nisms as insects (*3*, p. 87) and plants (*3*, p. 6), it seems reasonable to predict that these effects may be expected in the majority of normally outbreeding ungulate species. The evidence that inbreeding often leads to increased juvenile mortality and other deleterious effects in ungulates is at hand and the time has come to institute sound genetic management of small ungulate populations wherever practicable, without waiting for evidence of such effects in each species or population.

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12. The elephant data were obtained from the Washington Park Zoo in Portland. Ore., and the Japanese serow data from Atushi Komori, keeper of the studbook for this species. The sitatunga data were taken from a pedigree published by E. M. Lang [*Zool. Gart. N.F.* **49**, 8-16 (1978)] and the pygmy hippopotamus data from the published studbook [E. M. Lang, *Das Zwergflüsspferd* (Ziemsen, Wittenberg, Lutherstadt, 1975)]. Part of the sable data were obtained from the Baltimore Zoo. Additional sable data and all the data on the 11 other species were collected from the records of the National Zoological Park (NZP), Washington, D.C.
13. Inbreeding coefficients (*F*) were calculated by hand from the formula $F_x = {}^1/_2 \Sigma [({}^1/_2)^n (1 + F_a)]$ (*2*, p. 240). We assumed that the individuals used to found a population were unrelated, although we knew that this assumption was unjustified in some cases. Unless we knew the manner in which individuals subsequently obtained from outside sources were related to existing stock, we assumed they were unrelated. In some cases, it was not possible to calculate an exact inbreeding coefficient although we knew it must be greater than zero.
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Relatedness and Inbreeding Avoidance: Counterploys in the Communally Nesting Acorn Woodpecker

Abstract. *Acorn woodpeckers (*Melanerpes formicivorus*) live in family groups within which more than one female may lay eggs communally in a single nest. Communally nesting females are usually closely related and share evenly in nesting activities. Although birds of either sex may breed in their natal territory, reproductive inhibition of offspring by the presence of their parent of the opposite sex and dispersal by unisexual sibling units ensure that inbreeding between close relatives is rare.*

True communal nesting, in which more than one female regularly lays eggs in the same nest, is known from some ten species of birds (*1*). In none of these has either the genetic relatedness among such females or the consequences of communal nesting on amount of inbreeding been identified. We report such data for the acorn woodpecker. These data are difficult to gather and some of our sample sizes are small; but the results bring out significant components of social dynamics acting to prevent inbreeding and needing attention in studies of all cooperative breeding birds.

In California, the acorn woodpecker typically lives in permanently territorial family groups of 2 to 15 birds (*2*). Only a single nest is attended at any one time by a group, and most or all group members help to incubate and feed the young. Unlike many group-living species, either males or females may breed in their natal territory (*3*), thus apparently presenting unusually great opportunities for inbreeding among close relatives.

As part of a continuing long-term study of the social behavior of this species at the Hastings Natural History Reservation, we recorded intergroup transfers of marked birds and clutch size in relation to group composition (*3*). On the basis of the deposition of two eggs on each of one or more days in a nest (*4*), we found that two females were nesting together in at least 3 of 27 group breeding efforts in which the nest was found before hatching and two or more females were known to be members of the group. Evidence from clutches of groups with differing compositions permits an analysis of the restrictions placed on reproduction by females and the conditions under which more than one female may lay eggs in a nest. Our results suggest that (i) large sets of eggs are the result of true communal nesting rather than intraspecific nest parasitism by females from outside the group, (ii) females do not breed in their natal group as long as their known or presumed father is still in the group, and (iii) communally nesting fe-

Table 1. Relatedness of acorn woodpeckers immigrating in unisexual units of either sex.

Origin	Number of units	Number of individuals
Siblings from the same group	8 (42 percent)	18 (40 percent)
Birds from the same group, two of which were known siblings*	3 (16 percent)	9 (20 percent)
Birds from the same group, one or none of which was known to have been born there*	7 (37 percent)	16 (36 percent)
Birds from different groups	1 (5 percent)	2 (4 percent)
Total	19 (100 percent)	45 (100 percent)

*These units are also likely to have been siblings.

males often consist of siblings that emigrate as a unit from their natal group or, less frequently, of a mother and daughter in groups where the father of the latter has been replaced from outside the group.

