PATERNAL CARE IN THE COOPERATIVELY POLYANDROUS GALAPAGOS HAWK[1]

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Abstract. In cooperative breeding systems, males that share a nest face the prospect of providing for young that are not their own. Males of many species attempt to reduce the risk of losing paternity with aggressive behaviors, thereby limiting other males' access to the female during copulation. The Galapagos Hawk (*Buteo galapagoensis*) exhibits an extreme form of cooperative polyandry in which anecdotal data suggest all males in a territory share mating equally with the female, with very little to no interference, and care for young within the group. Males in a territory are unrelated adults and share paternity. We examine paternal care in relation to the shared parentage of the Galapagos Hawk and offer explanations for group cohesion. We found that paternal care was variable and that all males cared for the young on their territory without regard to the number of males residing together. There was evidence that males that sired young and those that sired none did not differ in quantity of care. However, we could not rule out a relationship between paternity and care. There was no obvious cue the males could use to discern paternity, since the only evidence of dominance was a subtle hierarchy expressed in larger groups. We suggest that the simple rule for paternal care in the Galapagos Hawk is that if a male is a group member, he will copulate with the female, have some probability to fertilize the eggs, and provide care for young produced at the nest.

Key words: breeding systems; cooperative polyandry; Galapagos Hawks; Buteo galapagoensis *paternal care.*

INTRODUCTION

General models for the evolution of mating systems often deal with the trade-offs between individual investments in a current mate or clutch and attempts to increase additional matings or clutches (Emlen and Oring 1977). The optimal solution for an individual may depend upon constraints of the local environment and opportunities to increase reproductive success. Once some investment in a clutch has occurred, models concerning parental behavior differ in whether or not paternal care should vary with parentage. Some authors have argued that parentage should not affect care, that reduced paternity to a brood would not affect a male's decision to desert and remate with a new female (Maynard Smith 1978), or to remate with the same female (Grafen 1980). These ideas assumed that paternity was the same for all broods and individuals could not assess their own parentage. Other authors concluded

that relatedness to the current brood should affect care, assuming that paternity differs between broods (Xia 1992) and parental care increases mortality of the male (Winkler 1987). Westneat and Sherman (1993) predicted that behavioral responses to parentage depend on the parents' ability to assess paternity, the patterns of parentage among offspring, and cues to the likelihood of relatedness. Werren et al. (1980) pointed out that other variables such as mate guarding and number of copulations could cause variance in parental effort regardless of paternity.

Recent parentage studies using DNA fingerprints have revealed genetic relationships among cooperative breeders differing from those determined by behavioral observations. DNA data have found "monogamous" groups of cooperative breeders with regular, though infrequent, polyandrous associations (e.g., *Campylorhychus nuchalis* [Rabenold et al. 1990, Piper and Slader 1993] and *C. griseus* [Haydock et al., in press]), while revealing genetic monogamy in facultatively polyandrous species (*Tribonyx mortierii* [Gibbs et al. 1994]). Among cooperative breeders, several studies have shown positive corre-

lations of parental care with presumed gamete contribution (e.g., Vehrencamp 1977, Dow 1978, Joste et al. 1982, Craig and Jamieson 1985, Reyer and Westerterp 1985, Clark 1989) or with actual genetic contribution (Davies et al. 1992). However, Jamieson et al. (1994) found populations of Pukeko (*Porphyrio porphyrio*) contributing equally in paternal care to the young regardless of the proportion of eggs sired.

The Galapagos Hawk (*Buteo galapagoensis*) has been described as having a cooperatively polyandrous breeding system based on observations that each male within the territory copulates with the female and cares for the offspring (Faaborg and Patterson 1982, Oring 1982). Typically groups composed of one female and up to five males defend a territory throughout the year. On the island of Santiago, 87% of the territories were polyandrous groups ($\bar{x} \pm SD = 2.6 \pm 0.9$ males per group, Faaborg and Bednarz 1990). In contrast to most cooperative breeders, juveniles do not stay within the breeding territories (Smith 1990), but are chased from the natal territory after three to five months and join non-territorial, non-breeding populations. Adult territory members were suggested to be unrelated due to small clutch size (one to three eggs), low fledging rates (usually one young), and the difficulty of forming kin groups away from the breeding territory (Faaborg et al. 1980); recent DNA fingerprinting analyses have supported this hypothesis (Faaborg et al. 1995). Observations suggested all males copulated with the group female, and genetic analyses have substantiated mixed parentage among males within a group (Faaborg et al. 1995). In general, polyandrous groups produce more young than monogamous pairs (Faaborg 1986), but polyandrous males average fewer young annually than monogamous males assuming equal probability of paternity. Faaborg and Bednarz (1990) argued that advantages of increased survival on group maintained territories compensated for reduced annual production of young.

