

POLYANDRY AND INCEST AVOIDANCE IN THE COOPERATIVE STRIPE-BACKED WREN OF VENEZUELA

by

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(With 2 Figures)

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Summary

We made behavioral observations in 37 social groups of the communal stripe-backed wren during 1990 and 1991 to investigate the recently-discovered shared paternity between dominant and subordinate males (or "SMs"). We found two distinct kinds of social groups that differed in terms of social behavior: "mother" groups, which contained only subordinate males that were sons of the dominant female (termed "DF-sons"), and "stepmother" groups, which contained at least one subordinate male unrelated to the dominant female (termed "DF-stepsons"). In mother groups only dominant males courted dominant females, mate-guarding was infrequent and aggression by dominant males toward other males was absent. On the other hand, stepmother groups were characterized by frequent association with and courtship of dominant females ("DFs") by both dominant males ("DMs") and DF-stepsons and relatively frequent aggression by dominant males toward DF-stepsons. DF-stepsons, moreover, sired 15% of all young in stepmother groups. Thus, incest avoidance dictated the behavior of subordinate males, and the mating system in wren groups was either monogamous or polyandrous, depending upon the relatedness between subordinate males and the dominant female.

Introduction

The discovery that some adult animals forego reproduction and help to raise young not their own (SKUTCH, 1935) and subsequent elaboration of

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theoretical models to explain helping behavior (*e.g.* HAMILTON, 1963) touched off an explosion of studies of helping behavior in the 1960s and 1970s, many of which continue today (see BROWN, 1987 for a review). The enormous amount of research on cooperative breeders, as species with helpers are called, has led to an understanding of the variability in helping behavior between species and has resulted in the formulation of numerous hypotheses to explain the evolution of helping behavior.

One point that has become clear to those studying cooperative breeders is that the terms "helper" and auxiliary" are often used to describe individuals that, in fact, exhibit a wide range of behaviors of which only a fraction are altruistic. A clear example of this underlying complexity is in the pied kingfisher (*Ceryle rudis*) of Kenya, in which REYER (1984, 1986) has recognized two distinct classes of helpers, primary and secondary. The behavior of primary helpers is altruistic (that is, resulting in loss in direct fitness by the donor and a gain in direct fitness by the recipient; BROWN, 1987) because they assist a breeding pair to raise young without receiving a benefit to their own direct fitness. Secondary helpers do not behave altruistically, because they provide assistance primarily as a means of establishing a social bond with a breeding female so that they can pair and breed with her in the future (REYER, 1986). Similar variability in degree of helping versus breeding behavior has been noted in other cooperative breeders (*e.g.* acorn woodpeckers *Melanerpes formicivorus*, MUMME *et al.*, 1983; Galapagos mockingbirds *Nesomimus parvulus*, CURRY & GRANT, 1990).

The stripe-backed wren (*Campylorhynchus nuchalis*), a cooperative breeder native to Colombia and Venezuela, is a species in which results of parentage analysis have revealed greater complexity in the behavior of male helpers than was recognized previously. In this species, helpers of both sexes (termed "subordinates") are usually young that have remained with their natal groups (69 of 74 subordinates in 1991, 93%), and they assist dominants in virtually all aspects of year-round territory maintenance and reproduction. The pattern in parentage, as revealed by DNA fingerprinting, is clear: 1) dominant females are mothers of all juveniles in all groups, 2) dominant males sire all offspring in "mother groups" (wherein all subordinate males are "DF-sons", sons of the dominant female), and 3) dominant males sire 85% of the offspring in "stepmother groups" (which contain "DF-stepsons", subordinate males unrelated to

the dominant female); the remaining 15% are sired by DF-stepsons (see RABENOLD *et al.*, 1990).

As a means of following up the discovery of shared paternity, we studied the associations between subordinate males ("SMs"), dominant males ("DMs") and dominant females ("DFs") to determine whether or not DF-stepsons systematically attempted to associate with DFs during their fertile periods. We made two simple predictions based on the idea that DMs and SMs should maximize their chance of siring offspring in their groups. Considering the ability of DF-stepsons to sire offspring, we predicted that DMs should guard DFs in stepmother groups. Since DMs in mother groups suffered no cuckoldry from SMs in their group or other males outside the group, we predicted little or no mate-guarding in mother groups.

Methods

Study area and study species.

Our study site was Hato Masaguaral, a cattle ranch in a lowland palm (*Copernicia tectorum*) savanna located about 300 km south of Caracas, Venezuela. The ranch contains stands of leguminous trees in which stripe-backed wrens forage and roost (for a more complete description of the study site, see RABENOLD, 1990). Two distinct seasons occur in the lowland savanna: a wet season from May to November when rainfall occurs commonly to the point where standing water from a few cm to a meter in depth covers most of the ground, and a dry season from December to April when little or no rain falls and the ground becomes dry except for scattered permanent water sources. Stripe-backed wrens, like most other species in the area (see THOMAS, 1979), breed during the wet season when the insects they consume and feed to their young are abundant.

The medium-sized (25 g) stripe-backed wren is a loud and conspicuous member of the avian community in the study area. Social groups of this species consist of a dominant pair and from 0 to 12 subordinates, which are usually offspring produced by the group that have not dispersed (see RABENOLD, 1990). Groups defend exclusive, all-purpose territories of roughly 1-4 ha in size, subsist on insects gleaned from trunks and small branches of large trees and often roost and breed in stick nests built by a sympatric thornbird (Furnariidae: *Phacellodomus rufifrons*).

