

## NESTLING HUNGER AND PARENTAL CARE IN RED-WINGED BLACKBIRDS

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**ABSTRACT.**—We examined the influence of nestling hunger and the settlement of additional mates on the parental behavior of polygynous male Red-winged Blackbirds (*Agelaius phoeniceus*). When brood size and nestling age were held constant, the begging behavior of food-deprived nestlings caused most males to begin provisioning nestlings. Males were not influenced by the presence of additional females settling on the territory. Males that did not respond to nestling hunger had a fertile female mate. In response to satiated nestlings, males stopped provisioning. These results suggest that polygynous male Red-winged Blackbirds may be withholding parental care at one nest in order to protect paternity at another nest. Females increased provisioning to food-deprived nestlings and reduced provisioning to satiated nestlings. Changes in female provisioning rate were associated with changes in foraging habitat and volume of prey delivered to nestlings. Received 2 October 1991, accepted 16 July 1992.

THE REPRODUCTIVE effort parents allocate to provisioning nestlings has been interpreted as balancing the parents' physical condition, food abundance, and clutch or brood size to maximize the number of offspring that will survive and reproduce (Royama 1966, Drent and Daan 1980, Nur 1984, Winkler 1987). Since offspring survival may depend on offspring condition (e.g. Magrath 1991), parental provisioning rate is expected to be adjusted to the condition or nutritional status of the nestlings during their development (Ricklefs et al. 1985, Hussell 1988). Nestlings can effectively communicate their nutritional requirements to parents by begging (Rydén and Bengtsson 1980, Smith and Montgomerie 1991), and nestlings deprived of food experimentally consistently beg louder, more frequently and more vigorously (Henderson 1975, Bengtsson and Rydén 1983, Smith and Montgomerie 1991). Conversely, nestlings satiated through artificial feeding reduce begging (Bengtsson and Rydén 1983). In response to increased begging, parents provision nestlings more frequently, whereas parents reduce provisioning to satiated nestlings (Bengtsson and Rydén 1983).

Research on the influence of nestling begging on parental behavior has focussed on monogamous species where both sexes provision

offspring (Henderson 1975, Muller and Smith 1978, Bengtsson and Rydén 1983, Harris 1983, Gottlander 1987, Lifjeld 1988, Stamps et al. 1989, Smith and Montgomerie 1991). However, nestling begging may not have a similar effect on the behavior of polygynous males. When breeding is asynchronous, the reproductive effort of a polygynous male may be divided between mating effort and parental effort (Trivers 1972). Polygynous males may be able to enhance their reproductive success relatively more by attracting and courting additional mates than by feeding hungry nestlings. Therefore, polygynous species provide an opportunity to investigate the relative influence of nestling hunger and the attraction of additional mates on male parental behavior.

Male Red-winged Blackbirds (*Agelaius phoeniceus*) are polygynous and females settle asynchronously (Allen 1914, Nero 1956, Orians 1980). Males as well as females provision nestlings at some nests, but at other nests, only females feed nestlings (Yasukawa and Searcy 1982, Muldal et al. 1986, Whittingham 1989, Yasukawa et al. 1990, Patterson 1991). Nestling provisioning by polygynous male Red-winged Blackbirds is strongly influenced by brood size and nestling age (Whittingham 1989, Yasukawa et al. 1990). However, it is not known whether male parental care is influenced by nestling hunger. Similarly, it is not known whether male parental care is influenced by the presence of fertile or settling females on the territory. In this paper, we present the results of two experiments de-

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signed to examine the influence of nestling hunger and female availability on male parental behavior.

In the first experiment, nestlings were deprived of food at nests where the male had not previously provisioned nestlings. We predicted that males would begin provisioning food-deprived nestlings if male parental behavior was influenced by nestling hunger level. If mate attraction activities had an overriding influence on male behavior, then we predicted that males would not provision food-deprived nestlings when a new mate was settling on the territory. In the second experiment, nestlings were fed by hand until satiated at nests where the male was currently provisioning nestlings. We predicted males would terminate provisioning satiated nestlings if male parental behavior was influenced by nestling hunger level.

