did not follow, but in many instances I observed a male leave a female even when he was not chasing an intruder. Poor mate guarding ought to be selected against, since males are cuckolded fairly often. Males might be cuckolded even when they guard their mates, in which case there might be less advantage in spending the extra effort to guard their females closely. Males could be seeking EPCs themselves instead of guarding their mates. Although two of the EPCs I witnessed were by males with nest-building females, males usually do not leave their territories when the female is nest building and mating.

#### Evolution of EPC Behaviour in Buntings

Indigo buntings have some ecological and life history characteristics that might be considered prerequisites for frequent EPCs. First, as the

breeding season progresses, females become fertile asynchronously. Since males are capable of mating at any time throughout the season, asynchrony of breeding skews the operational sex ratio (Emlen & Oring 1977) toward more males than females. This skew increases the number of males seeking EPCs per fertile female, which increases the likelihood that each female receives an EPC and decreases her mate's ability to protect her from the attentions of other males (Birkhead et al. 1985). Colonial species usually breed more synchronously and have lower levels of successful EPCs (McKinney et al. 1984) than found in non-colonial buntings.

Asynchrony is not the only factor that might explain the high frequency of EPCs in buntings. Male buntings could be pursuing EPCs at the expense of their ability to provide for their young. Maynard Smith (1977) outlined a model of the costs and benefits to an individual that provides for young versus an individual that pursues alternative matings. The strategy an individual follows will depend on how important its parental care is to the survival of its young and how many matings it is likely to gain by sacrificing parental care. Most male buntings spend little effort on parental care, especially during incubation (Verner & Willson 1969; Carey & Nolan 1979; Westneat, unpublished data). Female buntings might be capable of providing all the parental care needed by the young, thus freeing the males to pursue EPCs. However, the causal relationship between parental care and EPCs is not specified in Maynard Smith's model; male buntings could be providing little parental care because they can gain so much from EPCs.

Synchrony of breeding and the benefits of male parental care are likely to have counteracting influences on the evolution of EPC behaviour. Males of asynchronous breeders pursue EPCs at some cost to their effectiveness as a parent. Males of synchronous breeders do not make this tradeoff, but do pursue EPCs at a cost to their own likelihood of paternity or ability to guard their nest (Mineau & Cooke 1979; Werschkul 1982; Fitch & Shugart 1984; Frederick, in press). Thus the benefits of providing for young, or guarding a nest or mate will interact with the degree of synchrony to produce conditions favouring EPCs in species that have different ecologies.

The evolution of EPCs must also be considered in relation to the evolution of polygyny, since the pursuit of EPCs and additional mates are both strategies to increase a male's reproduction. If the

quality of a male's territory is high, then females might be able to raise the young without the help of a male. Males would then be freed either to advertise for additional mates or to seek EPCs. If, in addition, the variance in the quality of male territories is low, then females might not benefit by settling in territories already occupied by other females (Verner 1964; Willson 1966; Orians 1969). Males would gain more by pursuing EPCs instead of advertising for additional mates. Some male buntings pair with more than one female simultaneously (Carey & Nolan 1975, 1979; Payne 1982), but only 11–12% of fledged young come from additional nestings (Payne, unpublished data) whereas an observed 15% and an estimated 30–40% of all young come from extra-pair fertilizations.

An additional test of this relationship would be to compare buntings with a more polygynous species. For example, more male red-winged blackbirds, *Aegelaius phoeniceus*, are paired with more than one female and most males provide more parental care than in buntings (Verner & Willson 1969; Patterson 1979), although populations do vary considerably (Orians 1961; Payne 1969; Searcy 1979). If male redwings gain more from polygyny, I would predict that they devote less time to the pursuit of EPCs and more to the attraction of females to their territories than male buntings. There is some evidence that EPCs occur in redwings (Bray et al. 1975; Wittenberger 1981). No genetic analyses have been done, but Monnett et al. (1984) report in a behavioural study that less than 15% of all copulations were EPCs.

In conclusion, the presence of frequent EPCs in indigo buntings has important and fascinating consequences for theories on mating systems. However, many of these ramifications cannot be examined until quantitative studies are undertaken. My results highlight the difficulty of using observations alone to measure reproductive success. Genetic markers should be used in future studies of this sort.

