GENETIC VARIATION AND PARENTAGE IN A CALIFORNIA POPULATION OF ACORN WOODPECKERS

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ABSTRACT.—We examined genetic variation in a California population of the highly social Acorn Woodpecker (*Melanerpes formicivorus*) using starch-gel electrophoresis of 580 blood samples collected between 1975 and 1982. Eighteen genetic loci were resolvable from blood, 2 of which (*Mpi* and *Np*) were polymorphic. One additional locus (*Est-2*) showed variation that was not easily interpreted as an outcome of simple Mendelian inheritance. Average heterozygosity (0.032) was comparable to that of other bird species. Both variable loci showed a slight but not significant deficiency of heterozygotes relative to Hardy-Weinberg expectation. Of 186 nestlings from 62 nests, the genotypes of 4 nestlings (2.2%) from 2 nests (3.2%) were inconsistent with the genotypes of the group breeding males, thus indicating kleptogamy (cuckoldry) in our study population. The low level of genetic variation and the high degree of relatedness between males within groups prevented us from making definitive conclusions concerning the patterns of within-group paternity. Nonetheless, at 1 one-female nest the brood was probably, but not certainly, multiply sired. *Received 23 January 1984, accepted 13 September 1984.*

THE genetic structure of natural populations of social vertebrates is a topic of much current research. Of particular interest is the question of whether social structuring results in decreased effective population size and increased inbreeding, which could in turn promote more rapid rates of evolutionary divergence (Wilson et al. 1975, Bush et al. 1977, Schwartz and Armitage 1980) or the evolution of cooperative or altruistic traits (Brown 1974, Johnson and Brown 1980).

Electrophoretic and other genetic markers have proved useful in investigating alternative reproductive strategies. For example, Hanken and Sherman (1981) found that multiple matings by female Belding's ground squirrels (*Spermophilus beldingi*) result in multiple paternity of most litters. Gowaty and Karlin (1984) suggest that extrapair copulations and intraspecific nest parasitism result in frequent kleptogamy (Gowaty 1982) in the Eastern Bluebird (*Sialia sialis*). Joste (1983) used electrophoretic techniques to document the occurrence of multiply sired broods in a New Mexico population of the communally breeding Acorn Woodpecker (*Melanerpes formicivorus*). Findings similar to these have led Sherman (1981) to encourage a more widespread use of electrophoresis in avian genealogical studies.

We investigated population genetic structure, kleptogamy, and possible multiple paternity by assessing genetic variation in a California population of Acorn Woodpeckers through starch-gel electrophoresis of blood samples. Acorn Woodpeckers in California live in highly social, permanently territorial family groups of 2–15 individuals (MacRoberts and MacRoberts 1976). Groups typically consist of 1 female or 2 related females breeding with 1 male or 2–4 related males (Koenig and Pitelka 1979; Joste et al. 1982; Koenig et al. 1983, 1984; Mumme et al. 1983a, b). In addition to this breeding "core," groups contain 0–10 nonreproductive group offspring (helpers) still living on their natal territory. Among the birds representing the breeding core, pairing behavior and dominance interactions usually are absent (Stacey 1979), and all breeders may contribute to parentage of young (Mumme et al. 1983a, b). Thus, the mating system within Acorn Woodpecker groups may be monogamous, po-

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lygynous, polyandrous, or polygynandrous (Daly and Wilson 1978, Brown 1983), depending upon the composition of the group.

Acorn Woodpeckers show several characteristic behaviors that appear to minimize the frequency of incestuous matings. For example, helpers on their natal territory usually do not acquire breeding status unless their parent of the opposite sex disappears and is replaced by an unrelated immigrant (Koenig and Pitelka 1979, Mumme et al. 1983a, Koenig et al. 1984). Nonetheless, several cases of certain or apparent consanguineous matings have been recorded, either directly through failures of the usual behavioral inbreeding avoidance mechanisms, or indirectly from limited dispersal (Koenig et al. 1984). Thus, the behavioral and demographic data bearing on the extent of inbreeding are equivocal.

