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Ethics and Experimentation: Hard Choices for the Field Ornithologist

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Every scientist must make difficult ethical decisions when designing experiments, whether such experiments are conducted in the laboratory or in the field. Typically, these decisions require weighing the likely scientific gain (in terms of new information to be learned) against the animal cost (in terms of suffering of the individuals involved). The question of when the pursuit of knowledge justifies the imposition of suffering on animal subjects is one that should be honestly confronted and constantly reassessed. Most scientific societies have published guidelines to help individual scientists formulate their answers (e.g. Oring et al. 1988, Dawkins and Gosling 1992, Anonymous 1987, 1992). However, even with such guidelines, there is no magic "threshold" of agreement. Rather, there is a broad grey area within which different opinions are vehemently expressed. Peer feedback is useful in defining these grey areas and in stimulating discussion about them. It is in this light that I welcome the opportunity to reply to the commentary of Bekoff (1993).

Bekoff (1993) criticized our study (Emlen et al. 1989) of experimentally induced infanticide in jacanas on ethical grounds and chastised the American Ornithologists' Union for publishing our article in the *Auk*. As the senior author of the challenged paper, I wish to justify our specific experiments, as well as address the broader issue of ethical trade-offs in experimental science.

If asked, everyone would agree that unnecessary and unnatural pain and suffering in animals should be minimized wherever possible, but there exists a spectrum of opinions on when and whether intervention and experimentation are appropriate. At one end, few would disagree that many birds are kept in captivity under sufficiently inhumane conditions that no degree of scientific justification can excuse their poor care. At the other, field ornithologists routinely witness nestlings suffering from predation and starvation, yet few would advocate intervention to eliminate predators or to provide supplemental food to undernourished chicks. In between these extremes the answers are less clear-cut.

How then should scientists balance the trade-off of knowledge gained versus suffering caused (or permitted, by nonintervention)? Bateson (1986) and Driscoll and Bateson (1988) offered a useful "model" in the form of a decision cube with three dimensions: the certainty of benefit (knowledge gained), the quality of the research, and the amount of animal suffering. In relative terms, animal suffering is justified only when the research is of high quality and has a high certainty of benefit.

But what qualifies as "benefit"? Bateson (1986) and Driscoll and Bateson (1988) couched benefit largely in terms of knowledge that has obvious potential benefit to humans. In his original paper, Bateson used "certainty of *medical* benefit" as his first dimension (emphasis mine). I strongly disagree. In this era of diminishing biodiversity it is imperative that we increase our knowledge of organisms that can serve as general models for larger categories of species. Whether we wish it or not, we are becoming stewards for increasing numbers of threatened species on this planet. To be effective stewards, we must have better knowledge of a wide array of species representing different phylogenetic, ecological, physiological, and behavioral types. Gaining such knowledge frequently requires experimental testing of specific hypotheses.

I suggest that "scientific value" replace Bateson's "certainty of medical benefit" as a critical criterion in the decision of when, and whether, animal suffering can be justified. I further suggest two specific criteria as useful guidelines for assessing the scientific value of any study: (1) the conceptual importance of the question being asked; and (2) the degree to which the results will be generalizable to other species (so that, ultimately, fewer experiments will need to be conducted on other species). These considerations were critical factors in our decision to conduct an experimental test of infanticide in jacanas.

The question of the possible adaptive significance of the infanticidal killing of conspecific young is, in my view, one of considerable conceptual importance. Such behavior occurs commonly in a wide variety of species, including our own (Hrdy 1979, Hausfater and Hrdy 1984). When infanticide was found to be widespread among primates, it aroused considerable scientific interest among both evolutionary biologists and anthropologists. Hrdy (1974, 1977) offered a comprehensive adaptive hypothesis for one form of infanticide, that which occurs when a new male in a harem polygynous primate species displaces a male breeder and "takes-over" the breeder's assemblage of females. Such incoming males frequently kill young that are still dependent upon the female(s). Hrdy (1974, 1977) speculated that such behavior was adaptive to the infanticidal male because the removal of dependent young caused females to come into estrous and to reproduce with the new male much more rapidly than would otherwise be the case. This sexually selected infanticide hypothesis proposed specific benefits (enhanced reproductive success) for the perpetrator and predicted the conditions (following takeovers by new mates) under which it was expected to occur.