#### METHODS

We studied the effect of nestling hunger on parental behavior in Red-winged Blackbirds in central Alberta, 60 km east of Edmonton (53°38'N, 112°63'W). These experiments were conducted in 1990 on a population breeding in a 45-ha open-water marsh ringed by cattails (*Typha latifolia*) and surrounded by aspen (*Populus* spp.) woodland. The cattail ring averaged 15 m wide, and Red-winged Blackbird territories were arranged linearly around the edge of the marsh. Breeding males and females were captured with mist nets or a house trap baited with sunflower seeds and millet. We banded 23 of 38 males and 9 of 38 females with unique combinations of colored leg bands.

Each experimental and control nest was associated with a different territorial male. Therefore, samples were independent. For both the food-deprivation experiment and satiation experiment, brood size and nestling age were held constant. Each experimental and control nest had four nestlings that were six days old. The food-deprivation experiment involved males that had not previously provisioned nestlings at the experimental nest or at any other nest on their territory. The three largest of four nestlings were removed from the experimental nest and placed in an incubator for 2 h. The incubator consisted of a hot water bottle inside an 18 × 25 cm insulated cooler. Following 2 h of food deprivation, nestlings were returned to the nest. The satiation experiment was conducted at nests where the male was currently provisioning nestlings. Males only fed nestlings at one nest on their territory at a given time. All four nestlings in each experimental nest were fed mealworms until they refused additional food and ceased begging when the nest was jostled (simulating arrival of the parent with food). We refer to this condition as nest-

ling satiation. Satiation usually occurred after each nestling received approximately four to six large mealworms. All nests in the nestling satiation experiment were primary (first) nests on the territory; however, the status of nests in the food-deprivation experiment was variable (discussed below).

We observed the behavior of adult male and female Red-winged Blackbirds at each experimental nest for one 60-min period before the experimental manipulation and for one 60-min period following the manipulation. Following the return of young to the nest (food-deprivation experiment) or the artificial satiation of nestlings, we allowed a 10-min period for parents to recover from the disturbance before we initiated the second 60-min observation period. Provisioning rate was recorded as the number of deliveries per hour by each parent to each brood (prey were usually visible in parent's bill). The time that adults spent foraging was recorded using a stopwatch.

A control nest was paired with each experimental nest for date of hatching to reduce seasonal effects (maximum difference between experimental and control nests was two days). Control nests for the food-deprivation experiment were disturbed between the first (before) and second (after) observation sessions. Three of four nestlings were removed, taken away from the nest for approximately 10 min and then replaced in the nest. Thus, these control nests were disturbed on two occasions, when nestlings were removed and then later when nestlings were replaced, similar to experimental nests. Control nests for the satiation experiment also were disturbed between the first (before) and second (after) observation sessions. These nests were approached and the observer remained in the vicinity of the nest for 5 min disrupting parental behavior. All experimental and control manipulations were conducted between 0600 and 0700 EST. All observations were made from a canoe anchored in the open-water area of the marsh 20 to 30 m from the nest. Food-deprivation experiments may have caused some temporary discomfort to nestlings. Therefore, we used the minimum number of nests necessary to establish a pattern in the results. Nestlings in experimental and control nests fledged with similar body mass, and no nestling deaths occurred due to the experimental procedures.

We used four periods to describe the breeding stage of additional females on the territory at the time the experiment was conducted at the focal nest on that territory. The settling period was defined as 20 days prior to laying until 4 days before the first egg was laid. This period includes the time when males attracted their eventual mates and females chose a breeding site. The fertile period was defined as four days before the first egg through the day of the last egg (see Birkhead 1988). The nestling period was hatching through 10 days of age. The fledgling period was from the day most offspring left the nest (day 10) until they left the marsh.

