

MALE PARENTAL CARE AND EXTRAPAIR COPULATIONS IN THE INDIGO BUNTING

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ABSTRACT.—Levels of parental care by male Indigo Buntings (*Passerina cyanea*) were predicted to be lower and the tendency to pursue extrapair matings greater when (1) the opportunity of additional matings (extrapair copulations) was high, (2) the male was cuckolded, and (3) the clutch or brood size was small. Observations of male care revealed that approximately 10% of all males fed nestlings at least once, whereas more than 30% fed fledglings. Males in their first breeding season were never seen feeding young. Males made more trips off their territories when females were fertilizable on nearby territories, but other measures of parental care (feeding young and time spent within 10 m of nest) were not affected. Cuckolded males (known through genetic analyses of parents and offspring) tended to feed young less often, but forayed off their territories significantly less than apparently uncuckolded males. Finally, males with small clutches or broods gave slightly, but not significantly, less care than males with large clutches or broods. These results suggest that the relationship between mating effort and parental effort is complicated by the presence of extrapair copulations as a type of mating effort, and that factors not included in current theory on parental care might influence a male's parental care. *Received 18 June 1987, accepted 19 October 1987.*

WHEN an individual spends time and energy to help raise its offspring, it potentially sacrifices opportunities to pursue additional reproduction (Trivers 1972, Maynard Smith 1977). In other words, reproductive effort can be divided into two components, mating effort and parental effort (Low 1978). Because energy spent on one component often reduces the energy available to spend on the other component, parenting behavior can be thought of as a reproductive strategy in competition with other strategies.

Maynard Smith (1977) quantified the trade-off between the gain in reproduction from additional matings and the gain from parental care. In this model, deserting a mate with young will be favored if

$$pV_2 > (V_2 - V_1),$$

where p is the probability of mating with a second female, V_1 is the number of young surviving with single-parent care, and V_2 is the number surviving with two parents helping with care. Thus, the payoffs to an individual for deserting depend on the chances of finding a new

mate as well as the effect of desertion on the survival of present young.

Total desertion is not the only alternative to parental care. Males of some species can attempt to attract additional females to their territories and still provide some care to the offspring (Wittenberger 1981). Effort spent on the attraction of females cannot be spent on parental care, however. Studies of polygynous species bear this out; males that attract more than one female to their territories often reduce the amount of parental effort to one or more of their broods (Verner and Willson 1969, Patterson et al. 1980, Muldal et al. 1986).

The relationship between parental investment and polygyny has been the focus of numerous studies (e.g. Willson 1966; Martin 1974; Patterson 1979; Searcy 1979; Weatherhead 1979, 1984; Orians 1980; Smith et al. 1982; Wittenberger 1982; Yasukawa and Searcy 1982). Males could pursue other strategies besides polygyny, however, as an alternative to parental care that maximizes reproductive success. Detailed observations of the mating behavior of many monogamous birds have revealed that copulations between individuals paired to another are quite frequent (Ford 1983, McKinney et al. 1984, Birkhead et al. 1985, Frederick 1987a, Westneat 1987a). Extrapair copulations (EPCs) generally are pursued by males that are already paired

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(McKinney et al. 1984, Birkhead et al. 1985, Frederick 1987a) and, in some cases, by males that already have eggs or young (Westneat 1987a, b). EPCs result in viable offspring (Gavin and Bollinger 1985, Joste et al. 1985, Mumme et al. 1985, Burke and Bruford 1987, Westneat 1987b, Wetton et al. 1987). Thus, a male could pursue extrapair copulations as an alternative to parental care.

Extrapair copulations that succeed in fertilizing some eggs result in some males raising young that are not their own. Maynard Smith (1978) and Wittenberger (1981) argued that cuckoldry does not affect the decision to care for young because a male's confidence in his paternity will be the same from one pairing to the next. Confidence of paternity could depend on a number of factors that change over time, however, such as the ability to guard a mate, age, and the number of neighbors actively pursuing extrapair copulations (Westneat 1987a). A male's chance of being cuckolded might even vary randomly. If so, in such cases males that can assess the likelihood of their paternity should desert offspring in which they have a low probability of paternity because they probably will do better with the next brood. Finally, Werren et al. (1980) pointed out that if a male gives up promiscuous matings for parental care, then cuckoldry could affect the evolution of male care. Because males that pursue extrapair copulations generally do not give care to the resulting young (Frederick 1985), the probability of paternity in the young they raise can affect how much effort they expend on parental care. A cuckolded male loses less from reducing parental care than a male that is not cuckolded. All else being equal, a cuckolded male is more likely than a male not cuckolded to benefit by pursuing EPCs.

The possibility of extrapair copulations affects our view of the trade-off between parental care and the pursuit of additional matings. These modifications can be incorporated into Maynard Smith's (1977) model. In this revised model, withholding parental care is favored if

$$pNb > qR,$$

where p is the probability of achieving a mating, N is the availability of matings, b is the number of young resulting from a given mating, R is the number of current offspring in a male's nest (genetically descendent from the male), and q is the effect on mortality (in proportion of young

dying) of reduced parental care. Three predictions can be made from the revised model: (1) male care should be low when the availability of fertilizable females (N) is high, (2) cuckolded males should give less care and pursue additional matings more frequently than males not cuckolded (R is less for cuckolded males), and (3) males with small clutches should give less care and pursue additional matings more than males with large clutches (R is less when clutch size is small).

I present data on male parental care in the Indigo Bunting (*Passerina cyanea*). Male buntings occasionally have more than one female nesting on their territories (Carey and Nolan 1975, 1979; Payne 1982) and frequently pursue extrapair copulations (Westneat 1987a, b). Because males appear to pursue extrapair matings when they have nesting females on their territories, they provide an excellent opportunity to test the predictions of the revised Maynard Smith model of parental care.