Here we examine the relationship between care and paternity among unrelated males in polyandrous groups of the Galapagos Hawk. A male cooperating with a group to initially obtain a territory may be one path toward attaining monogamy and optimal reproduction. Under this scenario, one might expect males to adopt a strategy to minimize their own risk relative to the group in an attempt to outlive the rest (Faaborg

and Bednarz 1990). Assuming care given to the young is costly, we ask whether males without parentage care for the young at the nest. We also ask whether males adjust their parental care according to their paternity, assuming they could determine that probability. Our objective was to examine 1) relative contributions of care by males in polyandrous groups, 2) the relationship of paternity to male care of young at the nest, and 3) correlations of intra-territory male aggression, a possible cue to parentage, with several components of care or paternity.

METHODS

We studied polyandrous groups primarily on Isla Santiago where hawks had been marked and monitored during previous studies. Santiago is a large (58,464 ha) and high elevation (914 m) volcanic island with a range of vegetation zones from cactus-dominated thorn scrub to *Psidium*-dominated highlands. Santiago supported an estimated 50 hawk territories and a non-breeding population of approximately 200 birds, primarily adult females and juveniles (deVries 1975). We made limited observations on Isla Santa Fe, a small (2,413 ha), low (239 m maximum elevation) island with relatively few hawk territories (14–16).

We collected data from June to September in 1990 and 1991. The area within 5 km of each of our camps was searched for active nests. The number, sex, and age class of each bird in the territories as determined by size and plumage (deVries 1973) were recorded. All members on a territory were captured using either a Balchatri trap (Berger and Mueller 1959) or by using a rope-noose on a stick (Faaborg et al. 1980). Like most animals in the Galapagos, this hawk was relatively easy to observe from a small distance with little disturbance. Individual adults were banded with numbered metal bands and a unique combination of colored vinyl strips attached around the tarsi. We also carefully withdrew 50 μl of blood from the brachial vein from nearly all territory members, including young. Samples were stored in sterile buffer solution until DNA fingerprinting analyses for paternity were completed (Faaborg et al. 1995). Parentage was not determined until after the field study, so no biases in data collection should have occurred.

We closely monitored activities associated with nesting in six groups containing two males, three groups of three or four males, and one group of

TABLE 1. Male parental care and paternity assignments within 2-, 3-, 4-, and 8-male territories. Males are identified by their band numbers. Mean ranks are derived from the previous five care classes.

Territory		Male	Prey number	[1]Significance of prey deliveries	Prey biomass (g)	Feeding (min)	Nest attendance (min)	Attacks to observer	[2]Mean rank	[3]Paternity Chick #1	Chick #2
Two-male Groups											
S1	1990	B78	14	***	1,430	8.2	29.1	7	1	+	▓
		B77	2		364	0	8.2	1	0	−	▓
S1	1991	B78	50	**	1,952	2	45	7	0.75	+	▓
		B77	20		943	4	14	5	0.25	−	▓
S2	1990	B153	8	ns	378	0	86	10	0.63	−	▓
		B152	12		212	0	18	0	0.38	+	▓
S2	1991	B153	13	ns	241	2	15	5	0.5	na	▓
		B152	16		529	2	15	1	0.5	na	▓
S3	1990	B79	4	ns	262	na	na	na	0	+	▓
		B59	6		431	na	na	na	1	−	▓
[4]S3	1991	B69	8	*	322	1	8	10	0.25	−	▓
		B59	21		599	7	95	2	0.75	+	▓
T2	1990	A28	10	ns	150	na	na	na	1	+	▓
		D07	5		240	na	na	na	0	−	▓
T2	1991	A28	31	ns	639	3	35	0	0.63	+	−
		D07	34		1,237	1	32	0	0.38	−	+
B4	1990	B333	48	***	1,129	29	311	16	1	+	−
		B338	17		498	0	38	7	0	−	+
B4	1991	B333	49	***	826	89	172	19	1	+	+
		B338	17		373	17	36	12	0	−	−
SF3	1990	Hw21	28	**	970	0.5	12	3	1	−	▓
		B159	9		435	0	6	0	0	+	▓

[1] χ^2 test used for prey delivery comparisons (binomial test used when $n \le 25$); * $P \le 0.05$, ** $P \le 0.01$, *** $P \le 0.001$, ns = not significant; letters denote male pairwise comparisons.
[2] Within-group relative rank; rank 0 to 1, 1 = highest rank of care.
[3] Analysis of paternity using DNA fingerprinting (Faaborg et al. 1995).
[4] First documented change in male composition within a group (Faaborg et al. 1980, Faaborg 1986).
na = data not available.
▓ = only one chick at the nest.
? = paternity uncertain.

eight males. Most of these groups were monitored in both 1990 and 1991 (Table 1). Each active nest was observed for an average of 100 hours over ten to fourteen consecutive days when young were present at the nest. We continually monitored hawk behavior with the aid of 7 × 45 binoculars and 15–60 × spotting scopes. An area of 100 m radius around the nest was scanned every five minutes for position and behavior of group members using "all-occurrences sampling" (Altmann 1974) to record behavior associated with parental care, dominance, and copulations.

