

NESTING SUCCESS IS HIGHER FOR POLYGYNOUSLY MATED FEMALES THAN FOR MONOGAMOUSLY MATED FEMALES IN THE EASTERN MEADOWLARK

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ABSTRACT.—I compared nesting success of polygynously and monogamously mated females in a population of the Eastern Meadowlark (*Sturnella magna*). Clutch size, growth rates of nestlings, and mass at fledging of nestlings were not different in the two groups of females. Both hatching success and fledging success were significantly higher, however, for females mated with polygynous males than for those mated with monogamous males. Predation was the major cause of reproductive failure. I suggest that polygynous males are older males that provide better parental care when nest contents are faced with the risks of predation. *Received 31 July 1987, accepted 5 January 1988.*

THE evolution of polygynous mating systems continues to be a subject of much interest (Wittenberger 1982, Searcy 1982, Hannon 1984, Catchpole et al. 1985, Davies 1985, Kirkpatrick 1985). Polygyny is viewed as benefiting the resource-controlling male (Mock 1983) but entailing costs for primary and secondary females paired with one male (Wittenberger 1982). In some polygynous species the primary females receive most or all of the male's parental assistance, especially in feeding young, while secondary females receive little or none (e.g. Wittenberger 1980, 1982; Alatalo et al. 1981; Catchpole et al. 1985; Nakamura 1985; Dyrce 1986). The Eastern Meadowlark (*Sturnella magna*) has a polygynous mating system (Lanyon 1957, Verner and Willson 1966, Orians 1985, this study), and both parents feed nestlings and fledglings (Orians 1985, Knapton pers. obs.). Because males provide parental care, females may incur costs from the reduced male assistance, and such costs may manifest themselves in female reproductive success being depressed under polygyny. I compared the nesting success of females paired with monogamous males and with polygynous males in a population of the Eastern Meadowlark. For the two groups of females, I compared clutch size, hatching success, fledging success, growth rates of nestlings, and nestling mass at fledging.

METHODS

The study population was located in the Short Hills Provincial Park Reserve, Regional Municipality of Niagara, Ontario. The area consists of abandoned fields

and old vineyards, in which human disturbance to nesting habitat was essentially absent. The old fields were dominated by various graminoids, and the abandoned vineyards had grasses and forbs growing among rows of old posts and dead cultivated grape stalks.

Adult Eastern Meadowlarks were mist-netted and color-banded for individual recognition, mostly in late March and early April, 1982 through 1985, before the nesting season had started. Each bird was sexed by presence or absence of cloacal protuberance or brood patch, by plumage differences (females tended to be duller than males), and by size differences (females average about 10% smaller than males; Siderius 1984, Orians 1985). Subsequent behavioral differences (e.g. singing by males, incubating by females) confirmed these sexing methods.

Polygyny occurred in each year of the study, but the proportion of polygynous males varied from one year to the next. About half the males were polygynous for all four years combined, ranging from a low of 38% in 1985 to a high of 56% in 1982 (Knapton and Siderius unpubl. data).

Nests were located by flushing the incubating female or by watching females return to their nests after feeding or with nest material. Nest contents were monitored every third day in each year except during the nestling stage in 1983, when the nests were visited daily. A log of nest progress was kept until the nest was empty, either because the young fledged or because the nest contents were destroyed. Young were weighed and banded on the eleventh or twelfth day in the nest.

In 1983 each nestling was weighed to the nearest 0.1 g for the first 4 days post-hatching, and to the nearest 0.5 g each day thereafter, until it fledged or disappeared from the nest. Each nestling was marked uniquely on the tarsus with a felt marker, and individuals were identifiable from one day to the next. Following Ricklefs (1967, 1983), I determined the

TABLE 1. Clutch size of polygynously and monogamously mated female Eastern Meadowlarks.

	Clutch size			
	3	4	5	6
Monogamous	2	16	18	1
Polygynous	3	21	35	7

growth constant K by fitting individual logistic growth equations to each nestling. According to the logistic equation, mass at age t is

$$M(t) = a(1 + e^{-Kt})^{-1},$$

where a = asymptotic mass of the nestlings and K = a constant proportional to the growth rate. A Kruskal-Wallis test was used to compare K values between the two groups of nestlings. Furthermore, the masses of nestlings of polygynously and monogamously mated females were compared at days 0, 3, 6, and 9 post-hatch, using single-classification ANOVAs for unequal variances (Sokal and Rohlf 1981). Finally, I compared the mass at fledging between young of monogamously and polygynously paired females for all years combined.

RESULTS

A total of 103 nests was located in all years combined; of these, 37 were of monogamously mated females and 66 of polygynously mated females. Clutch sizes and hatching and fledging successes did not differ significantly among years between the two groups of females, and data for all four years were combined.