Alternative hypotheses were rapidly advanced, including several that considered infanticidal killing to be a nonadaptive behavior, aberrantly expressed under conditions of artificially high population density or excessive human disturbance (Curtin and Dolhinow 1978, 1979, Boggess 1979, Sommer 1987). One of the difficulties in differentiating among these hypotheses has been the scarcity of direct observations of the behavior. Infanticide is usually inferred. And even when infanticide is observed, we are left with descriptive and correlational data only; cause and effect can only be tested experimentally. Although a growing body of data are consistent with Hrdy's predictions (e.g. Hausfater and Hrdy 1984, Sommer 1987), we have only weak inference tests of the hypothesis.

Because of their behavioral role-reversal, jacanas offered a unique opportunity to examine the hypothesis of sexually selected infanticide. Jacanas provide a mirror image of the polygynous mating systems in which infanticide has been reported in mammals. In jacanas it is females that hold "harems" of males and that compete intensively for mates. Jenni and Collier (1972) reported that males frequently change "ownership" during their lifetime. Stephens (1982, 1984) concurred and speculated that infanticide might occur.

By inducing infanticide experimentally, we were able to confirm the specific predictions of the Hrdy hypothesis with a rigor not possible from descriptive observations alone. Further, by our choice of jacanas as the model species, we were able to extend the applicability of the hypothesis (1) across taxa (to birds as well as mammals) and (2) across sexes (since females, as predicted by theory, are the infanticidal sex under conditions of role reversal). Our results thus provided an unusually robust test of the hypothesis. An adaptive explanation for infanticide was strongly supported, and the generality of the Hrdy hypothesis was greatly extended.

What of Bekoff's specific criticisms? In the experiment, we removed two polyandrously breeding female jacanas and then observed the behavior of the incoming females that competed to take-over the residents' territories and the males that occupied them. Bekoff (1993) questioned: (1) the methods used to remove the two breeding females; and (2) the allowing of the "maiming and killing of seven of their chicks." He also challenged (3) the review process that allowed publication of a paper that he believes violated

AOU guidelines. Below I address each of these criticisms.

(1) The females were collected by shooting. According to the AOU guidelines, shooting is the most humane method of collection because individuals are killed outright. Our observations were part of a pilot study to determine the feasibility of a more intensive project on the social behavior and breeding biology of this species. The collected individuals served an additional purpose. Blood and tissue samples from these specimens confirmed the suitability of the molecular method of DNA fingerprinting (Jeffries et al. 1985, Westneat 1990) for assignment of paternity in jacanas. We determined that blood samples would be sufficient for later studies of promiscuity and paternity, eliminating any need for collection of additional individuals for tissue samples.

(2) Following the removal of each resident female, neighboring females rapidly expended their territories to encompass the vacated areas (and the resident males they contained). These replacement females actively sought out and attacked the chicks of the former female. The males attempted to defend their young, but were unsuccessful. The behavior was dramatic; it provided clear answers to Hrdy's predictions. It also caused the death of five chicks.

After removal of the second female, I called off further experiments. Our sample sizes were extremely small (three of three incoming females infanticidal; four of four broods attacked; five of nine chicks killed and two evicted); however, the results were sufficiently clear that I did not wish to induce further suffering. By terminating the experiment at two female removals, we were unable statistically to confirm that incoming females are infanticidal (a sample of three females or four broods is too small to achieve significance with a Fisher exact test). Ironically, this trade-off "cost" us the opportunity of publishing the results in an interdisciplinary journal of wider circulation because one reviewer felt that the sample sizes were insufficient.

(3) Did this research violate AOU guidelines? The guidelines state that researchers must "avoid or minimize distress and pain to the animals, consistent with sound research design." The design of this experiment, however, was to test whether infanticidal behavior would be induced under specific conditions. One cannot easily control behavior in field situations. Bekoff questioned why we did not intervene to recapture the injured chicks, nursing them back to health or, if fatally injured, killing them humanely. This was not logistically possible. The remaining way of minimizing suffering is to limit the number of individuals attacked. We did this by terminating the experiment after only two removals.

