PLASMA LUTEINIZING HORMONE, STEROID HORMONES, BEHAVIORAL ROLE, AND NEST STAGE IN COOPERATIVELY BREEDING HARRIS' HAWKS (*PARABUTEO UNICINCTUS*)

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ABSTRACT.—We measured plasma levels of testosterone (T), estradiol 17β (E), corticosterone, and luteinizing hormone (LH) in adult breeders, adult-plumaged helpers, and juvenal-plumaged helpers of the cooperatively breeding Harris' Hawk (*Parabuteo unicinctus*) in southeastern Arizona. In the males, both adult breeders and most adult-plumaged helpers had elevated T and LH during February and March, when nest building occurs, whereas most juvenal-plumaged helpers showed no change in LH, T, or E throughout the year. Thus adult-plumaged helpers, usually not related to the breeders, are hormonally ready to breed in the spring. We suggest that these helpers attain breeding readiness because potential benefits they can derive from either occasional successful copulations or possible attainment of the breeding position make reproductive readiness advantageous. In contrast, most juvenal-plumaged helpers are aiding their own parents on their natal territory and are not hormonally ready to breed, and thus they physiologically avoid the potential for inbreeding. An exception to this was a juvenal-plumaged male helper with elevated testosterone levels who was not helping his parents. The female breeders we examined had elevated T, LH, and E during the nest-building period, whereas the helpers (both adult- and juvenal-plumaged) did not show elevations at any time of the year. During the early part of the nesting cycle, the adult-plumaged female helpers weighed significantly less (ca. 10%) than the breeders. It is possible that poor body condition, subordinate status to the breeding females, or both were related to their lack of breeding readiness. In all birds, corticosterone levels increased with handling time, and were higher during the nesting periods than during non-nesting periods, but showed no consistent relation with helper or breeder status. As in other species that are relatively social, maintain long-term pair bonds, or are tropical in distribution, plasma concentrations of LH and sex steroids in Harris' Hawks, even when elevated, were relatively low. *Received 10 May 1990, accepted 13 January 1991.*

COOPERATIVE breeding, in which more than two adults assist in raising young, occurs in at least 222 species of birds and is taxonomically widespread among altricial species (Brown 1987). Although the evolutionary origins of cooperative breeding systems remain unclear (see Brown 1983, Emlen 1984, Jamieson and Craig 1987, Jamieson 1989) many authors have discussed the ecological factors that promote the development of cooperative breeding in different species (e.g. Emlen and Vehrencamp 1983) and the potential advantages accrued by non-breeding helpers (e.g. Ligon and Ligon 1978; Woolfenden and Fitzpatrick 1978, 1984; Brown and Brown 1981). Few studies, however, have addressed either the physiological basis of this type of behavior (Reyer et al. 1986, Wingfield et al. in press, Schoech et al. 1991) or physiological constraints involved in cooperative

breeding (Ligon et al. 1988). In this study we present endocrine evidence for reproductive readiness in breeders and helpers in the Harris' Hawk (*Parabuteo unicinctus*) and discuss possible proximate and ultimate causes for lack of breeding in helpers. In an accompanying paper (Vleck et al. 1991), we discuss the physiological basis of parental or helping behavior in the Harris' Hawk.

Harris' Hawk breeding biology.—Harris' Hawks breed cooperatively in New Mexico, Texas, and Arizona (Mader 1975a, Griffin 1976, Brannon 1980, Whaley 1986, Bednarz 1987a, Dawson and Mannan 1989). The mean number of hawks associated with a nest in the population we studied was 3.8 ($\pm$1.3 SD) and ranged from 2 to 7 birds. Harris' Hawks may be polyandrous (Mader 1979), but behavioral and electrophoretic evidence suggests that groups generally consist

of 1 breeding pair and 1–5 nonreproducing birds (Bednarz 1987a; Dawson and Mannan 1991a, b) that may or may not be related to the breeders. DNA analysis of all members of several Harris' Hawk groups indicates that polygyny and polyandry, as well as monogamy, occur in the Arizona population (Sheehy et al. MS), but the frequency of each of these mating systems in the population is unknown.

