

treatment seemed to disappear at about the time the pesticide would be expected to lose its effect. Furthermore, other possible causes—molting, wet plumage, and cool weather—were not observed to be associated with sunbathing in the present instance. However, it is not certain that swallows can subject ectoparasites to sufficient heat to kill or immobilize them. Specific data on thermal sensitivity of mites and lice seem to be lacking, although both are responsive to high ambient temperature (Slansky and Rodriguez [1987] and the eggs of some mites are killed by 15–30 min exposure to 60°C (Belding, 1965). However, Violet-green Swallows seldom sunbathe for more than 1–3 min. Such short sunning bouts seem to be common in small birds (Simmons, 1986). It seems plausible that short exposure to high temperature could discourage mite/louse populations or concentrate them for more effective removal during preening, but we have no direct evidence of this effect. It also is possible that other components of sunlight have pesticidal effects (e.g., ultraviolet light). Given the overt way in which the swallows in this study oriented their bodies to direct sunlight and spread their wings and tails in what appears to be an effort to expose these surfaces maximally and that application of pesticide significantly decreases the frequency of sunning, we maintain that pest control is a reasonable explanation of such behavior.

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EFFECTS OF NESTLING PROVISIONING ON THE TIME-ACTIVITY BUDGETS OF MALE RED-WINGED BLACKBIRDS¹

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Key words: Male parental care; mating effort; time-activity budgets; Red-winged Blackbird; Agelaius phoeniceus.

Parental effort, mating effort and somatic effort are generally viewed as the major components of reproductive effort (Williams 1966, Maynard Smith 1977).

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During the breeding season, time and energy expended in reproductive effort are expected to be limited (e.g., Ricklefs 1974, Hails and Bryant 1979). As a result, a conflict may arise in biparental species regarding the allocation of time and energy among parental, mating and maintenance activities. This conflict may be greater for males because they can influence positively their fitness by caring for offspring, gaining additional matings or performing maintenance activities. For male birds, a conflict may arise if the time required to feed and protect nestlings (parental effort) necessitates a reduction in the time spent attracting additional mates and pursuing extra-pair fertilizations (mating effort) or a reduction in their investment in maintenance activ-

ities (somatic effort), or both. It is not clear how changes in male parental investment affect mating or maintenance activities. Conflicting demands for limited time and energy are most likely to occur in species where males are polygynous and females nest asynchronously, such that periods of parental care and the opportunity for additional matings overlap in time.

I examined natural and experimental variation in the time-activity budgets of polygynous male Red-winged Blackbirds (*Agelaius phoeniceus*) to determine whether the time spent in parental care activities affected the time that males spent in mating or maintenance activities. In eastern North American populations, males often have one to five females nesting on each territory, and males vary considerably in the amount of parental care they provide (Muldal et al. 1986, Whittingham 1989, Yasukawa et al. 1990, Beletsky and Orians 1990, Patterson 1991). In addition, male Red-winged Blackbirds frequently gain extra-pair fertilizations with the mates of neighboring males (Gibbs et al. 1990, Westneat 1993). In many populations, females nest asynchronously, and thus, unmated females are present, and mates of neighboring males are fertile, when early nesting females have dependent young.

METHODS

I studied Red-winged Blackbirds in 1986 in two marshes at the University of Michigan E. S. George Reserve, Livingston County, Michigan. The marsh vegetation was predominantly cattail (*Typha latifolia*). All territorial males and most females were captured in mist nets or traps baited with cracked corn and millet. Birds were banded with USFWS bands, and each bird was given a unique combination of colored plastic leg bands.

Observation sessions were conducted between 06:00 and 12:00 on nestling day 2, 3, 4, 5, 6 and 8 (day 0 represents hatching). I recorded data continuously on a cassette recorder during 60-min observation periods and quantified time spent in each activity using a stopwatch. The time males spent foraging for young and watching for predators on their territories was considered time spent in parental care activities (min per hr of observation). Time spent foraging was easily quantified because males were frequently visible while they were foraging within the aquatic vegetation. I recorded male behavior as vigilant when the male was perched on a prominent point overlooking his territory in an alert posture and visually scanning the area (e.g., Yasukawa et al. 1992).

