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FEEDING OF SECONDARY NESTLINGS BY POLYGYNOUS MALE BOBOLINKS IN OREGON

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The manner by which individuals allocate their reproductive efforts to maximize fitness has recently attracted much attention in studies of animal behavior (Trivers 1972, Pianka and Parker 1975, Dawkins 1976, Stearns 1976, Wittenberger 1979). One important aspect of reproductive effort in birds is parental care of nestlings. The parental behavior of monogamous birds involves optimizing brood size, maximizing food delivery rates and enhancing protection from adverse weather, brood parasitism, or predation. In polygynous species males also have opportunities for distributing parental care among several concurrent sets of offspring, perhaps optimizing the distribution of their care among broods.

Bobolinks (*Dolichonyx oryzivorus*) are single-brooded polygynous birds that breed in a broad range of grassland habitats. In Wisconsin polygynous males feed their primary nestlings (i.e., those of their first mates) almost exclusively (Martin 1971, 1974). Only rarely do they deliver food items to secondary nestlings (i.e., those of their second mates). I report here that polygynous male Bobolinks in Oregon regularly provision both primary and secondary nestlings, and I examine some of the conditions associated with this behavior.

Polygynous males should theoretically deliver each load of food to the brood in which it will produce the largest incremental gain in male fitness. Since older nestlings have higher reproductive value, males should deliver most food items to primary nestlings, unless other factors have overriding importance (Willson 1966). One potentially overriding factor is the relative nutritional condition of primary and secondary broods. If primary nestlings are relatively satiated with food while secondary nestlings are undernourished, males might gain more by delivering the food to their secondary nestlings. Factors affecting the nutritional condition of primary and secondary nestlings would then be important in determining how polygynous males distribute food among their broods. Such factors may include brood size, weather conditions and food availability, all of which will be evaluated here.

STUDY AREA AND POPULATION

My study comprised 27.3 ha of mesic meadow 2 km NW of P-Ranch Patrol Station on Malheur National Wildlife Refuge, 100 km S of Burns, Oregon. The study site was situated in the area occupied by the earliest males and females to arrive on the refuge each spring (1973–1976), and it supported the highest breeding densities of both males and females on the refuge (Wittenberger 1976, 1978).

The habitat consisted of grassy meadows intermixed with conspicuous patches of sedge (*Carex* spp.) that grow in poorly drained places. Predominant forb species were dandelion (*Taraxacum officinale*), cinquefoil (*Potentilla glomerata*), yarrow (*Achillea millefolium*), thistle (*Cirsium arvense*), dock (*Rumex crispus*) in the wetter areas, cow parsnip (*Heracleum lanatum*), red clover (*Trifolium pratense*) and vetch (*Vicia americana*).

The study area was irrigated with a consistent water supply from March or April until late June each year, resulting in flooding of peripheral areas adjacent to where Bobolinks bred. It was also grazed by cattle in autumn and winter, though not while Bobolinks were present, and mowed for hay in late summer.

The Bobolink population at Malheur Refuge is an isolated one consisting of from 90–150 adults of each sex, depending on the year. From 20–27 males bred each year on my study area, of which 6–17 were polygynous. Only 2 males ever attracted 3 mates, both in 1975. Breeding is highly synchronous. Females selected mates from about 20 May to 10 June, and nests contained nestlings from about 11 June to 7 July. Additional details of Bobolink breeding biology on the refuge are presented elsewhere (Wittenberger 1978).

METHODS

Individual males and females were identified by both colored plastic leg bands and by unique plumage characteristics. All males and about half of all females discussed here were banded. In 1973 males were also marked on their scapulars with green or red Esterbrook Flo-Master ink to facilitate individual recognition from a distance.

Territories were mapped by flushing territorial males and recording at least 20 points where they landed (see Wiens 1969). Pair bonds were ascertained from prolonged association of a female with a particular male and, when possible, by the occurrence of copulations. Polygynous pairings were verified by simultaneous observation of all mates on a territory and by locating nests.

Nests were found by watching females return to them at dusk, by watching females carrying nest materials and by accidentally flushing females from them. Nest contents were monitored daily at mid-day. Nestlings in each nest were weighed collectively with a triple-beam balance to the nearest 0.1 g. Nestlings were assumed to have died of exposure when found dead with rain-soaked bodies and full stomachs. They were assumed to have starved when found with empty stomachs or when they disappeared singly during mild weather (known predators took entire broods). Predation was inferred from losses of entire broods and from signs of disturbance around the nest.

