

Parental-investment studies have frequently regarded attacks by predators as a fixed behavior to which a parent responds. Likewise, foraging studies often assume that prey items have a fixed "handling time"—the time it takes the predator to capture and consume the prey. When the prey is being guarded by a parent, the parent's defensive actions will influence a predator's attack decisions, and these in turn will affect the parent's decisions to defend. This kind of interaction, where the success of a behavior is determined in part by the actions of another individual, is ideally suited to game-theory analysis (Maynard Smith 1982), and future research should develop this area of parental-investment theory.

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#### Response to R. M. Coleman

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Coleman (1987) takes issue with our explanation for reported changes in nest-defense intensity (Knight and Temple 1986a) because it was not couched in evolutionary terms, but he overlooked a crucial point: we never touted our explanation as an ultimate one. Our explanation clearly provides only a proximate cause for observed trends in nest defense: "We propose that the increases are largely the result of methods used by researchers." Our primary goal was to show that previous studies, reviewed by Knight and Temple (1986a, b), lacked necessary controls, thereby making it impossible to accept their explanations for increased nest-defense intensity, of which parental investment was only one of several.

Coleman asserts incorrectly that our explanation for changes in nest-defense intensity was intended to invalidate parental-investment theory; that was not our intention. Instead, we identified four assumptions made in studies that have tried to explain observed patterns of nest defense on the basis of the existing theories: (1) that the reproductive value of the nest contents increases with age, (2) that the nest contents

become more conspicuous with increasing age, (3) that nest defense is costly and risky, and (4) that the intensity of nest defense is solely or primarily a reflection of either parental investment or the conspicuousness of the young. We concluded that the last two assumptions required closer scrutiny and focused our attention mainly on the last one. We found nothing that invalidated parental-investment theory but much that indicated there were methodological flaws in previous studies that sought to validate the theory.

Coleman uses a cost/benefit approach to argue that when parents have serial encounters with predators they should either defend with the same vigor on subsequent encounters or defend less intensely. We feel this is an inappropriate approach and prefer instead a risk/benefit analysis. The costs of nest defense (in terms of energy and time) are trivial compared with the risks of being killed or injured in the process, or of losing the entire nesting effort; nest defense is typically an all-or-none matter. Naive parents perceive the risks of attacking a potentially dangerous predator to be great until they have had experiences showing the contrary. In other words, we suggest that parents restrain their nest-defense aggressiveness during initial nest-defense efforts against a particular predator because of fear for their own safety. Despite what Coleman implies, natural selection should favor such behavior. A parent that unleashes an unrestrained defense against a predator of unknown threat

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risks death or injury as well as the consequent loss of its reproductive investment. A more prudent parent ensures its own safety and, thereby, retains the option of re-nesting even if the initial defense fails to prevent nest predation.

As an alternative to our explanation for why nest-defense intensity increases at multiple-visit nests, Coleman suggests that parents initially defend at a conservatively low level and increase that level only if they become frustrated that the predator has returned despite their previous defense. In this way, repeated visits by a predator would provoke increasing levels of defense. We believe this alternative explanation can be separated from ours (i.e. loss of fear and reinforcement) by a relatively simple test. If Coleman's idea is correct, the intensity of nest defense should increase during each visit as well as between successive visits; when a predator arrives at a nest, parents should defend at an initial low rate that increases if the predator remains near the nest (i.e. as parents become increasingly frustrated that the predator has not left). Under our hypothesis increases in nest-defense intensity should occur only between, not within, visits because the reinforcement of the behavior occurs only when the predator leaves.

During a single visit to each of six nests, we measured the nest-defense intensity of Red-winged Blackbirds (*Agelaius phoeniceus*) to a human intruder in the same manner described by Knight and Temple (1986a), but we scored nest-defense intensity separately during each of the six 30-s intervals during a

3-min visit. Using the same analytical techniques as Knight and Temple (1986a), we found no evidence that any of the measured responses of either males or females increased in intensity during a visit; instead, several actually decreased.

We appreciate Coleman's commentary but suggest that it is more interesting and important to explain why nest-defense intensity did not change through the nesting cycle of the nests we visited only once rather than why it increased at multiple-visit nests. We have no ready explanation and can only reiterate that this pattern is inconsistent with the predictions of parental-investment theory, as it has so far been applied to the phenomenon of parental nest defense in birds.

We appreciate the comments of T. L. George.

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