Letters

Discrepancy Between Successful Adaptation and Welfare

I was delighted to read Professor Beilharz's penetrating discussion of animal welfare in the *Journal (Int J Stud Anim Prob* 3(2):117, 1982). One point of disagreement I would like to raise concerns Beilharz's assumption about the welfare of animals in their species-typical environments. On p. 122 of his paper he says that "we can do no better than *to assume that the welfare of any adapted form of life is guaranteed, i.e.,* that it does not suffer in its particular environment" (his italics).

My particular doubts about this statement concern two aspects of genetic adaptation. The first of these is that animals are not ideally adapted to every aspect of their environments. Rather, animals are "complicated sets of compromises" (Morris, 1964) to all prevailing environmental pressures. For example, the injury (often serious) sustained during competition between conspecifics is a compromise resulting from the demand for resources exceeding supply (Geist, 1971; Wilkinson and Shank, 1976; Southwick, 1970). Also, the trauma of weaning in mammals is the compromise solution to parent-offspring conflict (Trivers, 1974). These are instances of considerable suffering occurring in well-adapted animals. The compromise nature of genetic adaptations, along with the inevitable variation between individual animals around the species norm suggests that, at most, only a few members of a few species will be sufficiently well adapted to have their welfare guaranteed.

It might be thought that this does not jeopardize the principle that Beilharz was trying to convey but merely requires it to be qualified. It could thus be suggested that "within the limits imposed by conflicting environmental pressures, welfare, in a species-typical environment, will be optimized by genetic adaptation." This brings me to the second aspect of genetic adaptation about which I have doubts.

A great contribution by Lehrman (1970) to the nature-nurture controversy was to point out that "nature selects for outcomes." By this he meant that natural selection operates on the consequences

of genetically adapted processes rather than on the actual processes themselves. For example, the experience of hunger evolved to regulate the intake of food. So long as an adequate intake of food is achieved without interfering with other biological processes, the nature of the feelings of hunger experienced by the animal will be irrelevant to natural selection. All psychological traits that increase an animal's reproductive fitness will be selected for *even if they cause discomfort and distress in the process.* It is the effects of psychological traits on reproductive fitness which are subject to genetic adaptation rather than their effects on welfare. All of animals' hedonic experiences will be the means of bringing about sexual, exploratory, feeding or other behaviors. Natural selection will genetically adapt animals according to the outcome of these behaviors, rather than the means by which they were brought about. In other words, what the animal experiences is generally unimportant for the purposes of genetic adaptation, provided that it induces the animal to interact appropriately with its environment.

From Beilharz's original suggestion - that we can do no better than to assume that the welfare of any adapted form of life is guaranteed - I have argued that: (1) all the characteristics of individual animals are compromises and not ideal adaptations to the environment; and (2) the welfare effects of psyc_hological traits will not be genetically adapted, provided the animal is induced to interact appropriately with its environment.

The welfare of any genetically adapted animal could therefore be unsatisfactory in the environment to which it is adapted.

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Dr. Beilharz Responds

I largely concur with Dr. Baxter's views, but wish to make the following additional comments.

1. I agree that when populations of animals adapt to their environment, compromises will be made among the different demands that the environment imposes. This must be particularly true in the variable and unpredictable environments of many wild animals and of domestic animals kept extensively.

· One can go further, however, to say that if, in nature, animals continue to be subject to conflicting environmental pressures that genetic adaptation of animals cannot adequately meet, then it is unreasonable for anyone to demand, as many do, that a more complete matching of the environment to the needs of animals should be achieved for farm animals. Even **in** farm animals kept intensively, genetic adaptation is occurring, unless we prevent it, and in due course, even in this "new" environment, welfare "will beoptimized by genetic adaptation."

2. I agree with Dr. Baxter's second point that "nature selects for outcomes." Yes, it is those genes that are passed on, which were carried by the individuals that achieved an adequate food intake resulting in survival and reproduction, regardless of how this came about. However, I believe that if an animal obtains adequate feed only after significant pain or hunger (in other words after some depression of its welfare), while another animal in the same environment does so with less discomfort, there will usually be some real side-effects accompanying the depression in welfare, so that in the long run selection will favor the genotypes whose welfare is not depressed. This leads me to repeat the point in my paper. I believe that the desert mammal no longer suffers frorri thirst (i.e., plagued by a feeling accompanying thirst) in the same way as would a human who had had nothing to drink for 3 days. Thus, I do believe that genetic adaptation will, in general, also take care of the welfare aspects of psychological traits. However, I realize that this is a question that is very difficult to resolve experimentally.

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