The maximum number of eggs in nests of groups with only a single female is five (Fig. 1a), whereas the minimum number in clutches with more than one egg deposited within a 24-hour period is six (Fig. 1b) (*5*). There is no significant difference (*6*) between the number of eggs found in nests of groups with one female (Fig. 1a) and those laid by groups (Fig. 1c) containing *both* of the following: (i) one or more females born into the group and (ii) the presumed or actual parents of (i). Moreover, in five groups with one adult female only, to which was added a female group offspring in the following season without change of parents, there was no change in number of eggs laid (−1,0,0,0,+1 eggs; mean difference = 0.0 egg). Thus female group offspring do not breed when their parents are present.

Reproductive immaturity of young females cannot account for this pattern. Of the 12 pertinent groups (Fig. 1c), four included second-year females that did not breed, even though females of this age can do so after having emigrated out of their natal group. Only rarely is a first-year female in a group without her parents, but in the one case documented during this study the first-year bird laid eggs.

But the effect is more specific. Our evidence suggests that female group offspring fail to breed as a result of the father's presence rather than that of the mother. We followed two groups consisting of a single adult female and one female group offspring but with the father of the latter previously replaced by immigrants. The completed nests of both groups contained seven eggs (Fig. 1d), significantly greater than clutches known to have been laid by a single female (*7*), or by a single adult female plus one or more female offspring when the father was still present (*8*). A third relevant case occurred when a third-year female living on her natal territory who had not reproduced while her parents had been alive laid eggs alone after both her parents disappeared. This is the first evidence to suggest that reproductive inhibition in group-living birds may be mediated by genetic relatives of the opposite sex (*9*) rather than by intrasexual dominance hierarchies (*10*).

Thus, only after the father has been replaced can female group offspring breed in their natal territories. This may occur and also result in communal nesting in two ways. First, a mother-daughter combination may result if the father dies and is replaced from outside the group (observed once). Second, loss of both parents of a female group offspring "releases" her to breed in her natal territory along with a newly immigrated, unrelated female (observed once). More commonly, communal nesting may result when two or more females immigrate together and replace the former breeding female in another group. The number of eggs laid in groups containing immigrant pairs of females averages 6.8 (Fig. 1e), significantly larger than and not overlapping with the number laid by single females (*11*). In four of these five cases, the two females were known or likely to have been siblings.

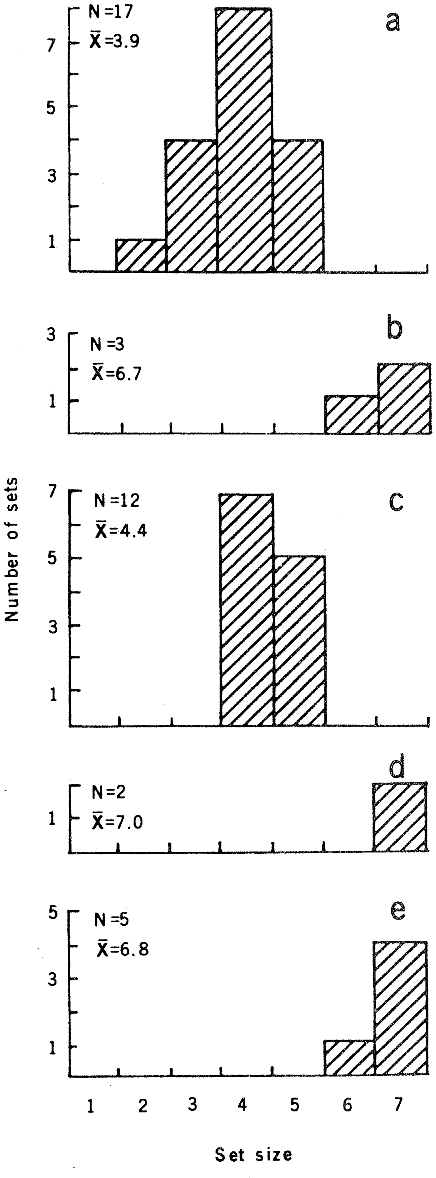

Fig. 1. Number of eggs laid in the completed nests of groups with differing compositions. (a) One female only in the group. (b) Nests in which two eggs were deposited within a 24-hour period on one or more days. (c) Groups containing an adult female, one or more female group offspring, and the presumed or known father of the offspring. (d) Groups with an adult female and one female group offspring whose father was no longer in the group. (e) Groups containing two female immigrants.