The features of Acorn Woodpecker biology discussed above make it a particularly interesting subject for a genetic investigation. The main objectives of our study were as follows: (1) To investigate the genetic structure of a population of Acorn Woodpeckers and to determine the extent to which genetic variability may have been affected by social structure and inbreeding. (2) To determine the frequency with which nestlings are produced either from eggs laid by nongroup females (intraspecific nest parasitism) or from eggs fertilized by nongroup males (cuckoldry). (3) To document the occurrence of multiply sired broods in groups containing 2 or more breeding males, as has been done for Acorn Woodpeckers in New Mexico by Joste (1983).

METHODS

Fieldwork was conducted at Hastings Natural History Reservation, 40 km southeast of Monterey in central coastal California. A color-banded population of Acorn Woodpeckers has been under continuous study at Hastings since 1971 (MacRoberts and MacRoberts 1976, Koenig and Pitelka 1979, Mumme et al. 1983a). Blood samples from 171 adults or independent young and 409 nestlings (18–27 days old) were collected between 1975 and 1982. Samples were obtained by piercing the brachial vein on the underside of the wing (at the "elbow") with a syringe needle, then collecting the blood in 75 μm heparinized microhematocrit capillary tubes. Two tubes of blood usually were obtained.

Whole blood samples were kept chilled at about 4°C until they could be returned to the laboratory for processing (usually within 2 h). Samples were processed by centrifuging them until the plasma and red cell components had separated. Red cells were then washed twice in 0.85% saline solution. After the second wash the red cells were lysed with 2–4 drops of distilled water. Plasma and red cells were kept frozen at −15°C for 1–6 months, then transferred on dry ice to ultracold (−76°C) freezers.

Electrophoretic methods followed standard procedures (e.g. Selander et al. 1971, Barrowclough and Corbin 1978, Yang and Patton 1981). Protein assays were prepared following the methods of Harris and Hopkinson (1976). For all loci at which variation was observed, heterozygotes exhibited the pattern expected based on the subunit structure of the enzyme observed in other vertebrates (see Harris and Hopkinson 1976, Avise et al. 1980). From the banding pattern on the gels, allelic frequencies were calculated for the breeding adults in each year. Heterozygosity was calculated by counting the number of heterozygous loci (maximum of 2) and dividing by 18 (number of loci surveyed). For each year, mean breeding adult heterozygosity was calculated (denoted as $\bar{H}$). Birds were assigned "breeding" or "helping" status based on criteria discussed by Koenig et al. (1984).

For the two variable loci, the Hardy-Weinberg frequencies of expected heterozygotes were calculated using Levene's formula for finite populations (Crow and Kimura 1970: 55–56, Johnson and Brown 1980):

$$H_E = \sum^{i} p_i(1 - p_i)[1 + 1/(2n - 1)],$$

where p_i is the frequency of allele i and n is the number of individuals in the sample. Expected and observed frequencies of heterozygotes were used to calculate the inbreeding coefficient, F, calculated as $F = 1 - (H_O/H_E)$, where H_O is the observed frequency of heterozygotes (Crow and Kimura 1970: 66, Johnson and Brown 1980). The standard error and 95% confidence limits of this estimate of F were calculated using the method of Rasmussen (1964).

RESULTS

Genetic variation.—Fifteen proteins encoded by 18 presumptive genetic loci were resolvable from blood. Sixteen loci were monomorphic: *La-1, Mdh-1, Mdh-2, 6-Pgd, Eap, Hb, Ldh-1, Lgg, Est-1, Est-4, Ab-2, Ab-3, Gpi, Sod-1, Pgm,* and *Icd-1.* Two loci, *Mpi* and *Np,* were polymorphic, with *Mpi* highly so. Four alleles were detected at *Mpi* and 3 at *Np.*

After applying a standard esterase stain (alpha NP-GBC) to plasma samples run on a LiOH gel/buffer system, a complex pattern of bands appeared. Variation was observed at a putative

TABLE 1. Frequencies of alleles at *Mpi* and *Np*, average observed heterozygosity ($\bar{H}$), and sample sizes for breeding Acorn Woodpeckers at Hastings Reservation, 1975–1982.

