INTERSPECIFIC AGGRESSION IN STEAMER-DUCKS

G. L. Nuechterlein and R. W. Storer (Condor 87:87–91, 1985) and B. C. Livezey and P. S. Humphrey (Condor 87: 154–157, 1985) recently described interspecific aggression between species of steamer-ducks (*Tachyeres* spp.) and other waterbirds, including grebes, ducks, and coots. Although these authors refer to my papers on interspecific territoriality (B. G. Murray, Jr., Ecology 52:414–423, 1971; Biol. Rev. 56:1–22, 1981), their interpretations of interspecific aggression are different from each other and are contrary to mine.

Nuechterlein and Storer (1985) could not believe that Flying Steamer-Ducks (T. patachonicus) misidentified grebes, ducks, and coots as conspecifics and suggested that interspecific aggression by the males either showed "their belligerency and fighting abilities to their females" or served to reduce competition for food. In contrast, in a study of all four species of steamer-ducks in a variety of situations, Livezey and Humphrey (1985) rejected the notion that interspecific aggression was related to competition for food and accepted the probability that there is "little selective pressure for discrimination of targets for interspecific aggression." Yet, they proposed that "interspecific aggression in steamer-ducks [is] a suite of secondary adaptations for protection of young, defense of food resources from marginal competitors, sexually selected ritualized behavior for assessment of males by females, and practice for intrageneric combat." Such an inclusive list of benefits seems necessary to cover the observed variety of interspecific aggressive interactions, if each is to be considered adaptive.

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We read with interest the comments by B. G. Murray, Jr., concerning our earlier discussion (Condor 87:154–157, 1985) of aggression in steamer-ducks (*Tachyeres*). Although Murray focused primarily on proximate stimuli and we emphasized ultimate evolutionary implications, his views are nonetheless thought-provoking. The paucity of data on this genus makes the contribution of Nuechterlein and Storer (Condor 87:87–91, 1985) and the remarks of Murray particularly welcome.

Murray's speculation that a radio-controlled model boat might provide an insight into the discrimination of targets by steamer-ducks is intriguing, although the outcome of such an encounter might prove difficult to interpret. We often have discussed the possible utility of a remote-controlled decoy in the live capture of steamer-ducks. Based on our observations of the reactions of steamer-ducks to southern sea lions (Otaria byronia) and humans and on known instances of predation on steamer-ducks by marine mammals (Straneck et al., Condor 85:255-256, 1983), however, we suspect that an investigator who was snorkeling would drive steamer-ducks ashore rather than elicit an attack. It is also worth mentioning that not all birds that enter territories of steamer-ducks are attacked; we have observed uneventful trespasses by a number of species, including shorebirds, penguins, and domestic ducks.

We share the view that the empirical value of a hypothesis is commensurate with its testability. Fortunately,

In the search for evolutionary explanations, one can either invent ad hoc adaptive stories, an all too common but not very fruitful approach, as pointed out by S. J. Gould and R. C. Lewontin (Proc. R. Soc. Lond. B Biol. Sci. 205:581-598, 1979), or look for patterns and try to construct general theories (B. G. Murray, Jr., BioScience 25:149, 1975; Oikos, in press). In this case, the latter approach seems appropriate because the kind of generalized aggression exhibited by steamer-ducks occurs in some other species. For example, a reef fish, Pomacentrus jenkinsi, attacked not only several other species of fish, but also moving buttons, shells, and human beings. O. A. E. Rasa (Z. Tierpsychol. 26:825-845, 1969) concluded that the stimulus for attack was an "object moving through [the] territory." After reviewing interspecific aggression in hummingbirds, I suggested that the stimulus for attack was "any flying organism near the food resources" (Murray 1981). Thus, in these cases, aggression is toward classes of intruders rather than toward specific intruders. Such a hypothesis could account for aggression toward inappropriate as well as toward appropriate targets. Thus, one does not have to find an adaptive explanation for every attack of one species on another.

With regard to steamer-ducks, Livezey and Humphrey (1985) recognized that the diversity of targets—including apparently inappropriate ones—indicated that steamer-ducks do not distinguish targets. I have little doubt that steamer-ducks would attack a radio-controlled model boat or even a snorkeling human who might be cruising through their territories. Rather than propose several advantages of interspecific aggression simply to be able to cover all possible cases, should we not consider the possibility that the stimulus for attack in steamer-ducks is "an object moving through the territory or near the nest or chicks"? At the very least, this seems a testable hypothesis.

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like the "non-discrimination" explanation of Murray, the alternative hypotheses which we proposed are equally testable. A variety of somewhat more elaborate field experiments would be informative, including: (1) a contingency analysis of interspecific attacks, including the intensity and socio-environmental circumstances of the attack, the identities of attacked and unmolested birds, and the species, sex, age, and reproductive status (including presence of broods, etc.) of the steamer-ducks; (2) studies using remote-controlled models, including a range of sizes and species imitations, a variety of speeds and directions of approach, employed throughout the year and involving steamer-ducks of diverse species, sex, age, and reproductive status; or (3) comparison of the reproductive success of marked birds that show different levels of interspecific aggression (naturally occurring or perhaps chemically induced).