Observations of parental behavior were made with binoculars from blinds mounted on 2 stationary 2-m tall towers, from a small portable blind and from the top of a step-ladder placed 75–125 m from the nearest nest under observation. Food items fed to nestlings were identified with 10× binoculars from a blind placed about 5 m from the nest.

Food abundance was sampled in 1975 and 1976 with a 38-cm diameter sweep net. In both years 2 samples of 50 sweeps were taken daily on each of 14 contiguous territories in the area where most polygynous matings occurred (1 sample was taken at random on each half of each territory). Caterpillar biomass was calculated by regression analysis after measuring specimen lengths, drying specimens of each length until no further weight reductions could be obtained and weighing specimens to the nearest 0.1 mg (see Wittenberger 1976).

RESULTS

Male feeding of secondary nestlings.—All polygynous males fed secondary nestlings in 1973, 1974 and 1975, but only 1 of 5 did in 1976. They began feeding secondary nestlings when their primary nestlings reached

TABLE 1
AGE OF PRIMARY AND SECONDARY YOUNG OF POLYGYNOUS MALES AT THE TIME THEY BEGAN FEEDING SECONDARY NESTLINGS[1]

Year	No. of polygynous males	No. of males that fed secondary young	Age of primary young (range)	Age of secondary young (range)
1973	4	4	10[2]	4–6
1974	4	4	7[2]	1–4
1975	5	5	12–13	7–10
1976	5	1	15	8

[1] Data include all territories on which both nests were found; in 1975 and 1976 many polygnous males were not included because either their primary or their secondary nest was destroyed by flooding, or predators at an early stage.

[2] Age of primary nestlings was the same for every male.

a specific age that differed each year (Table 1). No relationship between age of secondary nestlings and the beginning of male assistance at secondary nests was evident.

Polygynous males continued to feed nestlings and fledglings from their primary nests after beginning to feed secondary nestlings. I did not examine this behavior closely in 1973, but 1 indication that males continued feeding primary fledglings that year was the discovery of a 13-day-old banded fledgling in 1 male's secondary nest. That fledgling had been reared in the male's primary nest about 23 m away. In 1974 and 1975 every male continued feeding primary fledglings while feeding secondary nestlings. In 1975 I determined that 4 of 5 males were feeding only 1 primary fledgling at the time they began feeding their secondary nestlings. I did not ascertain how many were being fed by the remaining male. The primary fledglings fed by each male were not being fed by the corresponding primary female. Bobolinks divide their broods a few days after fledging, with each parent exclusively feeding about half the brood (Martin 1971, pers. obs.).

Nutritional condition of nestlings.—One indication of a nestling's nutritional condition is its weight at a standard age. The mean weight of 10-day-old primary nestlings just prior to forced fledging was similar in 1973 and 1974, but was significantly lower ($P < 0.05$) in 1975 and 1976 (Table 2). The fledging weights of all nestlings belonging to both monogamous and polygynous males were used for this analysis because they did not differ significantly as a function of male mated status. The data for 1975 were analyzed separately for early and late nests because young that hatched more than 5 days before a storm of 13–25 June ended, fledged at significantly lower weights. The primary nestlings of all polygynous males studied that year were hatched in early nests.

TABLE 2

MEAN NESTLING WEIGHTS ± SD (G) JUST PRIOR TO FLEDGING ON DAY 10 POST-HATCHING[1]

Year	Primary nests[2]	Secondary nests[2]
1973	23.5 ± 2.3 (5)^{a}	24.2 ± 1.9 (4)^{a}
1974	24.0 ± 1.5 (17)^{a}	22.8 ± 2.2 (3)
1975 (early)[3]	20.0 ± 1.4 (6)^{b}	—
1975 (late)[3]	23.3 ± 0.8 (7)^{a}	19.4 ± 2.1 (4)^{b}
1976	20.7 ± 2.2 (9)^{b}	22.2 ± 0.1 (2)

[1] Significant differences between years are indicated by superscripts for each status of nests, with a > b (Student's *t*-test, $P < 0.05$). Number of nests is given in parentheses.