We examined the effect of changes in provisioning rate on parents' choice of foraging habitat (marsh or woods), type of prey, and prey-load volume brought to nestlings. Foraging habitat was recorded for each feeding visit made by parents to both food-deprived and satiated broods. Since prey samples could not be obtained without disrupting parental behavior, we collected food samples from nests that were not part of the experiments, but were similar in habitat and time of season. To obtain food samples, six-day-old nestlings were fitted with pipe-cleaner neck collars (Willson 1966), which prevented them from swallowing food but permitted normal respiration. Food brought by parents was collected immediately after each feeding and neck collars were removed after 60 min. Food samples were collected for only one 60-min period per brood. The length and width (excluding wings) of each food item was measured to the nearest 0.01 mm. Prey-load volume was estimated (i.e.  $\pi r^2 l$ , where  $r$  is the estimated radius and  $l$  the length of the food bolus) as an index of the food volume received by nestlings. Means are presented with their standard errors, and significance was designated at the 0.05 probability level.

## RESULTS

Nestling Red-winged Blackbirds that were deprived of food begged almost continuously while satiated nestlings ceased begging (see also Bengtsson and Rydén 1983). Under nonexperimental conditions, nestlings began begging when the nest was jostled lightly by investigators or when a parent arrived at the nest with food (see also Tinbergen 1973). Early in the food-deprivation period nestlings began to beg when the incubator was jostled. However, later in the food-deprivation period, nestlings begged almost constantly without stimulation. Furthermore, food-deprived nestlings could be heard begging throughout the first 30 min of the second observation period. Satiated nestlings did not beg when the nest was jostled following supplemental feeding. Satiated nestlings were not heard begging when the female approached the nest with prey during the observation session following supplemental feeding.

*Food-deprivation experiment.*—In general, male Red-winged Blackbirds responded to the hunger level of food-deprived nestlings (Table 1). Nine of 11 (82%) males that were not previously provisioning young began feeding nestlings that had been deprived of food ( $P = 0.03$ , binomial test). When both responding and nonresponding experimental males were considered ( $n = 11$ ), the average provisioning rate was  $3.2 \pm 0.5$  deliveries/h (Table 1). The nine males that re-

sponded to nestling hunger made  $4.0 \pm 0.7$  deliveries/h. None of the 11 control males provisioned nestlings before or after nest disturbance. Female parents also responded to increased nestling hunger. The female provisioning rate increased significantly following the period of food deprivation at experimental nests (Table 1).

The two males that did not initiate nestling provisioning in response to increased nestling hunger were apparently not influenced by nest status or by the time of the breeding season in which the experiment was conducted. Of the 11 experimental nests, 5 were the primary nest on the territory, 3 were secondary, 2 were tertiary, and 1 was quaternary. For the two nonresponding males, one nest was primary and one nest was secondary on their territories. The hatch date for the 11 experimental nests ranged evenly from 8 June to 3 July. The hatch dates for the two nests of nonresponding males were 12 June and 24 June.

The presence of fertile females on the territory differed between males that did and did not respond to nestling begging in the food-deprivation experiment. Both of the nonresponding males had a fertile female on their territory at the time of the experiment. In contrast, none of the responding males had a fertile female on their territories ( $X^2$  with continuity correction = 5.3,  $P = 0.02$ ).

The presence of settling females, nestlings or fledglings on the territory did not influence male response to food-deprived nestlings. Four of the nine responding males had one or two females settling on their territories, while neither of the two nonresponding males had females settling on their territory. Over 30 females settled on territories later in the season following the food-deprivation experiment. This suggests that unmated females were available throughout the experiments, and all males in the food-deprivation experiment had the opportunity to attract additional females. Four responding and one nonresponding male had at least one other nest with nestlings on their territory. Three responding males, but neither of the two nonresponding males, had fledglings present on their territory. In summary, the only factor consistently associated with nonresponding males in the experiment was the presence of a fertile female on the territory.

The change in parental behavior of experimental males and females was associated with changes in time spent foraging and foraging

TABLE 1. Male and female behavior during food-deprivation experiment. Behaviors ( $\bar{x} \pm SE$ ) compared before and after treatment within nests for experimental or control groups, and between experimental and control groups before or after treatment.  $n$  = number of males and nests.