The social groups of wrens observed at Hato Masaguaral have been individually marked with colored leg bands since 1985 or before. From 1985 to the present, demographic data on histories of about 60 groups have been maintained by twice-annual censuses and annual banding of unmarked immigrants and juveniles. These data have shown that wrens of both sexes usually remain with their natal groups for a year or more, after which all females and many males (31 of 49 males since 1985, 63%) disperse from their natal groups to breed in unrelated groups (RABENOLD, 1990). The remaining 37% of surviving subordinate males rise to breeding status through the death or dispersal of older, more dominant males in their natal groups. As a result of the female-biased dispersal system and 63% annual survival rate of dominant females (RABENOLD, 1990), about two-thirds of all wren groups are stepmother groups (*i.e.* those that contain at least one DF-stepson) and the remainder are mother groups.

Focal samples.

From April through June of 1990 and 1991, we carried out focal samples in color-banded groups containing at least one subordinate male to determine patterns of association between group members and dominant females during the fertile periods of DFs. Focal samples commenced when the observer first identified the DF in a group and were carried out by following the DF and simply recording the identities of any other group members within 2m of her at every minute for 15 minutes. The distance of 2m was selected both because this simplified the recording of data and because a first wren, regardless of its status in the group, usually remained within 2m of the second wren with which it was associating. We also recorded all behavioral interactions that occurred before and during the samples including following of one wren by another, duets (between group members of opposite sex; see RABENOLD, 1990), courtship (see below), aggression and allopreening. Observations were done consistently from 0600-1200 and 1700-1800 each day, and the sequence in which groups were visited was rotated so that there was no bias in the time of day during which groups were observed. Few enough behaviors occurred during observation periods that few or none of the behaviors analyzed below were missed during any observation period.

We selected 15 stepmother groups and 9 mother groups for focal sampling every other day in 1990. In 1991, focal samples were done every day in 9 stepmother and 4 mother groups. Of 9 stepmother groups observed in 1991, 5 contained the same dominants and subordinates as in 1990, 3 contained a new DF and had been observed as mother groups the previous year, and 1 had not been observed in 1990. Of 4 mother groups observed in 1991, 1 was unchanged from 1990, 2 had changed from stepmother groups to mother groups after the disappearance of the DM, and the fourth was a new group. Observation of the same groups in two consecutive years offered a chance to investigate the behavior of individuals over time and as the compositions of their groups changed.

Determination of fertile periods.

The fertile period, the period during which copulations by males were capable of fertilizing eggs laid by females, has never been determined precisely for any free-living passerine (BIRKHEAD & MØLLER, 1992). We estimated fertile periods for stripe-backed wrens as follows. First, we used observations of nesting behavior to establish, for each nesting attempt, the date on which feeding of young was first observed. Then we subtracted from this date a fixed number of days based on: 1) an estimate of 18 d for the incubation period, 2) incubation commencing with the laying of the penultimate egg, 3) a clutch size of four, and 4) an estimate of eight days for viability of sperm (see BIRKHEAD & MØLLER, 1992). For example, the LD group in 1991 was first observed feeding young on 3 May. We subtracted 28 and 18 days, respectively, from 3 May to establish the first (5 April) and last (15 April) days of the fertile period for this breeding attempt. In the case of three group attempts that resulted in the fledging of shiny cowbirds *Molothrus bonariensis* (which hatch in 11 days; CRUZ *et al.*, 1990), we subtracted 21 and 11 d, respectively, to define the beginning and end of the fertile period for wren eggs.

Analysis of parentage.

We used DNA fingerprinting to determine the parentage of offspring produced by focal groups. The techniques used are presented in detail elsewhere (RABENOLD *et al.*, 1990), and here we will only summarize them briefly. Blood samples were taken from the brachial veins of adults, fledglings or nestlings and blood cells preserved in phosphate-buffered saline solution at 4° C. We extracted DNA from samples using phenol followed by chloroform/isoamyl alcohol, digested DNA with the *HaeIII* or *HinfI* enzymes, and ran the

resulting fragments on agarose gels. After Southern transfer, we probed filters with radioactively-labelled Jeffreys' probes 33.6 and 33.15 and produced autoradiographs on X-ray film to visualize fragments. We assigned parentage by looking for unique bands in fingerprints of adult group members that were present also in lanes of juveniles (see RABENOLD *et al.*, 1990 for a more complete description of scoring methods and for photos of autoradiographs).

Statistical analysis.

Sample sizes varied in statistical tests because some groups had begun breeding before observations commenced in 1990 and because we had to exclude some groups from analyses when the difficulty of observing them resulted in less than 30 minutes of consistent focal sampling on the DF being recorded during the season. In addition, only data from 1991 (in which more data were available) were used in cases where the same pair of dominants was observed in both 1990 and 1991. All statistical tests were based on SOKAL & ROHLF (1981).

Results

Associations between males and females.

The only group members observed to associate with dominant females consistently were dominant males and DF-stepsons, and the general pattern in their associations was fairly constant between social groups. Males typically associated with DFs for "bouts" of 5-10 minutes and then left them, presumably to forage elsewhere. Bouts of association by DF-stepsons were often curtailed by the arrival of the DM, which then often began a bout of his own. Subordinate females and DF-sons rarely associated with dominant females for more than a few minutes at a time. For their part, dominant females appeared indifferent to the behavior of males and were never observed trying to escape the attention of one male in order to associate with another as has been reported in dunnocks (DAVIES, 1992).

