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AN INCREASE IN PARENTAL INVESTMENT DURING THE BREEDING SEASON

BY GLORIA C. BIERMANN* & RALEIGH J. ROBERTSON
Department of Biology, Queen's University, Kingston, Ontario, Canada, K7L 3N6

Abstract. The intensity of nest-defence aggression by female redwinged blackbirds (*Agelaius phoeniceus*) with eggs decreased late in the breeding season, while aggression at this time increased amongst females defending broods. High predation pressure late in the breeding season decreased the probability of survival of the late nesting attempts, so that females with young had a much greater chance of success than females with eggs at this time. The observed changes in aggressive responses are predicted by the theory of parental investment.

Parental investment has been defined as 'anything done by the parent for the offspring that increases the offspring's chance of survival while decreasing the parent's ability to invest in other offspring' (Trivers 1972). The reproductive strategy of any individual is therefore a balance between the benefits of energy expenditure on reproductive processes (reproductive effort), expressed as increased fecundity, and the costs in terms of decreased probability of successfully reproducing in the future (Cody 1971; Hirshfield & Tinkle 1975; Wilson 1975). It has been predicted that, all other factors being equal, as an individual's probability of reproducing decreases, due to ageing or any other factor that increases mortality, its reproductive effort should increase (Pianka 1974).

To test this prediction, the nest-defence aggression by female redwinged blackbirds (*Agelaius phoeniceus*) with different clutch and brood sizes was measured when they were confronted with a simulated nest predation event.

Methods

Redwinged blackbird nests were monitored from late May to early July 1977 in two small marshes on Lake Opinicon, approximately 45 km north of Kingston, Ontario, Canada. Clutch and brood manipulations were conducted for a separate study (Robertson & Biermann 1979).

A nest predator was simulated by a 70-cm-long black-and-green rubber snake wrapped around the nest-supporting vegetation with its head in the nest cup. Water snakes (*Natrix sipedon sipedon*) are common marsh predators (Robertson 1972; Clark & Robertson 1979) that female redwinged blackbirds can occasionally deter from destroying an entire nesting attempt.

Behaviours were scored based on the distance of the females from the nest, calling, movement near the nest, and attacking. A scoring scheme was devised to rank the females' aggression toward the snake, incorporating both the behavioural acts performed and the duration of the acts during the first 5 min after the females returned to their nests. Behaviour acts were scored as follows: distant (> 5 m) silent observation $= 1$; close (> 1, < 5 m) silent observation $= 2$; distant 'check' calling $= 3$; close 'check' calling $= 4$; circling nest or fly-by investigations $= 5$; nest attentiveness (perching near or on nest, silent) $= 6$; close harsh calling $= 7$; nest attentiveness with calling $= 8$; circling the nest closely (< 1 m), silently $= 9$; circling the nest closely with calling $= 10$; attacking silently $= 15$; attacking with calling $= 20$. Duration scores, with the scale designed to reflect what we felt were differences in aggression are: act elicited briefly or only once $= 1$; given several times or continuously up to 1 min $= 2$; given for 1 to 3 min $= 4$; given for 3 to 5 min $= 6$; given for 5 min $= 8$. The score for a given trial was computed as the sum of the products of the behaviour scores and duration scores obtained during the 5-min trial (for details see Robertson & Biermann 1979). High scores were recorded for more aggressive females. Of all trials conducted on nests prior to hatching the mean score was 62 ± 7 (SE) (range: 7–170). After hatching, the mean score was 60 ± 6 (range: 7–160). Results approximated normal distributions.

Aggression toward a predator is a very risky undertaking, and greater aggression incurs a larger cost in reproductive attempts. Thus, aggression may be used as a measure of relative parental investment.

*Present address: Department of Zoology, University of Manitoba, Winnipeg, Manitoba R3T 2N2.

Results and Discussion

As the breeding season progresses, the probability that a female can successfully renest decreases, due to increased predation pressure, decreased availability of resources, or lack of time before moulting and migration must occur. Late in the breeding season, there is a high probability of a nest being preyed upon (Fig. 1). A female with young in the nest has a fairly high probability of successfully fledging the young if she can protect them from predators for a short while longer. With higher predation pressure, more parental investment in the form of increased nest defence is needed to fledge the young successfully.

There is a high (48.3%) annual adult mortality rate for redwinged blackbirds, with most deaths occurring over the non-breeding period (Fankhauser 1971). Thus, there is a very high probability that a female will not survive until the next breeding season. Therefore, from the beginning to the end of the reproductive season, the reproductive potential of an individual decreases by a large amount since the possibility of successfully renesting in the present or future breeding seasons greatly decreases. If Pianka's (1974) prediction holds, one would expect a greater degree of nest-defence aggression amongst females defending nests later in the season than amongst females defending nests at the same stage of development earlier in the season, assuming that the effort required for other forms of parental investment, such as incubating and feeding the young, remains relatively constant throughout the breeding period.