In most *Buteo* species during breeding, the male captures and transports prey while the female feeds and broods the young until late in the nesting period (Newton 1979). We quantified parental care of each male in terms of: 1) Number of prey delivered to the nest and the total estimated biomass of prey (no. prey × the prey species' mean mass [g]); mean mass of each prey species was obtained from the literature (Armas and deVries 1978, Grant and Grant 1980) and H. Snell (pers. comm.); 2) Total time (min.) feeding the young on the nest per 100 hrs. observation; 3) Total time (min.) individuals spent in nest attendance per 100 hrs.; 4) Intensity of nest defense (measured as the number of attacks directed at observers entering the territory).

We recorded all aggressive encounters between territory members while young were associated with the nest, measured as both direct attacks and supplants or chases. As a possible measure of a male's social dominance, several morphological characters of size were examined for their association with care: claw, culmen, hallux, tail,

TABLE 1. Continued.

Territory		Male	Prey number	¹Significance of prey (comparisons)	Prey biomass (g)	Feeding (min)	Nest attendance (min)	Attacks to observer	²Mean rank	Chick #1	Chick #2
				Care classes (based on 100 hrs. observation) Nest effort				Defense		³Paternity	
Three to Four-male groups											
T3	1990	B161 (a)	6	(ab) ns, (bc) ns	423	na	na	na	0.00	+	▨
		B081 (b)	10	(ac) **, (ad) *	877	na	na	na	0.33	−	▨
		A027 (c)	21	(bd) ns	695	na	na	na	1.00	−	▨
		B080 (d)	16	(cd) ns	285	na	na	na	0.67	−	▨
T3	1991	B161 (a)	13	(ab) ns	854	8	94	6	0.38	−	▨
		B081 (b)	6	(bc) ***	621	65	193	0	0.31	−	▨
		A027 (c)	47	(ac) **	1,916	160	306	0	0.81	+?	▨
S4	1991	B105 (a)	19	(ab) ns	1,709	16	46	182	0.25	−	+
		B107 (b)	23	(bc) ns	1,107	39	104	78	0.63	+	−
		B104 (c)	30	(ac) ns	1,830	19	85	181	0.63	−	−
S5	1991	B109 (a)	13	(ab) ns	855	49	104	23	0.63	−	▨
		B108 (b)	6	(bc) ns	316	20	95	25	0.38	+	▨
		Alum (c)	15	(ac) ns	1,301	9	27	26	0.50	−	▨
Eight-male group											
B3	1990	B164	24		923	30	132	3	0.96	−	+
		A026	16		742	18	95	1	0.63	−	−
		B165	20		1,023	17	55	2	0.66	+	−
		B157	8		660	22	56	1	0.48	−	−
		B163	13		923	16	136	0	0.50	−	−
		B155	11		415	0.5	32	1	0.25	−	−
		B160	11		148	5	42	2	0.43	−	−
		B156	7		670	0	9	1	0.09	−	−
B3	1991	B164	19		672	11	68	12	0.96	+?	−
		A026	12		978	3	56	10	0.79	−	−
		B165	10		963	0	22	5	0.38	−	−
		B157	9		523	1	21	2	0.25	−	+
		B163	10		1,253	4	96	5	0.79	+?	−
		B155	3		135	0	24	2	0.14	−	−
		B160	9		309	1	46	4	0.45	−	−
		B156	8		400	1	35	1	0.25	+?	−

and wing lengths. Body weight was not considered because we could not account for variation due to recent prey consumption. In 1990, we witnessed chance copulations between males and the female of an eight-male territory prior to egg-laying. A copulation was considered successful when a male landed on the female's back and twisted his lower abdomen toward the female's cloaca. Using this criteria, we witnessed no unsuccessful copulations.

Comparisons of parental care among individual males were made with nonparametric tests due to small sample sizes and ranking of the data (Siegel and Castellan 1988). We examined whether the frequency of a male's prey delivery was different from those of another within the territory (excluding the eight- male group) by using chi-squared and two-tailed binomial tests. Associations of care classes with intra-male aggression or aggression to the observer were tested using two-tailed Spearman rank correlations r_s (SYSTAT 1992).