METHODS

During the breeding seasons of 1983–1985, I studied a population of Indigo Buntings located 5 km northeast of Niles in Cass Co., Michigan. This population has been studied since 1978 (Payne et al. 1981; Payne 1982, 1983a, b, 1984; Westneat 1987a, b).

Males and females were caught with mist nets and banded with unique sequences of colored plastic leg bands (see Westneat 1987a, b for details). Attempts were made to capture males throughout the season except when females on the territory were fertilizable. I banded females and young at the nest when the young were 4–7 days old. Male age was determined by examination of the greater primary coverts; males in their first season have at least one brown covert, whereas all the coverts of older males are blue (Taber and Johnston 1968; Carey and Nolan 1975, 1979; Payne 1982).

I located nests by observing females building nests, by following them to the nest, or by searching likely nesting areas. All territories were visited several times a week throughout the breeding season. Nearly all of the nests that fledged young were found; although unmarked fledglings sometimes appeared, they made up less than 5% of the total number of fledglings seen on the study area (Payne pers. comm.).

Females were considered fertilizable from their arrival on the study area until the first egg was laid. Because I observed a decrease in copulations, intrusions, and mate guarding during the period of laying (Westneat 1987a), I did not consider laying females to be fertilizable. Some nests were found after the female had begun incubating. The date of laying could be calculated by assuming a 13-day incubation period and a 9-day nestling period (Taber and Johnston 1968,

Payne 1982). Females averaged a period of 11 days from first copulation to the laying of the first egg (unpubl. data).

Observations of male behavior were conducted throughout the nesting cycle. I began observation sessions of focal males at all times of day, though more were begun in the morning and middle of the day than in the afternoon. In 1983 sessions lasted 45 min, in 1984 and 1985, 45–90 min. Each session was begun as soon as the male was spotted after the observer entered the territory (the area defended by the male, as evidenced by singing or chasing of intruders). A running account of the location and behavior (singing, sitting, alarm calling, foraging, and flying) of the focal bird was recorded on a cassette tape until the predetermined time had elapsed. If I lost sight of the focal bird, I searched the territory until I resighted it. These searches were focused around the area where the bird disappeared or near the nest. If a male left the territory, I waited in a spot where I could see his return.

I observed 15 males on 15 territories in 1983. The study was expanded to 24 territories in 1984 and 1985; 27 and 28 males were observed in those two years, respectively (some males were replaced in the middle of the season). Two males were observed in all three years, 18 for two of three, and 28 for only one year.

I observed these 48 males for a total of 792 h. The observation sessions were distributed among 9 stages of the nesting cycle: prefemale (59 sessions), mating (216), laying (32), early (days 1–6; 84 sessions) and late (days 7–12; 63) incubation, early (days 1–4; 71) and late (day 5–fledging; 65) nestlings, and fledglings (84). The prefemale stage covered the time from male arrival to the arrival of a female on his territory.

I compared offspring genotypes with those of their putative parents for the broods that survived to be biopsied. Genotypes were determined by protein electrophoresis, and the results are reported elsewhere (Westneat 1986b, 1987b). Biopsies of adults were performed upon capture and of young when they were 4–7 days old (for details see Westneat 1986a, Westneat et al. 1986).

In my observations of male behavior I assumed that I was equally likely to see the male no matter what he was doing. This assumption probably is not true, but any biases should be the same for all males. Because some males were out of sight some of the time, most behavior was summarized as a proportion of the time the male was seen. Because I could always tell if a male was singing or not (males sang only on their territories), I calculated the amount of time spent singing as a proportion of the total time spent in observation sessions. The forays a male made off his territory were summarized as the number made per hour of time the male was seen. I defined a foray as a trip by the male outside the boundaries of his territory and, in most cases, over the boundary of another male's territory. A few males had a territory on the edge of a field that was not defended by any other

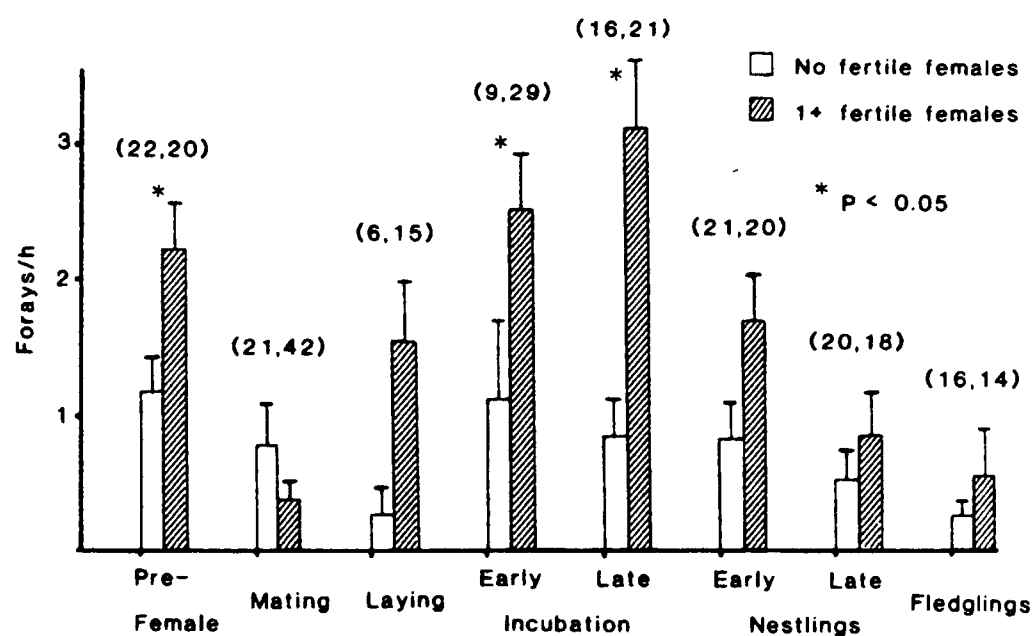


Fig. 1. Comparison of the number of forays a male made per hour if no females were mating within 200 m vs. if one or more females were mating nearby. Means and standard errors are shown, with sample sizes in parentheses. Groups were compared with Mann-Whitney *U*-tests.