[2] Standard deviation indicates variability between broods, not nestlings.

[3] Early nests hatched more than 5 days before a rainstorm of 13–25 June ended; late nests hatched fewer than 5 days before a rainstorm of 13–25 June ended.

Males delivered as much food as females to older secondary nestlings in 1973 and 1974, and this probably accounts for the high fledging weights of secondary nestlings in those years. The low fledging weights of secondary nestlings in 1975 reflect the lateness that males began feeding them. In 1976 brood reductions caused smaller brood sizes in secondary nests, and this probably allowed secondary females to deliver as much food per nestling as the male and female combined could deliver to primary nests.

A second indication of a nestling's nutritional condition is the strength of its gaping response. Both primary and secondary nestlings nearly always displayed very strong gaping respones in 1975 and 1976, but they rarely did so in 1973 or 1974. In the former 2 years nestlings always extended their necks to the fullest extent possible and gaped vigorously whenever I visited the nest (except in the late nests in 1975). In 1973 and 1974

TABLE 3

NESTLING MORTALITY RATES FOR POLYGNOUS AND MONOGAMOUS MALE BOBOLINKS

	Primary nests of polygynous males			Secondary nests of polygynous males			Nests of monogamous males		
		% mortality			% mortality			% mortality	
Year	No. nestlings (and nests)	All causes	Starved	No. nestlings (and nests)	All causes	Starved	No. nestlings (and nests)	All causes	Starved
1973	25 (5)	0.0	0.0	26 (5)	7.7	7.7	67 (14)	9.0	0.0
1974	39 (8)	2.6	0.0	23 (5)	34.8	8.7	66 (12)	10.6	3.0
1975	59 (11)	50.8	1.7	61 (13)	55.7	29.5	47 (9)	65.7	2.1
1976	60 (11)	45.0	5.0	49 (12)	73.3	32.7	23 (4)	56.5	39.2

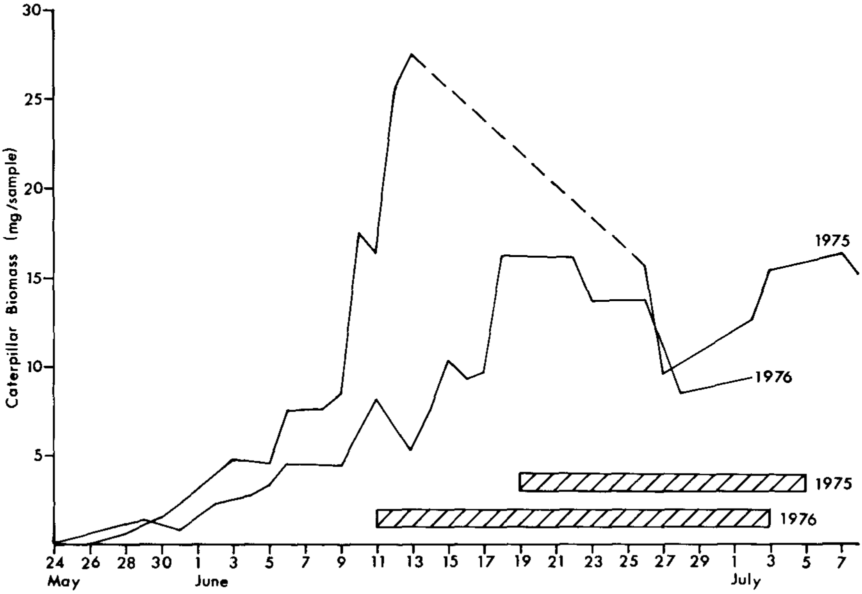

FIG. 1. Relative abundance of caterpillars on the study area during 1975 and 1976. Diagonally-hatched bars indicate the period when primary nests contained young each year. The dashed line from 13–25 June 1975 spans a period of continuous rainstorms when samples could not be taken.

nestlings never extended their necks fully, and they exhibited little or no gaping response when I visited the nest.

Few primary nestlings of polygynous males starved in any year of the study, but significantly more nestlings of nearby monogamous males starved in 1976 than in 1973–1975 (Table 3). The territories of monogamous males were often adjacent to those of polygynous males, but many were in wetter areas, 100–400 m from the mesic meadows occupied by polygynous males (Wittenberger 1976). Starvation rates were markedly higher among secondary nestlings in 1975 and 1976 than in 1973 or 1974, possibly because males provided them with less food in the former 2 years.