We examined the relationships between a male's parental care and parentage by ranking the magnitude of care provided by individuals and relating these data to paternity, excluding territories where we were uncertain of parentage. We ranked each male according to his within-group relative care index $(1 - ((rank - 1)/(n - 1)))$, where rank is a male's standing within his group and n is the number of males in the group. This scale ranks parental care from 0 (lowest rank) to 1 (highest rank) and adjusts for group size. Our analysis included ranking males by each

care category separately and the mean of four of those categories thought to be independent (number of prey, feeding young, nest attendance, and attacks to observers). We used a Mann-Whitney U test to compare ranks of males that sired young to those that sired none.

We examined the power of our data to predict changes in behavior due to parentage by examining the degree of difference in mean prey deliveries of fathers and non-fathers of a territory. New data sets were created from the original by randomly reassigning parentage to males within a territory. We added a percentage of the average deliveries within a group to the father's contribution and subtracted the same percentage from that of the nonfather to keep the group average unchanged, thereby creating five alternative data sets with successive disparity in prey deliveries (10, 20, 30, 40, and 50%). As a rough measure of power, we computed beta for the z distribution using the hypothesized null mean (difference in deliveries is zero) and the alternative mean values calculated from our new data sets.

RESULTS

Of 12 territories surveyed, two male polyandrous groups were the most common (67%); other territories contained three or more males. Eight adults that occurred in six groups and were banded in 1977 and 1979 were still residing in their territories and would be at least 14 to 16 years old. All were males but one previously banded bird. We analyzed ten of the territories for which we had both behavioral and paternity information, nine from Santiago and territory SF3 from Santa Fe (Table 1).

PATERNAL CARE

All males within a territory contributed to the care of the young in both years in all categories of effort, no matter how many males resided there (Table 1). Prey were delivered to the nest primarily by males while the female remained on the nest with the brood. Over both years ($n = 19$ territories), $12 \pm 3\%$ SE (min. 0%, max. 48%) of the prey deliveries were by the female; most of these were probably retrieved from the male out of view of the observer. A male's within-group ranking by the number of prey delivered to the nest was correlated with the resulting prey biomass in 1991 ($r_s = 0.90$, $P < 0.0001$, $n = 24$) but not in 1990 ($r_s = 0.31$, $P = 0.14$, $n = 24$).

Previous studies (deVries 1973, Faaborg et al. 1980) showed that the most common polyandrous groups were composed of two males with a maximum of five. We discovered an eight-male group (B3) where all males participated in food deliveries and defense of the young at the nest (Table 1). The mean parental care scores were not skewed obviously to one male. The top two ranking males (B164 and A026) in that group maintained their relative status over two years. Over all nests there was no significant association of the ranking of male parental care between 1990 and 1991 ($r_s = 0.48$, $P = 0.23$).

The relative contribution of number of prey delivered to the nest by males in a group varied among territories and years (Table 1). Of the five two-male territories studied in 1990 and 1991, males from two groups (S1 and B4) differed significantly in their relative prey deliveries both years (χ^2 tests of independence, $P < 0.01$, Table 1). The remaining three groups consisted of males that did not differ in their deliveries of prey or differed in one year only. Males within three- and four-male groups showed less skew in intra-territory prey deliveries where only male (A027) in 1991 made more deliveries within his group (Table 1).

Individual males were consistent in their rank of mean care when comparing territories observed over two years (calculation using prey number, feeding young, nest attendance, and defense; $r_s = 0.79$, $P < 0.0001$, $n = 21$ males). A lack of negative correlations between a male's relative ranking in prey delivery and attacks to observers (1990: $r_s = 0.50$, $P = 0.052$, $n = 16$, 1991: $r_s = 0.18$, $P = 0.34$, $n = 27$) signifies no obvious division in labor within groups between food provisioning and defense of the territory.

