HOLMES, W. G., & P. W. SHERMAN. In press. Ontogeny of kin recognition in two species of ground squirrels. Amer. Zool.

INGRAM, C. 1959. The importance of juvenile cannibalism in the breeding biology of certain birds of prey. Auk 76: 218–226.

JENNI, D. A., & G. COLLIER. 1972. Polyandry in the American Jacana (*Jacana spinosa*). Auk 89: 743–765.

JOHNSON, M. S., & J. L. BROWN. 1980. Genetic variation among trait groups and apparent absence of close inbreeding in Grey-crowned Babblers. Behav. Ecol. Sociobiol. 7: 93–98.

KOENIG, W. D., & F. A. PITELKA. 1979. Relatedness and inbreeding avoidance: counterploys in the communally nesting Acorn Woodpecker. Science 206: 1103–1105.

LEWONTIN, R. C. 1974. The genetic basis of evolutionary change. New York, Columbia Univ. Press.

LIGON, J. D., & S. H. LIGON. 1978. The communal social system of the Green Woodhoopoe in Kenya. Living Bird 17: 159–197.

LILL, A. 1974. Sexual behavior of the lek-forming White-bearded Manakin (*Manacus manacus trinitatis,* Hertert). Zeit. Tierpsychol. 36: 1–36.

MADER, W. J. 1975. Biology of the Harris' Hawk in southern Arizona. Living Bird 14: 59–85.

MAYNARD SMITH, J., & M. G. RIDPATH. 1972. Wife sharing in the Tasmanian Native Hen, *Tribonyx mortierii*: a case of kin selection? Amer. Natur. 106: 447–452.

MCCRACKEN, G. F., & J. W. BRADBURY. 1977. Paternity and genetic heterogeneity in the polygynous bat, *Phyllostomus hastatus*. Science 198: 303– 306.

NEVO, E. 1978. Genetic variation in natural populations: patterns and theory. Theor. Popul. Biol. 13: 121–177.

O'CONNER, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide. Anim. Behav. 26: 79–96.

ORING, L. W., & M. L. KNUDSON. 1972. Monogamy and polyandry in the Spotted Sandpiper. Living Bird 11: 59–73.

SAUER, E. G. F., & E. M. SAUER. 1966. The behavior and ecology of the South African Ostrich. Living Bird 5: 45–75.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, & J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Stud. Genet. 6: 49–90 (Univ. Texas Publ. 7103).

SMITH, D. G. 1980. Paternity exclusion in six captive groups of rhesus monkeys (*Macaca mulatta*). Amer. J. Phys. Anthropol. 53: 243–249.

SMITH, R. I. 1968. The social aspects of reproductive behavior in the pintail. Auk 85: 381–396.

STACEY, P. B. 1979. Kinship, promiscuity, and communal breeding in the Acorn Woodpecker. Behav. Ecol. Sociobiol. 6: 53–66.

VEHRENCAMP, S. L. 1978. The adaptive significance of communal nesting in Groove-billed Anis (*Crotophaga sulcirostris*). Behav. Ecol. Sociobiol. 4: 1–33.

WELLER, M. W. 1959. Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. Ecol. Monogr. 29: 333–365.

WERSCHKUL, D. F., & J. A. JACKSON. 1979. Sibling competition and avian growth rates. Ibis 121: 97–102.

YOM-TOV, Y., G. M. DUNNET, & A. ANDERSON. 1974. Intraspecific nest parasitism in the Starling *Sturnus vulgaris*. Ibis 116: 87–90.