Variable	Experimental ( $n = 11$ )			Control ( $n = 11$ )			Experimental vs. control	
	Before	After	$P^a$	Before	After	$P^a$	Before	After
<b>Males</b>								
Provisioning rate (deliveries/h)	0.00 $\pm$ 0.00	3.2 $\pm$ 0.5	0.003	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	1.000	1.000	0.0001
Foraging (min/h)	21.2 $\pm$ 3.0	33.4 $\pm$ 5.4	0.01	18.9 $\pm$ 3.3	17.9 $\pm$ 1.7	0.534	0.870	0.009
<b>Females</b>								
Provisioning rate (deliveries/h)	11.7 $\pm$ 0.8	18.1 $\pm$ 1.1	0.007	11.9 $\pm$ 1.0	11.9 $\pm$ 0.7	0.944	0.837	0.0008
Foraging (min/h)	51.7 $\pm$ 2.0	56.1 $\pm$ 1.5	0.02	51.9 $\pm$ 1.5	51.6 $\pm$ 1.2	1.000	0.724	0.0178
Percent food from woods <sup>c</sup>	51 $\pm$ 5	79 $\pm$ 5	0.01	46 $\pm$ 4	44 $\pm$ 3	0.735	0.289	0.0008

<sup>a</sup> Wilcoxon signed-rank test comparing behavior before and after treatment.  
<sup>b</sup> Mann-Whitney  $U$ -test comparing experimental versus control birds.  
<sup>c</sup> Percent food delivered from woods versus marsh.

location (Table 1). Increased provisioning rate was associated with increased time spent foraging and more food deliveries from the marsh.

**Satiation experiment.**—Male and female Red-winged Blackbirds responded to nestling satiation as predicted. All eight experimental males stopped provisioning nestlings after the nestlings had been satiated by supplemental feeding. Control males provisioned nestlings at a similar rate before and after nest disturbance (Table 2). None of the experimental or control males had a fertile female on the territory at the time of the experiment. Females also re-

duced their provisioning of satiated broods. The changes in parental behavior associated with nestling satiation did not affect time spent foraging for either sex. However, the reduced provisioning rate of females was associated with a greater proportion of food deliveries from the woods.

**Male provisioning rate.**—Prior to treatment, 16 males in the satiation experiment provisioned nestlings at an average of  $5.6 \pm 0.3$  deliveries/h. We assume this represents male provisioning rate under natural conditions. These males provisioned nestlings at a significantly higher rate

TABLE 2. Male and female behavior during satiation experiment. Behaviors ( $\bar{x} \pm SE$ ) compared before and after treatment within nests for experimental or control groups, and between experimental and control groups before or after treatment.  $n$  = number of males and nests.

Variable	Experimental ( $n = 8$ )			Control ( $n = 8$ )			Experimental vs. control	
	Before	After	$P^a$	Before	After	$P^a$	Before	After
<b>Males</b>								
Provisioning rate (deliveries/h)	5.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.025	5.5 $\pm$ 0.4	5.3 $\pm$ 0.3	0.414	0.867	0.0003
Foraging (min/h)	41.5 $\pm$ 3.1	36.0 $\pm$ 6.2	0.463	40.7 $\pm$ 2.7	44.5 $\pm$ 3.0	0.463	0.522	0.282
<b>Females</b>								
Provisioning rate (deliveries/h)	12.2 $\pm$ 0.5	10.3 $\pm$ 0.4	0.034	12.3 $\pm$ 1.1	12.7 $\pm$ 0.6	0.765	0.871	0.0126
Foraging (min/h)	55.0 $\pm$ 1.5	54.3 $\pm$ 0.5	0.500	54.3 $\pm$ 1.1	54.0 $\pm$ 1.1	0.763	0.749	0.631
Percent food from woods <sup>c</sup>	56 $\pm$ 6	28 $\pm$ 7	0.027	41 $\pm$ 3	46 $\pm$ 3	0.207	0.029	0.004

<sup>a</sup> Wilcoxon signed-rank test comparing behavior before and after treatment.  
<sup>b</sup> Mann-Whitney  $U$ -test comparing experimental versus control birds.  
<sup>c</sup> Percent food delivered from woods versus marsh.

than the nine experimental males that provisioned nestlings in the food-deprivation experiment ( $4.0 \pm 0.7$ ; Mann-Whitney  $U = 121$ ,  $P < 0.01$ ).