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## REFERENCES

- Abele, L. G. & Gilchrist, S. 1977. Homosexual rape and sexual selection in acanthocephalan worms. *Science, N. Y.*, **197**, 81–83.
- Afton, A. D. 1985. Forced copulation as a reproductive strategy of male lesser scaup: a field test of some predictions. *Behaviour*, **92**, 146–167.
- Beecher, M. D. & Beecher, I. M. 1979. Sociobiology of bank swallows: reproductive strategy of the male. *Science, N. Y.*, **205**, 1282–1285.
- Birkhead, T. R. 1978. Behavioural adaptations to high density nesting in the common guillemot *Uria aalge*. *Anim. Behav.*, **26**, 321–331.
- Birkhead, T. R. 1979. Timing and duration of mate guarding in magpies *Pica pica*. *Anim. Behav.*, **30**, 277–283.
- Birkhead, T. R., Johnson, S. D. & Nettleship, D. N. 1985. Extra-pair matings and mate guarding in the common murre *Uria aalge*. *Anim. Behav.*, **33**, 608–619.
- Bjorklund, M. & Westman, B. 1983. Extra-pair copulations in the pied flycatcher *Ficedula hypoleuca*: a removal experiment. *Behav. Ecol. Sociobiol.*, **13**, 271–275.
- Bray, O. E., Kennelly, J. J. & Guarino, T. L. 1975. Fertility of eggs produced on territories of vasectomized red-winged blackbirds. *Wilson Bull.*, **87**, 187–195.
- Buitron, D. 1983. Extra-pair courtship in black-billed magpies. *Anim. Behav.*, **31**, 211–220.
- Carey, M. & Nolan, V. 1975. Polygyny in indigo buntings: a hypothesis tested. *Science, N. Y.*, **190**, 1296–1297.
- Carey, M. & Nolan, V. 1979. Population dynamics of indigo buntings and the evolution of avian polygyny. *Evolution*, **33**, 1180–1192.
- Cheng, K. M., Burns, J. T. & McKinney, F. 1983. Forced copulation in captive mallards: III. Sperm competition. *Auk*, **100**, 302–310.
- Compton, M. M., Van Krey, H. P. & Siegel, P. B. 1978. The filling and emptying of the uterovaginal sperm host glands in the domestic hen. *Poult. Sci.*, **57**, 1696–1700.
- Cox, C. R. & LeBoeuf, B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *Am. Nat.*, **111**, 317–335.
- Davies, N. B. 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. *Anim. Behav.*, **33**, 628–648.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science, N. Y.*, **197**, 215–223.
- Erickson, C. J. & Zenone, P. G. 1976. Courtship differences in male ring doves: avoidance of cuckoldry? *Science, N. Y.*, **192**, 1353–1354.
- Fitch, M. A. & Shugart, G. W. 1984. Requirements for a mixed reproductive strategy in avian species. *Am. Nat.*, **124**, 116–126.
- Ford, N. L. 1983. Variation in mate fidelity in monogamous birds. In: *Current Ornithology, Vol. I* (Ed. by R. F. Johnston), pp. 329–356. New York: Plenum Press.
- Frederick, P. C. In press. Extra-pair copulations in the mating system of white ibis (*Eudocimus albus*). *Behaviour*.
- Fujioka, A. & Yamagishi, S. 1981. Extra-marital and pair copulations in the cattle egret. *Auk*, **98**, 134–144.
- Gladstone, D. E. 1979. Promiscuity in monogamous colonial birds. *Am. Nat.*, **114**, 545–577.
- Krebs, J. R. 1970. The efficiency of courtship feeding in the blue tit *Parus caeruleus*. *Ibis*, **112**, 108–110.
- Lumpkin, S. 1981. Avoidance of cuckoldry in birds: the role of the female. *Anim. Behav.*, **29**, 303–304.
- McKinney, F., Cheng, K. M. & Bruggers, D. J. 1984. Sperm competition in apparently monogamous birds. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 523–545. New York: Academic Press.
- McKinney, F., Derrickson, S. R. & Mineau, P. 1983. Forced copulation in waterfowl. *Behaviour*, **86**, 250–294.
- MacRoberts, M. H. 1973. Extramarital courting in the lesser black-backed and herring gulls. *Z. Tierpsychol.*, **32**, 62–74.
- Martin, P. A., Reimers, T. J., Lodge, J. R. & Dzuik, P. J. 1974. The effect of ratios and number of spermatozoa mixed from two males on the proportion of offspring. *J. Reprod. Fert.*, **39**, 251–258.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.*, **25**, 1–7.
- Mineau, P. & Cooke, F. 1979. Rape in the lesser snow goose. *Behaviour*, **70**, 280–291.
- Monnett, C., Rotterman, L. M., Worlein, C. & Halupka, K. 1984. Copulation patterns of red-winged blackbirds (*Agelaius phoeniceus*). *Am. Nat.*, **124**, 757–764.
- Nisbet, I. C. T. 1977. Courtship feeding and clutch size in common terns *Sterna hirundo*. In: *Evolutionary Ecology* (Ed. by B. Stonehouse & C. M. Perrins), pp. 101–109. London: Macmillan.
- Orians, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. *Ecol. Monogr.*, **31**, 285–312.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.*, **103**, 589–603.
- Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.*, **45**, 525–567.
- Patterson, C. B. 1979. Relative parental investment in the red-winged blackbird. Ph. D. thesis, Indiana University, Bloomington.
- Payne, L. F. & Kahrs, A. J. 1961. Competitive efficiency of turkey sperm. *Poult. Sci.*, **40**, 1598–1604.
- Payne, R. B. 1969. The breeding seasons and reproductive physiology of tricolored blackbirds and redwinged blackbirds. *Univ. Calif. Publ. Zool.*, **90**, 1–137.