The behavioral roles of different members of the group have been described in detail elsewhere (Dawson and Mannan 1991a) for this Arizona population. The dominant pair in each group (termed the alpha male and female) provides direct care of the eggs and young, including nest building, egg laying, incubation and brooding, and shading and feeding the nestlings. The dominant pair also participates in group hunting although the alpha female rarely leaves the nest area during the breeding season and is usually supplied with food by the alpha male or helpers. (Approximately 9% of the groups also have another alpha-level female, an alpha-2 bird, but none of the females we captured in this study were of this type.) In Harris' Hawks, alpha breeders remain on the same territory year after year; thus helpers that remain on natal territories are likely to be helping their parents and those that disperse are likely to be helping birds that are not their parents. The helpers' major contributions to the breeding effort are to capture and transport prey to the nest area, detect and harass predators, and help with defense of the nesting territory. Bednarz (1988) and Bednarz and Ligon (1988) suggested that cooperative hunting may be the basis for the social organization of the Harris' Hawk and participation in hunting may be one of the largest contributions that helpers make to the breeding effort.

Based on behavior, Dawson and Mannan (1991a) distinguish two types of helpers in Harris' Hawks: beta males and gamma males or females. They find that approximately 80% of adult-plumaged male helpers are beta birds (Dawson and Mannan 1991a: table 3) and are not related to the breeders. Gamma helpers may be in adult plumage (~22%) but are more frequently in juvenal plumage (~78%). They may be either male (~63%) or female (~37%) and are usually offspring of the breeding pair. The evidence for the relatedness of these two types of helpers comes from 4 yr of group-composition analysis, banding, and dispersal data (Daw-

son and Mannan 1991a). Approximately three fourths of observed juvenal-plumaged gamma helpers were banded offspring of the breeders they were helping, and about one fourth were immigrants. Furthermore, no birds banded in the nest were observed to attain alpha or beta status within their natal group or territory, although three males were observed to do so within unrelated groups. Adult male helpers can be older than 4 yr; three adult beta helpers on the study area had been banded more than 8 yr previously by earlier workers (Dawson unpubl. data).

We did not divide our helpers into beta and gamma types because we did not always have enough information to do so. Rather, we classified them as either in adult plumage or in juvenal plumage (Table 1). Based on the above information, however, the probability that our adult-plumaged male helpers were of the unrelated, beta type is ca. 80%; the other 20% of adult-plumaged helpers were probably nondispersed gamma helpers. In Arizona <6% of female offspring remain on natal territories by their second year (after molting into adult plumage), and none remain by their third year (Dawson and Mannan 1991a). Thus, the adult female helpers we caught were even less likely to have been offspring of the breeders they were helping. All of our juvenal-plumaged birds were gamma helpers (no juvenal-plumaged beta birds have been observed). Approximately 75% of them were probably helping their parents, and 25% were not.

Endocrine mechanisms and lack of breeding in helpers.—Elevations in reproductive hormones are commonly interpreted as an indication of readiness to breed. In all seasonally breeding birds in which annual cycles in reproductive hormones have been studied, there are seasonal increases in plasma levels of gonadotropin and sex steroids associated with gonadal maturation or recrudescence (Wingfield and Farner 1980, Wingfield and Moore 1987). The extent of the elevation varies between species, however, and hormone levels often decline after the initiation of breeding cycles. If gonadotropin and sex steroid levels in a species are not elevated in helpers at the same time that they are elevated in breeders, then it seems reasonable that lack of breeding in helpers must be causally related, at least in part, to this hormonal difference.

We use analyses of hormones known to be involved in avian breeding cycles and a com-

TABLE 1. Categories and sample size for each sex of the composite variable called *nest role* used in the statistical analysis of hormone levels in Harris' Hawks. The 12 categories of nest role for each sex are determined by the individual's behavioral role and stage of the nest when the blood sample was taken.