*Prey type and load volume.*—Red-winged Blackbird parents foraged in woodland and marsh habitats. Prey brought to nestlings from the woods were lepidopteran larvae or pupae, whereas prey from the marsh were mostly larvae or recently emerged adult odonates (94% Zygoptera, 4% Anisoptera). Lepidopterans were delivered as single prey, whereas one or more odonates were fed to nestlings at each delivery. The volume of food brought from the woods by males ( $701.5 \pm 147.2 \text{ mm}^3$ ,  $n = 3$  males) was significantly greater than the volume of a load brought from the marsh by males ( $48.2 \pm 10.7 \text{ mm}^3$ ,  $n = 3$ ;  $U = 9$ ,  $P < 0.05$ ). Similarly, the volume of food brought from the woods by females ( $706.6 \pm 114.1 \text{ mm}^3$ ,  $n = 13$ ) was significantly greater than the volume of a load brought from the marsh by females ( $327.8 \pm 125.5 \text{ mm}^3$ ,  $n = 12$ ;  $U = 122$ ,  $P < 0.02$ ).

#### DISCUSSION

*Factors influencing male parental care.*—The results of this study demonstrate that the extent of nestling hunger or satiation can cause polygynous males to initiate or terminate nestling provisioning. These results are consistent with the hypothesis that parents respond to nestling food demands as communicated by nestling begging behavior. We also expected the parental behavior of polygynous males to be influenced by the availability of other mates. However, we found no influence of settling females on male response to nestling hunger. The only apparent difference between males that responded and did not respond to food-deprived nestlings was that nonresponding males had fertile mates already settled on their territory. In contrast to the findings of Muldal et al. (1986), there apparently was no trade-off between the presence of a settling female and paternal care. Instead, our results suggest that polygynous male Red-winged Blackbirds may be withholding parental care at one nest in order to guard a mate and ensure paternity at another nest.

Time and energy invested in either mate guarding or parental care is expected to enhance male reproductive success. Red-winged Blackbird males appear to guard their mate by following her closely during her fertile period

(Westneat 1992), and mate guarding is assumed to be correlated positively with the number of genetically descendent offspring produced (e.g. Birkhead and Lessells 1988). Male parental care is expected to improve offspring survival. When male Red-winged Blackbirds provision nestlings, fledging success increases; however, females often can raise some of the brood unassisted (Muldal et al. 1986, Whittingham 1989, Yasukawa et al. 1990, Patterson 1991). Polygynous males may not be able to simultaneously provision nestlings and guard a mate. If there is a trade-off between these behaviors then mate guarding should be favored over parental care when the reduction in nestling survival due to uniparental care is more than compensated for by the number of genetically descendent offspring at the other nest. Clearly, the costs and benefits of these alternative behaviors need to be studied in more detail for polygynous species.

Red-winged Blackbird females increased their provisioning rate in response to the begging of food-deprived nestlings and reduced provisioning rates in response to satiated offspring. These results concur with those reported for similar experiments on monogamous species (Henderson 1975, Muller and Smith 1978, Bengtsson and Rydén 1983, Harris 1983, Hussell 1988, Smith and Montgomerie 1991). Similar to monogamous species, nestling begging intensity increased with hunger level and increased the probability that nestlings obtained food from both parents. Overall, nestling begging behavior acts as an efficient communication system that enables parents to adjust their provisioning rate to the needs of their young.

Although male Red-winged Blackbirds that were not previously provisioning young did feed experimentally food-deprived nestlings, they did so significantly less often than males that provisioned nestlings under natural conditions (before treatment in the satiation experiment). In addition to nestling hunger, other factors can influence male provisioning rates. Variation in brood size and nestling age also cause male Red-winged Blackbirds to initiate or cease provisioning nestlings (Whittingham 1989, Yasukawa et al. in press). In the food-deprivation experiment it is possible that males were responding to the sudden changes in brood size (from one to four young) immediately following the food-deprivation period rather than to a change in nestling hunger and begging be-

havior. However, in this experiment, males responded more quickly than males in a brood-size manipulation experiment. Male Red-winged Blackbirds averaged a one-day delay in their response to changes in brood size (Yasukawa et al. in press); whereas, males in our experiment began feeding food-deprived nestlings within 10 to 20 min of their return to the nest. Male response to hungry nestlings was temporary (2 to 3 h), but males responding to increased brood size continue to provision young into the fledging period (Whittingham unpubl. data). Furthermore, males in the satiation experiment stopped provisioning nestlings when their hunger level was reduced and there were no concurrent changes in brood size. We conclude that males in the food-deprivation and satiation experiments were responding to the hunger level of the nestlings.