The frequency of songs, female chases, and intrusions onto territories of other males were considered mating activities. These activities were very brief. For example, a male song averaged 1.1 sec (± 0.3 ; $n = 21$ males), a female chase averaged 0.6 sec (± 1.6 ; $n = 21$ males) and male intrusion averaged 1.9 sec (± 2.9 ; $n = 21$ males). Therefore, songs, female chases and male intrusions are presented as frequencies (number per hr of observation). Male song is important in mate attraction, either directly when song rate is related to mating success, as in this study (see below), or indirectly because it is important in defending and maintaining a territory where females will nest (Peek 1972; Smith 1979; Searcy 1979, 1988). Female chases and intrusions onto other male's territories were also con-

sidered mating activities because males frequently chase their mates during courtship (Nero 1956, Westneat 1992), and males also frequently intrude onto neighboring male's territories in pursuit of extra-pair fertilizations (Westneat 1992). The time males spent preening or perched low in the vegetation and apparently resting was considered time spent in maintenance activities.

The breeding season extended from mid April through late July. On average, first nestlings hatched on 9 May (± 0.6 ; $n = 2$ years) and last nestlings hatched on 29 June (± 6.0 ; $n = 2$ years). Data used in these analyses were from experiments and observations conducted early in the breeding season, 15 May–22 May, before all females had settled on breeding territories. Time of day (Mann-Whitney $U = 60$, $df = 1$, $P > 0.5$) and date (Mann-Whitney $U = 53$, $df = 1$, $P > 0.3$) of observations did not differ between treatment groups. Furthermore, the frequency of activities and the time males spent in each activity were not related to the hour of the observation period (r^2 values < 0.06 , P values > 0.4), or time of the season ($r^2 < 0.2$, $P > 0.1$).

Unmanipulated males. If males fed nestlings, they began when the nestlings were four or five days old (Whittingham 1989). Thus, I compared the change in time-activity budgets of unmanipulated males prior to day 4 and following day 5. This comparison was made for two groups of unmanipulated males: (1) males that fed nestlings and, (2) males that did not feed nestlings. Mean values of the change in each activity, from two observation sessions before day 4 and two observation sessions after day 5, were compared for these two groups of males with Mann-Whitney U tests.

The frequency of songs and conspecific chases were examined for correlation with number of female mates for all males that did not feed nestlings ($n = 14$). A mean value for each activity from four 60-min observation sessions (on nestling days 2, 3, 6 and 8) was used in the analysis.

Experimental males. Experimental nests were chosen randomly and brood size increase experiments were alternated with brood size decrease experiments. Brood size was manipulated experimentally on nestling day 5 (Whittingham 1989). Brood size was increased at nests where the male ($n = 5$) was not feeding young. All males at these nests subsequently started feeding nestlings. Brood size was decreased at nests where the male ($n = 5$) was feeding young, and all males stopped feeding nestlings at these nests (see Whittingham 1989 for details). Brood size was increased from three to five nestlings and brood size was decreased from four to two nestlings or from three to one nestling. Time spent in activities before and after the experimental change in parental behavior were compared for both groups of males. Mean values of each activity, from two observation sessions before and two observation sessions after manipulation, were compared with Wilcoxon paired-sample tests. Mean values are reported with standard errors and significance was designated at the 0.05 level.

RESULTS

Unmanipulated males. The change in frequency or time spent in activities was compared for unmanipulated males that did and did not feed nestlings (Table 1).

TABLE 1. Change (mean \pm SE) before and after nestling day 5 in parental, mating and maintenance activities of unmanipulated males that fed ($n = 7$) and did not feed ($n = 7$) nestlings.

Activity	Fed nestlings	Did not feed nestlings	U^1	P
Foraging (min/hr)	14.6 \pm 2.6	0.8 \pm 2.4	44	0.01
Vigilance (min/hr)	-0.5 \pm 1.1	1.2 \pm 1.4	31.5	0.37
Maintenance (min/hr)	-5.8 \pm 0.4	-1.1 \pm 1.1	48	0.003
Songs (hr ⁻¹)	-15.0 \pm 1.8	-2.4 \pm 4.4	42	0.03
Female chases (hr ⁻¹)	0.2 \pm 0.6	-0.9 \pm 0.9	29.5	0.5
Male intrusions (hr ⁻¹)	-2.4 \pm 1.0	-0.6 \pm 0.5	40	0.04

¹ Mann-Whitney U test. Means were calculated from the change in behavior of each male.

The frequency of songs and intrusions, as well as the time spent in maintenance activities, was reduced more when males fed nestlings than when males did not feed nestlings. Conversely, the time spent foraging increased more when males fed nestlings than when males did not feed nestlings. There was no difference in the frequency of female chases or time spent in vigilance activities.