Such approaches would permit the evaluation of a number of hypotheses and would provide insights into both the proximate stimuli for attack and the ultimate adaptive significance of interspecific aggression in *Tachyeres*. We think that field research on territoriality and aggression of steamer-ducks would be most worthwhile, despite the logistic difficulties involved. Only through the empirical rejection of alternate hypotheses can one determine whether a given "general" model is preferable or even partially explanatory, and until more information is available, all hypotheses—adaptive or non-adaptive, discriminatory or non-discriminatory—must remain reasoned, but untested, "inventions."

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Questions concerning the biological basis of observations of animal behavior are frequently the primary focus in studies of avian behavioral ecology. In such studies, it is important to realize that hypotheses concerning the proximal stimuli that elicit a response are not necessarily in conflict with those that concern its ultimate evolutionary basis (Alcock, Animal behavior: an evolutionary approach. Sinauer Associates, Sunderland, MA, 1975).

We welcome B. G. Murray's suggestion that the stimulus for attack by a male Flying Steamer-Duck (*Tachyeres patachonicus*) may be simply any object that moves through its territory or approaches its nest or young, for this is a testable hypothesis concerning a question not addressed in our paper. Murray's hypothesis, however, has little bearing on the primary evolutionary question that we posed in our paper, namely: "Why has such strong interspecific aggression evolved in Flying Steamer-Ducks?" (i.e., as compared to other bird species; Nuechterlein and Storer, Condor 87:87–91, 1985).

Although notoriously difficult to test, hypotheses that concern such ultimate evolutionary questions are *not* untestable. Our sexual selection hypothesis, for example, states that male steamer-ducks may be victimizing birds of other species "to display their belligerency and fighting abilities to their females." This hypothesis predicts that males will be interspecifically aggressive particularly during pair formation and then only when a female is present. In contrast, the food competition hypothesis predicts interspecific aggression throughout the breeding season by both male and female. Both of these predictions could be tested but we had to leave the area shortly after making our initial observations: neither of our hypotheses addresses what proximal stimuli elicit this response.

Finally, although the aggressive responses of male steamer-ducks during pair formation appear to be "almost indiscriminate," this does not mean that males cannot or do not distinguish other species from conspecifics. In fact, by examining their behavior in other contexts, we conclude the opposite. During our observations of their behavior, we never saw unpaired male steamer-ducks at tempting to court a member of another species. This suggests that they can and do distinguish conspecifics from birds of other species and that their aggressive responses are very intense to both classes of stimuli.

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NEWS AND NOTES

55TH ANNUAL MEETING OF THE C.O.S.

The Cooper Ornithological Society held its 55th Annual Meeting jointly with the Wilson Ornithological Society on 5–9 June 1985 at the University of Colorado, Boulder. Cynthia Carey was the chairperson of the Local Committee on Arrangements, and Carl Bock was the chairperson of the Committee on the Scientific Program.

The following people were elected as officers: C. J. Ralph, President; Russell Balda, President-elect; Charles Collins, Treasurer; Michael Morrison, Secretary; and, James Northern, Assistant Treasurer. Four new members of the board were elected: Daniel Anderson, Charles van Riper, Robert Ohmart, and Richard Hutto (who was elected to fill out the term of C. J. Ralph). Martin Morton was chosen to be Editor of *The Condor* to replace Peter Stettenheim, who had asked to step down.

Ninety-two papers were on the three-day program. The Harry R. Painton Award was given to Stephen R. Sabo and Richard T. Holmes for their paper, "Foraging niches and the structure of forest bird communities in contrasting montane habitats" (Condor 85:121–138). The A. Brazier Howell Award was presented to Brian Obst, and the Francis F. Roberts Award was presented to David Westmoreland. The two Board of Directors' Awards were presented to Mary McDonald and to Jerry W. Hupp.

The Board of Directors conferred honorary membership

on Peter Stettenheim for his outstanding service to our Society as Editor of *The Condor*.

The Conservation Committee drafted, in letter form, several resolutions to be sent to the appropriate officials and legislators: one to the Fish and Wildlife Service recommending that federal employees be supported to attend professional meetings; one regarding the preservation of Spotted Owls; one regarding the preservation of the California Condor; one encouraging implementation of the National Forest Management Act of 1976; and, one supporting the Fish and Wildlife Conservation Act of 1980. The membership passed a resolution of thanks to the Local Committee that hosted this year's C.O.S. meeting.

1986 ANNUAL MEETING OF THE C.O.S.

The 56th Annual Meeting will be held in Davis, California, in early September, 1986. Charles van Riper is in charge of local arrangements. Announcements of the schedule and a call for papers will be mailed to members at a later date.

NOMINEES FOR C.O.S. BOARD OF DIRECTORS

In 1986, the members of the Cooper Ornithological Society shall elect to the Board of Directors three people to replace retiring members William R. Dawson, Sandra L. L. Gaunt, and Richard L. Hutto.

The Nominating Committee, consisting of Jared Verner (chairperson), Frank B. Gill, and David Balph, therefore

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