	Behavioral role							
	Adult breeders		Adult-plumaged helpers		Juvenal-plumaged helpers		Total	
Nest stage	M	F	M	F	M	F	M	F
Nonbreeding	—	4	3	1	3	1	6	6
Nest building	5	10	7	5	4	9	16	24
Incubation	9	7	3	1	1	1	13	9
Feeding young	9	12	6	1	2	1	17	14
Total	23	33	19	8	10	12		

parison of levels between helpers and breeders to investigate whether or not Harris' Hawk helpers are physiologically ready to breed. We describe the way that plasma concentrations of luteinizing hormone (LH), testosterone (T), estradiol-17β (E), and corticosterone vary with season, behavior, social status and relatedness among individual Harris' Hawks. We measured corticosterone levels as an indicator of stress (e.g. Wingfield, Smith, and Farner 1982, Deviche 1983, Harvey et al. 1984, Wingfield 1985, Wingfield and Silverin 1986), in order to explore the possibility that lack of breeding by helpers is due to high stress levels associated with their subordinate social status.

METHODS

Study areas.—This study was conducted from May 1985 through August 1987 on an approx. 200-km² site north of Tucson, Arizona, and south of Florence, Arizona. Approx. 25% of the site overlaps that used by Dawson and Mannan (1991a, b). Harris' Hawks commonly nest in saguaro cactus and paloverde and mesquite trees in this habitat.

Field measurements.—To capture 157 Harris' Hawks (n = 157), we set a balchatri trap (Berger and Mueller 1959) near a perched bird and watched from 300–400 m until the bird was caught, or we staked traps within 200 m of active nests and checked traps every 1–2 h. Birds usually do not hunt when closely observed and will not approach a trap if humans are within sight. We were thus forced to remain away from the traps for long periods of time to increase the probability of capturing a bird. The maximum possible time a bird could have been ensnared on a trap was recorded as time elapsed since the trap was set until the bird was removed from the trap. Mean (±SD) maximum time birds spent on the trap was 55 ±58 min (median time = 30 min).

We withdrew 3 ml of blood from a wing vein of captured birds with a heparinized syringe and 25-gauge ⅝-in needle. Handling time was then calculated as maximum possible time on trap plus processing time. The mean maximum handling time was 70 ± 61 min. Blood was stored on ice in heparinized test tubes until the end of the field day when it was centrifuged. The plasma was then removed and stored at −20°C until analyzed.

We banded each bird with a unique combination of three colored bands and a numbered aluminum USFWS service band (permit no. 09335). Morphological measurements were taken, and each bird was weighed. A 2,000-g pesola scale was used to weigh each bird to ±25 g.

To assess the breeding condition of males, we examined the cloacal contents of 26 males for the presence or absence of sperm. The cloacal contents were extruded onto a slide (Bird et al. 1976), the slide was air-dried and later examined for the presence of sperm under a phase contrast light microscope. We found sperm in 4 of 8 breeding males and no sperm in the cloacal contents of 7 adult helpers, 4 juvenal-plumaged helpers, and 7 males whose role was unknown. We believe, however, that detection of cloacal sperm in Harris' Hawks by the "stripping" technique may reflect only the remnants of a recent sperm ejaculation, rather than evidence of spermatogenesis. For instance, we found no sperm in the cloaca of one alpha breeder 5 days before the first egg. This male was the only male at a nest lacking helpers, and the eggs in the nest hatched. When sperm were present, we found only a few per microliter. Others have also noted low levels of sperm in cloacal samples collected from breeding raptors (Corten 1973).

Age and sex of individuals.—Based on their appearance, we identified banded hawks as belonging to one of two age categories: adult or juvenal-plumaged. The juvenal plumage is retained through one breeding season after fledging (Brown and Amadon 1968). The sexes are monomorphic in plumage coloration. We assigned a sex to each individual in the field (after separation by age) on the basis of mass (Hamerstrom and Hamerstrom 1978). Mass of adult males (range:

610–900 g; $\bar{x} = 726$ g) overlapped that of adult females (range: 900–1,225 g; $\bar{x} = 1,046$ g) in only one male. The next largest male weighed 825 g, and the sex of the one unusually large male was supported using principal components analysis of seven morphological measurements (Mays 1989). The mass of juvenal-plumaged males (range: 650–800 g; $\bar{x} = 706$ g) did not overlap that of juvenal-plumaged females (range: 850–1,086 g; $\bar{x} = 942$ g).

Field observations.—We identified a hawk as a member of a group if it was trapped or seen within 300 m of an active nest. Harris' Hawks actively expel trespassers from within at least 500 m of an active nest (Dawson and Mannan 1991b); therefore trapping a nonmember within this zone is unlikely.