male. A trip into the field was considered a foray only if the male flew farther than 50 m from his nearest singing perch.

If I saw a male leave his territory, but did not see him return, I assumed he was off the territory the entire time. If I lost sight of a male and then saw him return to his territory, I assumed he had been off the territory the whole time. Sometimes I lost track of the male but later heard alarm calls or had evidence that he was on the territory. If the male was later seen returning to his territory, I assumed he had been on his territory when I heard the alarm calls and off his territory from then until his return.

In the analysis of male tendencies to feed young, I assumed that each brood was an independent event because male feeding behavior was observed to change between broods and sample sizes were small. For all remaining analyses a male's behavior was assumed to be independent between seasons but not between broods.

Most males were observed more than once during a particular stage of the nesting cycle in a season. In such cases, I combined those sessions for a single measure of that male's behavior. In some of the analyses, a few males had observation sessions in both categories of the independent variable. To keep the sample of males independent between categories, I omitted sessions to minimize the difference in sample sizes between categories. For example, in the analysis of forays by males with and without fertilizable females on nearby territories during early incubation, there were 9 observation sessions on males without such females and 33 on males with at least one such female. Four males had sessions that fell into both categories. I omitted the sessions of those 4 that were in the category of at least one fertilizable female nearby, giving final independent samples of 9 and 29 (see Fig. 1).

The availability of fertilizable females (*N* in revised model) was measured by counting the number of fe-

males that were in their fertilizable periods on nearby territories (territories with 50% of area within 200 m of center of focal bird's territory). This distance was determined from observations of marked males; the majority of intruders onto a male's territory came from within 200 m (Westneat 1987a). I assumed that $b = 1$ for successful EPCs in the revised model.

Proportions were transformed with the arcsin transformation (Sokal and Rohlf 1969) and analyzed with parametric statistics. Untransformed data were analyzed with the appropriate nonparametric statistic, usually Mann-Whitney U or the Kruskal-Wallis H (Siegel 1956).

RESULTS

MALE PARENTAL CARE

The observations indicated that male parental behavior varied considerably. During incubation all males did very little that could be considered parental care. Males occasionally appeared to guard their mates' nests by giving alarm calls when the nests were approached. Most, however, did no more than follow the females some of the time they were off the nest.

Once the young hatched, some males began to help more with their care. Of 65 broods where the male was observed during the first 4 days of the nestlings' lives, only once was a male seen carrying food to the nest. Of 58 broods where the male was observed when the young were at least 4 days old, the male carried food at least once to 6 of the nests (10.3%). Males that did not feed young were often found near the nest and nearly always gave alarm calls if the nest was approached. Some males, however, spent little time near the nest, especially when the female was not present, and did not always respond to potential danger by alarm calling.

Of 35 broods of fledglings, in 11 (31.4%) the male fed at least one fledgling at some point before independence. All but one male that fed nestlings eventually fed fledglings if the young survived. The degree of male care of the fledglings varied. Five males eventually appeared to take sole responsibility for feeding the fledglings, but the other males that fed young did so infrequently late in the fledgling stage.

Males that did not feed usually followed the female and fledglings. These males responded to any approach with rapid alarm calls and short, excited flights through the vegetation. This behavior reached a peak in the week after fledging and diminished until the young reached in-

dependence, about 14–25 days after fledging. A few males spent little time with the fledglings. In two cases the male stayed on his territory after the female left with the fledglings. One of these males renested quickly with a second female; the first female eventually settled on another male's territory nearly 4 weeks after the young fledged. The other male remained unpaired until the female returned to renest.

Male feeding and age.—A male's ability to gain EPCs and his susceptibility to EPCs are strongly correlated with the age of the male (Westneat 1986b, 1987b). For this reason, male parental care was analyzed with respect to age; males were categorized as subadult (first breeding season) or adult (second or greater breeding season). To be sure males that I did not see feeding were observed the same length of time as those that were, I selected only broods of nestlings I had observed for at least 2 h (3 sessions in 1983, 2 in 1984 and 1985). I selected broods of fledglings that I had observed for at least 90 min.

No subadult male was observed feeding nestlings ($n = 11$) or fledglings ($n = 6$), whereas 7 of 34 adult males fed nestlings and 11 of 27 fed fledglings. Although these differences were large, they were not significant (Fisher exact probability; nestlings, $P = 0.12$; fledglings, $P = 0.07$).

Male feeding and the availability of fertilizable females.—Two of 12 males with fertilizable females on nearby territories (within 200 m of the focal bird's nest) fed nestlings. A similar proportion of males (5 of 28) without fertilizable females on nearby territories also fed nestlings. The proportions of males with and without fertilizable females on nearby territories that fed fledglings also were not significantly different (6 of 12 vs. 5 of 21; $G = 2.32$, $df = 1$, $P > 0.05$).

