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Does Experience With Predators Affect Parental Investment?

RONALD M. COLEMAN^{1,2}

Recently, Knight and Temple (1986) offered a new explanation for observed patterns of nest defense by parental birds, based on experience with predators. They proposed that increases in nest defense through the brood cycle are the result of the methods used by researchers. Repeated visits to a nest induce "positive reinforcement" and "loss of fear" in a parent, which leads to the observed pattern. For example, if a potential predator (intruder) retreats after being harassed by a parent, then the parent is positively reinforced by its "success." Thus they argue that the parent should attack more vigorously the next time the intruder appears because the parent has learned that the intruder is not dangerous to the parent but is still a threat to the brood. The result for nest-defense studies is that each time the investigator tests the parent's willingness to defend, the defense score increases.

Knight and Temple's suggestion centers on the motivation of the parent; however, motivation is the proximate manifestation of underlying selective pressures. As such, we can analyze the costs and benefits of their suggested parental behavior and ask whether it can evolve by natural selection.

For a behavior to evolve, the benefits of the behavior must exceed the costs. If the predator's retreat in the first encounter causes the parent to feel "successful," and if the parent defends more vigorously on subsequent encounters, again causing the predator to retreat, then the parent will have paid a greater cost to achieve the same benefit, namely "success." This behavior cannot evolve by natural selection. The parent should at most defend the same amount on subsequent encounters if it is going to receive only the same benefit. It might even defend less, rather than more, to determine if this lower defense level also achieves "success." Undoubtedly, there is substantial risk in doing this, but if less defense were sufficient to achieve "success," the parent could reduce its future defense expenditures to this lower level.

The parent could perhaps achieve additional benefits by defending more vigorously when the predator returns. For example, the parent might make the predator retreat a greater distance than it did the first time. If this is necessary, however, then we must conclude that the parent did not in fact achieve "success" in the first encounter. Therefore, it could not be "pos-

itively reinforced," nor should it experience "loss of fear."

Another possibility is that the parent defends more vigorously to inflict injury to the intruder in addition to achieving "success" at deterring it. Such injury would presumably incapacitate the predator in some way. This idea is also untenable, however. The behavior cannot evolve because other parents in the population also reap the benefits of an incapacitated predator while expending less energy to achieve "success." This behavior is altruistic and cannot evolve without recourse to kin selection or reciprocity (see Tullock 1979, Davies and Houston 1984 for discussions of similar behaviors).

It appears that Knight and Temple's suggestion cannot explain increases in nest defense; however, many studies have found such increases (see Knight and Temple 1986). These increases may not be due to experience with predators, but rather to some other component of parental-investment theory, such as changes in the value of the brood to the parent (e.g. Sargent and Gross 1986). Alternatively, some mechanism may be operating between the predator and the parent other than the one suggested by Knight and Temple.

It is possible to explain an increase in nest defense due to experience with predators if (in contrast to Knight and Temple) we assume that the defender interprets the reappearance of the predator as indicating that it was *unsuccessful* in deterring the predator previously. In this case the defender should increase its defensive effort to ensure that it is successful in the present encounter. Thus, experience with predators (natural or artificial) may influence nest defense but not in the manner Knight and Temple proposed.

Knight and Temple implied that their explanation for increases in nest defense is an alternative to parental-investment theory. Parental-investment theory attempts to understand the factors that influence a parent's allocation of resources to its young (Coleman et al. 1985, Sargent and Gross 1985). These include the interactions between a parent and offspring, the environment, another parent, helpers at the nest, and predators. Knight and Temple's ideas are not an alternative to this. Rather, they are suggesting that one of these factors operating on a parent, namely the parent-predator interaction, is more important than other factors, such as the parent-offspring interaction, for explaining observed patterns of parental allocation. Determining which interactions are important in any given parental situation is a valid issue within the realm of parental-investment theory, not an alternative to it.

I agree with Knight and Temple that the parent-predator interaction deserves more careful analysis.

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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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