- Payne, R. B. 1979. Sexual selection and intersexual differences in variation of mating success. *Am. Nat.*, **114**, 447–452.
- Payne, R. B. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in indigo buntings. *Ecology*, **63**, 401–411.
- Payne, R. B. 1983a. Bird songs, sexual selection, and female mating strategies. In: *Social Behavior of Female Vertebrates* (Ed. by S. K. Wasser), pp. 55–90. New York: Academic Press.
- Payne, R. B. 1983b. The social context of song mimicry: song matching dialects in indigo buntings (*Passerina cyanea*). *Anim. Behav.*, **31**, 788–805.
- Payne, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithol. Monogr.*, **33**, 1–52.
- Payne, R. B., Thompson, W. L., Fiala, K. L. & Sweany, L. L. 1981. Local song traditions in indigo buntings: cultural transmission of behaviour patterns across generations. *Behaviour*, **77**, 199–221.
- Røskaft, E. 1983. Male promiscuity and female adultery by the rook (*Corvus frugilegus*). *Ornis Scand.*, **14**, 174–179.
- Rothschild, Lord, 1955. The spermatozoa of the honeybee. *Trans. R. entomol. Soc. Lond.*, **107**, 289–294.
- Searcy, W. J. 1979. Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). *Am. Nat.*, **114**, 77–100.
- Sturkie, P. D. & Mueller, N. J. 1976. Reproduction in the female and egg formation. In: *Avian Physiology* (Ed. by P. D. Sturkie), p. 302–330. New York: Springer-Verlag.
- Summers-Smith, D. 1963. *The House Sparrow*. London: Collins.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.
- Verner, J. 1964. The evolution of polygamy in the long-billed marsh wren. *Evolution*, **18**, 252–261.
- Verner, J. & Willson, M. F. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. *Ornithol. Monogr.*, **9**, 1–76.
- Waage, J. K. 1979. Dual function of the damselfly penis: sperm removal and transfer. *Science, N. Y.*, **203**, 916–918.
- Welty, J. C. 1982. *The Life of Birds*. Philadelphia: Saunders College.
- Werschkul, D. F. 1982. Nesting ecology of the little blue heron: promiscuous behavior. *Condor*, **84**, 381–384.
- Westneat, D. F. 1987. Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. *Anim. Behav.*, **35**, 877–886.
- Willson, M. F. 1966. The breeding ecology of the yellow-headed blackbird. *Ecol. Monogr.*, **36**, 51–77.
- Wittenberger, J. F. 1981. Male quality and polygyny: the sexy son hypothesis revisited. *Am. Nat.*, **117**, 329–342.

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