I have no disagreement with Bekoff that animal pain and suffering are sometimes caused by scientific research, that such pain and suffering should be minimized whenever possible, and that scientists have a moral and ethical obligation to weigh carefully the scientific value of their research against the magnitude of suffering that it might cause. However, he and I differ on how such trade-offs should be decided, and on where the line of justification lies. Medical researchers argue that animal experimentation is required if we are to combat human diseases and avoid pain and suffering in our own species. I would expand their argument to encompass the need for selective animal experimentation to enhance our general knowledge of the behavior and ecology of representative species, knowledge that is required if we are to protect and conserve the diversity of life and, ultimately, to minimize pain and suffering in nonhuman species.

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The Variably Plumaged Gulls of Iceland

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I (Ingolfsson 1970, 1987) described a situation in Iceland where apparent extensive hybridization occurred when Herring Gulls (*Larus argentatus*; comparatively small, with strongly pigmented primaries) immigrated to Iceland starting about 1920 and encountered Glaucous Gulls (*L. hyperboreus*; larger, with light unpatterned primaries). At present the majority of the gulls that breed in western Iceland appear still to be pure *hyperboreus*. In eastern and southern Iceland pure *hyperboreus* are scarce or absent, and most of the gulls appear to be hybrids or pure *argentatus*.

Snell (1991a, b) recently questioned whether hybridization in fact has occurred in Iceland. He considered it more likely that the intermediate plumage pattern of Icelandic gulls "represents the genetic legacy of light-winged *L. argentatus* founders, possibly dispersed from Scandinavia, where light-winged *L. argentatus* are present" (1991b:329). This conclusion was based mainly on two lines of argument. First, "There is no evidence Icelandic populations of either *argentatus* or *hyperboreus* are more variable than allopatric populations of either species morphologically" (1991a:325). Second, there is no correlation between amount of melanin (pigment) in primaries and body measurements.

Snell's reasoning fails on both accounts. This is partly the result of an unfortunate, but understandable, choice of Skrudur as a study colony in eastern Iceland. This colony contains a higher proportion of *argentatus*-like birds than most other colonies in eastern and southern Iceland. My previous account (Ingolfsson 1970) should have made this clear.

Snell (1991b) stated that his samples of *hyperboreus*-like gulls from Bjarnarhafnarfjall (western Iceland), Svalbard (off northern Norway), and Home Bay (Canada) do not differ significantly in melanism scores. This is not so. Significantly larger numbers of gulls have traces of melanistic patterns on their primaries at Bjarnarhafnarfjall (11 of 53) than in Svalbard (1 of 48; Fisher exact test [two-tailed], $P = 0.004$) and Home Bay (0 of 48). My own data, comparing a larger sample of birds from Bjarnarhafnarfjall with *hyperboreus* from Greenland, indicate an even clearer difference. Only 3 of 80 Greenland birds had faint traces of melanin on the primaries (Ingolfsson 1970), while 67 of 167 birds from Bjarnarhafnarfjall showed a melanistic pattern on one or more primaries (Ingolfsson 1987). There can be no doubt that the *hyperboreus*-like gulls of western Iceland are more variable in pigmentation of primaries than neighboring populations of Greenland and Svalbard.

Snell found that the Skrudur gulls of eastern Iceland were no more variable in primary pigmentation than *argentatus* from northern Norway, but were more variable than several other *argentatus* populations sampled. I had noted that some birds from northern Norway and the adjacent Kola Peninsula in Russia were so hybridlike that extensive hybridization in the area was suspected (Ingolfsson 1970). In any case, some of the Icelandic *argentatus*-like populations, especially those I studied at Hromundarey and Horn (Ingolfsson 1987), are considerably more variable in degree of primary melanism than those from Europe, including northern Norway. Snell did not mention this point.

It is not possible to attach much significance to Snell's conclusion that the variability in 16 skeletal measurements of Icelandic gulls he studied was no greater than found in allopatric populations. The two populations he analyzed in Iceland, at Bjarnarhaf-