RELATIONSHIPS BETWEEN PATERNITY AND CARE

We were able to compare paternal care and parentage from ten territories (Table 1). Of the territories with certain paternity assignment, 11 of 19 young (58%, all groups) and eight of 13 young (61%, two-male groups) were sired by the males that provided the higher care (Table 1). There was no significant difference in the quantity of care (relative within-group index) by males that sired young and those that sired none when examining years separately ($P > 0.20$, Fig. 1). Males that produced young did not contribute more to overall mean care in either year (Mann-Whitney $U = 87$, 1990 and $U = 33$, 1991), nor to a greater
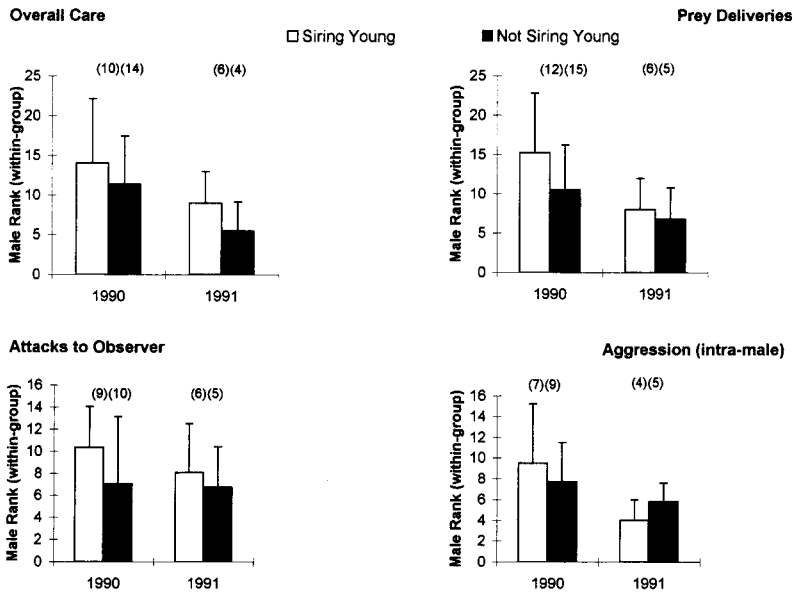
FIGURE 1. Comparisons of the mean rank of males in several components of parental care and parentage. Ranking of males is a within-group relative index of care corrected for ties and represented here as 1) overall care (mean of prey number, feeding young, nest attendance, and attacks to observers), 2) prey deliveries to the nest, 3) attacks directed at observers, and 4) male-male aggression during 1990 and 1991. Includes males from eight territories, including one from Santa Fe, (1990) and six (1991) territories. Symbol () denotes the number of males and bars represent standard errors.

number of prey deliveries ($U = 92$, 1990 and $U = 28$, 1991), attacks toward observers ($U = 35$, 1990 and $U = 28$, 1991), or male-male aggression ($U = 38$, 1990 and $U = 14$, 1991). However, seven of the eight pairs of histograms are in the predicted direction for a hypothesis that links quantity of care to parentage (Fig. 1). Because the values of beta were large and consistent (0.50 to 0.51) for each data set, even for a 50% disparity in prey deliveries, power of the data are low and we cannot accept the null that males contribute equally in favor of alternate hypotheses that skews in prey deliveries depend on parentage.

Male ranking within the eight-male group (B3) differed greatly from one paternal care category to another and was not obviously skewed towards one male in terms of effort in either year (Table 1). Fathers of the two chicks in territory B3 (B164 and B165) were also the first and third highest contributors in terms of their mean ranks and second and fifth in terms of the amount of time they spent attending the nest during 1990. However, 1991 paternity analysis could only determine, with certainty, the father for one of the two young (Table 1).

CUES TO PRESUMED GAMETE CONTRIBUTION

To gain insight into the maintenance of such a cooperative breeding system, we considered possible behavioral assessments of paternity, though a relationship between paternity and care may not require behavioral assessment (Westneat and Sherman 1993). Possible behavioral cues available to males for determining their probability of fathering young of the territory could be dominance status (limiting access to the female) and number of successful copulations (Emlen 1978, Craig and Jamieson 1985). Male group-members rarely interacted aggressively under normal conditions (Table 2). Observed aggressive encounters between males, however, did occur during or just prior to prey capture. As the number of males in a territory increased, so did the number of aggressive acts per male (over the study: 3.1 attacks per male within the eight-male group both years; 1.0 [1990] and 0.62 [1991] acts per male over four two-male territories).

There was an association between intra-territory male aggression of a male who sired young and his mean contribution to care, as well as to

TABLE 2.   Aggressive interactions between males within 2-, 3-, and 8-male territories on Isla Santiago during 1990 and 1991. Interactions included attacks, chases, and supplants.

| | | Within-group aggressive acts | | | | | | |
| | | 1990 | | | 1991 | | | |
Territory	Male	Hours territory observed	Wins	Losses	Male	Hours territory observed	Wins	Losses
Two-male groups								
S1	B78	110	1	0	B78	100	0	0
	B77		0	1	B77		0	0
S2	B153	50	1	0	B153	100	5	0
	B152		0	1	B152		0	5
S3	B79		na	na	B69	80	0	0
	B59		na	na	B59		0	0
B4	B333	100	3	0	B333	100	0	0
	B338		0	3	B338		0	0
SF3	HW26	100	2	1	HW26		na	na
	B159		1	2	B159		na	na
Three-male groups								
S4	B104		na	na	B104	103	5	1
	B105		na	na	B105		3	2
	B107		na	na	B107		1	5
S5	B109		na	na	B109	97	5	1
	ALUM		na	na	ALUM		4	3
	B108		na	na	B108		0	3
Eight-male group								
B3	B164	100	13	0	B164	100	16	2
	A026		2	12	A026		2	1
	B165		0	5	B165		2	2
	B157		0	3	B157		0	5
	B163		2	1	B163		0	3
	B155		3	2	B155		5	7
	B160		2	4	B160		0	2
	B156		3	2	B156		0	0

na = data not available.