SEARCHING FOR ALTRUISM IN BIRDS

HARRY W. POWER[1]

Sociobiology is the application of selection theory to the study of adaptation in general and the evolution of social behavior in particular. Ornithology has played a major role in sociobiology, beginning with Darwin (1859), who frequently used

[1] Department of Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903 USA.

birds to illustrate the role of selection. In turn, sociobiology has influenced almost every area of concern to ornithologists, but here I have space to consider only one of them. Do birds act to maximize their individual fitnesses, or do they act to promote the survival of their species even when that requires a reduction in their own fitness? This problem can be conveniently referred to as *the question of altruism.*

The question of altruism is the central question of sociobiology because upon its resolution rests the veracity of the Darwinian theory of evolution (Alexander 1974). If organisms have evolved to help one another at net cost to their own fitness (altruism), then evolution by natural selection is not possible because selection acting at the level of the individual or lower cannot produce altruism, and selection acting at the level of the group or higher (which can produce altruism) is not sufficiently potent to counteract selection operating at lower levels (Williams 1966). Contrarily, if organisms have evolved selfishly to promote their own fitnesses (reproductive selfishness), then evolution by natural selection is corroborated, and the Darwinian paradigm serves as a fruitful analytical and predictive tool.

Despite the centrality of the question of altruism, few attempts have been made to resolve it by experimental means. Most biologists have been convinced by persuasive pro-selection interpretations, but this is not a substitute for performing an experiment. The difference between science and ideology is that science attempts to falsify its theories through experimentation, while ideology merely rationalizes them.

The question of altruism cannot be resolved in a simple either/or way. It must be resolved on the basis of the frequency of altruistic vs. reproductively selfish acts. Only a high frequency of altruistic acts in nature can be taken as convincing evidence that altruism is a *trait* rather than an *error.* This is because rare acts of altruism can be expected to result from errors in attempts to promote reproductive selfishness, just as fractures can be expected to result from errors in limb movement.

In testing for the presence and frequency of altruistic acts, it is important to separate "altruism" from "beneficence." The latter is a generic term (West Eberhard 1975, Power 1976b) referring to any act helpful to another regardless of its effect upon the donor's fitness. "Altruism" refers only to beneficence that is injurious to the donor's inclusive fitness. Thus "altruism" does not include acts helpful to relatives ("nepotism"; Alexander 1974, Sherman 1980) or helpful to cooperators ("reciprocity"; Trivers 1971, Alexander 1979) *unless* the cost-benefit ratios of those acts generate a decline in the donor's inclusive fitness.

The easiest way to approach the question of altruism is to design an experiment in which potential donors have the option of being beneficient to potential recipients that are *not* related to them but that can use their beneficence and actively seek it. This design eliminates nepotism, insuring that any observed beneficence is either altruism or reciprocity. Altricial birds are excellent subjects for this kind of experiment because adults can be provided with the opportunity to care for nestlings that are unrelated to them and that seek their care through begging.

Power (1975) adapted the classic experiment of biology, the removal experiment, to the study of altruism in Mountain Bluebirds (*Sialia currucoides*). I removed one adult from each of 25 nests (12 males, 13 females) during the nestling period. Ten of the 25 adults were replaced by "consorts," adults that courted mateless birds but that could not be said to have yet formed pair bonds with them. Eight of the consorts were males, two females. No male consorts fed young or cleaned nests, and all gave alarm notes seemingly only in response to the alarm notes of female parents (Power

1975). Males at unmolested nests, however, typically provided care to young about equal to that of females. Of the two female consorts, one was not seen until after fledging of the semi-orphaned young, while the other provided care to the motherless chicks. Thus, with the exception of the second female, consorts were not beneficent.

Pierotti (1980) removed one adult (2 males, 5 females) from each of 7 nests of the Western Gull (*Larus occidentalis*). Both widowed females deserted their nests, but the five widowed males attracted female consorts. All female consorts were beneficent, two of them helping to incubate the unhatched eggs of the removed female parents, and three of them helping to attend, guard, and feed chicks. Pierotti interpreted this beneficence as reciprocity because the two females that he color-banded remained with their males for at least 2 years, i.e. the female consorts helped widowed males rear young in return for permanent pair bonds with them.