Locus allele[a]	1975	1976	1977	1978	1979	1980	1981	1982	1975–1982
Mpi									
F	0.03	0.07	0.04	0.04	0.04	0.06	0.03	0.02	0.04
M	0.47	0.37	0.52	0.69	0.57	0.55	0.68	0.58	0.61
S	0.47	0.53	0.40	0.27	0.36	0.37	0.26	0.33	0.31
S−	0.03	0.03	0.04	—	0.03	0.02	0.03	0.07	0.04
Np									
F	0.06	0.09	0.06	0.07	0.11	0.11	0.12	0.11	0.07
M	0.91	0.88	0.92	0.93	0.89	0.89	0.88	0.88	0.92
S	0.03	0.03	0.02	—	—	—	—	0.01	0.01
$\bar{H}$	0.028	0.033	0.026	0.019	0.034	0.036	0.034	0.033	0.032
n[b]	16	15	26	24	38	43	61	62	113
N[c]	89	113	104	110	48	52	82	103	—

[a] Alleles coded by mobility relative to origin: F = fast, M = medium, S = slow, S− = slow "minus."
[b] Average number of individuals scored for both loci.
[c] Total size of breeding population on study area.

locus, *Est-2*, with 4 "alleles." Individuals exhibited either 1 or 2 bands, implying that the protein is monomeric in the active state, i.e. heterozygotes exhibit 2 bands. We concluded, however, that the observed variation may not have a simple genetic basis. In 3 of 6 groups in which only a single male and female were presumed breeders, the "genotypes" of the young could not be attributed to the parents. The genotypes of the offspring at *Mpi* and *Np*, however, were consistent with the parental genotypes. Thus, we think it unlikely that variation at this locus is inherited in a simple Mendelian fashion. This conclusion is supported by the findings of other studies. For example, plasma esterases in the dove *Streptopelia senagalensis* exhibit a pattern of variation in which only a single "allele" is expressed in all individuals, with no evidence of codominance. In at least some cases, the phenotype of an individual dove can show no similarity to its parental phenotypes (Boehm and Irwin 1970). Similar results have been obtained by Bowen and Yang (1978) for esterases of the microtine rodent *Microtus californicus*.

Allelic frequencies for *Mpi* and *Np* in the breeding population during the 8 yr of the study are shown in Table 1. Temporal variation was observed at *Mpi*, especially for the "M" and "S" alleles; the frequency of the "M" allele ranged from 0.37 (1976) to 0.69 (1978), and the "S" allele from 0.26 (1981) to 0.53 (1976). Allelic frequencies at *Np* were temporally stable. Considering only the breeding adults sampled, average individual heterozygosity/yr ranged from 0.019 (1978) to 0.036 (1980). The average heterozygosity across all 8 yr was 0.030, and was 0.032 for the total sample of 113 individual breeders (Table 1). Heterozygosity was similar between the sexes (0.030, $n = 67$ for males; 0.036, $n = 46$ for females), as were gene frequencies at both *Mpi* or *Np*.

Among our sample of breeding Acorn Woodpeckers, a slight deficiency of heterozygotes relative to Hardy-Weinberg expectation was detected at both *Mpi* (observed, 53; expected, 60.45) and *Np* (observed, 13; expected, 16.67). However, neither difference is significant (both $P > 0.1$ by Chi-square test). The observed and expected frequencies of heterozygotes can be used to estimate the inbreeding coefficient, F (see Methods); $F = 0.123$ for the *Mpi* locus, and $F = 0.220$ for *Np* ($\bar{F} = 0.172$). The 95% confidence intervals of these estimates, however, are very large; -0.077 ± 0.323 for *Mpi*, -0.068 ± 0.508 for *Np*. Thus, these results must be interpreted cautiously.

Between-group parentage exclusion analysis.—We obtained blood samples from all adult group members and all nestlings for a total of 52 nests and 160 nestlings from 16 different groups. Genotypes at the *Mpi* and *Np* loci were determined for all the individuals in these groups for parentage-exclusion analysis. Because of the low variability at *Np*, only *Mpi* proved useful in this regard.

TABLE 2. Cases where *Mpi* genotypes of nestlings were not consistent with paternal genotypes. Individual bird identification numbers are shown in parentheses after the genotype. Nestlings identified with an asterisk are inconsistent with the breeding males. See text for details. Genotypes are coded as in Table 1.