In other species of birds, several additional factors have been shown to influence parental provisioning rates. Monogamous male Budgerigars (*Melopsittacus undulatus*) preferentially provision nestlings that are older and beg more intensely (Stamps et al. 1985). Stamps et al. (1989) suggested that provisioning rate was influenced more by brood size and brood sex ratio than nestling begging. Higher provisioning rates are correlated with male-biased broods in Red-winged Blackbirds as well (Yasukawa et al. 1990). In contrast, Bengtsson and Rydén (1983) showed that nestling provisioning by monogamous Great Tits (*Parus major*) was influenced more by the nutritional needs of nestlings, expressed by the intensity of begging calls, than by brood size. In Tree Swallows (*Tachycineta bicolor*) provisioning rate also is influenced directly by nestling begging calls, which reflect nestling condition and the food supply in the environment (Hussell 1988). In addition, experiments on Pied Flycatchers (*Ficedula hypoleuca*) show that the breeding experience and condition of the parents influence the rate at which they feed nestlings (Lifjeld 1988). In our food-deprivation and satiation experiments, brood size and nestling age were held constant. Thus, the difference in provisioning rate between males that provisioned food-deprived nestlings and males that provisioned control nestlings may be related to differences in male breeding experience and condition of parents, brood sex ratio, or other factors such as female quality. Our study has shown that nestling hunger can influence the parental behavior of polygynous

males; however, further experiments will be necessary to determine the relative influence of nestling hunger and other variables on male parental behavior.

*Foraging behavior and prey selection.*—Lifjeld (1988) predicted that parents should choose prey less selectively in response to intense nestling hunger. This change in foraging behavior is expected to reduce the time between food deliveries. In several species, provisioning rate is correlated negatively with prey size. In Great Tits, European Starlings (*Sturnus vulgaris*), and Pied Flycatchers, parents fed a larger proportion of small or low-quality prey when the brood's demand for food was increased experimentally (Royama 1966, Tinbergen 1981, Lifjeld 1988). By foraging more often in the marsh, Red-winged Blackbird parents reduced the travel distance and the time between each nest visit. When parents spent more time foraging in the marsh, the average number of visits per hour increased 89%, but the volume per load decreased by at least 54%. Thus, Red-winged Blackbird nestlings received less food per visit but at a faster rate. This change in foraging behavior may represent a parental response to avoid deterioration of nestling condition and possible starvation (Lifjeld 1988).

In summary, male and female Red-winged Blackbird parents adjusted provisioning rate in response to the hunger level of nestlings. In contrast to monogamous species, the effect of nestling hunger on the behavior of polygynous males seems to depend on the male's activities with other mates. Although polygynous males provide relatively low levels of parental care, their responses to experimental manipulations of brood size and nestling hunger suggest that they have evolved the ability to assess the reproductive options in their environment and rapidly adjust their reproductive behavior in response to changes in expected fitness.

#### ACKNOWLEDGMENTS

We thank Ducks Unlimited Canada in Camrose and Tofield, Alberta for logistical support, and D. Hansen and L. Munro who provided excellent assistance in the field. We appreciate permission from the Muir and Penner families to study Red-winged Blackbirds on their property. We are grateful to P. O. Dunn, D. Hussell, J. T. Lifjeld, and K. Yasukawa for helpful comments on previous drafts of this manuscript. Financial support for this study was provided by grants from the Frank M. Chapman Memorial Fund (Amer-

ican Museum of Natural History), the James L. Baillie Memorial Fund (Society of Canadian Ornithologists), and Sigma Xi to L.A.W., as well as a grant from Natural Sciences and Engineering Research Council of Canada to R.J.R.

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