The circumstances under which more than one female breeds in a group are thus predictable on the basis of group composition and history. In addition, in no instance was any overt sign of competition observed between communally nesting females, who in one intensively watched case cooperated nearly evenly in incubation and feeding of young. Thus, true communal nesting, rather than intraspecific nest parasitism (*12*), best describes this phenomenon.

When all available data are used, the frequency of communal nesting can be estimated. Of 42 nests discovered during incubation between 1975 and 1978, 11 (26 percent) contained six or seven eggs. Of 131 eggs sets of Californian acorn woodpeckers we examined in museum collections, 48 (37 percent) contained six or more eggs; the most eggs found in any set was 13. Thus, on the average in any 1 year, 26 to 37 percent of all nests are the product of two or more females and at least 41 to 54 percent of all breeding females nest communally.

In addition to reproductive inhibition of offspring in their natal territory by parents of the opposite sex, the probability of inbreeding in the acorn woodpecker is further reduced because intergroup transfer, although frequently done by groups, is always by unisexual units of either sex. Male units average 1.7 individuals (range 1 to 4), whereas female units average 1.3 individuals (range 1 to 2). Sixty-five percent of males (N = 65) and 50 percent of females (N = 48) immigrate in the company of at least one other individual of the same sex. These units are nearly always composed of siblings (whether full or half is usually unknown) born in the same group, though not always in the same year. Among 19 immigrating units of either sex and of known origin (Table 1), most were known or suspected to be composed entirely of siblings.

Despite this high incidence of relatedness, the observed patterns of reproductive inhibition and unisexual sibling dispersal ensure that inbreeding is rare. Furthermore, it is significant that exogamy is not merely an automatic consequence of dispersal; instead, parent-offspring incest is actively avoided despite ample opportunity for it to occur. A set of three behavioral rules accounts for this pattern: (i) If a female is in her natal group and a male who was reproductively active when the female was born is still in the group, the female does not breed. (ii) Once a female disperses, she breeds. (iii) Birds disperse alone or in unisexual units only.

That these rules may also be sufficient to account for the pattern of inbreeding avoidance is suggested by two types of rare anomalies which have led to possible inbreeding. First, by rule (i) above group offspring are inhibited from reproduction by their parent of the opposite sex. But siblings may inbreed if the parents of a bisexual set of offspring both die at about the same time (observed once). Second, by rules (ii) and (iii), the probability of relatives of both sexes moving to new groups and breeding together outside their natal territory is reduced. But, individuals of common group origin have been observed to immigrate separately to the same group and subsequently to breed together (observed twice). A mating between siblings is presumably as deleterious as that of parent-offspring incest (both result in an equivalent degree of inbreeding). However, the conditions leading to the former are apparently so unusual that no mechanism has evolved to avoid it on the rare occasions when the opportunity arises.

Another consequence of the acorn woodpecker's mating system is that group offspring are frequently not full siblings, even when all have fledged from the same nest. This will be the case whenever communal nesting occurs, even if the females themselves are closely related. This diminution of relatedness between siblings will be further accentuated if more than one male breeds in a group. Such promiscuity within groups means that nonbreeding nest helpers (group offspring still in their natal group) are *less* closely related to subsequent siblings whom they help to feed than a hypothetical helper in a permanently territorial monogamous species, where siblings more often share both parents even when born in successive broods (*13*). Similarly, individuals in unisexual sibling units of the acorn woodpecker who immigrate together and ultimately nest communally are likely to share fewer of their genes than siblings in monogamous societies. Thus, our data reveal mechanisms that lower the genetic relatedness between cooperating individuals by promoting multiple parentage of nest helpers, a phenomenon not previously predicted to occur among cooperative breeders (*14*).