Group	Breeding males	Breeding females	Nestlings	Adult male helpers
Plaque 1982	SS (473) FS (521)	MS (494) MS (496)	MS (721) SS (722) MM (723)* SS (724) SS (725) SS (726)	SS (660)
Road 3 1982	FS (68)	MS (265)	SS (792) MM (793)* MM (794)* MM (795)*	FS (537) SS (654) MS (655) FS (656)

In addition to the 52 nests with complete information, for 20 additional nests with 61 nestlings we lacked blood samples from 1 or more breeding males but had samples from the breeding female(s) and all nestlings. For this total of 221 nestlings from 72 nests, all nestlings were attributable to the breeding female or females within the group. Thus, unlike the situation for Eastern Bluebirds (Gowaty and Karlin 1984), we find no electrophoretic evidence of intraspecific nest parasitism from outside the group. This finding also is supported by our behavioral observations: we have never observed extragroup females entering nests, despite having observed egg-laying at many nests (Mumme et al. 1983b). Other than true communal or joint nesting, it appears that intraspecific nest parasitism occurs rarely, if ever, in Acorn Woodpeckers.

For paternity exclusion analysis, we obtained blood samples from all breeding males and all nestlings for 62 nests and 186 nestlings. Of these, 4 nestlings (2.2%) from 2 nests (3.2%) had *Mpi* genotypes that could not be attributed to the breeding males within the group. The genetic data relevant to these cases are shown in Table 2.

In the first case, group Plaque 1982, 1 of 6 nestlings produced by 2 breeding females could not have been fathered by either of the 2 breeding males, or by the male helper present in the group. Behavioral data are also available for this group. During the prenesting and early egg-laying period, both breeding males closely guarded 1 of the 2 females, but not the other. Two of the 6 nestlings were hatched from eggs laid by the nonguarded female (♀496). Although we do not know if the particular nestling in question belonged to this latter female, it seems to us unlikely that an extragroup male would have been able to successfully copulate with ♀494, who was closely attended during the egg-laying period.

In group Road 3 in 1982, 3 of 4 nestlings were not attributable to the only breeding male (♂68). All the nestings could have been fathered by 1 of the first-year male helpers present in the group, ♂655, but this is unlikely. Male 655 was not the dominant male helper in the group, and never followed the female (his mother) during the prenesting period. During 1976–1981, 2 breeding males (♂68 and ♂184) were present in the group, and both strongly guarded the breeding female (see Mumme et al. 1983a: 1099). Just before the 1982 breeding season, ♂184 disappeared, and ♂68's guarding behavior declined significantly (Mumme et al. 1983a). As all the young from 1976 to 1981 were attributable to the 2 breeding males, it seems likely that the apparent kleptogamy in 1982 was related to ♂68's decreased guarding of the breeding female.

Within-group paternity exclusion analysis.— Blood samples were available from all adult group members and all nestlings for 33 nests (103 nestlings) of groups that contained 2 or more breeding males. All offspring in these groups had *Mpi* genotypes that were attributable to the parental genotypes. Using information from the *Mpi* locus, we attempted to determine the patterns of paternity within the group. In this analysis, we assumed that all offspring were produced by the breeding female or females within the group (see above).

Within-group paternity exclusion proved difficult. Because potentially breeding males within groups are nearly always closely related (Koenig and Pitelka 1979, Koenig et al. 1984), breeders of the same sex are likely to share one or both alleles at even highly variable loci like *Mpi*. For example, of the 33 nests that contained 2 or more breeding males, the males' *Mpi* genotypes were identical in 25 cases, thus ruling out any possibility of paternity exclusion based on this locus. At 7 nests the males shared one allele, and at only 1 nest did the 2 breeding males have different alleles.

TABLE 3. Probable case of multiple paternity in a group of Acorn Woodpeckers. *Mpi* genotypes and individual bird identification number (in parentheses) are shown. Assuming that female 483 was the mother, male 234 could not have sired nestlings 664–666, and male 252 could not have sired nestling 663. However, all nestlings could have been sired by the first-year male helper, male 619. See text for details. Genotypes are coded as in Table 1.

