The Relationships among Polygyny, Male Parental Care, and Female Breeding Success in the Indigo Bunting

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The reproductive success of males and females in a polygynous, territorial bird species is affected by the ability of the male to provide care to some or all of the young and by the benefits of pairing polygynously (Orians 1969, Patterson et al. 1980, Muldal et al. 1986). The benefits to males of attracting a second mate will be reduced if the pursuit of additional females affects a male's ability to care for present young (Maynard Smith 1977). For female reproductive success the benefits of nesting on the territory of an already-mated male will also depend in part on that male's ability to care for the female's young. To understand the evolution of polygyny, it is critical to know the effect of male parental care on the reproductive success of both males and females and how polygyny determines the levels of male parental care.

In many species polygynous males feed the young infrequently in some or all of their broods (reviewed by Verner and Willson 1969, Wittenberger 1981). Usually, the young in these neglected broods suffer increased mortality either before or after fledging (Patterson 1979, Muldal et al. 1986). In other populations males show no parental care (Orians 1961, Payne 1969, Patterson et al. 1980), but presumably the number of surviving young would be increased if males helped feed the young even in these species.

Indigo Bunting (*Passerina cyanea*) males are occasionally polygynous (Carey and Nolan 1979, Payne 1982) and reportedly provide little help with the care of the offspring (Verner and Willson 1969, Carey and Nolan 1979). In breeding Indigo Buntings studied in detail by Carey and Nolan (1975, 1979), males showed little tendency to feed young. This lack of male care made the effects of polygyny on female reproductive success appear negligible. In a separate population with a similar frequency of polygyny (Payne 1982), however, I found that some males feed nestlings and over a third feed fledglings (Westneat 1988). This difference between populations led me to study the effect of male parental care on male and female reproductive success and to investigate the role polygyny might play in determining the levels of male parental care in this second population.

I collected data as part of a larger study on the mating behavior and parental care of Indigo Buntings (Westneat 1987a, b, 1988). The study was conducted in May–August 1983–1985 along an active railroad line 5 km northeast of Niles in Cass Co., Michigan. This population has been the subject of intensive fieldwork since 1978 (Payne 1982, 1983a, b; Payne et al. 1987).

Individual buntings were marked with unique combinations of colored bands (see Payne 1982, Westneat 1987a for details). Territories (areas males defended by singing or chasing intruders) were censused several times a week, and attempts were made to find all nests for all females seen on a male's territory.

I observed the behavior of males throughout the season in the 3 yr of study. Observation sessions lasted 45–90 min. Each session was started as soon as the focal male was spotted and continued until a predetermined time had elapsed. A running account of the male's behavior was kept on cassette tape. In the 3 yr I observed 15, 27, and 28 males. Some of these males returned and were observed in subsequent years; 48 different males were observed for a total of 792 h.

I completed at least 2 observation sessions during the nestling stage of 52 broods; in 7 (13.5%) of these the male fed nestlings at least once (Westneat 1986, 1988). To calculate the effect of male feeding on the production of fledglings, I counted the number of young known to have fledged, including Brown-headed Cowbird (*Molothrus ater*) young, for all nests observed at least twice. The nests where males fed young fledged an average of 1.71 young ($n = 7$, range = 0–4), not significantly different from the average of 1.77 young fledged from nests that were not provisioned in part by males ($n = 45$, range = 0–4; Mann-Whitney U-test, $P > 0.05$). In the 3 yr of study only two broods apparently starved (nestlings found dead in nest after growing more slowly than normal); in both cases the male did not feed the young. A third brood of young appeared to be smaller than normal when a male began provisioning them. I did not weigh nestlings repeatedly, however, so I have no quantitative evidence on the condition of young in broods provisioned by males.

A test of the effect of feeding on survival of the fledglings to independence could not be made. Fledglings were usually secretive and so were difficult to locate and count consistently. Male feeding of fledglings appeared to have a considerable impact on the length of time from fledging until the female renested. I analyzed this relationship by considering only those broods for which (1) the brood was observed at least three times after fledging, (2) the fledglings were known to be alive, and (3) the female eventually renested. Females of males that fed fledglings renested an average of 8.8 days sooner than females of males that did not feed (Table 1). Males

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usually did not feed fledglings while the female was fertilizable, but started feeding when she began incubating the second clutch.

To assess the impact the additional 9 days might have on female reproductive success, I examined nesting dates in two ways. I attempted to see if any unassisted females that did not renest might have done so if their mates had fed young. First, among females that laid second clutches in each year I picked the female whose first clutch had the latest fledging date. Any female that fledged young before that date and did not renest might have been affected by lack of male assistance with the young. Alternatively, I determined the date of laying of the first egg for the last successful nest in each season. Females that fledged young 11 days before that date (average renesting time for females with male help; see Table 1) might have been able to renest if their males had helped.