Clutch size.—Clutch sizes ranged from 3 to 6 eggs, with 4 and 5 the most common (35.9% and 51.5%, respectively) (Table 1). Seven of the 8 6-egg clutches were laid by polygynously mated females; however, mean clutch sizes of polygynously mated females (4.70 ± 0.72) and of monogamously mated females (4.51 ± 0.65) were not different ($t = 1.28$, not significant).

Hatching success.—Young hatched in more nests of polygynously mated females (44 of 66 nests) than of monogamously mated females (17 of 37 nests). The difference was significant ($\chi^2 = 4.22$, $P < 0.05$).

To eliminate the influence of clutch-size differences on hatching success, I considered the number of young hatched as a function of the number of eggs laid (Table 2). The nests of polygynously mated females produced significantly more hatched young per eggs laid (66.5%)

TABLE 2. Nesting success of monogamously and polygynously mated female Eastern Meadowlarks, 1982–1985.

	Monogamous	Polygynous
Number of nests	37	66
Eggs laid	167	310
Young hatched	81 (48.5%)	206 (66.5%)
Young fledged	48 (59.3%)	161 (78.2%)
Eggs resulting in fledged young	28.9%	51.9%

than did those of monogamously mated females (48.5%) ($\chi^2 = 14.1$, $P < 0.01$).

Fledging success.—Young fledged from 11 nests of monogamously mated females (29.7%) and from 34 nests of polygynously mated females (51.5%). The difference was significant ($\chi^2 = 4.57$, $P < 0.05$).

To eliminate the influence of brood-size differences, I calculated fledging success in two additional ways: the number of young fledged as a function of the number of young hatched, and the number of young fledged as a function of the number of eggs laid (Table 2). In both analyses significantly more young fledged from the nests of polygynously mated females than from those of monogamously mated ones. Of the total young hatched, 59.3% fledged from nests of monogamously paired females and 78.2% from those of polygynously paired females (Table 2; $\chi^2 = 10.5$, $P < 0.05$). Of the total eggs laid, 28.9% resulted in fledged young in monogamously paired females and 51.9% in polygynously paired females (Table 2; $\chi^2 = 23.3$, $P < 0.001$).

Growth rates and fledging mass.—There was no difference in the rate of growth of nestlings in nests of monogamously paired females compared with polygynously paired females. The growth rate constant K for the former group was 0.53 ± 0.016 , and for the latter group 0.54 ± 0.014 ($F = 1.38$, $df = 1.13$, not significant).

To determine if nestling growth was influenced by the number of young present in a nest, I compared nestling mass among different brood sizes at days 0, 3, 6, and 9 after hatching (Table 3). There were no significant differences in mass among broods of different sizes; therefore, data were pooled regardless of brood size.

ANOVAs revealed no differences in the mass of nestlings of monogamously and polygynously mated females at any of the four ages

TABLE 3. Nestling mass (g) among different brood sizes at 4 ages post-hatch in Eastern Meadowlarks.

Brood size	Age [$\bar{x} \pm SD (n)$]			
	0	3	6	9
3	4.9 \pm 0.18 (12)	11.8 \pm 0.63 (12)	26.2 \pm 0.92 (12)	44.6 \pm 2.32 (9)
4	4.8 \pm 0.14 (28)	11.4 \pm 0.52 (28)	25.5 \pm 1.19 (24)	43.8 \pm 2.42 (20)
5	4.9 \pm 0.12 (10)	11.3 \pm 0.58 (10)	25.9 \pm 1.14 (10)	44.2 \pm 1.96 (5)
F^a	2.95	2.23	1.86	0.35

^a All F -values are nonsignificant.

post-hatching (Table 4). None of the F -values was significant, indicating that the mating status of the female did not influence mass gain in nestlings.

Finally, I compared the mass of nestlings when they left the nest for all years combined between the two groups of females. Again, there were no differences in fledging mass of young of monogamously and polygynously mated females (Table 5; $t = 0.63$, not significant).

DISCUSSION

The nesting success of female Eastern Meadowlarks mated with polygynous males was significantly higher than that of females mated with monogamous males. This higher success rate was not due to a difference in clutch size (Table 1) or to differences in growth rates or mass at fledging (Tables 4 and 5). Young hatched in and fledged from significantly more nests of polygynously mated than of monogamously mated females, a result at variance with the predicted cost of polygyny to primary or secondary females. I could not easily distinguish primary and secondary females. There was no detectable temporal pattern to pairing of a polygynous male with one and then a second female, or of a temporal separation of nest initiation between two females in the territory of a polygynous male. Thus, comparisons of nesting success between primary and secondary females of po-

lygynous males were not made, and data from females mated polygynously were pooled.