As predicted, DMs in stepmother groups tended to be observed more often within 2 m of DFs during the fertile period (mean = $43 \pm 14\%$ SD of DF's time, $N=17$) than were DMs in mother groups ($28 \pm 17\%$, $N=9$; $U_s=97$, $p<0.05$, two-tailed Mann-Whitney U Test). In particular, DMs in stepmother groups spent more time near DFs on days -2 to 1 of the nesting cycle, near the end of the fertile period (Fig. 1).

The absolute number of males in mother groups also affected the amount of association between DMs and DFs during the fertile period. DMs in mother groups with only one DF-son spent significantly less time

($18 \pm 12\%$ SD, $N=5$) with DFs than did DMs in mother groups containing 2 or more sons ($40 \pm 15\%$ SD, $N=4$; $U_s=19$, $p<0.05$, two-tailed Mann-Whitney U Test). In stepmother groups there was also a non-significant tendency for DMs to associate more with DFs in groups containing more than one DF-stepson ($39 \pm 15\%$, $N=10$ with only one DF-stepson; $49 \pm 10\%$, $N=7$ with ≥ 2 DF-stepsons; $U_s=50$, $p=0.2$, two-tailed Mann-Whitney U Test).

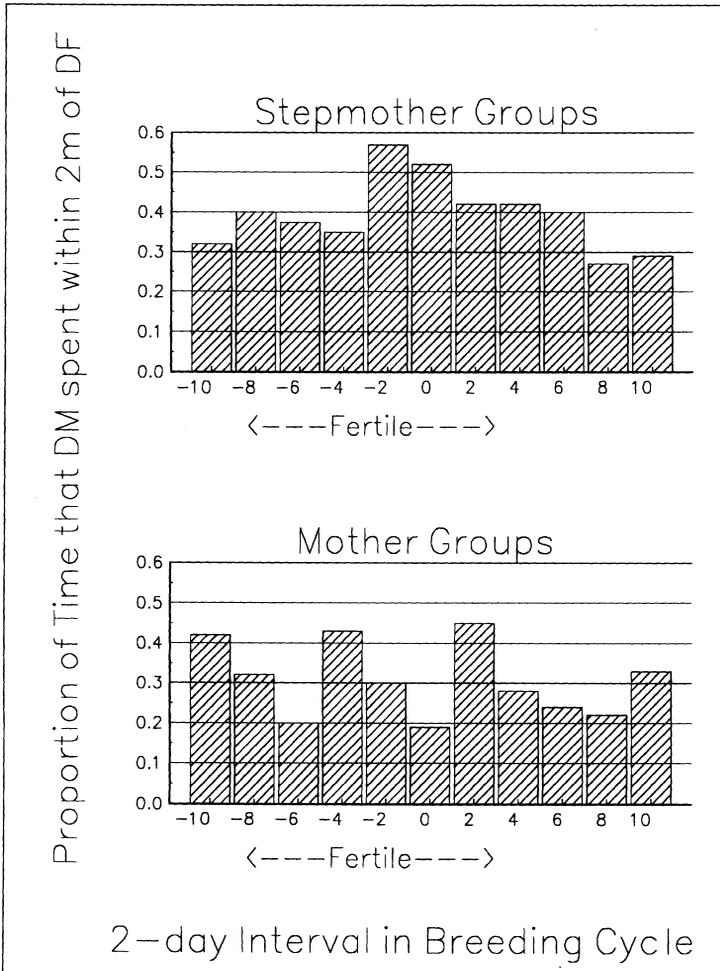


Fig. 1. Mate-guarding by dominant males and females in mother and stepmother groups. During the fertile period, DMs in stepmother groups guarded DFs more than did DMs in mother groups.

The association between DMs and DFs during the fertile period resulted mainly from DMs following DFs and not the reverse; this was especially true in stepmother groups. In groups wherein 5 or more follows were observed between DMs and DFs, DMs followed in 89% (± 13 SD, $N=146$ follows in 11 groups) of the cases in stepmother groups and 74% (± 16 SD, $N=42$ follows in 5 groups) of the cases in mother groups, a significant difference ($U_s=85.5$, $p<0.05$, two-tailed Mann-Whitney U Test by group).

In some groups DMs obviously "shadowed" DFs intermittently over a period of several days. During these periods, DMs often sat for minutes at a time watching DFs feed while feeding little or not at all themselves. Shadowing of DFs by DMs was observed in 7 stepmother and 2 mother groups and reported once each on days -10, -9, -8, -7 and -6, twice each on days -1 and 0, and 3 times on day 2. Thus, incidents of shadowing by DMs were clustered somewhat on the few days just prior to the onset of incubation.

Although the absolute amount of time spent by SMs within 2m of DFs was small, DF-stepsons spent significantly more time within 2m of DFs ($9.5 \pm 7.0\%$ SD of DF's time, $N=27$) than did DF-sons ($4.4 \pm 3.2\%$, $N=17$) during the fertile period ($U_s=330$, $p<0.02$, two-tailed Mann-Whitney U Test). As with DMs, these patterns in association resulted primarily from SMs following DFs and not *vice-versa*. Out of a total of 88 cases in which a DF followed a subordinate male or *vice-versa*, in 78 (89%) the SM followed the DF (20 out of 25 cases were DF-sons following their mothers; 58 of 63 were DF-stepsons following DFs).