Food availability.—The preferred food items fed to nestling Bobolinks are lepidopteran and sawfly (Tentridididae [Hymenoptera]) caterpillars (Wiens 1969, Martin 1971, Wittenberger 1978). The diet of nestlings on my study area consisted of 65.6% caterpillars in 1974 (N = 2318), 59.0% in 1975 (N = 2064) and 54.2% in 1976 (N = 2818). I did not record the types of food items delivered to nestlings in 1973. The proportion of caterpillars in the nestling diet was significantly different every year (χ^2 =

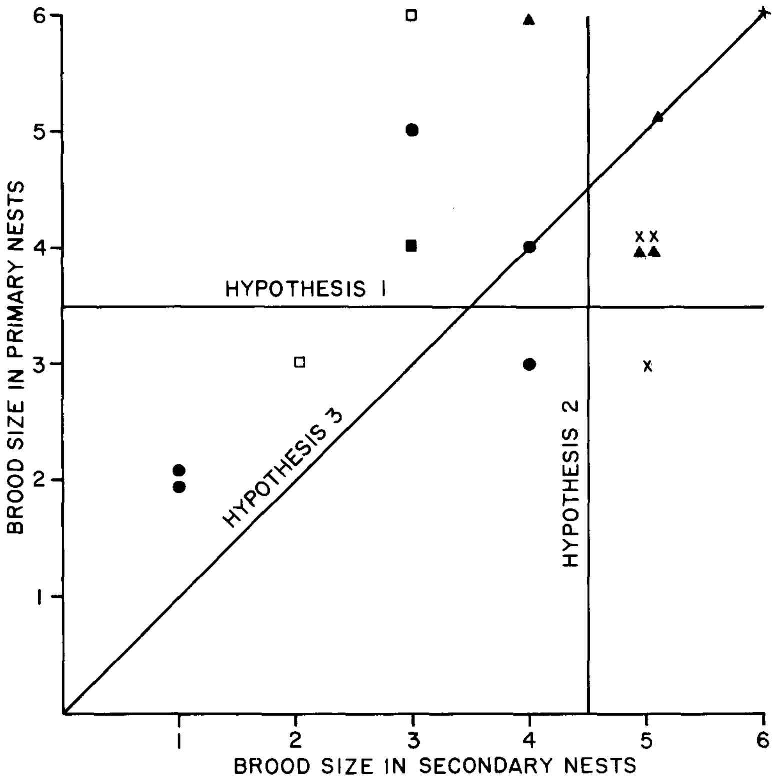

FIG. 2. A test of 3 hypotheses relating brood size to the propensity for males to feed secondary nestlings (see text). An hypothesis is supported if all points fall to the right or below the line representing it. X = 1973, ▲ = 1974, ● = 1975, ■ = 1976. □ = instances when males did not feed their secondary nestlings at all. In cases where males began feeding secondary nestlings after their primary nestlings had fledged, brood size for the primary nest was assumed equal to the number of young that had successfully fledged because fledgling mortality could not be monitored.

68.9, df = 2, $P < 0.001$), suggesting that caterpillars were less available relative to alternative food resources in the latter 2 years.

Caterpillar densities were sampled with a sweep net only in 1975 and 1976. A quadrat sampling method used in 1974 proved unsatisfactory, and caterpillars were not sampled in 1973.

In 1975 caterpillar densities increased exponentially, until shortly before nestlings hatched, and then declined markedly during the continuous heavy rains and cold weather of 13–25 June (Fig. 1). Caterpillar densities increased again after the storm ended, but they never reached the level

TABLE 4

RATE THAT POLYGYNOUS MALES FED THEIR SECONDARY NESTLINGS AS A FUNCTION OF BROOD SIZE IN THEIR PRIMARY NESTS[1]

Brood size in primary nest	No. males	H of observation	Mean brood size in secondary nest	Mean age of secondary broods	Trips/h to secondary nest[2]
4	3	16	4.96	6.7	5.49
5	2	22	5.00	2.5	1.92
6	2	20	4.50	6.0	0.40

[1] Data based on first 2 days that males fed seondary nestlings (only data from 1973 and 1974 were used).
[2] Trips/h differ significantly at $P < 0.001$ between all sizes of primary broods (Student's t-test).

prior to the storm. In 1976 caterpillar densities were even lower than in 1975, despite fair weather throughout June and July.

