EVOLUTION OF DISTRACTION DISPLAY BEHAVIOR IN BIRDS

by William E. Davis, Jr.

In a previous article (Davis 1989) I discussed some aspects of distraction displays, or "injury feigning," in birds. This article speculates about the question, how did this fascinating behavior evolve?

In attempting to work out a feasible scenario for the evolution of distraction displays, it may be helpful to examine the diversity of bird species that utilize this behavior to see what patterns emerge. This phenomenon is most common in ground nesters. Skutch (1976) points out that most species that nest in burrows or cavities do not perform distraction displays, and it is rare among birds that construct open nests in trees. He further suggests that the species that do, which include some of the Parulidae such as the American Redstart and Pine Warbler and many doves, may have had ancestors that nested on the ground. The occurrence of injury feigning chiefly in ground-nesting birds suggests that the displays were evolved primarily under selective pressures related to terrestrial mammals.

In most species that share responsibility for rearing young, both males and females give distraction displays. However, in some species, such as the Prairie Warbler, the females seem to be more prone to display (Nolan 1978). The major focus for the display in altricial birds seems to be the nest. Nolan found, for example, that when he banded chicks at the nest the adult bird displayed and when he took the chicks to an adjacent territory the bird stopped displaying. But when he returned them to their nest, the adult resumed the display. For precocial birds like grouse, the nest plays a minor role since it is abandoned soon after the chicks hatch. These observations, together with the correlation of display intensity with the stage in the nesting cycle, suggest the hypothesis that distraction displays have evolved as a device against predators for the protection of the young.

Varied observations of distraction displays have led some workers to conclude that these represent intelligent and thoughtful acts, whereas others have concluded that the displays are a purely instinctive response. Taverner (1936), for example, found that an individual bird could behave differently toward different predators. A Killdeer flew into the face of a cow or horse grazing too close to its nest with "a great outcry" but feigned injury to lead off a dog. Taverner suggested that "the feigning is more or less calculated." Griffin (1984) explored the possible role of thinking and learning in distraction displays. But several lines of evidence argue that, at least in some species, the display is an automatic, instinctive response. Wheatears, for example, in an apparently meaningless behavior, continued to display after their nest and eggs

were removed (Armstrong 1965). Welty (1975) states that "both the stereotyped nature of the performance and its occasional nonadaptive application (for example, by a Ringed Plover, *Charadrius hiaticula*, to a strange egg in its nest) argue against its being interpreted as an intelligent, purposive act." Since many bird species give distraction displays but many do not, and since each species has its own characteristic display, it is possible that distraction-display behavior has evolved independently in different families of birds and perhaps even in different species within the same family. Hence, there could be substantial variability in the learned versus the instinctive component of the behavior.

Clearly, feigning injury has survival advantages for the nestlings and fledglings and is a behavior character that natural selection would favor. Those birds that performed the act would, on the average, raise more offspring and thus spread into the next generation the genetic trait that produced the display. If this advantage persisted, eventually it would become a normal component of the gene pool of the species.

How can the mechanism for the production of distraction displays be explained? One of the most widely accepted suggestions was presented by Friedmann (1936). "Injury feigning is a compromise between fear and reproductive emotions. Fear impels the bird to leave its nest; the bond to the nest and eggs or young prevents the bird from doing so; the result is a crippled departure." Welty (1975) sums up this position: "Perhaps the best current interpretation of distraction display is that it originated in the bird's inability to react simultaneously to two great drives: one to protect the nest or young, and



Killdeer on eggs

Photo by Wilfred Kimber Courtesy of MAS

the other to flee from the predator. The result is a frenzied compromise refined in its more convincing aspects by years of natural selection into what today appears to be 'injury feigning'." Support for the fear component of this hypothesis has come from Lorenz (see Armstrong 1965) with the observation that he could not elicit a distraction display from tame birds, thus suggesting that fear was an important component in the display. Griffin (1984), on the other hand, seems to discount fear as an important factor in the evolution of distraction displays and argues that a displaying bird is in control of its behavior and modifies the details of its behavior depending on what the predator does. He concludes, "There are many well-orchestrated complexities to the behavior, and its adjustments to circumstances strongly suggests intentional reaction to the situation rather than crippling confusion."

Perhaps one of the major unanswered questions is why is there so much intraspecific and interspecific variability in the use of distraction displays? In some species like the Killdeer most individuals perform distraction displays. But even within families that are prone to display, such as the Parulidae, there are species that rarely exhibit the behavior. For example, I could find only two references (Lawrence 1948, Pitelka 1940) to injury feigning by Nashville Warblers. Chisholm (1936) reported that in thirty years of experience with the ground-nesting Pilotbird of Australia a colleague had seen injury feigning but once. Perhaps there is some threshold of response in which the necessary conditions of nesting stage, predator type, hormonal levels, and perhaps fear combine to elicit a response. The threshold may be low for Killdeers but high for Nashville Warblers and thus rarely exceeded. Perhaps learning and individual experience plays a greater role than is currently held by many behavioral ecologists. Distraction display may be only weakly evolved in many species because it puts the parent bird at risk, and it may be a better reproductive strategy in the long run to abandon the nest and start over again, especially in the early phases of the nesting cycle (Davis 1989).

Whether or not these questions are eventually resolved, the distraction display will remain a fascinating behavior to observe.

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