Like dominant males, DF-stepsons shadowed DFs from time to time, but shadowing by DF-stepsons tended to occur at times other than during the fertile period. One DF-stepson was observed to shadow the DF on day 4 (the day that the last egg was laid) and a second DF-stepson in a different group shadowed the DF in his group on days 20 and 27 of the breeding cycle.

Finally, age appeared to affect the degree to which DF-stepsons associated with dominant females. First-year DF-stepsons associated less with DFs (mean of $3.0 \pm 3.1\%$ SD of DF's time spent within 2m of first-years, $N=5$) than did DF-stepsons at least 2 years of age (mean= $10.3 \pm 6.7\%$, $N=21$; $U_s=87$, $p<0.05$, two-tailed Mann-Whitney U Test).

There is some evidence that the amount of time dominant males spent near dominant females was affected by associations between DFs and DF-stepsons. Those groups in which DF-stepsons associated often with DFs were also those in which DMs spent large percentages of time near DFs (associations combined for all DF-stepsons; product-moment correlation coefficient=0.49, $p < 0.05$).

Visits to the nest by males.

In four cases, repeated entries by a male into the brood chamber coincided with the onset of egg-laying and appeared to signify substantial interest in this event on the male's part. For example, of 12 cases of subordinate males entering brood chambers, 10 involved a yearling DF-son in the CF group that entered repeatedly on day 1 of the breeding cycle, the day on which his mother laid her first egg of the clutch (nest checked). In three other groups, dominant males entered the brood chamber four or more times in quick succession between estimated days 0 and 2 of the breeding cycle.

Courtship by subordinate and dominant males.

Male stripe-backed wrens exhibit distinctive courtship, termed the aggressive chase, which occurs before and during the fertile period of the dominant female but appears not to be linked behaviorally with copulation. Each aggressive chase consists of a series of pecks at the cloacal area of a dominant female while the latter is in flight and is accompanied by a vocalization indistinguishable from that used while chasing away other species from the vicinity of the wren nest (PIPER, MS).

A revealing pattern in the occurrence of aggressive chases was the tendency of SMs to engage in aggressive chases of the DFs in their groups only when they were unrelated to the DFs. In focal groups, 16 of 33 (48%) DF-stepsons were observed to carry out aggressive chases of the DF in their groups, while none of the 23 DF-sons ever aggressively chases his mother ($G=15.5$, $p < 0.001$, G-test).

A comparison of the behaviors of 3 subordinate males in 1990 and 1991 confirmed the tendency for SMs to carry out aggressive chases only on DFs unrelated to them. None of the 3 DF-sons observed in the RW,

GL, and NM groups carried out a single aggressive chase of his mother in 1990. The subordinate male in RW again did not carry out a single aggressive chase of his mother in 1991, but the SMs in GL and NM, which had become DF-stepsons after the disappearances of their mothers in 1991, carried out 7 and 10 aggressive chases (0.25 and 0.31 aggressive chases per hour) of the new DFs.

A striking temporal pattern in the occurrence of aggressive chases was the tendency of DMs and DF-stepsons to engage in aggressive chases at different stages in the breeding cycle (Fig. 2). Aggressive chases by DMs fell closer to the midpoint of the fertile period than did chases by DF-stepsons in 10 of 11 groups wherein both DF-stepsons and DMs carried out aggressive chases (sign test, $p < 0.01$). Altogether, 66% of all aggressive chases by DMs in stepmother groups ($N = 88$ chases in 16 groups) fell within the fertile period of the DF in their group, while only 35% of the aggressive chases by DF-stepsons in the same groups ($N = 31$ chases) fell

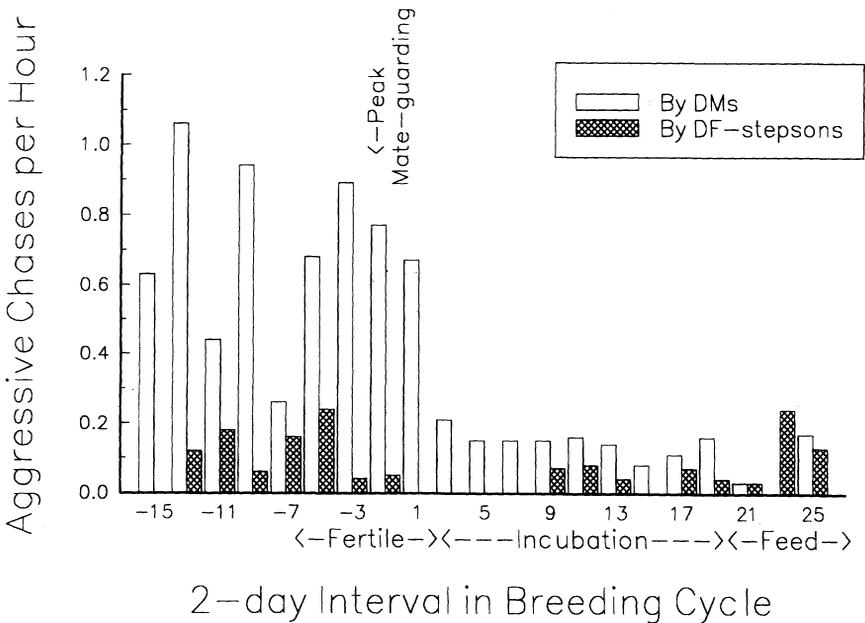


Fig. 2. Timing of aggressive chases relative to the breeding cycle. The figure shows that: 1) in general, aggressive chases peaked in frequency before incubation, and 2) most aggressive chases by DMs occurred before or during the fertile period, while a large proportion of aggressive chases by DF-stepsons occurred well after the fertile period.

within this period (Fig. 2). The clear tendency of DF-stepsons to court DFs outside of the fertile period was consistent with their tendency to shadow DFs outside of this period.