If song rate and female chases indicate mating effort, then these variables might be associated with the number of mates breeding with each male. Song rate and the frequency that males chased females were correlated positively with the total number of female mates ($r^2 = 0.64$, $df = 12$, $P < 0.001$; $r^2 = 0.70$, $df = 12$, $P < 0.001$, respectively).

Experimental males. When males began provisioning young in response to experimentally increased brood size, their time-activity budgets changed similarly to that of unmanipulated males that provisioned young (Table 2). Males experimentally induced to provision nestlings decreased the time they spent in maintenance activities, their song rate and frequency of intrusions

onto other male's territories. Experimental males also increased the time spent foraging when they began feeding nestlings. Conversely, males that stopped provisioning young in response to experimentally reduced brood size, increased their song rate, intrusion rate and time spent in maintenance activities, while they decreased their time spent foraging. The frequency that males chased females and time spent in vigilance behavior did not change when males provisioned young (Table 2).

DISCUSSION

My results suggest that male Red-winged Blackbirds provisioning nestlings reduce both their mating and maintenance activities. When male Red-winged Blackbirds began feeding nestlings they increased the amount of time they spent foraging. For all males not feeding nestlings (experimental and non-experimental), the amount of time spent foraging was similar. This suggests that this was the amount of time spent foraging for self maintenance. From this perspective, it appears that there was no trade-off between parental and maintenance activities (i.e., foraging time was not similar between parental and non-parental males). However, when males fed nestlings the amount of time they spent preening and resting decreased significantly. Thus, there does appear to be a trade-off between some maintenance activities and parental care. The behavior of male Red-winged Blackbirds suggests that the cost of temporarily reducing preening and resting may have been lower than the cost of reducing energy acquisition (foraging). The parental care period is often considered the most energetically demanding for parents (e.g., Hails and Bryant 1979, Moreno and Hillström 1992) and thus, male Red-winged Blackbirds probably need to maintain their own level of energy intake in order to provide sufficient parental care.

For Red-winged Blackbirds mating activities include singing, chasing females and intruding onto other male's territories. When feeding nestlings, males reduced their song rate and the frequency of intrusions onto other males' territories, however, the frequency that males chased females did not change. Male song rate was correlated positively with the number of female mates, suggesting an important role in male mating success (but see Shutler and Weatherhead 1991). Although song rate was reduced during parental care, males did not lose their territories. This suggests that the reduced song rate was sufficient for territory maintenance and

TABLE 2. Parental, mating and maintenance activities of experimental male Red-winged Blackbirds. $n = 5$ males in each experimental group.¹

Activity		Experimental group	
		Brood size increase	Brood size decrease
Foraging (min/hr)	before	12.2 \pm 2.5*	42.2 \pm 3.9*
	after	31.4 \pm 6.9	20.3 \pm 4.2
Vigilance (min/hr)	before	19.5 \pm 1.1	15.4 \pm 0.8
	after	17.1 \pm 0.7	17.4 \pm 1.2
Maintenance (min/hr)	before	8.2 \pm 0.3*	1.3 \pm 0.1*
	after	1.9 \pm 0.2	6.8 \pm 0.4
Songs (hr ⁻¹)	before	41.1 \pm 7.0*	10.4 \pm 2.3*
	after	10.5 \pm 1.8	25.0 \pm 5.3
Female chases (hr ⁻¹)	before	0	0.4 \pm 0.2
	after	0.6 \pm 0.4	1.2 \pm 0.4
Male intrusions (hr ⁻¹)	before	3.4 \pm 0.6*	1.1 \pm 0.2*
	after	0.8 \pm 0.1	3.4 \pm 0.6

¹ Wilcoxon paired-sample tests were used to compare male behaviors (mean \pm SE) before and after experimental change in brood size on nestling day 5 (* $P < 0.05$).

that the higher song rate may function in mate attraction. In other species of birds, increased male song rate has been associated specifically with mate attraction. For example, the song rate of male Willow Warblers (*Phylloscopus trochilus*) is significantly higher during mate attraction and courtship than during territory establishment (Radesater and Jakobsson 1988).