Because age could be confounding this analysis, I also compared adult males with and without fertilizable females on nearby territories. Five of 23 adult males without fertilizable females nearby fed nestlings, and a similar proportion (2 of 9) with at least one fertilizable female fed nestlings. More males with fertilizable females nearby fed fledglings than those without such females (6 of 11 vs. 5 of 16), but this difference was not significant ($G = 1.43$, $df = 1$, $P > 0.05$), and it is opposite to that expected.

Male feeding and cuckoldry.—I obtained information on the paternity of the young for 44 of 45 broods observed for 2 h or more as nestlings.

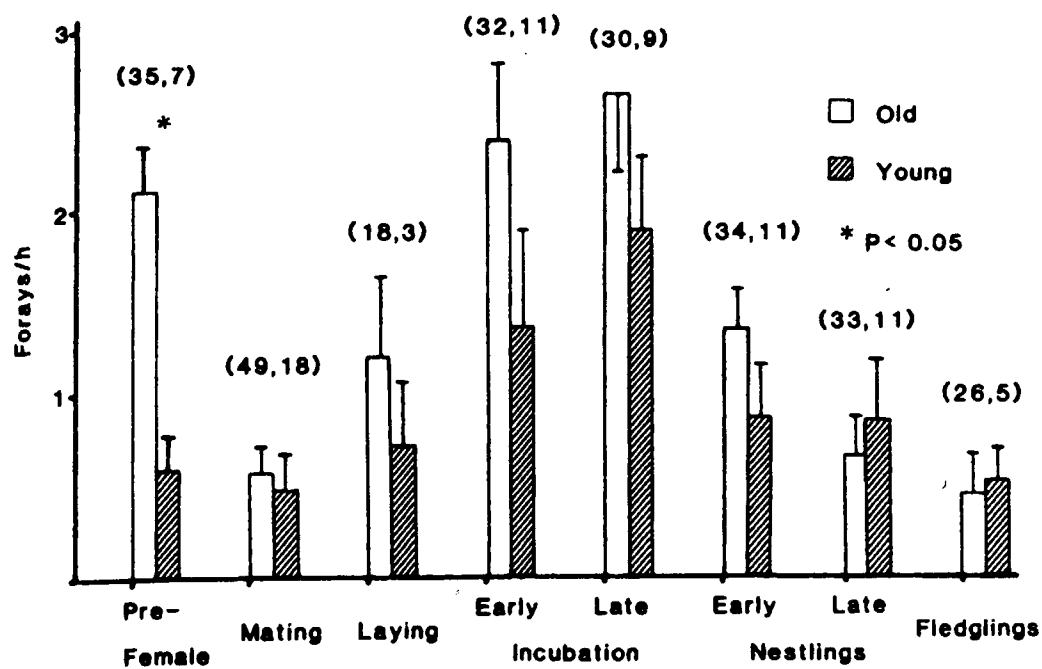


Fig. 2. Number of forays off a male's territory by his age and the stage in the nesting cycle. Young males (subadults) were in their first breeding season and older males (adults) in their second or greater season (see text). Means and standard errors of the raw data are shown, with sample sizes in parentheses. Mann-Whitney *U*-tests were used to compare age groups.

In 11 of those at least one of the young was not the offspring of the putative father. The proportion of excluded males feeding nestlings did not differ from that of apparently unexcluded males (1 of 12 vs. 5 of 29; Fisher exact probability, $P > 0.05$). Omission of subadult males from this analysis did not affect the general result; 1 of 9 (11.1%) excluded adult males fed nestlings, whereas 5 of 26 (19.2%) unexcluded adults fed nestlings. One male fed young in a nest containing two Brown-headed Cowbird (*Molothrus ater*) young and no buntings.

Nine of 31 broods of fledglings had at least one young not the offspring of the putative father. Two of 9 (22.2%) excluded males fed fledglings, and 9 of 22 (40.9%) unexcluded males fed. The difference was not significant ($G = 1.03$, $df = 1$, $P > 0.05$). Omission of the subadult males did not change the difference in proportions much; 2 of 6 (33.3%) excluded adults fed fledglings, whereas 9 of 19 (47.4%) unexcluded males fed fledglings. Each of the excluded males that fed fledglings fed the young bunting that was not his own.

It is important to note that electrophoresis detects only about 40% of the young that result from extrapair fertilizations in this population (Westneat et al. 1987). This means some of the males that had offspring with consistent genotypes were actually cuckolded. On average, about 20% of the offspring of these apparently uncuckolded males were actually fathered by another male. The above analyses should thus