Most behavioral information on color-marked birds was gathered from fully enclosed, elevated blinds, which were erected 3–10 m from the nest gradually over a period of several days. Blinds were entered either before dawn or by two people, one of whom later left the area. We used a 20× spotting scope and 9× binoculars to identify and observe the behavior of marked birds. We recorded behavioral activity of marked individuals for a minimum of 10 h at each nest (see Dawson and Mannan 1989, 1991a, b). At some nests, we used a fully enclosed cloth blind erected on the ground within 10 m of active nests and recorded behavioral activity of marked individuals at the nest for 3–16 h per nest. Behavioral observations at 47 different nests allowed us to identify the behavioral role (breeder or helper) of 105 of the 157 trapped individuals for whom we had blood samples.

Nest stage.—We classified the nest stage for each hawk for the time the blood sample was taken by counting forward or backward from the estimated date of the first-laid egg. The date of the first-laid egg was either observed directly, calculated from observations of the first-hatched chick, or calculated from estimates of the age of the nestlings based on plumage development (Bednarz 1987a). Nest building begins approx. 36 days before egg laying (Mader 1975b). Defense of a nest site from human intruders (circling and screaming) begins approximately the same time as nest building, and we observed it a maximum of 66 days before the first-laid egg ($\bar{x} = 32 \pm 16$ days, $n = 14$ nests). We used the mean time of nest-site defense plus one SD to indicate the early beginning of the nesting cycle. Thus samples collected >50 days before the first-laid egg were considered to be from the nonbreeding stage of the annual cycles (approximately August through early January). Samples collected 50 days before the first egg up to the date of the first egg were considered to be from the nest-building and gamete-production stage. Samples collected from the date of the first-laid egg to 35 days later were from the incubation stage (Mader 1975b), and those collected from 36 to 100 days after the first-laid egg were from the stage when young were being fed. The chicks remain in or near the nest for approx.

45 days post-hatch (Mader 1975a), and group members continue to feed the young for several months after fledging (pers. obs.).

Hormone assays.—Testosterone (T) and Estradiol-17β (E) in 200 μl plasma were assayed after extraction in 2.5 ml diethyl ether and chromatographic separation on celite columns by radioimmunoassay (RIA) following the methods of Abraham (1974) with modifications described by Wingfield and Farner (1975) for use with avian plasma. For the corticosterone RIA, the hormone was extracted from 30 μl plasma in 3 ml dichloromethane, and it was then assayed in duplicate. Least detectable concentrations were 15 pg/ml for T, 1 ng/ml for corticosterone, and 12 pg/ml for E. Interassay variability and intraassay variability (SD/mean × 100) for T were 10.8% and 7.0%; for corticosterone, 7.0% and 10.9%; and for E, 23.2% and 8.7%, respectively.

We assayed luteinizing hormone (LH) in the laboratory of John Wingfield (Univ. Washington, Seattle, Washington) with a double-antibody, postprecipitation RIA for avian LH developed by Follett et al. (1972) and modified by Follett et al. (1975). Luteinizing antiserum (anti 3/3) and LH standard (PRC-AEI-I) were kindly provided by Peter Sharp (Poultry Research Centre, Roslin Edinburgh). The least detectable concentration was approx. 0.1 ng/ml.

Statistical analysis of effect of season.—All values were first transformed with natural logs to minimize the effects of outliers and normalize the data. Statistical tests were performed using general linear models contained in SAS statistical package (SAS 1984). To elucidate seasonal patterns in hormone levels, we did three-way ANOVAs for each hormone after separating samples by sex. To test for the effect of age of the bird, month of year, and maximum possible handling time on hormone levels, we used samples from all years combined (Table 2A). All 157 samples could be used for this analysis. Two-way ANOVAs were performed (after separation of the data by sex and age) to determine whether values changed significantly in a given month from the previous month. Handling time was included in all two- and three-way ANOVAs because handling times were long. A pilot study showed that testosterone and corticosterone levels in serial samples tend to increase with handling time, although estradiol and luteinizing hormone levels do not change (Mays and Vleck 1987; unpubl. data). We excluded handling time from one-way ANOVAs only after it showed no significant effect in two- or three-way ANOVAs.