Pierotti (1980) also made a discovery that shows that the removal experiment is a valid way of exploring the question of altruism. Emlen (1976) had attacked Power's (1975) experiment, asserting that it did not really give birds a choice of behaving altruistically or selfishly because consorts were not in the proper hormonal state to behave beneficently toward nestlings, since they had not gone through the nesting stages prior to hatching. Power (1976a) rebutted by showing that consorts were capable of beneficence in giving alarm calls and providing food to the female parents they courted. Pierotti's (1980) discovery is an even more convincing demonstration of Power's (1976a) position. Neither of the female consorts he captured showed any sign of brood patches, implying that they had not gone through the previous stages of nesting, yet both incubated the eggs of the males they courted and subsequently cared for the chicks they hatched.

Weatherhead and Robertson (1980) removed eight male Savannah Sparrows (*Passerculus sandwichensis*) from their territories just before hatching of their clutches. Six of these were replaced by consorts. One consort was also removed, but it too was replaced. Six of the seven consorts gave persistent alarm calls when the observer was near the nest, and one carried food to the nest. Weatherhead and Robertson considered the beneficence of consorts to be true altruism in the form of reproductive errors, because the breeding season at their study site was too short to permit a nesting attempt after fledging of a first brood and there seemed to be very little mate fidelity between breeding seasons. However, Weatherhead and Robertson did not consider that low-cost acts of beneficence, such as giving alarm calls toward a human, might be necessary to avoid aggression from female parents that could make it difficult for male consorts to establish territories in the present year that could be defended against the same neighbors in subsequent years. Nevertheless, Weatherhead and Robertson may be correct because one cannot assume that every act is adaptive (Williams 1966).

Rutberg and Rohwer (1980) removed 21 male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) from their breeding territories while some nests of this harem-forming species were still being initiated. All males were replaced within a few days. Replacement males appeared to attack predators indiscriminately, probably because clumping of nests prevented males from determining which nests on their territories a predator might attack; some of these nests probably contained eggs sired by the replacement males. Replacement males, however, did appear to discriminate against foster chicks in dispensing food.

Because each removal experiment has yielded different results and all have been based on small samples, it is clear that the question of altruism is not closed. Considering the openness of the question, its intrinsic importance, and the special suitability of birds as experimental subjects, ornithologists have an opportunity of truly historic dimensions to contribute to the resolution of this most important of questions. Among the many felicitous effects of this contribution will be the return of ornithology to the center stage of biology. Let there be 1,000 experiments on 1,000 species!

Literature Cited

ALEXANDER, R. D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5: 325–383.

———. 1979. Darwinism and human affairs. Seattle, Univ. Washington Press.

DARWIN, C. R. 1859. On the origin of species. London, John Murray.

EMLEN, S. T. 1976. Altruism in Mountain Bluebirds? Science 191: 808–809.

PIEROTTI, R. 1980. Spite and altruism in gulls. Amer. Natur. 115: 290–300.

POWER, H. W. 1975. Mountain Bluebirds: experimental evidence against altruism. Science 189: 142–143.

———. 1976a. Altruism in Mountain Bluebirds? (Reply). Science 191: 809–810.

———. 1976b. Altruism: methodological and definitional issues. Science 194: 562–563.

RUTBERG, A. T., & S. ROHWER. 1980. Breeding strategies of male Yellow-headed Blackbirds: results of a removal experiment. Auk 97: 619–622.

SHERMAN, P. W. 1980. The meaning of nepotism. Amer. Natur. 116: 604–606.

TRIVERS, R. L. 1971. The evolution of reciprocal altruism. Quart. Rev. Biol. 46: 35–57.

WEATHERHEAD, P. J., & R. J. ROBERTSON. 1980. Altruism in the Savannah Sparrow? Behav. Ecol. Sociobiol. 6: 185–186.

WEST EBERHARD, M. J. 1975. The evolution of social behavior by kin selection. Quart. Rev. Biol. 50: 1–33.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton, New Jersey, Princeton Univ. Press.