Aggressive chases were much more frequent in stepmother (0.46 ± 0.26 SD aggressive chases per hour, $N=16$) than in mother groups (0.16 ± 0.14 SD, $N=10$). This greater frequency of courtship in stepmother groups resulted partly from the fact that stepmother groups contained DF-stepsons, the only SMs that courted DFs, but DMs in stepmother groups also courted significantly more frequently (mean of 0.34 ± 0.25 SD aggressive chases per hour, $N=16$ groups) than DMs in mother groups (0.16 ± 0.14 SD, $N=10$; $U_s=120$, $p<0.05$; two-tailed Mann-Whitney U Test).

The data suggest that first-year DF-stepsons engaged in fewer aggressive chases than DF-stepsons at least 2 years old, but the sample of first-year DF-stepsons is too small for a reliable test. Only one of 5 first-year DF-stepsons (20%; mean of 0.008 ± 0.017 SD aggressive chases per hour, $N=5$) was observed to aggressively chase a dominant female, while 14 of 23 DF-stepsons (61%; mean of 0.11 ± 0.13 SD aggressive chases per hour, $N=23$) that were at least two years old did so ($U_s=85$, $t_s=1.74$, $0.10>p>0.05$, two-tailed Mann-Whitney U test with correction for ties).

Finally, although aggressive chases appeared to be a clear indication of the potential for copulation between a DF-stepson and the DF he courted, there was no strong evidence that DMs increased their level of mate-guarding in groups where DF-stepsons engaged in aggressive chases. DMs guarded somewhat but not significantly more in stepmother groups wherein at least one aggressive chase by a DF-stepson occurred ($50 \pm 0.18\%$ SD association in stepmother groups with at least one aggressive chase by a DF-stepson, $N=11$; $40 \pm 18\%$ SD, $N=6$ in stepmother groups with no aggressive chases by DF-stepsons; $U_s=43$, $p>0.2$, two-tailed Mann-Whitney U Test).

Occurrence of copulations.

We witnessed too few copulations to be able to make strong statements concerning their importance to the behavior of DFs, DMs and DF-stepsons. Indeed, only 5 solicitations for copulations (4 of which were followed by copulations) were observed in 1990 and 2 solicitations (1 of

which resulted in a copulation) were recorded in 1991. All copulations were between DMs and DFs and were in plain view, either on the outside of the nest or in bushes or trees nearby. Dominant females always emitted a loud and distinctive vocalization while soliciting a copulation (see also PIPER, MS).

Paternity of offspring.

Altogether, 40 of 47 juveniles (85%) from focal stepmother groups were sired by DMs, while the remaining 7 were sired by DF-stepsons. All juveniles in mother groups were offspring of the DF and DM. This pattern of parentage is similar to that reported for the two previous years in this population (RABENOLD *et al.*, 1990).

Four of 5 DF-stepsons that sired offspring (1 of 3, 1 of 3, 1 of 2 and 1 of 1 young) were in focal groups for which behavioral data were complete, and thus it is possible to compare the breeding behavior of such DF-stepsons with those that sired no young (data for a 5th DF-stepson that sired 3 of 4 young in a focal group were too meager for analysis). Though the difference is not statistically significant, DF-stepsons with paternity tended to have associated longer with DFs during the fertile period ($10.7 \pm 9.6\%$ SD, $N=4$) than DF-stepsons without paternity ($5.9 \pm 4.3\%$ SD, $N=19$; $U_s=49.5$, $p>0.2$, two-tailed Mann-Whitney U Test). However, DF-stepsons that sired offspring were never observed to carry out aggressive chases (mean of 0 aggressive chases per hour among 4 DF-stepsons that sired young; mean of 0.10 ± 0.13 SD, $N=26$ among DF-stepsons that sired no offspring; $U_s=80$, $t_s=1.85$, $0.10>p>0.05$, two-tailed Mann-Whitney U Test with correction for ties).

Aggression between males.

Aggression in stable, well-established groups was uncommon during the breeding season, as it is throughout the year. The most frequent and conspicuous aggression during the breeding season was directed by DMs toward DF-stepsons and often followed duets or aggressive chases between the DF-stepsons and DFs. Attacks by DMs were observed in 69% of all stepmother groups ($N=16$) and were always directed at DF-stepsons; in contrast, DMs in mother groups were never observed to attack DF-sons

(0 of 11 groups; $G=16.6$, $p<0.001$, G-test of independence). The nature of aggression by DMs towards DF-stepsons ranged from simple and often subtle supplantations, to half-hearted pecks, to protracted chases and violent pecking accompanied by loud screaming by the victim.

