ELECTROPHORESIS AND AVIAN GENEALOGICAL ANALYSES[1]

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Genealogical relationships between adult birds and the young they attend or among fledglings within a nest cannot always be determined from behavioral observations alone. This is due mainly to internal fertilization, egg laying, and the difficulty of seeing copulations, which are often quick and surreptitious. Kinship may be especially uncertain when females mate with more than one male prior to laying (and vice versa), when females parasitize conspecifics, and when several individuals or pairs contribute eggs to a shared nest. Thus avian polygyny, polyandry, promiscuity, and parasitism pose intriguing genetic as well as behavioral questions. In this essay I reemphasize some of these questions and suggest a central role for electrophoresis in answering them. Because of the importance of testing W. D. Hamilton's (1964) "kin selection" hypothesis to developing a general theory of social behavior, detailed investigations of avian nepotism (favoring relatives) are particularly timely and valuable.

When females copulate with more than one male before laying, which mate or mates are genetically represented in their broods? This question is obviously relevant to birds in which groups of males "force" females to mate multiply (e.g. various ducks; Smith 1968, Burns et al. 1980). It may also be relevant to a wide range of "monogamous" species among which extra-pair copulations turn out to be more common than was once supposed (e.g. various gulls, herons, and swallows; Gladstone 1979), and to those polygynous (e.g. Red-winged Blackbirds, *Agelaius phoeniceus*; Bray et al. 1975), lekking (e.g. White-bearded Manakins, *Manacus manacus*; Lill 1974), and parasitic birds (e.g. Brown-headed Cowbirds, *Molothrus ater*; Elliott 1980) among which at least some females mate polygamously. The paternity question is perhaps most complex among polyandrous species, in which males regularly attend clutches laid by a female that did not mate solely with them. In one extreme, male Galapagos Hawks (*Buteo galapagoensis*; Faaborg et al. 1980), Harris's Hawks (*Parabuteo unicinctus*; Mader 1975), and Tasmanian Native Hens (*Tribonyx mortierii*; Maynard Smith and Ridpath 1972) live in multi-male groups and rear the young of their shared mate in a single nest. No less interesting in this regard are simultaneously polyandrous birds like the American Jacana (*Jacana spinosa*; Jenni and Collier 1972) and sequentially polyandrous species like the Spotted Sandpiper (*Actitis macularia*; Oring and Knudson 1972), in which males nest alone but rear young produced by a female that has multiply mated. Finally, the polygynous/polyandrous mating systems of Greater Rheas (*Rhea americana*; Bruning 1974) and Ostriches (*Struthio camelus*; Sauer and Sauer 1966, Bertram 1979) raise fascinating questions about both paternity and maternity within clutches.

Among cooperatively breeding birds like Mexican Jays (*Aphelocoma ultramarina*; Brown 1970), Acorn Woodpeckers (*Melanerpes formicivorus*; Stacey 1979, Koenig and Pitelka 1979), Noisy Miners (*Manorina melanocephala*; Dow 1977), and Green Woodhoopoes (*Phoeniculus purpureus*; Ligon and Ligon 1978) a slightly different question arises: which males and females contribute genetic material directly to each

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nest? In other words, are such societies most appropriately viewed as pairs plus helpers, groups of reciprocators, polyandrous bands, or communal associations? Among known communal nesters (i.e. several pairs contribute eggs to the same nest), like the Pukeko (*Porphyrio melanotus*; Craig 1980) and the Groove-billed Ani (*Crotophaga sulcirostris*; Vehrencamp 1978), are parents equally genetically represented among broods? Perhaps most important, for all cases of cooperative breeding, do asymmetries in relatedness to eggs and nestlings underly among-helper differences in the intensity of brood care?

The possibility of multiple maternity and paternity within clutches raises a third sort of question: how frequently are nestmates not full-siblings, and what, if any, are the behavioral consequences of intra-brood kinship asymmetries? Intraspecific parasitism obviously results in broods of mixed relatedness (Weller 1959, Yom-Tov et al. 1974). Multiple mating by a female with different males may also create heterogeneous clutches, containing full- and half-sibs. Is it possible that the frequency or intensity of between-chick competition reflects such genetic asymmetries, as well as food abundance and nestling body size differences (see Werschkul and Jackson 1979)? For example, could intra-nest killing and cannibalism in gulls, herons, swallows, and birds of prey (Ingram 1959, O'Conner 1978) sometimes involve differential fratricide of half-sib or nonsibling nestmates? Similarly, do helpers at the nest ever behave as discriminative nepotists, feeding and protecting offspring or full-sibling chicks in preference to equally helpless half-sibs, nieces and nephews, or nonkin?

Answering such questions will probably require a combination of two research strategies. First, it will certainly involve detailed, long-term observations of individually marked birds. Second, it will likely require the use of phenotypic markers to assess genetic similarity due to recent common ancestry. Here I spotlight electrophoresis as a tool for performing such genealogical analyses.