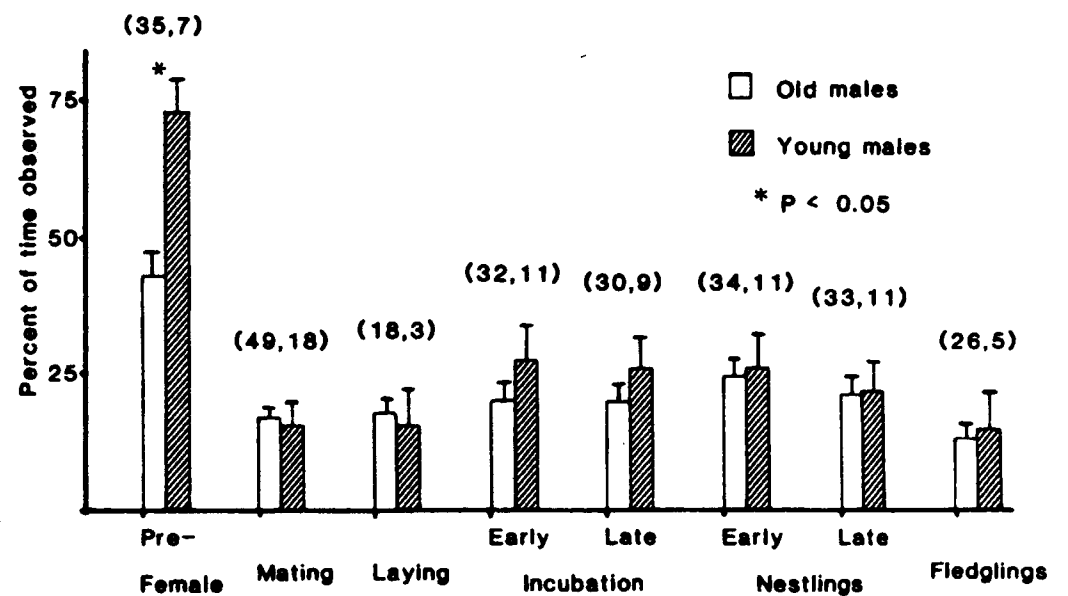


Fig. 3. Comparison of the amount of time males spent singing over the stages in the nesting cycle and by male age. Means and standard errors of the raw data are shown, with sample sizes in parentheses. Age groups were compared by a two-tailed *t*-test of the arcsine transformations of proportions.

be conservative tests of the behavior of cuckolded males.

Male feeding and brood size.—Clutch and brood size varied between 1 and 7, including cowbird eggs or young in parasitized nests. The modal clutch and brood size was 3. To analyze the relationship between male feeding and brood size, I classified broods into large (3 or more young, including cowbirds) and small (1 or 2 young). Because the number of young was difficult to count after fledging, I used as the brood size the number of young known to have fledged.

Brood size seemed to have no effect on whether a male fed nestlings (small, 0.19, $n = 16$; large, 0.14, $n = 29$; Fisher exact probability, $P > 0.05$). Fewer males with small broods fed fledglings than those with large broods (2 of 12 vs. 9 of 21), but this difference was not significant (Fisher exact probability with Tocher's modification, $P > 0.05$; Siegel 1956). Omission of subadult males did not change the general tendencies.

FORAYS OFF THE TERRITORY

Because males did not bring food from other males' territories to the young, I assumed forays off the territory were attempts to achieve extrapair copulations. I analyzed the rate of forays (forays/h) away from the territory with respect to the stage of nesting, age, presence of fertilizable females on nearby territories, cuckoldry, and clutch size.

The rate of forays varied considerably over the nesting cycle (Fig. 2). Males left their ter-

TABLE 1. Number of forays off the territory per hour by excluded and unexcluded males over the nesting cycle.

	Incubation		Nestlings		Fledglings
	Early	Late	Early	Late	
Excluded					
Mean	1.4	0.7	0.8	0.3	0.5
SD	1.5	1.0	0.9	0.5	0.4
<i>n</i>	8	7	13	12	9
Unexcluded					
Mean	2.0	3.2	1.5	1.0	0.3
SD	2.1	2.9	1.3	1.3	0.8
<i>n</i>	21	19	23	27	21
<i>P</i> ^a	NS	<0.05	NS	NS	NS

^a Mann-Whitney *U*-test.

territories least often when they were following a fertilizable female or a brood of fledglings on their own territory. The rate of forays peaked during incubation.

Forays and age.—Adult males left their territories significantly more than subadults early in the season before a female settled on their territories (Fig. 2). After a female began to lay eggs on a male's territory, adults continued to leave their territories more than subadults, although this difference was not significant.

Subadult male buntings are less likely to acquire a territory than older males (Payne 1982). Thus, subadults might defer pursuing EPCs when the acquisition of a territory is more important. To test this notion I examined the amount of time a male spent singing.

Both adults and subadults sang most early in the season (Fig. 3; see also Thompson 1972). Once females arrived, the time spent singing dropped to about 15%. Singing increased slightly to about 25% during the later stages of nesting.

Subadults sang significantly more than adults early in the season (Fig. 3). Subadults continued to sing slightly more during incubation. This extra effort spent on singing does not serve to attract additional females; fewer subadult males than adults mate polygynously (Payne 1982, unpubl. data).

Forays and the availability of fertilizable females.—The presence of fertilizable females on neighboring territories had a major effect on the rates of forays outside the territory (Fig. 1). The greatest effect of fertilizable females on the number of forays occurred before the focal male's own female arrived and during incu-

TABLE 2. Effect of clutch or brood size on the frequency of forays off the territory. Clutch and brood sizes include cowbird eggs and young.

Clutch size	Forays/h				
	Incubation		Nestlings		Fledglings
	Early	Late	Early	Late	
Small (1 or 2)					
Mean	2.3	3.0	1.0	1.6	0.3
SD	1.6	1.6	1.1	1.2	0.6
<i>n</i>	10	9	11	11	14
Medium (3)					
Mean	2.1	1.9	0.9	0.4	
SD	2.4	2.0	0.9	0.9	
<i>n</i>	23	17	23	25	
Large (4+)					
Mean	1.4	2.5	2.2	0.9	0.4 ^a
SD	1.6	1.9	1.9	1.4	0.8
<i>n</i>	9	13	10	8	17
<i>P</i> ^b	NS	NS	NS	NS	NS ^c

^a Medium and large classes lumped to increase sample size.

^b Kruskal-Wallis test.