The frequency with which DMs attacked DF-stepsons varied greatly from group to group but was fairly constant within groups, even between years. Attacks, unlike aggressive chases, occurred with roughly equal frequency throughout the breeding cycle. In most groups attacks by DMs were rare, occurring at a rate of 0.1 attacks per hr of observation during courtship and the fertile period. The four group-years during which attacks were most frequent were in the BR group in 1990 (0.4 attacks per hr), the BR group in 1991 (0.9 attacks per hr), the IN group in 1990 (0.4 attacks per hr) and the IN group in 1991 (0.5 attacks per hr). In both BR and IN, the identities of the attacking DM and the attacked DF-stepson were the same in both years. Thus, patterns of aggression between the same individuals tended to remain constant over long periods.

Dominant males focussed their attacks on the oldest DF-stepsons, which were presumably also the highest-ranking, though too few observations were recorded to describe social relationships of SMs. Of 6 stepmother groups that contained more than one DF-stepson and in which at least one attack had occurred, there was a strong tendency for the DM to attack the oldest DF-stepson most frequently ($p<0.002$ by multiplying probabilities across groups). In fact only 1 of 17 total attacks by DMs in these groups was on a DF-stepson other than the oldest one.

While the relatedness between the DF and SMs in a group was closely related to the likelihood of a DM attacking an SM, the relatedness between the males themselves appeared unimportant. In 7 of 10 groups wherein DMs pecked or chased DF-stepsons, the DM was a first-order relative of the victim (in 5 cases a full sib and 2 cases the father), while such attacks occurred in an additional 4 of 5 groups wherein the DM was less than a first-order relative of the attacked bird.

More frequent than overt aggression between males were an assortment of behaviors by DF-stepsons elicited by the approach of DMs. These behaviors by DF-stepsons included subordinate behaviors like squatting low and emitting soft buzzy vocalizations when DMs approached and departing at the approach of DMs.

Discussion

General.

The consistent pattern that emerged from the data presented above was that subordinate male stripe-backed wrens only showed reproductive interest in dominant females that were not their mothers. Apparently as a consequence of this rule, the breeding season in mother groups was rather subdued, involving infrequent association of the dominant male with the dominant female, little courtship and very little aggression between males. In contrast to the strictly monogamous mother groups, polyandrous stepmother groups were distinguished by courtship and association with the DF by DF-stepsons, high levels of association with and courtship of the DF by DMs, and attacks by DMs on DF-stepsons.

Patterns in aggressive chases.

Although it was clearly associated with the onset of breeding behavior and was only carried out by males capable of mating with the dominant female non-incestuously, the significance of the aggressive chase is not known. However, the greater frequency of aggressive chases by DMs in stepmother groups and the striking tendency of DF-stepsons to court DFs outside of the fertile period (*e.g.* long after incubation had begun, see Fig. 2) might provide some insight into the function of this conspicuous behavior.

It is possible that the aggressive chase was a means by which males signalled their readiness for reproduction to females. This hypothesis is consistent with the occurrence of many aggressive chases well before the fertile period; these early aggressive chases might have triggered reproductive behavior in females. Furthermore, the greater frequency of aggressive chases by DMs in stepmother groups might have reflected competition between DMs and DF-stepsons over the control of the female's receptivity to copulation. If so, then the aggressive chases that occurred during incubation and feeding, particularly those by DF-stepsons, might have been attempts on the part of males to initiate second broods overlapping the first. (Such overlapping does occur occasionally in large groups.) Perhaps DF-stepsons that were able to induce the female into beginning a second fertile period stood a better chance of fertilizing

the eggs in the second clutch, since the dominant male was likely to be consumed with his effort to fledge the first brood. At this point, we lack the data to test the prediction that paternity by DF-stepsons should be higher in second broods overlapping the first.

Mate-guarding by stripe-backed wrens.

Our data imply that, even in groups with relatively high levels of mate-guarding, dominant females spent substantial periods of time away from dominant males during their fertile periods. This pattern did not result from our failure to select a biologically meaningful criterion of association (*i.e.* the distance of 2m). A male stripe-backed wren attempting to remain near the dominant female usually remained quite close to her, seldom allowing her to venture more than 2m from him, though this did occasionally occur when both foraged in a single tree and the vegetation was sparse enough for good visibility over distances of several meters.

In general, DMs associated with DFs during only 20-50% of the time within the fertile period. These data are not directly comparable with those on mate-guarding by male acorn woodpeckers (MUMME *et al.*, 1983) or dunnocks (HATCHWELL & DAVIES, 1982), because more liberal criteria were used to determine associations in those species (males within 15 m and within 10m, respectively, were regarded as associating with females). It is clear, however, that dominant male stripe-backed wrens spent much less than the 91-99% of the time spent by breeding male acorn woodpeckers and the 70-80% spent by alpha male dunnocks within sight of the dominant female. The extended periods during which female stripe-backed wrens were not guarded appeared to leave ample opportunity for DF-stepsons to associate with DFs and has no obvious explanation. It is probable that DMs, because they were able to feed very little during their bouts of mate-guarding, simply could not both guard the dominant female continuously and satisfy their own metabolic needs.

From a relative standpoint, the pattern of mate-guarding observed in stripe-backed wrens was consistent with our first prediction: that DMs should guard DFs in stepmother groups, wherein paternity was shared with DF-stepsons, and not in mother groups, where DMs enjoyed exclusive paternity. A similar pattern in mate-guarding behavior has been reported by MUMME *et al.* (1983) in the acorn woodpecker. The substantial

differences between mate-guarding levels in mother and stepmother groups indicate that, as in the acorn woodpecker, dominant male stripe-backed wrens guarded DFs mainly to minimize the risk of cuckoldry by DF-stepsons in their own group and not by extra-group males, which do not sire young (see RABENOLD *et al.*, 1990).