Group	Breeding males	Breeding female	Nestlings	Adult male helper
Buckeye 1981	MM (234) SS− (252)	SS− (483)	MS (663) SS− (664) SS (665) SS− (666)	MS (619)

The one nest where the two breeding males shared no alleles at *Mpi* provides compelling, but not conclusive, evidence of within-group multiple paternity in our study population. Genetic information pertaining to this case, group Buckeye 1981, is shown in Table 3. One of the 2 breeding males, ♂234, could not have fathered 3 of the 4 nestlings, while the other breeding male, ♂252, could not have fathered the fourth nestling. Unfortunately, even this fairly clear example is confounded by the presence of a first-year male helper in the group that could have fathered all 4 of the offspring produced by his mother (Table 3). Nonetheless, it seems likely that 3 of the 4 offspring were fathered by ♂252 and 1 by ♂234. In groups with 2 breeding males and 1 breeding female, both males characteristically guard the female during egg-laying, while male helpers do not guard (Mumme et al. 1983a). Males 234 and 252 and a third unsampled male immigrated to group Buckeye in 1979, and these 3 males bred with the same female in both 1979 and 1980. In 1979, ♂234 could not have fathered either of the 2 offspring; in 1980, ♂252 could not have fathered either of the 2 offspring. Although the presence of the unsampled male in 1979 and 1980 introduces difficulties in interpretation, these results nonetheless suggest that within-group reproductive success can be highly variable from year to year, with no individual consistently siring all the offspring (Mumme et al. 1983a, b).

In 4 of the 7 nests where breeding males shared only one allele, 1 male was excluded as the father of 1 or more nestlings. For example, group Plaque in 1980 contained an old breeding male (♂473), his first-year male offspring (♂521), and 2 immigrant sibling females (♀494 and ♀496), neither of which was the mother of ♂521 (Table 4). Male 521 was thus a potential breeder (Koenig et al. 1984). Five nestlings were produced, 4 hatching from eggs laid by ♀494 and 1 from ♀496. Male 473 strongly guarded ♀494 during egg-laying; all of her offspring nonetheless are attributable to either male (Table 4). Male 521 guarded neither female. However, ♀496's lone offspring was fathered by a male carrying the relatively rare ($P = 0.04$) "F" allele at the *Mpi* locus. This allele was absent in ♂473 but carried by ♂521. Thus, based on behavioral and genetic evidence, it seems likely that ♂521 fathered ♀496's single nestling, while most or all of ♀494's were fathered by ♂473. The following year, 1981, both males closely guarded ♀494, and 1 of 3 nestlings that year also contained the "F" allele. In this case, however, we were unable to determine which female was the mother of that nestling.

The two other cases of partial paternity exclusion also are shown in Table 4. In School Hill 1977, 1 of the 2 males could not have fathered 3 of the 4 offspring. In group Y 1977, 1 of the 3 males was excluded as the father of all 3 offspring, even though this male followed the breeding female during egg-laying and performed all nocturnal incubation and brooding (Koenig unpubl. data).

DISCUSSION

Genetic variation.—Few multilocus surveys of avian populations exist (reviewed by Barrowclough 1983); only Johnson and Zink (1983) report on genetic variation in woodpeckers. The average H for Acorn Woodpeckers, 0.032, is slightly lower but nonetheless comparable to that found by Johnson and Zink (1983) for sapsuckers (mean over 4 species = 0.041), and to the avian average of 0.053 (Barrowclough 1983).

The extent to which the social system of the Acorn Woodpecker has affected its genetic

TABLE 4. Cases where *Mpi* genotypes exclude one breeding male as the father of one or more nestlings. Individual bird identification numbers are shown in parentheses after the genotype. Males identified with an asterisk could not have sired the young identified with an asterisk. See text for details. Genotypes are coded as in Table 1.