^c Mann-Whitney *U*-test.

bation. Omission of the subadult males from this analysis revealed that adult males continued to foray more late in the nesting cycle if there were fertilizable females on nearby territories. Adult males averaged 0.76 forays/h ($n = 16$, $SD = 1.20$) during the early nestling stage with no fertilizable females nearby, whereas males with one or more fertilizable females nearby forayed significantly more ($\bar{x} = 1.93$, $n = 16$, $SD = 1.53$; Mann-Whitney *U*, $P < 0.05$). A similar, but not significant, tendency occurred for adult males with old nestlings (no females: $\bar{x} = 0.24$, $n = 14$, $SD = 0.57$; one or more females: $\bar{x} = 1.05$, $n = 14$, $SD = 1.42$; Mann-Whitney *U*, $P > 0.05$). This provides strong evidence for the notion that forays are attempts to gain extrapair matings and that males should pursue EPCs more and care for young less when fertilizable females are available.

Forays and cuckoldry.—I analyzed the relationship between forays off the territory and cuckoldry by classifying males as cuckolded only when they were excluded genetically. Inclusion of males with cowbird young in the cuckolded class did not change the result of any comparisons.

Excluded males did not leave their territories more than unexcluded males (Table 1). In fact, during incubation, excluded males left their territories significantly less than unexcluded males.

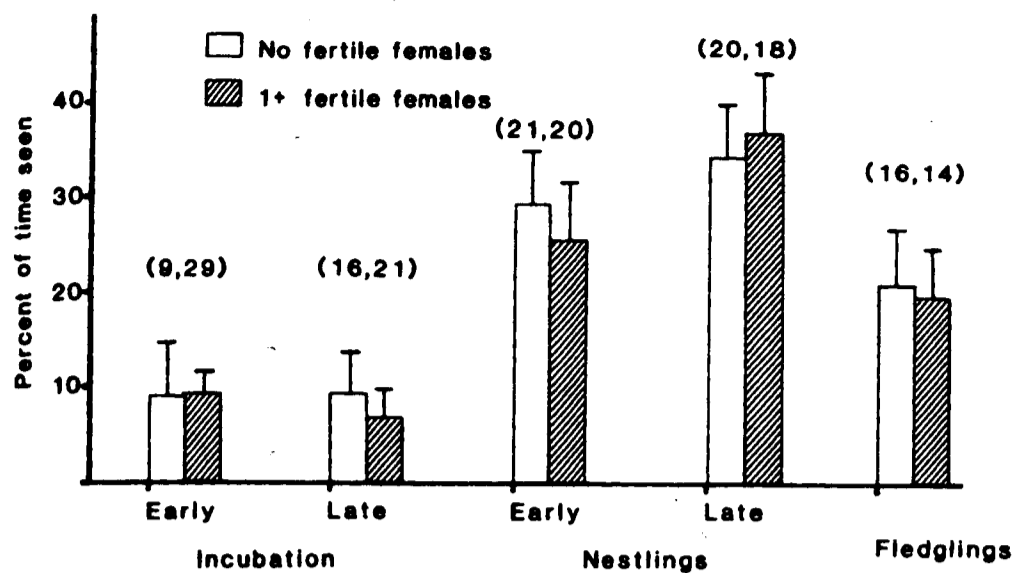


Fig. 4. Comparison of the time males spent near (within 10 m) their nests or young (as a percentage of time males were seen) over the nesting cycle and by whether or not at least one fertilizable female was present within 200 m. Means and standard errors are of the raw data, and sample sizes are in parentheses. Groups were compared with two-tailed *t*-tests of the arcsine transformation of proportions.

Omission of subadult males from this analysis either did not affect the differences observed, or increased them. This result refutes the prediction that cuckolded males should spend more effort on the pursuit of extrapair matings. Caution must be taken when interpreting this result because not all instances of cuckoldry could be detected (Westneat et al. 1987).

Forays and clutch or brood size.—For this analysis, nests were grouped into three classes: 1 and 2 eggs or young, 3 eggs or young, and 4 or more eggs or young. Cowbird eggs and young were included. There was no consistent difference in the number of forays per hour for different sizes of the male's clutch across the five stages of the nesting cycle (Table 2).

TIME NEAR THE NEST

Males cannot contribute to the defense of the nest or young while they are off their territories. Although the best measure of a male's tendency to guard his nest might be the amount of time spent with the nest in sight, I had difficulty deciding when a male could or could not see the nest. Accordingly, I considered the amount of time a male spent within 10 m of the nest or young as a possible indicator of male protective behavior. This time changed dramatically over the course of the nesting cycle (Fig. 4). During incubation males spent very little time near the nest. Once the young hatched, the activity of males became much more centered around the nest site. This activity dissipated as the young fledglings became more mobile.

TABLE 3. Effect of age on the time males spent near (within 10 m) their nests or young. Means and standard deviations are of untransformed data.

Age	Time near nest or young (%)				Fledglings
	Incubation		Nestlings		
	Early	Late	Early	Late	
Adult					
Mean	8.8	7.9	27.4	31.5	18.0
SD	10.8	13.3	22.2	23.8	19.1
<i>n</i>	32	30	34	33	26
Subadult					
Mean	6.3	6.8	24.7	40.5	33.6
SD	10.3	7.6	18.7	22.0	26.2
<i>n</i>	11	9	11	11	5
<i>P</i> ^a	NS	NS	NS	NS	NS

^a Two-tailed *t*-test with arcsine transformation.

The time a male spent near the nest was independent of his age (Table 3). Furthermore, the time a male spent near the nest or young was not related to the availability of fertilizable females on nearby territories (Fig. 4). This result does not support the prediction that parental care should be affected by the availability of potential additional mates.

Cuckoldry seemed to have some effect on the amount of time a male spent near the nest. In four of the five stages excluded males spent more time near the nest than unexcluded males (Table 4), although in no stage was this difference significant. This result is opposite that expected from the revised Maynard Smith model.