The significant positive correlation between the time spent associating with DFs by DMs and by DF-stepsons might be seen as evidence that DMs responded to increased associations between DFs and DF-stepsons by increasing their own level of association with DFs, but the meaning of this correlation is, in fact, not clear. Such a correlation might have been expected, for example, if DFs in some groups foraged in peripheral areas and thus limited the access that all males had to them.

The fact that a higher level of mate-guarding was detected in mother groups containing two or more DF-sons than in groups containing only one DF-son failed to support our prediction that DMs would not guard their mates in mother groups. Mate-guarding related to the number of males in addition to their relatedness to the DF has been reported also in the acorn woodpecker (MUMME *et al.*, 1983).

It is difficult to understand why mate-guarding by dominant males increased with the number of DF-sons in the group, since DF-sons, regardless of their number, were no threat to a DM's paternity. The pattern seems to be nonadaptive and to reflect the inability of dominant males to assess the likelihood of subordinate males mating with the dominant female.

On the other hand, the tendency for mate-guarding to increase with number of DF-sons might have been, in reality, part of a more general tendency for dominant males to increase their guarding not merely in mother groups with many SMs but in all groups that contained many subordinate males, regardless of their relatedness to the DF (note the trend, though nonsignificant, for DMs in stepmother groups to guard more in groups containing more DF-stepsons). If so, then DMs, by basing their guarding on the sheer number of subordinate males as well as on their relatedness to DFs, might have reduced the likelihood of paternity by DF-stepsons that did not openly court or associate with the DF. Since DF-stepsons that sired offspring in their groups engaged in no more (and possibly less, see Results) courtship than DF-stepsons that sired no young, DMs might have been unable to use behavioral interactions alone to

assess the likelihood of any one subordinate male siring offspring with the DF.

A mate-guarding system based in part upon the number of subordinate males might have permitted DMs to guard also against paternity by DF-stepsons that dispersed into the group as juveniles. DNA fingerprinting has shown that juvenile males commonly disperse into unrelated groups (unpublished data). By treating all males in his group as potential sires of offspring, DMs might have reduced the likelihood of paternity by juvenile male dispersers (which, because they joined the groups as juveniles, might have appeared unable to mate with the DF because of incest avoidance).

The tendency of first-year DF-stepsons to associate with DFs less than older DF-stepsons did probably resulted not from age, *per se*, but from the subordinate status of first-year males. In groups with more than one DF-stepson, subordinate DF-stepsons had difficulty associating for long periods with DFs because they were often interrupted by the dominant male or other DF-stepsons dominant to them. In fact, 4 of the 5 first-year DF-stepsons used in this analysis were in groups containing at least one other DF-stepson dominant to them.

Timing and effectiveness of mate-guarding.

Many factors, including the occurrence of rainfall and solicitation of copulations by DFs, might have acted as cues to allow DMs to engage in mate-guarding at the appropriate times. The observation that several DMs visited the brood chamber repeatedly on a single day around estimated days 0-2 of the breeding cycle (roughly when the first egg should have been laid) suggests that the presence of eggs in the nest might have been an additional means by which DMs determined when to guard their mates (as in the polyandrous dunnock, see HATCHWELL & DAVIES, 1992).

The value of observation of eggs in the brood chamber as a cue indicating days on which dominant females could be fertilized might explain the peculiar tendency of dominant males to guard nests at very high rates at the end of the fertile period and beginning of incubation (RABENOLD, 1990; PIPER, MS). By guarding the entrance of the brood chamber and preventing the entrance of DF-stepsons before the clutch was completed, DMs might have been able to keep them from learning

that copulations with the DF were likely to fertilize eggs at that time. Though guarding the nest was not as safe as guarding the DF herself, it probably consumed less energy and might have been a suitable substitute for mate-guarding for DMs under energy stress.

The occurrence of loud and conspicuous courtship and copulation suggested that subordinate males did obtain some temporal information concerning the occurrence of the fertile period. In theory, DF-stepsons could have maximized their likelihood of fertilizing DFs merely by remaining near the DFs during the period when aggressive chases by DMs were frequent and waiting for DMs to copulate (see Fig. 2). DF-stepsons able to copulate with the DF soon after the DM did so would have been likely to fertilize eggs (assuming precedence of sperm of the last male to copulate, see BIRKHEAD & MØLLER, 1992). This scenario depends upon the ability of DF-stepsons to inseminate the DF at will, however.

Did dominant females solicit copulations selectively?

Few enough copulations were seen that it was impossible to detect any preference by DFs for soliciting copulations from DMs or DF-stepsons. However, our data on mate-guarding and paternity seem to indicate that, on a population-wide basis, neither DMs nor DF-stepsons experienced a higher level of paternity than would have been expected from the relative lengths of their associations with DFs during the fertile period. The mean ratio of time spent by DMs within 2m of DFs to time spent by DF-stepsons within 2m of DFs during the fertile period across all stepmother groups, 5.4:1, was nearly equal to the ratio of young sired by DMs to young sired by DF-stepsons of 5.7:1 in these groups. These data could be interpreted to mean that DFs solicited copulations “*at random*” from males in the group so that a male’s likelihood of siring offspring depended solely on the amount of time he spent with the DF relative to other reproductive males in the group. This hypothesis requires further investigation, as nothing is known about the factors leading to solicitation of copulations by females.