In 1983, 1984, and 1985 the last female to fledge young and renest did so on 20 July, 22 July, and 5 July, respectively. In the 3 yr only 1 of 17 females that fledged young before the above dates did not subsequently renest. The one female fledged 4 young on 4 July 1984. Between 7 July and 10 July the entire family disappeared from the territory. I never saw the adults again, but I saw one fledgling foraging alone several weeks later. Because the male disappeared, I have little information on his behavior. Thus, whether or not male help with fledglings might have affected this female's behavior is unclear.

The dates a female would have had to fledge young to renest before the last successful nest of the season was started were 23 July in 1983, 2 August in 1984, and 27 July in 1985. Seven females in the 3 yr fledged young before those dates and did not renest. In 4 of these cases I completed at least 2 observation sessions in which I did not witness the male feeding the young. Lack of male help might have affected the female's reproductive success in these cases. Two of the remaining females that did not renest had some male help with the fledglings, however. One female appeared to try to renest, but either she could not lay eggs or the contents were immediately taken by a predator, because I never saw eggs in the nest. In the other case, the female disappeared from the territory immediately after fledging and so might have been killed.

Male help might make the difference between one renesting attempt and two. For example, in 1984 male ROSX helped feed fledglings that left the nest on 15 July. The female attempted to renest on 26 July, but the eggs vanished before hatching. The female renested again on 14 August and eventually fledged 3 young. Without the male's help with the first brood, the second renesting attempt probably would not have succeeded and might not have been attempted.

Females thus appear to benefit from male help in some instances, but translating the effect of shorter renesting times into reproductive success is difficult. Many nests fledged on dates when the female had time to renest, regardless of male help. In addition, renesting probably depends on the female's age and condition and on factors specific to her male's territory. Finally, most nests fail (Carey and Nolan 1979, Payne unpub. data), so females can expect to succeed in only 30–50% of their nesting attempts (depending on the time in the season).

TABLE 1. The effect of male feeding of fledglings on the number of days until the female renested, measured from the date of fledging to the date the first egg was laid. Data are shown as means ± standard deviations.

Male fed fledglings[a]	Male often with fledglings[b]	Male left with fledglings[c]	Male did not feed fledglings[a]
11.2 ± 2.7 ($n = 5$)	12.0 ± 1.0 ($n = 2$)	7.0 ± 0.0 ($n = 2$)	20.0 ± 6.1 ($n = 7$)

[a] Two-tailed t-test; $t = 3.14$, df = 10, $P < 0.01$.

[b] These 2 males were frequently observed near the fledglings for 3 weeks after fledging, but were never seen carrying food.

[c] These 2 males disappeared soon after their female renested (same female on same territory but with different males in 2 different years). Only one of several young that fledged was seen after the male left.

Males that did not feed nestlings or fledglings often attracted a second female to their territories. Of the 7 males that did not feed fledglings, 5 had a second female that nested either before the first brood fledged or soon thereafter. This suggestion of a relationship between pairing status and male feeding of young is supported on closer inspection. To be sure I had made equally thorough observations of males that did and did not feed young, I selected only broods of nestlings I had observed for at least 2 h (3 sessions in 1983, 2 in 1984 and 1985) and broods of fledglings observed for at least 90 min (2 sessions in 1983, 1 in 1984 and 1985).

No polygynous male ($n = 14$) was seen feeding nestlings, whereas 7 monogamous males ($n = 31$) fed nestlings at least once; however, this difference is not significant (Fisher exact probability, $P = 0.058$). Two males fed nestlings in one season when they were monogamous but did not feed nestlings in another season when they were polygynous.

Only 1 of 10 polygynous males fed fledglings, as opposed to 10 of 13 monogamous males, a significant difference (Fisher exact probability with Tocher's modification, $P < 0.05$; Siegel 1956). The one polygynous male that did feed fledglings had only one fledgling at that time, but his second female was feeding two nestlings.

These results suggest that in Indigo Buntings female reproductive success is affected by male parental care. In addition, the levels of male parental care may depend on whether the male has one mate or two. Calculations of the impact of polygyny and male parental care on reproductive success (especially the male's) are made more difficult because in this population males are often victims of extrapair fertilizations (Westneat 1987a, b; Westneat et al. 1987), yet the precise effect on reproductive success of these matings is unknown because parentage cannot be assigned. Nevertheless, polygyny in this species is associated with a decrease in male parental care, which probably affects female reproductive success by lengthening the time between fledging and renesting and makes it less likely that a female will attempt a second brood.

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Seasonal Changes in Food Preferences of American Robins in Captivity

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Virtually all birds change their diets over the course of the year (e.g. Martin et al. 1951, Hintz and Dyer 1970, Smith et al. 1978). Seasonal shifts in diet are especially striking in birds that eat fruits. Fruits may comprise more than 95% of the diet in some seasons while in other seasons they are not eaten at all (Martin et al. 1951), despite the fact that in most habitats at least some fruits are available year-round (Jones and Wheelwright 1987, Skeate 1987). The simplest explanation for such diet shifts is that birds track food

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