the number of attacks directed at the observer ($P = 0.001$, $n = 13$, Fig. 2). Males that did not father young showed no such correlation ($P < 0.1$, $n = 15$, Fig. 2). The correlation between a father's aggression and care was highly significant in 1990 but not so in 1991 ($r_s = 0.93$, $P < 0.002$, $n = 7$ and $r_s = 0.42$, $P = 0.41$, $n = 6$, respectively), with a similar relationship of male-to-male aggression to attacks ($r_s = 1.00$, $P < 0.0001$ and $r_s = 0.56$, $P = 0.25$, respectively). Males not fathering young showed a correlation between aggression and attacks in 1990 ($r_s = 0.70$, $P = 0.04$, $n = 9$), as well as to care in 1991 ($r_s = 0.85$, $P = 0.03$, $n = 6$). However, no relationship was found between aggression and care in 1990 ($r_s = 0.50$, $P = 0.17$), as well as to attacks in 1991 ($r_s = -0.22$, $P = 0.67$).

Because of the above relationships of intra-territory male aggression and attacks to a would-be predator, we compared a male's attack ranks to those of other care categories. Males that attacked the observer most often also ranked the highest in their groups in terms of care giving in both 1990 and 1991 ($r_s = 0.89$, $P < 0.001$, $n = 16$, and $r_s = 0.21$, $P = 0.35$, $n = 22$, respectively). In spite of any association, male-to-male aggression did not predict his success in siring young (Mann-Whitney $U = 35$, $P < 0.2$, 1990; $U = 28$, $P < 0.2$, 1991).

In a social system with little aggression, dominance might be conveyed by the size of a male. Tail length was the morphological measure showing the most variation among males (min. = 196 cm, max. = 400 cm, variance $v = 1,153.0$,
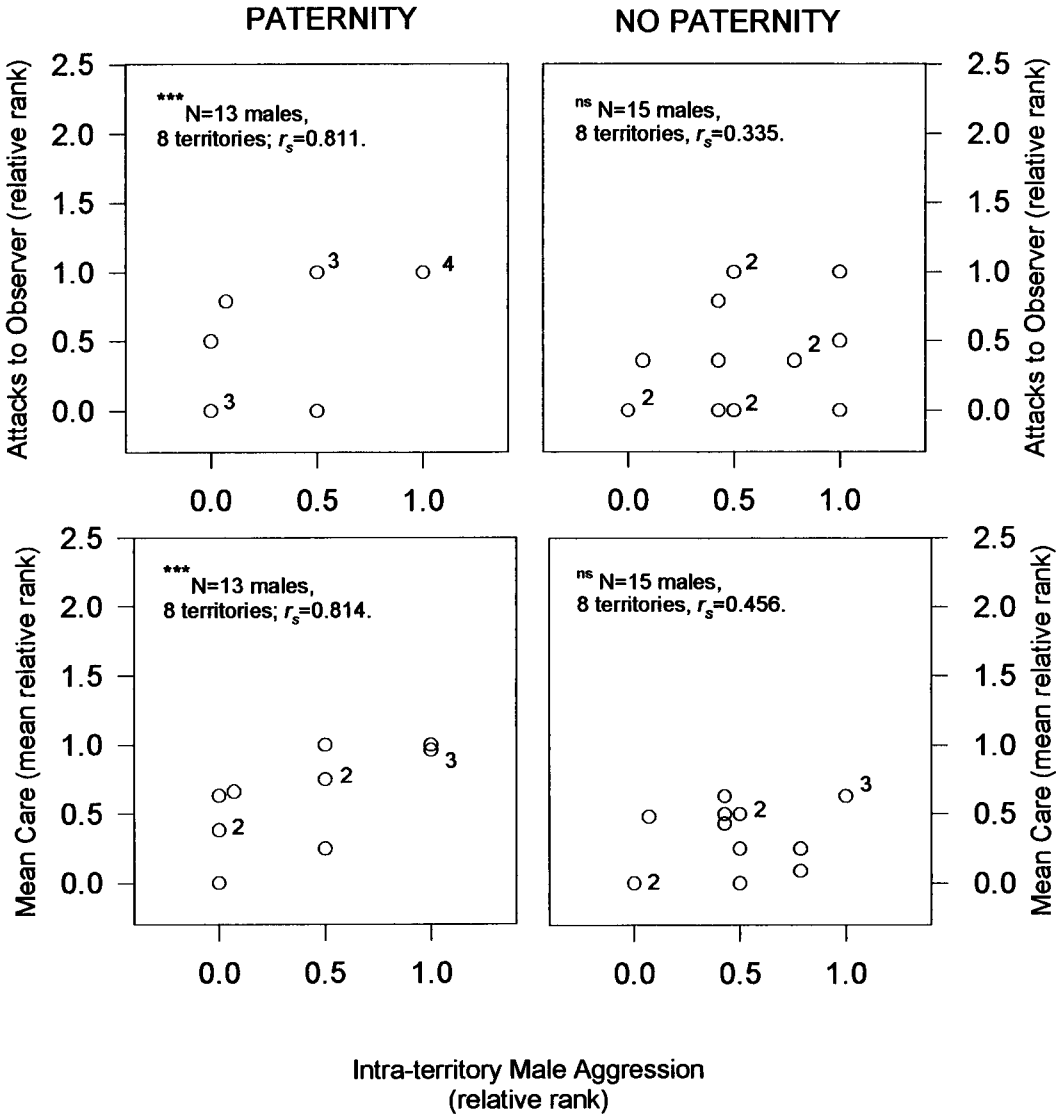
FIGURE 2.   The relationships between intra-territory male aggression and paternal care illustrated as the mean of four care categories (prey number, feeding, nest attendance, and attacks to observers), and attacks to the observer. All values are expressed as within-group relative index. **Symbols denote a significant Spearman rank correlation at $P<0.001$, ns = not significant. Numbers adjacent to points indicate repeated values.