Male-male aggression.

Aggression in male stripe-backed wrens during the breeding season appeared to reflect efforts of DMs to suppress DF-stepsons reproduc-

tively. Dominant males only attacked SMs when the latter were DF-stepsons, and attacks often followed duets or aggressive chases between DF-stepsons and the DF. This pattern showed that attacks were, in many cases, direct responses to specific efforts of DF-stepsons to associate with DFs, perhaps because any affiliative behaviors by DF-stepsons might have increased the likelihood that DFs would later choose to associate with and solicit copulations from DF-stepsons. It is possible that a history of having been attacked by the DM when associating with the DF discouraged DF-stepsons from doing so even in the absence of the DM. This effect would explain the occurrence of male-male aggression before, during and after the breeding cycle and even during the dry season (W. PIPER, personal observation).

Dominant males probably singled out the highest ranking DF-stepson for attack because lower ranking DF-stepsons had greater difficulty associating and copulating with DFs. For example, associations between the second-ranking DF-stepson and the dominant female could be interrupted by either the DM himself or by the highest-ranking DF-stepson and thus seldom lasted long.

Incest avoidance.

The consistent tendency of DF-stepsons to associate with dominant females during their fertile periods and court them throughout the breeding cycle together with the complete lack of these behaviors among DF-sons shows that one of the most critical ingredients in the breeding system of the stripe-backed wrens was incest avoidance. This pattern is wholly consistent with the siring of offspring only by dominant males and DF-stepsons (RABENOLD *et al.*, 1990) and with the peculiar tendency of the dominant female to disperse after the death of the dominant male in cases where the new dominant male is her son (RABENOLD, 1990).

Although logical from the standpoint of avoidance of potentially deleterious inbreeding (GREENWOOD *et al.*, 1978), incest avoidance of this kind is not universal among cooperative breeders. For instance, acorn woodpeckers (KOENIG *et al.*, 1984) and Arabian babblers (*Turdoides squamiceps*; ZAHAVI, 1990) show incest avoidance of the kind described here, but Galápagos mockingbirds (CURRY & GRANT, 1990) and Splendid Fairy-

wrens (*Malurus splendens*; ROWLEY & RUSSELL, 1990; but see also BROOKER *et al.*, 1990) do not.

The recognition of incest avoidance as the key determinant of breeding behavior by subordinate male stripe-backed wrens adds greater complexity to our original view of their helping behavior (*e.g.* WILEY & RABENOLD, 1984). We now can see that the death of his mother and her subsequent replacement by an immigrant female is a critical event for a SM that has remained with his natal group because: 1) it results in the SM being related by 1/4 to all future juveniles (his half-sibs) and thus causes a sudden decrease in the benefit he can gain, in terms of indirect fitness, by raising the young of the group, and 2) it removes a barrier to his reproduction.

The clear distinction between mother and stepmother groups offers an opportunity to examine the options available to a subordinate male for increasing his inclusive fitness. If a SM favors increasing inclusive fitness through its direct component (*i.e.* his own reproduction), then he might be expected to remain for a longer period in a stepmother group, where he might reproduce, than in a mother group, wherein he cannot. Just the opposite dispersal pattern would be expected from SMs favoring the indirect component of inclusive fitness. In fact, subordinate males tended to disperse more often from mother than from stepmother groups, and thus appeared to favor the direct component of inclusive fitness (mean of 1.7 ± 1.1 SD seasons remaining with mother groups; 3.4 ± 2.1 SD seasons remaining with stepmother groups; $U_s=169.5$, $t_s=2.3$, $p<0.05$, two tailed Mann-Whitney U test with correction for ties). The greater dispersal of SMs from mother groups is surprising, considering that: 1) the indirect benefit for a SM helping to raise his full siblings in a mother group can be substantial, especially if he is one of a group of 3 or 4 (which are far more successful in producing offspring than groups of 2 or 3, respectively; see RABENOLD, 1990), and 2) most dispersing males move to small groups where they are unlikely to produce many offspring (RABENOLD, 1990).

Categories of helping.

Subordinate male stripe-backed wrens clearly fell into 2 distinct categories with regard to their helping behavior. DF-sons, like subordinate females, were altruistic in the sense that they assisted with many aspects

of breeding and territoriality (and suffered higher mortality as a result; see RABENOLD, 1990) but did not reproduce. On the other hand, DF-stepsons were "would-be" dominant males that attempted to participate in all aspects of breeding behavior including mate-guarding, courtship and copulation with the dominant female. Thus, the chief distinction between DF-stepsons and dominant males was social status. The breeding system of the stripe-backed wren resembled that of the acorn woodpecker (MUMME *et al.*, 1983) in that both reproductive and nonreproductive male helpers were present.

Conclusion.

The monogamous/polyandrous mating system of the stripe-backed wren was discovered in the wake of the genetic analysis of parentage, which suggested incest avoidance in the copulation patterns of subordinate males. The availability of genetic techniques for determining parentage promises to revolutionize the study of breeding behavior in cooperative breeders. As we have demonstrated here, the use of these techniques together with thorough behavioral observations can reveal basic patterns in breeding behavior that observation alone cannot detect (see also BROOKER *et al.*, 1990). It seems likely that this dual approach will be necessary to recognize patterns in parentage that will, in turn, lead to a fuller understanding of the evolution of cooperative mating systems.

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