Brood size in primary and secondary nests.—The impact of male food deliveries on nestling survival should be a function of brood size. Females should be better able to feed small broods without male assistance, other factors being equal, so small broods in the primary nest or large broods in the secondary nest should increase the propensity for polygynous males to feed secondary nestlings.

I examined 3 hypotheses relating brood size to the occurrence of male feeding of secondary nestlings: (1) males begin feeding secondary nestlings when brood size in the primary nest drops below a specific level; (2) males begin feeding secondary nestlings when brood size in the secondary nest exceeds a certain level and (3) males begin feeding secondary nestlings when brood size in the secondary nest exceeds that in the primary nest. I chose as my threshold levels a brood size of 4 primary nestlings for hypothesis 1 and a brood size of 4 secondary nestlings for hypothesis 2, but any other level can be evaluated with the same data.

I tested the 3 hypotheses by plotting the brood size present in each male's primary nest at the time he began feeding secondary nestlings against brood size in the same male's secondary nest at that time (Fig. 2). The results do not fit any of the 3 hypotheses, regardless of which specific brood size or combination of brood sizes is postulated as the threshold stimulus.

Although brood sizes in a male's primary and secondary nests evidently do not determine whether a male will feed secondary nestlings, they may affect the amount of effort he invests in each brood. Data taken during the first 2 days of male assistance at secondary nests indicate that the amount of care allocated to secondary nestlings is inversely related to brood size in the corresponding primary nest (Table 4). Sample sizes were

TABLE 5
MORTALITY OF NESTLINGS CAUSED BY PREDATION AND FLOODING CONVERTED TO A DAILY RATE

	1973	1974	1975	1976
Primary nests				
Number of nestlings	92	97	106	83
Predation	0	4	5	16
Adverse weather	2	3	53	12
Total due to environmental hazards	2	7	58	28
No. of nestling-days	794	947	685	649
Risk of mortality/day	0.003	0.007	0.085	0.043
Secondary nests				
Number of nestlings	26	23	61	49
Predation	0	0	0	17
Adverse weather	0	7	16	3
Total due to environmental hazards	0	7	16	20
No. of nestling-days	243	178	398	290
Risk of mortality/day	0.000	0.039	0.040	0.069

not sufficient to control for nestling age or other factors and the data are based on relatively few males, but these variables are unlikely to explain the large differences observed. The data for males with primary broods of 5 young were based on younger secondary nestlings, but males fed 7–8 day old primary nestlings only 30% faster than 2–3 day old primary nestlings ($N = 248$ nest-h of observations), suggesting that age alone is not responsible for the observed difference.

Relative reproductive value of primary and secondary nestlings.—The reproductive value of secondary nestlings decreases relative to that of primary nestlings when hatching interval between primary and secondary nests increases or when nestling mortality caused by predation or flooding increases. The mean interval between hatching of primary and secondary nestlings of polygynous males was 6.0 days in 1973 ($N = 5$, range = 4–9), 4.4 days in 1974 ($N = 5$, range = 3–6), 3.8 days in 1975 ($N = 10$, range = 2–5) and 7.2 days in 1976 ($N = 5$, range = 3–9). The interval averaged significantly longer in 1973 and 1976 than in 1975 (Student's t-test, $P < 0.05$).

Mortality of secondary nestlings caused by predation and flooding was low in 1973, intermediate in 1974 and 1975 and high in 1976 (Table 5). Mortality risk per nestling-day was calculated by dividing the number of nestling-days monitored each year into total mortality. The risk per day was higher for secondary than for primary nestlings in 1974 and 1976, lower in 1975 when many primary nestlings hatched during heavy rainstorms and similar in 1973. Much of the predation in 1976 was by a single pair of Sandhill Cranes (*Grus canadensis*) that fed regularly on the study area that year. (In the previous 3 years cranes were absent from my study area.)