$n = 33$) compared to claw ($v = 1.9$), culmen ($v = 0.5$), hallux ($v = 1.3$), and wing length ($v = 926.2$). However, there was no relationship between an adult male's size (tail length) and his aggressive behavior towards other males within the same territory ($r_s = 0.26$, $P = 0.31$, $n = 16$, 1990; $r_s = 0.22$, $P = 0.54$, $n = 9$ males, 1991). Also, males siring young were not the largest of

the males within a group ($U = 74$, $P < 0.20$, 1990 and $U = 87$ $P < 0.20$, 1991).

We counted copulations in the eight-male group over a six-day period (48 hr of observation) previous to egg-laying. Seven of the eight males copulated with the female and all males made prey deliveries to the female at the nest. We found no statistical association between copulation fre-

quency and visits to the nest ($r_s = 0.15$, $P = 0.36$). While the male that copulated the most was a father (B164 copulating nine times), so was a male that had copulated much less frequently (B165 copulating one time).

DISCUSSION

Although past behavioral observations suggested that this breeding system is cooperative polyandry, genetic information had been lacking to eliminate the possibility that groups comprise a monogamous pair with helpers such as found in populations of Harris' Hawks (Bednarz 1987) and among many cooperative breeders (Stacey and Koenig 1990). Paternity analysis data (Faaborg et al. 1995) confirm that this mating system is cooperative polyandry (Faaborg and Patterson 1982). Although the distribution of paternity within the sample presented by Faaborg et al. (1995) agreed with a random mating hypothesis, sample sizes were small. It is possible that we might still find skews in paternity, which may then correlate with paternal effort in more subtle ways. The distribution of paternity was, however, almost significantly even (64 hawks in ten territories, Faaborg et al. 1995).

Our data are sufficient to reject the idea that paternity is a major factor in determining provisioning and defense behavior. Males contribute to the care of the young even when they had sired none of the offspring. The amount of care a male exhibited was not correlated with his success in siring offspring in any obvious way, although there were some indications of what may be subtle correlations between paternal care and paternity. Expanded samples would be needed to prove that subtle differences in male effort were also correlated with male paternity. Currently, our work suggests that males are responding to behavioral cures of possible paternity in an all-or-none manner by caring for all young in the nest. They do not appear to be responding in a graded fashion related to the probability of paternity as might be predicted in groups with multiple males (Whittingham et al. 1992) or has been observed with the Dunnock, *Prunella modularis* (Burke et al. 1989), but we cannot rule out this possibility with the current data.