Clutch or brood size was the only variable that had the predicted effect on the time a male spent near the nest or young. In four of the five stages males with small clutches spent less time near the nest than males with large clutches (Table 5). None of these tendencies was significant, however, so at best these results are weak evidence that males reduce parental care to small clutches.

DISCUSSION

Availability of matings.—Male behavior was affected by the availability of fertilizable females. Males left their territories considerably more when females on nearby territories were fertilizable. Other measures of parental care did not show similar relationships. For example, males spent similar amounts of time near the nest regardless of the presence of mating females on

TABLE 4. Comparison of the time excluded and unexcluded males spent near (within 10 m) their nests or young. Means and standard deviations are of untransformed data.

Parentage of male	Time near nest or young (%)				
	Incubation		Nestlings		Fledglings
	Early	Late	Early	Late	
Excluded					
Mean	15.6	16.0	31.5	34.4	31.0
SD	17.2	15.2	27.0	27.1	31.8
<i>n</i>	8	7	13	12	9
Unexcluded					
Mean	7.5	7.1	25.3	38.8	14.8
SD	11.9	13.6	19.5	23.5	12.0
<i>n</i>	21	19	23	27	21
<i>P</i> ^a	NS	NS	NS	NS	NS

^a Two-tailed *t*-test with arcsine transformation.

nearby territories. One possible reason for this is that males often left their territories when their own females were incubating, even though no females within 200 m were fertilizable. Because a male's presence near the nest during incubation might confer little benefit to the survival of those young, males might search farther afield for fertilizable females. Once the young hatched, male presence near the nest increased dramatically. During this time males might gain more by staying near the nest even if females are mating on nearby territories. The trade-off between the gains from parental care and the gains from pursuit of additional matings may switch during the course of the nesting cycle. The data presented here are not sufficient to evaluate the potential gains and losses of leaving the territory at different times in the nesting cycle.

The present study focused exclusively on the effect of opportunities for extrapair copulations on male parental behavior. Male Indigo Buntings also occasionally attract more than one female to their territories (Carey and Nolan 1975, 1979; Payne 1982). Unpaired females are another source of additional matings that can be incorporated into the revised model presented here (the variable *b* would be the brood size of the second nest). If so, the model would predict that males should reduce parental care if the opportunity for attracting unpaired females is high. Fewer male buntings that attract a second female feed young than males with a single mate (Westneat 1988).

TABLE 5. Effect of clutch or brood size on the time males spent near (within 10 m) their nests or young.

Clutch or brood size	Time near nest or young (%)				
	Incubation		Nestlings		Fledglings
	Early	Late	Early	Late	
Small (1 or 2)					
Mean	9.9	0.9	26.4	26.4	16.8
SD	15.2	2.0	28.4	24.1	20.0
<i>n</i>	10	9	11	11	14
Medium (3)					
Mean	10.9	7.8	24.9	38.2	
SD	12.4	11.6	19.1	25.2	
<i>n</i>	23	17	23	25	
Large (4+)					
Mean	7.0	8.6	32.2	34.8	22.7 ^a
SD	9.8	15.0	26.2	16.2	22.1
<i>n</i>	9	13	10	8	17
<i>P</i> ^b	NS	NS	NS	NS	NS ^c

^a Medium and large lumped to increase sample size.

^b Kruskal-Wallis test.

^c Mann-Whitney *U*-test.

Cuckoldry.—Cuckolded males were predicted by the revised model to reduce parental care and increase their efforts in pursuing additional matings. The evidence bearing on this prediction was equivocal. Fewer excluded males fed young, although the differences were not significant. Subadult males never fed young and were twice as likely as adults to be victims of extrapair fertilizations (Westneat 1986b, 1987b). This result suggests that cuckoldry may have affected the evolution of male parental behavior. Several previous studies have found no effect of cuckoldry, but behavioral observations were used to determine the likelihood of a male's parentage (Frederick 1987b, Morton 1987). Unfortunately, the results of my study must be viewed with caution because of small sample sizes and the incomplete knowledge of paternity.

None of the other measures of parental care examined supported the prediction that cuckolded males should reduce parental care. In fact, excluded males appeared to spend slightly more time near the nest and to fly off their territories less frequently than unexcluded males, especially during incubation. These results suggest that parts of the revised model may not apply. This could be true if the model is wrong, or if males cannot detect that they are cuckolded.

An additional reason for the disagreement with the prediction is that susceptibility to

cuckoldry might be correlated inversely with the ability to gain extrapair copulations (R related to p in revised model). Males incapable of defending their own females against the advances of other males might be unable to overcome the defense of mates by other males and thereby gain an EPC. Fighting ability over extrapair females was correlated with success at obtaining EPCs in Cattle Egrets (*Bubulcus ibis*; Fujioka and Yamagishi 1981) and White Ibis (*Eudocimus albus*; Frederick 1987a). In addition, Frederick (1985) found that males that were poor at gaining EPCs were also poor at defending their own females, primarily because they spent more time off the colony.

Two results from the allozyme analysis suggest that in buntings susceptibility to cuckoldry might be related to the ability to gain EPCs. First, males known to be successful at gaining EPCs (by matches of their genotype to that of an excluded offspring on a neighbor's territory) were excluded less than expected by chance (Westneat 1986b). Second, subadult males were excluded more often than adult males and also achieved fewer extrapair fertilizations than adults (Westneat 1987b).