The frequency of male intrusions onto a neighboring male's territory, and subsequent chases by the territorial male, decreased when males were feeding nestlings. In many species of birds, territorial intrusions by conspecific males are most frequent when resident females are nest-building or egg-laying and less frequent prior to female arrival during territory establishment (Ford 1983, Møller 1987). This suggests that male intrusions may be associated closely with the pursuit of extra-pair fertilizations. Male Indigo Buntings (*Passerina cyanea*) made more trips off their territory when nearby females were fertilizable, and males gained most of their extra-pair fertilizations with the mates of neighboring males (Westneat 1987, 1988). Similarly, territorial male Red-winged Blackbirds gain extra-pair fertilizations most frequently with mates of neighboring males (Gibbs et al. 1990, Westneat 1993), apparently through intrusions onto the neighboring male's territory (Westneat 1992). If the frequency of intrusions is proportional to the effort that males expend in pursuit of extra-pair fertilizations, then the results of this study suggest that male Red-winged Blackbirds expend less effort pursuing extra-pair fertilizations when they are provisioning nestlings.

Male Red-winged Blackbirds frequently chase their mates within the territory during courtship (Nero 1956). These chases may be associated with mating effort because they occur during pairing and during the female's fertile period (Nero 1956, Westneat 1992). However, when males provisioned nestlings the frequency that males chased females was not influenced negatively, as was the frequency of intrusions onto other males' territories. This study was conducted early in the breeding season before all females had settled on breeding territories, and as a result, males may have continued their pursuit of additional mates whether or not they were feeding nestlings. Since female chases occurred on the male's territory they may not be incompatible with foraging for and feeding nestlings within the same area. Alternatively, the pursuit of extra-pair fertilizations involves entering another male's territory to pursue the female as well as the risk of retaliation by the territorial male.

Reduced mating effort associated with increased paternal care will only be costly in terms of male reproductive success if decreased mating effort results in fewer mates or reduced paternity. In previous studies of Red-winged Blackbirds there was no difference in the number of mates attracted by males that fed nestlings and those that did not feed nestlings (Mulda et al. 1986, Patterson 1991), although some data do suggest that males refrain from feeding nestlings until the last female has settled on his territory (Yasukawa et al. 1990). Similarly, in this population, the number of mates per male did not differ between males that fed (2.1 ± 0.3) and did not feed nestlings (2.0 ± 0.2 ; $U = 21$, $df = 1$, $P > 0.5$).

Both provisioning nestlings and guarding nestlings

are forms of parental care, and thus, we may not expect one to occur at the expense of the other. During the nestling period male Red-winged Blackbirds spend a considerable amount of time guarding their nests and females against predators (Yasukawa et al. 1992). Vigilant males scan and call from prominent perches, and respond aggressively to potential predators (Yasukawa et al. 1992). In this study, the time spent foraging for and provisioning nestlings did not affect the vigilance behavior of male Red-winged Blackbirds. Furthermore, there was no difference in the frequency of predation at nests where the male fed nestlings versus nests where the male did not provision nestlings. In this study, only two nests for each group of males were depredated following nestling day 4. Thus, there is no indication that males provisioning nestlings were less vigilant.

Male Red-winged Blackbirds appear to reduce some of their mating and maintenance activities, but not others, when provisioning nestlings. These relationships may be influenced by additional factors such as male age or breeding experience. Females appear to prefer nesting on territories of males with more breeding experience, and more experienced males provision nestlings at higher rates (Searcy 1979, Yasukawa 1981, Yasukawa et al. 1990). Thus, it is possible that experienced males are also more successful at feeding nestlings and attracting additional mates simultaneously. If this is the case, the influence of paternal care on mating effort may change as males gain breeding experience.

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MAXIMUM DIVING DEPTHS OF CAPE GANNETS¹

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Key words: *Cape Gannets; diving depths; foraging; Morus capensis.*

An important factor determining the availability of marine prey to seabird predators is the depth to which they may capture prey. The remarkable diving abilities of three families of pursuit-diving seabirds, penguins

(Spheniscidae) (Wilson 1985, Burger 1991), auks (Alcidae) (Burger 1991, Burger and Powell 1990, Piatt and Nettleship 1985) and cormorants (family Phalacrocoracidae) (Wanless et al. 1991) are now recognized. Plunge diving seabirds are probably restricted to feeding in the top few meters of the water column. We report here the maximum diving depths of plunge diving Cape Gannets (*Morus capensis*) determined by use of maximum dive recorders. In addition, we examined interspecific differences in the availability of particular prey to gannets by combining measurements of dive depth with diet analysis. Cape Gannets are important consumers of commercially important pelagic fish off the coast of southern Africa (Berruti and Colclough 1987). Depth gauges (see Burger and Wilson 1988) were

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