Statistical analysis of effect of nest role.—Harris' Hawks do not breed synchronously; first-egg dates ranged from 21 February through 5 May. Hormone levels are probably more closely correlated with nest stage than with day of the year. Thus, we analyzed separately the data from the 105 hawks for which we knew the behavioral role and the stage of its associated nest. Due to the incomplete design inherent in our study,

we designated a composite variable that we called *nest role* for use in the ANOVA. We defined this variable based on the combined behavioral role of the individual at the nest, the stage of the nest, and the age of the bird. Nest role separates the values for each sex into 12 possible categories; sample sizes for each nest role are shown in Table 1.

For the 105 hawks for whom we knew nest role, we examined the effects of sex, nest role, and handling time on the levels of each of the hormones with a three-way ANOVA (statistics not shown). After separation by sex, we tested the 105 samples for the combined effects of nest role and handling time with a two-way ANOVA (Table 2B). For cases in which handling time showed no effect, we did one-way ANOVAs for each role category, to test whether means differed between nest stages for each behavioral role (Table 2C). One-way ANOVAs were also done for each nest stage, to test whether hormone levels differed between roles during the same nest stage (Table 2D). Each variable that showed a significant effect (P < 0.05) was further examined using Bonferroni multiple-comparison tests (BON) to indicate which means differed (SAS 1984).

RESULTS

TESTOSTERONE

Effect of season in males.—Mean plasma T concentrations varied significantly by month in male Harris Hawks (Fig. 1a), but handling time did not significantly affect T levels (Table 2A). In adult-plumaged males exclusively, mean T levels differed significantly between months (two-way ANOVA, $F = 4.94$, $P = 0.007$, $n = 33$). Levels rose during February and remained elevated during March (nest-building period for most birds). Levels of T declined in April, which coincided with incubation at most nests. In juvenal-plumaged males, T levels did not vary among months. Adult levels were higher than those in juvenal-plumaged birds, but the differences in T between age groups did not quite reach significance (Table 2A). One juvenal-plumaged male plotted individually (Fig. 1a) had an elevated T level late in February, 30 days before the first egg was laid in the nest at which he helped. This individual was the only juvenal-plumaged male sampled during the nest-building stage that was known to be helping at a nest *not* belonging to his parents. The other three had been banded in the previous years' nests of the birds they were currently helping.

We examined the male T and LH data from March in more detail because the average first-

egg date for both study sites and all 3 yr was 30 March (± 17 days, $n = 113$ nests) and previous studies (Balthazart 1983; Wingfield and Farner 1978a, b; Fivizzani and Oring 1986; Wingfield and Moore 1987; Wingfield 1984a) have shown that these two hormones are highest in the period before egg laying in most species. During March, T levels were significantly higher in adult males than in juvenal-plumaged males (one-way ANOVA, $F = 5.68$, $P = 0.038$, $n = 12$).

Effect of nest role in males.—Average plasma T levels differed significantly depending on nest roles (Fig. 1b, Table 2B). In adult breeders, T was significantly higher during the nest-building stage than during incubation or feeding of young (BON, $t = 2.63$, $P < 0.05$, $n = 22$). In the adult helpers, T was also significantly higher during the nest-building stage than during incubation (BON, $t = 3.07$, $P < 0.05$, $n = 18$). There were no statistically significant changes in T between nest stages in juvenal-plumaged helpers (Table 2C). Sample sizes were small for juvenal-plumaged helpers (total $n = 10$), but T levels were low in all but the individual who was not on his natal territory (Fig. 1b).

We also examined the effect of role during each nest stage (Table 2D). During the nest-building stage, T levels in breeder and adult helper were similar to each other and higher than juvenal-plumaged helpers, but this difference was not significant. Excluding the T value for the one male helper that was not on his parents' territory decreased the mean T value for juvenal-plumaged helpers during nest building, and the differences in breeders and adult helpers from the three remaining juvenal-plumaged helpers approached significance ($F = 2.24$, $P = 0.08$, $n = 14$). Nest role did have a significant effect in the two-way ANOVA (Table 2B), so the inability of the one-way ANOVA to detect significant differences between the groups during the nest-building stage was presumably due to small sample sizes that resulted from partitioning the data by nest stages.