These results support the findings of others in pointing out some of the complexities underlying social organizations that superficially seem to entail considerably reduced gene flow and low effective population sizes (*15*). In the case of the acorn woodpecker, the apparent stability of family groups is deceiving; specific behavioral mechanisms, detectable only in long-term study of banded individuals, act to reduce inbreeding. Genetic heterogeneity within social units is thus maintained despite their communality in nesting.

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3. W. D. Koenig, thesis, University of California, Berkeley (1978). Birds were individually color-banded and many were fitted with plastic wing streamers. Histories of 477 birds have been followed since 1971, when banding was begun. Our work, based on 68 nest histories, was conducted between July 1974 and September 1978. Some data were also drawn from 24 earlier such histories (*2*). Hastings Reservation is located 30 miles southeast of Monterey in central coastal California.
4. In birds, the minimum interval between eggs laid by a single female is 1 day [D. Lack, *Ecological Adaptations for Breeding in Birds* (Methuen, London, 1968), p. 187].
5. The latter is significantly larger (Mann-Whitney U test, $n_1 = 17$, $n_2 = 3$, $U = 0$, $P < .01$).
6. Mann-Whitney U test, $n_1 = 17$, $n_2 = 12$, $U = 66$, $P > .10$.
7. Mann-Whitney U test, $n_1 = 17$, $n_2 = 2$, $U = 0$, $P < .05$.
8. Mann-Whitney U test, $n_1 = 12$, $n_2 = 2$, $U = 0$, $P < .05$.
9. We also have evidence that male group offspring may suffer reproductive inhibition in the presence of their mothers.
10. Intrasexual subordinance has been implicated as being responsible for reproductive inhibition in the Australian magpie *Gymnorhina tibicen* [R. Carrick, *U.S. Dep. Inter. Wildl. Res. Rep.* **2**, 41 (1972)], and has been shown to result in inhibition of sexual maturation in other natural populations of vertebrates [R. Borowsky, *Science* **201**, 933 (1978)].
11. Mann-Whitney U test, $n_1 = 17$, $n_2 = 5$, $U = 0$, $P < .001$.
12. See Y. Yom-Tov, G. M. Dunnet, A. Anderson, *Ibis* **116**, 87 (1974).
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Parabolic Flight: Loss of Sense of Orientation

Abstract. *On the earth, or in level flight, a blindfolded subject being rotated at constant velocity about his recumbent long body axis experiences illusory orbital motion of his body in the opposite direction. By contrast, during comparable rotation in the free-fall phase of parabolic flight, no body motion is perceived and all sense of external orientation may be lost; when touch and pressure stimulation is applied to the body surface, a sense of orientation is reestablished immediately. The increased gravitoinertial force period of a parabola produces an exaggeration of the orbital motion experienced in level flight. These observations reveal an important influence of touch, pressure, and kinesthetic information on spatial orientation and provide a basis for understanding many of the postural illusions reported by astronauts in space flight.*

Many sensory channels provide information about body orientation. Normally, these representations are concordant and specify the same relations of the body to the environment. We describe here the dynamic sensory interactions that determine apparent posture when the body is exposed to increases and decreases in gravitoinertial force while horizontal and being rotated about its long body axis, the Z axis. These observations indicate that when touch and pressure stimulation and vision are denied during exposure to free fall, all sense of orientation to the environment may be lost. They also provide a basis for understanding many of the postural and sensory illusions experienced by astronauts and cosmonauts during orbital space flight.

Several receptor systems transduce information about acceleration. The semicircular canals respond to angular accelerations and are activated minimally or not at all when one is rotated at constant velocity about his horizontal Z axis. The otolith organs respond to linear acceleration and are dynamically active during horizontal Z-axis rotation under normal gravitational conditions, because they are being continually reoriented in relation to the gravitoinertial force vector. The pressure on the surface of the body also changes systematically during rotation as a consequence of the contact forces of support provided by the me-