The major source of mortality for eggs and nestlings in meadowlark nests was predation. Infertility and abandonment of eggs were negligible factors in the calculation of hatching success. Starvation rarely occurred and was not important in the calculation of fledging success. This is not surprising as food items and rates of food delivered to nests did not differ between nests of females mated monogamously and those mated polygynously (Knapton unpubl. data). Nests of single females suffered a higher rate of predation than did those of females mated polygynously. Eight habitat variables of vegetation structure and composition, two measures of arthropod abundance, and territory size did not differ between the territories of monogamous and polygynous males (Siderius 1984). Nests did not appear to differ in their degree of concealment (all nests were well hidden). Furthermore, when numbers of females were controlled, there was no consistent trend for nesting success among territories. This indicates that territory quality did not influence nesting success.

Older individuals generally experience higher reproductive success than younger ones (e.g. De Steven 1978, Harvey et al. 1979, Middleton 1979, Perrins and McCleery 1985), and one would predict that females should choose an older over a younger male, all else being equal (but see

TABLE 4. Nestling mass (g) of polygynously and monogamously mated Eastern Meadowlark females at 4 ages post-hatch.

	Age [$\bar{x} \pm SD (n)$]			
	0	3	6	9
Polygynous	4.9 \pm 0.15 (28)	11.3 \pm 0.57 (28)	26.1 \pm 1.14 (28)	43.8 \pm 2.29 (23)
Monogamous	4.8 \pm 0.16 (22)	11.5 \pm 0.55 (22)	25.7 \pm 1.10 (18)	44.2 \pm 2.39 (11)
F^a	1.29	1.56	1.39	0.22

^a All F -values are nonsignificant.

TABLE 5. Mass (g) of young Eastern Meadowlarks at fledging of polygynously and monogamously mated females.

	Fledging mass [$\bar{x} \pm SD (n)$]
Monogamous	59.6 \pm 5.3 (35)
Polygynous	58.7 \pm 7.8 (94)

Reid and Sealy 1986). In the Eastern Meadowlark there is some evidence to suggest that polygynous males are older males. Six meadowlarks that returned to the same territories in successive years changed from being monogamous males in early years to bigamous males in later years. A similar situation was found in Red-winged Blackbirds (*Agelaius phoeniceus*; Picman 1980, Yasukawa 1981) and perhaps in Pied Flycatchers (*Ficedula hypoleuca*; Jarvi et al. 1982). Only one returning meadowlark changed from polygyny to monogamy. He was polygynous for the first 3 years of the study, but was monogamous, and changed his territory, in the final year. The very low rate of return of banded females did not allow comparison of the breeding success of young vs. older females.

Females may prefer older males because such males provide better parental care and allow the female to fledge more young (Searcy 1982; but see Weatherhead 1984 for alternative explanations). In the Eastern Meadowlark better parental care does not include provisioning of food for the young, as starvation was rare and nestlings of monogamously and polygynously mated females grew at similar rates and fledged at similar masses. If females choose their mates, then the difference must lie in male behavior when the nest is approached or threatened by a predator. Presumably, a polygynous male behaves differently from a monogamous male in the presence of a predator.

Several hypotheses have been proposed to explain the evolution of polygyny (reviews in Mock 1983, Vehrencamp and Bradbury 1984). The predicted nesting success of monogamously and polygynously mated females differs among the hypotheses.

The *polygyny-threshold model* has been the subject of considerable debate (e.g. Emlen and Oring 1977, Weatherhead and Robertson 1979, Garson et al. 1981) since its development by Verner and Willson (1966) and Orians (1969). A major prediction is that breeding success of

secondary females will be as high as that of single females paired with monogamous males. In contrast, the *sexy-son hypothesis* (Weatherhead and Robertson 1979) and the *deception hypothesis* (Alatalo et al. 1981, 1982) predict lowered breeding success for the secondary females compared with primary or single females. None of these hypotheses is adequate to explain the results I obtained, specifically, that female Eastern Meadowlarks paired with polygynous males enjoyed a higher rate of breeding success than did those paired with monogamous males. In addition, no polyterritoriality was found, and polygyny did not occur as a result of female site tenacity and random female dispersion (Wootton et al. 1986) or female site attachment and differences in arrival dates of adults and yearlings (Eliason 1986); female return rates were very low and territories were established before female arrival. Furthermore, there did not appear to be cooperation between the two females on a polygynous male's territory in detecting predators. My results suggest that females probably choose to pair with an already-mated male, and that such males are older males that provide better parental care when the eggs or nestlings, or both, face high risks of predation.

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