Group	Breeding males	Breeding females	Nestlings
Plaque 1980–1981	SS (473)*	MS (494)	SS (605)
	FS (521)	MS (496)	SS (606)
			MS (607)
			FS (608)*
			MS (609)
			SS (660)
			MS (661)
			FM (662)*
School Hill 1977	MS (86)	MM (419)	MS (399)*
	MM (256)*		MS (400)*
			MM (401)
			MS (402)*
Y 1977	SS (261)	MS− (16)	SS− (414)*
	MM (322)*		MS (415)*
	MS (364)		MS (416)*

structure is unclear. Our estimate of the inbreeding coefficient F in Acorn Woodpeckers (0.172) is high compared to that of communally breeding Gray-crowned Babblers (*Pomatostomus temporalis*, 0.015; Johnson and Brown 1980) and the nonsocial Great Tit (*Parus major*, 0.0035; Bulmer 1973, Greenwood et al. 1978). Furthermore, it is consistent with our data that indicate that consanguineous matings do occur occasionally in Acorn Woodpeckers, in spite of behavioral and demographic characteristics that promote outbreeding (Koenig et al. 1984). However, the confidence limits around our estimates of F are so large that our data, like Johnson and Brown's (1980) data for Gray-crowned Babblers, are consistent with interpretations of both no inbreeding and high inbreeding. Thus, the genetic data, in addition to the behavioral and demographic data, are equivocal concerning the extent of inbreeding in this population.

Parentage exclusion analysis.—Although electrophoretic parentage-exclusion analyses have potential in avian population studies (Sherman 1981), our work emphasizes some of the difficulties involved. First, genetic variability in our study population was low; only two variable loci were detected from blood samples (compared to the six found by Hanken and Sherman 1981), and only one of these proved useful in parental exclusion. The problem of low variability can be ameliorated somewhat by using muscle (e.g. Baker 1981, Joste 1983), feather pulp (Marsden and May 1984), or other tissue for which a greater number of enzyme systems, and hence possibly more variable loci, can be scored. Second, interpreting banding patterns on gels can be difficult; all results ideally should be corroborated by detailed behavioral observations (e.g. Hanken and Sherman 1981). Third, some loci may show patterns of variation not attributable to simple Mendelian models of inheritance (Boehm and Irwin 1970, Bowen and Yang 1978). Other loci may show phenotypic variation within individuals (McGovern and Tracy 1981). While low-frequency scoring errors and use of questionably Mendelian loci are not critical in general electrophoretic surveys, they must be avoided in parental-exclusion analyses.

A fourth difficulty in avian parental exclusion analyses is the actual effort expended. In our study, 580 blood samples collected over 8 yr and comprising 127 group-yr, 409 nestlings, and 52 completely sampled group-yr yielded minimal information on the frequency of multiple paternity and among-group kleptogamy in Acorn Woodpeckers. Thus, unless several certainly Mendelian, reliable, highly variable loci can be identified (e.g. Hanken and Sherman 1981), the minimal gain from parental exclusion studies simply may not justify the considerable expense and effort involved.

We were unable to make any conclusive statements about patterns of within-group paternity in multimale groups of Acorn Woodpeckers. A factor that contributed importantly to this failure was the close genetic relationship of potentially breeding males within groups. Of 33 nests of groups containing 2 or more breeding males, the males were electrophoretically identical at the *Mpi* locus in 25 cases, and shared one allele in 7 cases. The one instance where the breeding males differed (Table 3) provided a very likely, but not conclusive, case of multiple paternity. In 4 of the 7 nests where the males shared one allele, we were able to exclude 1 of the males as the father of 1 or more offspring (Table 4). From these results, however, it simply is not possible to make an estimate of the frequency of multiply

sired broods in the Acorn Woodpecker. Electrophoretic studies of this species where breeding males are usually unrelated (e.g. Joste 1983) could be potentially more fruitful.

Barrowclough et al. (1984) have summarized allozymic variation within avian populations and discussed its utility in resolving paternity. In most bird populations, most loci are monomorphic, some are moderately polymorphic, and a few are highly polymorphic. It is the latter class of loci that are, on average, the most useful for assessing questions of parentage (Barrowclough et al. 1984). Therefore, we recommend surveying at least 20 individuals from a single breeding population for as many loci as possible. The results of the survey should form the basis for whether proceeding with more electrophoresis would be profitable. For example, if only 1-2 loci are found with alleles segregating at a frequency of approximately 0.40-0.50, only a small percentage of cases of parentage can be resolved (this study). Researchers thus should weigh the costs in time and funds against the potential return, based on the preliminary analysis.

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