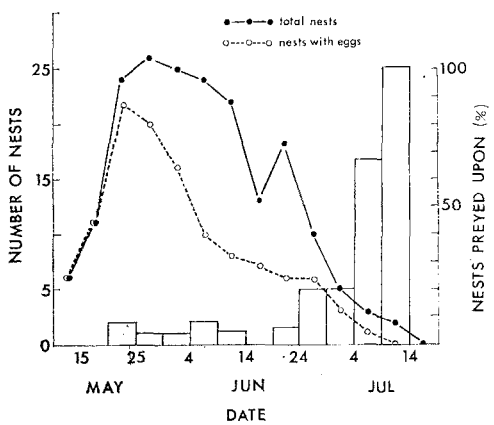

Fig. 1. The number of active redwinged blackbird nests throughout the breeding season, the number of active nests with eggs, and the proportion of currently active nests preyed upon throughout the breeding season.

Although there are significant differences between responses with varying clutch sizes (Robertson & Biermann 1979), responses by all females with all clutch sizes throughout the incubation period were used to determine changes in intensity of response during the breeding season, since tests of females with each clutch size were conducted throughout the season. Responses by females with all brood sizes were similarly obtained and treated although, again, there were significant differences in the intensity of response amongst females with different brood sizes. The testing period was arbitrarily divided into three equal-length periods for this analysis.

Amongst females defending nests with eggs, there was a decrease in the nest-defence response intensity at the end of the season (Fig. 2) although the decrease is not significant (One-way Analysis of Variance: $F = 1.86$, $df = 2, 41$; $P > 0.1$). With young in the nest, there was a significant increase in the nest-defence response of the females at the end of the season (Fig. 3; One-way Analysis of Variance: $F = 4.32$, $df = 2, 45$; $P < 0.025$). At the end of the nesting season, females with broods appear to invest the extra effort needed to attempt to complete the nesting effort successfully. Females with clutches do not increase investment in nest-defence late in the breeding season, and may actually decrease nest-defence aggression at this time.

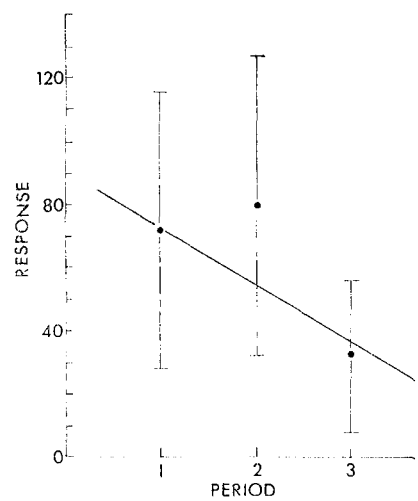

Fig. 2. Mean response to a predator model placed on nests with eggs throughout the testing period. Standard deviation lines are shown. Regression line: $r = -0.283$, $df = 41$, $P > 0.05$.

This may improve their chances of surviving to the next breeding season (see Askenmo 1979; also DeSteven 1980).

Although parental investment should increase as a nesting attempt progresses from eggs to young (Trivers 1972), during the first two periods there is no significant difference in nest-defence aggression amongst females defending eggs and young (Analysis of Variance: May 23 to June 6, $F = 2.12$, $df = 1, 32$; $P > 0.05$; June 7 to June 21, $F = 0.51$, $df = 1, 36$; $P > 0.05$). During these periods the probability of a nest being preyed upon was small (Fig. 1), so that the females could devote more energy to other forms of parental investment. Since energy demands are greater in other forms of parental investment after hatching than before, because of the necessity of feeding the young, nest-defence aggression should not necessarily increase after hatching.

Females with clutches defend them less intensely than females with broods late in the breeding season (Analysis of Variance: $F = 5.21$, $df = 1, 19$; $P < 0.05$). Late in the season, increased predation decreases the probability of a brood fledging, while the probability of a clutch surviving to fledging is even smaller. The difference in survival probabilities between clutches and broods is larger at this time than earlier in the breeding season. In order to complete nesting successfully, more parental investment in the form of nest-defence is required. Since nestlings represent greater possible reproductive success than eggs, with a lower expected cost since the expected remaining period of parental investment is shorter, greater effort should be expended on broods than clutches. Female redwinged blackbirds apparently differentiate between the nesting attempts and allocate maternal investment accordingly.

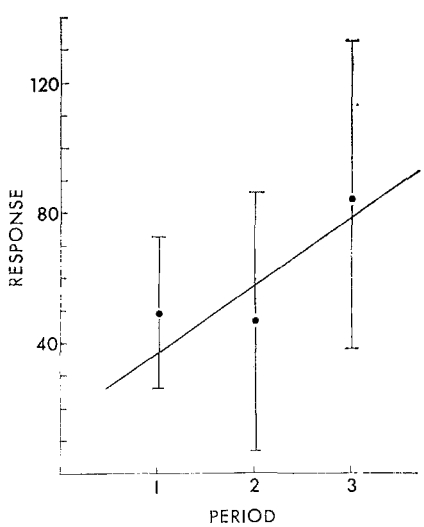

Fig. 3. Mean response to the predator model placed on nests with young throughout the breeding season. Standard deviation lines are shown. Regression line: $r = 0.332$, $df = 45$, $P < 0.05$.

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