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Non-Breeder Asymmetry in Florida Scrub Jays

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KEYWORDS

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ABSTRACT

The data of Woolfenden and Fitzpatrick (1984) show a statistically significant asymmetry in the sex ratio of non-breeders when one of the breeders is not the non-breeder's parent. 1 propose that the asymmetry is attributable to a combination of two factors acting on non-breeders: the value of inheriting a territory, and incest avoidance. Although natal territories are only occasionally inherited by non-breeders, and then apparently only by males, the rate of inheritance is significantly higher for parent/step-parent breeders (n = 6) than when both breeders are the non-breeder's parents (n = 1). An alternative hypothesis, that step-parents determine the non-breeder asymmetry by ousting potential rivals, might also explain the data, but evidence is currently lacking.

In their long-term study of communal breeding in the Florida Scrub Jay, *Aphelocoma coerulescens coerulescens,* Woolfenden and Fitzpatrick (1984; 1986) have described a number of asymmetries in the behavior of males and females. I wish to add to their list by noting a provocative asymmetry in their data that has implications for different benefits of communal breeding behavior. The asymmetry I consider to be interesting is that, in cases where a nonbreeder accompanies a breeding pair comprising its parent and a step-parent (n = 61), there is a significant propensity for the non-breeder and parent to be of the same sex (χ^2 = 6.27; df = 1; $p < 0.025$). The relevant data are reproduced in Table 1.

I propose the following hypothesis to explain the asymmetry shown in Table 1. Non-breeders tend to accompany a same-sex parent/step-parent breeding pair because, should the parent die, the non-breeder can form a non-incestuous pairing with the remaining breeder. In this way, the non-breeder improves its chances of acquiring the territory and breeding on it. Thus, the asymmetry in question is governed by two factors: the value of inheriting a territory, and incest avoidance. Although Woolfenden and Fitzpatrick (1984) use the term 'helper' almost exclusively, I have replaced the term with 'non-breeder' in this paper since not all non-breeders are necessarily helpers (Brown, 1987). The term 'helper' is used only when I distinctly mean a nonbreeder who engages in helping behavior.

Florida Scrub Jays form large breeding units comprising a single breeding pair and up to six non-breeders (Woolfenden and Fitzpatrick, 1984). Suitable habitat appears to be saturated and each breeding unit defends a territory. A Florida Scrub Jay non-breeder attains breeding status through acquiring a territory. According to Woolfenden and Fitzpatrick (1984), territories may be acquired: (1) by replacing a dead or impaired breeder away from home; (2) by occupying a segment of one's own family's territory (budding); (3) by inheriting the natal territory following the death of one or both of the breeders; or (4) by establishing a new territory between existing territories.

Table 1. Relationship of non-breeders to recipient breeders for those cases where the relationship between breeders and non-breeders is either parent/parent or parent/step-parent. Percentage column represents the percentage of all breeder/non-breeder relationships observed by Woolfenden and Fitzpatrick (1984), some of which (for example uncles, aunts, and grandparental relationships) are not included in this table.

Breeders	Non-breeders				
	Males	**Females**	**Sex unknown**	**Total**	**%**
Father/mother	69	76	16	161	64.1
Father/stepmother	21	9	---	30	12.0
Stepfather/mother	10	17	4	31	12.4
	Total percentage of all non-breeder/breeder relationships =				88.5

In terms of indirect selection, the optimal breeding pair to help is one's own parents because the offspring produced are the helper's full sibs. If only one of the breeding pair is the helper's parent, then the offspring produced are the helper's half-sibs; the sex of the parent makes no difference to the helper with respect to indirect selection. But, if the parent and the helper are of the *same* sex, it should improve the helper's prospects of acquiring the territory. An example will illustrate this point. If a male is helping his mother paired with a stepfather and the stepfather should happen to die, the helper is not in a good position to assume the vacancy left by the stepfather because the resultant pairing would be incestuous. Alternatively, if the male were helping his father paired with a stepmother, death of the father leaves the prospect of a fruitful pairing with the surviving stepmother.

So, while a parent/parent breeding pair is best for the non-breeder in terms of indirect selection, a parent/step-parent mating for which the parent is the same sex as the non-breeder should offer the best prospects for full natal territory acquisition. In a majority of cases, non-breeders are with both their parents (see Table 1), and thus can maximize indirect selection benefits. The existence of parent/step-parent pairs in which the parent is the opposite sex from the non-breeder (n = 19) further suggests indirect selection benefits. The significantly greater proportion of parent/stepparent relationships for which the parent is the same sex as the non-breeder (n = 38) suggests an added benefit of increased chances of territory inheritance.

While incest avoidance seems a reasonable explanation for the asymmetrical non-breeder structure of Florida Scrub Jays, observations by Woolfenden and Fitzpatrick (1984) would seem at first to lend only limited support to this hypothesis. As they assert (p. 93), inheritance of the natal territory seems to be the best option for a non-breeder since breeding space is limited and space familiar to a potential breeder is optimal. However, they observed this mode of inheritance only occasionally. In 48 observations of male non-breeders becoming breeders during the 1970s, only six (13%) involved inheritance of the full natal territory (Woolfenden and Fitzpatrick, 1984). Inheritance of natal territory by a female has been observed on just three occasions, and in none of these did it involve directly replacing the previous female breeder.

Of greater significance than the *absolute* rate of natal territory inheritance might be the *relative* rate. Woolfenden and Fitzpatrick (1986) report that at least six times, successful pairing by a nonbreeder on his natal territory has occurred when the surviving breeder was a step-parent of the non-breeder rather than its natural parent. (It is not clear as to whether all six of these observations comprise the 13% of territory inheritances cited earlier.) Only one case of an incestuous pairing (mother/son) on the natal territory has been observed, although opportunities for step-parental pairings should arise about 2.5 times less frequently than should opportunities for incestuous pairings (see percentage column in Table 1). Assuming that death of a breeder is equally likely for parent/parent and parent/step-parent breeding pairs,

the greater incidence of step-parental compared with incestuous pairings is statistically significant when weighted for the relative frequency (72% : 28%) of each pair type (binomial $p = 0.004$).

J. L. Brown (pers. comm.) has offered an alternative hypothesis to account for the nonbreeder asymmetry discussed in this paper. He suggests that it is the step-parent, and not the nonbreeder, that determines the inequality in the non-breeder proportions. If the non-breeder is of different sex than the step-parent, the step-parent regards the non-breeder as a potential mate; if the non-breeder and step-parent are of the same sex, the non-breeder is regarded as a potential rival. Since step-parents probably make life more miserable for potential rivals than potential mates, potential rivals tend to leave the group more than potential mates.

Brown's hypothesis assumes that a step-parent has no way of knowing that, in practically every case, the 'potential rival' is the offspring of the parent and therefore, based on incest avoidance, is not a rival at all. Although Woolfenden and Fitzpatrick (1984) suggest that Florida Scrub Jays are poor at identifying genetic relatives, I know of only one observation of a step-parent acting aggressively towards non-breeders, that of two males that were apparently driven from their natal territory by an aggressive stepfather. Brown's hypothesis deserves closer scrutiny, but it currently suffers from an unproven assumption and a paucity of supportive data.

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