An index of relative reproductive value of secondary nestlings was calculated as R × I, where R = mortality risk/day and I = mean hatching interval between primary and secondary nests. The index represents the cumulative probability that the secondary nest will fail due to predation or flooding before it reaches the stage already reached by the primary nest. The higher the index value, the lower is the relative reproductive value of secondary nestlings that year. The index values are 0.00 for 1973, 0.17 for 1974, 0.15 for 1975 and 0.50 for 1976.

DISCUSSION

The results show that males adjust the distribution of their parental allocations according to prevailing conditions. Polygynous males began feeding secondary nestlings when their primary nestlings reached a specific, but different, age each year, suggesting that the nutritional condition of primary nestlings is important in determining how polygynous males distribute their parental investments. Additional evidence supports the same conclusion. Primary nestlings fledged at significantly heavier weights and exhibited noticeably weaker gaping responses in the 2 years (1973, 1974) when polygynous males began feeding secondary nestlings earliest, and nestling starvation was highest in the year (1976) when most polygynous males did not feed secondary nestlings at all.

The behavior of polygynous males just prior to feeding secondary nestlings shows that males could be responding directly to the condition of primary nestlings. Before delivering food at their secondary nests, polygynous males almost invariably landed first near their primary nests and cocked their heads downward, apparently listening for the high-pitched squeaks given by hungry nestlings. Then they usually flew to their secondary nests and fed the nestlings there, although sometimes they dropped down and fed their primary nestlings instead. Occasionally males showed similar behavior before going off to forage, first perching near the primary nest and then perching near the secondary nest, cocking their heads each time. Upon returning with food, they usually repeated the sequence before finally feeding their secondary nestlings. In 1 extreme instance a male flew back and forth between his primary and secondary nest 4 times, landing and cocking his head each time, before finally feeding his secondary nestlings.

The annual variations in nestling condition may have resulted from annual variations in food availability and weather conditions. The poor condition of primary nestlings in 1975 was associated with cold rainy weather during mid-June, which reduced caterpillar abundance and probably also increased the maintenance energy requirements of nestlings. In 1976 caterpillars were even less abundant than 1975, and again nestlings were undernourished (despite fair weather).

Brood size per se in the primary and secondary nest does not act as a proximate stimulus for evoking the onset of male parental care at secondary nests, but brood size in the primary nest does appear important in determining how much food males deliver to secondary nestlings. Patterson, Erckmann and Orians (in press) found that polygynous male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) shift their parental care to secondary nests following experimental reduction of primary broods, but this response appears to differ from that of male Bobolinks. Only 1 of 7 male Bobolinks on my study area abandoned his primary nest entirely following natural brood reductions, and none did so in Martin's (1971) study area. That male abandoned his 7-day-old primary nestlings after 4 of 6 had died. His secondary nest contained six 5-day-old nestlings when he began feeding them exclusively. None of his primary nestlings fledged, but 5 of his secondary nestlings did.

The relative reproductive value of secondary nestlings may affect whether males deliver food at secondary nests, since it was lowest in the 1 year when males failed to feed secondary nestlings. However, the earliness that males began feeding secondary nestlings in the other nests was not correlated with their relative reproductive value. Secondary nestlings had the highest reproductive value in 1973, but polygynous males began feeding them later than in 1974. They had similar reproductive value in 1974 and 1975, but polygynous males began feeding them substantially later in 1975 than in 1974. Also, in order to adjust their parental allocations to the relative reproductive value of secondary nestlings, males would have to detect annual changes in the likelihood that their nests will be destroyed by predators or adverse weather. Since both predation pressure and weather conditions are often unpredictable, there may not be any cues that males could use to detect such changes.

SUMMARY

Polygynous male Bobolinks in Oregon helped feed secondary nestlings (i.e., those of their second mates) in 3 of 4 years studied. This behavior differed from that of male Bobolinks in Wisconsin, which rarely feed secondary nestlings (Martin 1971, 1974). In Oregon, males began feeding secondary nestlings when their primary nestlings reached a specific age that varied between years, regardless of brood size in either of their nests. However, the number of trips made by males to their secondary nests was correlated with brood size in their primary nests. Males began feeding secondary nestlings later, or not at all, in years when

primary nestlings were in poorer nutritional condition. Their poorer condition in those years was associated with reduced food availability. The relative reproductive value of secondary nestlings was lower in the 1 year when polygynous males did not feed them, but it was not correlated with the earliness that males began feeding them in the other 3 years.

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