Behavioral cues resulting in a threshold (yes-or-no) care response could include unencumbered copulations with the female and lack of dominance which allows each male full access to the female (Craig and Jamieson 1985). This contrasts to "continuous cues" such as the frequency of copulations or relative standing in a hierarchy which may influence access to the female. Although early observations with the Galapagos Hawk suggested group members shared equally in dominance status, copulation frequency, and defense (Faaborg and Bednarz 1990; deVries 1973), subtle dominance orders may exist in larger groups. Data from three-male groups and the eight-male group suggested that an increase in the number of males in a territory resulted in an increase in the number of aggressive encounters. In the eight-male group, for example, one male (B164) exhibited dominance over the other seven males within his unusually large group (Table 2). Males show aggressive and submissive posturing (deVries 1973), particularly in larger groups (pers. obs.); the rarity of these displays in small groups may be a result of less competition for prey. We may have also witnessed greater aggression among males had we done observations during the female's fertile period.

This lack of obvious dominance contrasts to the Arizona Harris' Hawk (*Parabuteo unicinctus*) population where alpha males actively chased subordinates from the nests (Dawson and Mannan 1991). As a result, beta and gamma males rarely participated in direct care of eggs and young. All Galapagos Hawk group members have access to the nest and there was no obvious division of labor in paternal care contributions. The strong dominance hierarchy present in Dunnock males affects a male's access to the female which predicts his chances of paternity and, therefore, his degree of paternal care (Burke et al. 1989); alpha males attempt to prevent beta males from copulating with the female, while the females encourage such copulations.

Although evidence of subtle dominance relationships within male groups now exists, we have seen no evidence of mate guarding or male aggression during copulations, and often many males mate with the female within seconds of each other without aggression. Observations within the eight-male group did illustrate a skew in numbers of copulations towards the dominant male (B164), yet all males contributed to care of the young. In this group, the male who copulated the most shared paternity with a male that copulated much less frequently, speculating that males are unable to estimate the proportion of eggs they have fertilized. We will, however, need more observations of the frequency of copulations in relation to paternity. Likewise, Jamieson et al. (1994) have found that in some populations

of cooperatively breeding Pukeko, unrelated males within the group do not guard matings or interrupt copulations and still care for the young equally. Unlike the Galapagos Hawk, Pukeko exhibit a dominance order among males where the alpha male appears to sire more of the young. If male Galapagos Hawks and Pukekos cannot assess their individual parentage but their shared paternity is predictable from year to year, then equivalent care is a response that fits into Westneat and Sherman's (1993) hierarchical model of parental care. Equivalent care is also predicted if the chances of recruiting any one young of the brood increases with overall parental effort (Whittingham et al. 1992). Though we have no information on the importance of multiple males to chick survival, all care contributed by males benefits the whole brood and appeared to be controlled by the female. Alternatively, males may simply feed all chicks with which they come into contact and are familiar from the nest of their territory (Jamieson and Craig 1987).

A survey of cooperative breeders revealed that maximum group size is smaller in polyandrous breeders, presumably because the resulting average male relatedness to the brood is reduced with an increase in male membership (Hartley and Davies 1994). Although we have observed an eight-male group, average group size on Santiago was shown to be 2.6 males per polyandrous group ($n = 16$ territories; Faaborg et al. 1980). A cursory examination of the effects of group size on prey delivery rates suggests no obvious advantage in terms of care of young for such a large number of males to coexist, particularly given limitations to clutch size and the increased occurrence of male-male aggression in this group. Certainly, trading higher survival rates on a territory for only a one-eighth chance at paternity may not be adaptive. On the other hand, this group maintained identical membership through two breeding seasons, suggesting it was stable. This large group represents the only territory consisting of more than five males found during three decades of observations (de Vries 1973, Faaborg et al. 1980, Faaborg and Bednarz 1990). Surplus females of breeding age occur on the highlands of the island (Faaborg et al. 1980). This suggests that the large group size is probably not adaptive, but possibly may reflect an unnatural combination of conditions, such as the habitat degradation by browsers occurring on that island (Santiago).

To date, the Galapagos Hawk system appears to be one of cooperating males of relatively equal status with little dominance and little variation in male care. Small sample sizes prevent us from using parental investment models such as that of Whittingham et al. (1992), but we suggest that any differences between relationships of care and paternity will be fairly small within groups of males. Perhaps this is not surprising, since a dominant aspect of the Galapagos Hawk breeding system is the acquisition and maintenance of a territory which group members share equally and defend together.

Survival rates on a territory exceed 90% per year, and some birds originally banded in 1977 were still alive on territories in 1991. One pair of males (group B4) had been banded on territory B4 in 1977 and presumable have stayed for 16 years, and all but one adult banded in 1990 remained in their groups the next year. Polyandrous groups, therefore, seem to be very stable where member survival rates are high. In contrast, production of young is always low, often one fledged young per nesting attempt, and the chances of any offspring making its way into the breeding population is low. As a result, membership within a group on a territory may result in high enough survival rates that small differences in reproductive success between males may be relatively unimportant at least when compared to the potential cost of loss of territory.

ACKNOWLEDGMENTS

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