If cuckolded Indigo Buntings are less able to gain EPCs, they might benefit by not trying. These males might gain by increasing parental care, even if they are cuckolded. Subadults were victimized often and did not foray off their territories in search of EPCs more than adults, nor did they gain as many EPCs (Westneat 1986b, 1987b). They also did not feed young, however, so they probably lose some reproduction by not feeding the young in their nests that are their own. Continued effort spent on territorial defense might compensate subadults for this lost reproductive success. Although subadults sang slightly more than adult males, the difference was very small during the stages when males might be feeding young.

Feeding young requires complex foraging skills, and subadult males might not have obtained the experience necessary for this task. Inexperience might cause inefficient foraging for self-maintenance as well as for provisioning the young. If so, subadult males might be expected to spend more time foraging than adult males. Subadults do not do so, however (Table 6). Furthermore, experience cannot be the only difference between subadult and adult male Indigo Buntings. Other studies have found that younger birds are less capable of parenting than

TABLE 6. Comparison of time spent foraging for adult and subadult males during each stage of the nesting cycle.

Stage of nesting	Age of male		P^a
	Adult	Subadult	
Prefemale			
Mean	11.5	15.1	NS
SD	9.7	8.3	
n	35	7	
Mating			
Mean	14.4	13.1	NS
SD	12.3	11.9	
n	49	18	
Laying			
Mean	21.9	37.0	NS
SD	22.0	26.2	
n	18	3	
Early incubation			
Mean	11.0	12.4	NS
SD	14.6	14.8	
n	32	11	
Late incubation			
Mean	11.0	9.7	NS
SD	10.3	9.8	
n	30	9	
Early nestlings			
Mean	8.4	15.4	NS
SD	10.3	14.9	
n	34	11	
Late nestlings			
Mean	12.7	7.5	NS
SD	13.8	8.4	
n	33	11	
Fledglings			
Mean	12.1	4.2	NS
SD	11.7	6.1	
n	26	5	

^a Two-tailed t -test on arcsine transformation.

older birds (Coulson and White 1958, Mills 1973, Crawford 1977, Curio 1983, Loman 1984), primarily because of inefficient foraging. In these species, however, subadults at least make an attempt to care for young, whereas in Indigo Buntings they do not try to feed young.

Finally, selection might have acted on subadult males to defer stressful care to broods likely to be only partially theirs in exchange for increased chances of survival to the next breeding season. The impact of feeding young on the chances of survival into the next breeding season is not known in this species.

Clutch or brood size.—Males with smaller clutches lose less by providing less parental care,

so they were predicted to increase the pursuit of alternative matings. The data I collected do not permit a rejection of this prediction, but neither do they constitute convincing evidence in support. None of the measures of parental care varied significantly with clutch size, yet nearly all showed weak tendencies in the predicted direction.

Curio and Regelman (1982) predicted on the basis of measurements of residual reproductive value that both parents should give less care to small broods. Other studies have indicated that clutch or brood size does affect levels of parental effort (Robertson and Biermann 1979, Patterson et al. 1980, Biermann and Sealy 1982, Johnson and Best 1982; but see Bjerke et al. 1985, Simmons 1986). Therefore, it is surprising that I did not find a stronger relationship between clutch size and parental effort in buntings. One possibility is that males in general expend little effort on raising their young. The size of the clutch or brood might not matter much in such cases, or males may have poor information on the size of their clutch or brood.

Changes in levels of nest defense might reflect changes in the probability of predation (Harvey and Greenwood 1978). If so, and if the probability of predation on small broods is similar to that of large broods, then nest-defense behavior should not depend on brood size. The frequency of male feeding is the only measure of parental care not at least indirectly related to nest defense. This is also the measure with the strongest relationship to brood size.

Maynard Smith's (1977) model of parental care has generated some new ideas on the relationship between parental care and mating behavior. Application of the original model to Indigo Buntings suggested that males might be seeking additional matings from extrapair copulations as well as from second mates. Observations of copulations (Westneat 1987a) and the analysis of parentage (Westneat 1987b) suggest that EPCs are a major component of the reproductive biology of Indigo Buntings.

The presence of frequent and successful extrapair copulations led me to revise Maynard Smith's (1977) original model. The specific predictions of the revised model generally were not supported in this study, however. In part, this result might have come from my assumption that the variance in male behavior resulted from male buntings behaving facultatively. This might not be so, and even though nonfaculta-

tive levels of male parental care might be adaptive, they would not be amenable to the tests have presented here.

In some circumstances male buntings behave facultatively. For example, males leave their territories more frequently when females are mating on nearby territories. Thus, the results from tests of the predictions of the revised model probably are meaningful. Even though the predictions of the model generally were not supported, the process of testing the predictions has generated new ideas about the relationship between parental care and alternative mating tactics, and about the behavioral options individual birds can pursue. For example, I predicted that males should reduce parental care when females were mating on nearby territories. I found that the trade-off between gains from parental care and from pursuit of additional matings might switch during the nesting cycle.

I also predicted that cuckolded males should reduce parental care and increase the pursuit of additional matings. I found that cuckolded males might not pursue additional matings because they have trouble succeeding. That subadult males are likely to be victimized by EPCs and do not feed young suggests that cuckoldry can affect male parental care, yet it is not clear how the behavior of subadults is adaptive, because by not feeding they lower the chances that their own young survive.

This study points out the continuing need to measure more accurately the effects of male parental care and the pursuit of additional matings on reproductive success and survival. In particular, we need to be able to assign parentage of all offspring. Quantitative methods of assigning parentage are being developed (Burke and Bruford 1987, Quinn et al. 1987, Wetton et al. 1987) and show promise. Once reproductive success can be measured more accurately, additional observations and manipulations of behavior may allow tests of the revised predictions suggested here and may lead to a more precise understanding of the evolution of mating behavior and parental care.

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