"Electrophoresis" defines a family of molecular genetic techniques that involve separating enzyme products of different alleles at a single locus (allozymes) based on uniqueness of their electrical charges (e.g. Selander et al. 1971). Through the use of electrophoresis an increased understanding of the genetic organization of natural populations has emerged (Lewontin 1974: 95–157, Nevo 1978). Electrophoresis has been particularly valuable to avian biologists in investigations of genetic distances and the likely evolutionary relationships among various taxa (Corbin and Sibley 1977, Avise et al. 1980a), levels of genetic heterozygosity and their possible behavioral consequences (Corbin 1977, Baker and Fox 1978), and population sub-structuring (Baker 1975, Johnson and Brown 1980). "Recipes" are currently available for separating and staining allozyme products of about 30 avian structural genes (Barrowclough and Corbin 1978), and average heterozygosity values ($\bar{H}$) range from 0.128 in Northern Waterthrushes (*Seiurus noveboracensis*) to 0.004 in Magnolia Warblers (*Dendroica magnolia*; Avise et al. 1980b). Thus $\bar{H}$ values for birds ($\bar{x} = 0.05$) are roughly equivalent to those found among other vertebrates. Certainly they are high enough to encourage electrophoretic analyses of avian breeding units.

Among other vertebrates such analyses are just beginning also; they are already yielding intriguing results (e.g. McCracken and Bradbury 1977, Smith 1980). For example, James Hanken and I (1981) recently used allozymes as phenotypic markers in an investigation of paternity within litters of Belding's ground squirrels (*Spermophilus beldingi*). Which mate or mates sire young is an interesting question because at the Tioga Pass, California study site, female *S. beldingi* copulate with one to five different males during their yearly half-day of sexual receptivity. By combining field observations of mating with electrophoretic analyses of the allozymes from six polymorphic loci detectable in blood, we discovered that most litters (78%) are sired by more than one male. Furthermore, there appears to be an unexpected behavioral consequence of the intra-litter genetic asymmetries. In the field, 1-yr-old littermate full-sisters and (maternal) half-sisters treat each other differently: full-sisters fight and chase each other less often, and cooperatively defend territories more often than do half-sibs (Holmes and Sherman in press). The mechanisms by which closely and more distantly related littermates can be distinguished are currently under investigation.

Do similar asymmetries in relatedness exist within clutches of birds? Is genetic monogamy as widespread as biparental care in birds? Does discriminative nepotism occur within nests, between adults and chicks or among nestmates? It is too soon to know, but clearly we need to begin finding out. Integrating long-term field observations with electrophoretic pedigree analyses will allow the separation of putative and genetic kinship, and thus the testing of Hamilton's (1964) hypothesis. The results of such investigations promise not only to expand our knowledge of avian biology, but also to enrich our understanding of the fundamental bases of vertebrate social behavior.

LITERATURE CITED

AVISE, J. C., J. C. PATTON, & C. F. AQUADRO. 1980a. Evolutionary genetics of birds I. Relationships among North American thrushes and allies. Auk 97: 135–147.

———, ———, & ———. 1980b. Evolutionary genetics of birds. J. Heredity 71: 303–310.

BAKER, M. C. 1975. Song dialects and genetic differences in White-crowned Sparrows (*Zonotrichia leucophrys*). Evolution 29: 226–241.

———, & S. F. FOX. 1978. Dominance, survival, and enzyme polymorphism in Dark-eyed Juncos, *Junco hyemalis*. Evolution 32: 697–711.

BARROWCLOUGH, G. F., & K. W. CORBIN. 1978. Genetic variation and differentiation in the Parulidae. Auk 95: 691–702.

BERTRAM, B. C. R. 1979. Ostriches recognize their own eggs and discard others. Nature 279: 233–234.

BRAY, O. E., J. KENNELLY, & J. L. GUARINO. 1975. Fertility of eggs produced on territories of vasectomized Red-winged Blackbirds. Wilson Bull. 87: 187–195.

BROWN, J. L. 1970. Cooperative breeding and altruistic behaviour in the Mexican Jay, *Aphelocoma ultramarina*. Anim. Behav. 18: 366–378.

BRUNING, D. F. 1974. Social structure and reproductive behavior in the Greater Rhea. Living Bird 13: 251–294.

BURNS, J. T., K. M. CHENG, & F. MCKINNEY. 1980. Forced copulation in captive mallards I. Fertilization of eggs. Auk 97: 875–879.

CORBIN, K. W. 1977. Genetic diversity in avian populations. Pp. 291–302 *in* Endangered birds: management techniques for preserving threatened species (S. A. Temple, Ed.). Madison, Wisconsin, Univ. of Wisconsin Press.

———, & C. G. SIBLEY. 1977. Rapid evolution in orioles of the genus *Icterus*. Condor 79: 335–342.

CRAIG, J. L. 1980. Pair and group breeding behaviour of a communal gallinule, the Pukeko, *Porphyrio p. melanotus*. Anim. Behav. 28: 593–603.

DOW, D. D. 1977. Reproductive behavior of the noisy miner, a communally breeding honeyeater. Living Bird 16: 163–186.

ELLIOTT, P. F. 1980. Evolution of promiscuity in the Brown-headed Cowbird. Condor 82: 138–141.

FAABORG, J., T. DEVRIES, C. B. PATTERSON, & C. R. GRIFFIN. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galapagos Hawk (*Buteo galapagoensis*). Auk 97: 581–590.

GLADSTONE, D. E. 1979. Promiscuity in monogamous colonial birds. Amer. Natur. 114: 545–557.

HAMILTON, W. D. 1964. The genetical evolution of social behaviour, I and II. J. Theor. Biol. 7: 1–52.

HANKEN, J., & P. W. SHERMAN. 1981. Multiple paternity in Belding's ground squirrel litters. Science 212: 351–353.

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

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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

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