Effect of season in females.—Levels of T in the 82 females differed significantly between age groups and months, and due to handling time (Table 2A); average T levels were lower than in males (three-way ANOVA, $F = 10.66$, $P = 0.002$, $n = 101$). In adult females, T levels differed significantly among months (two-way ANOVA, $F = 2.94$, $P = 0.005$, $n = 67$), rising during March (Fig. 1c), but there were no significant changes between months in juvenal-plumaged females.

TABLE 2. Analyses of variance (ANOVA) statistical results for Harris' Hawk hormones and body mass. Abbreviations: df = numerator degrees of freedom, T is testosterone, E is estradiol-17β, LH is luteinizing hormone, and B is corticosterone. The categories of nest role are shown in Table 1. Asterisks signify statistical significance.

A. Three-way ANOVA—effect of season. Model: hormone = age, month, handling time.

	|	Combined				Age			Month			Handling time		
	n	r^2	F	P	df	F	P	df	F	P	df	F	P	df
Male T	67	0.365	3.63	0.001*	9	3.58	0.064	1	3.96	0.001*	7	0.17	0.682	1
Female T	82	0.351	2.82	0.003*	13	4.08	0.021*	2	2.62	0.009*	10	6.04	0.017*	1
Male E	65	0.146	1.04	0.419	9	0.03	0.865	1	1.31	0.261	7	1.05	0.309	1
Female E	81	0.345	2.71	0.004*	13	3.42	0.039*	2	1.98	0.049*	10	2.13	0.149	1
Male LH	65	0.503	6.19	<0.001*	9	3.65	0.061	1	6.28	<0.001*	7	3.90	0.053	1
Female LH	77	0.292	2.00	0.035*	13	0.04	0.964	2	2.41	0.017*	10	0.18	0.669	1
Male B	67	0.500	6.33	<0.001*	9	6.64	0.013*	1	5.06	<0.001*	7	27.74	<0.001*	1
Female B	80	0.464	4.39	<0.001*	13	0.01	0.995	2	3.03	0.003*	10	10.11	0.002*	1

B. Two-way ANOVA—effect of nest role (after separation by sex). Model: hormone = nest role, handling time.

	|	Combined				Nest role			Handling time		
	n	r^2	F	P	df	F	P	df	F	P	df
Male T	48	0.451	2.69	0.012*	11	2.65	0.016*	3	<0.01	0.991	1
Female T	53	0.570	4.94	<0.001*	11	4.26	<0.001*	3	4.58	0.038*	1
Female E	53	0.599	5.58	<0.001*	11	5.08	<0.001*	3	1.67	0.203	1
Male LH	46	0.569	4.08	0.001*	11	3.83	0.002*	3	3.45	0.072	1
Female LH	52	0.317	1.69	0.111	11	1.71	0.112	3	0.02	0.888	1
Male B	47	0.456	2.67	0.013*	11	2.09	0.052	3	11.58	0.002*	1
Female B	53	0.418	2.68	0.011*	11	1.22	0.306	3	16.17	<0.001*	1

C. One-way ANOVA—effect of nest stage. Model: hormone = nest stage.

	Breeders					Adult auxiliaries					Juvenal-plumages auxiliaries				
	n	r^2	F	P	df	n	r^2	F	P	df	n	r^2	F	P	df
Male T	22	0.415	6.73	0.006*	2	18	0.557	5.87	0.008*	3	10	0.147	0.35	0.794	3
Female E	34	0.556	12.54	<0.001*	3	9	0.222	0.48	0.713	3	12	0.231	0.80	0.527	3
Male LH	22	0.592	13.06	<0.001*	2	18	0.270	1.72	0.208	3	9	0.544	1.99	0.234	3
Female LH	34	0.285	3.99	0.017*	3	8	0.334	0.67	0.615	3	12	0.310	1.20	0.372	3

TABLE 2. Continued.

D. One-way ANOVA—effect of role. Model: hormone = role.

	Nonbreeding					Nest building					Incubation					Feeding young				
	n	r^2	F	P	df	n	r^2	F	P	df	n	r^2	F	P	df	n	r^2	F	P	df
Male T	6	0.416	2.85	0.167	1	15	0.156	1.11	0.362	2	12	0.166	0.89	0.443	2	17	0.071	0.53	0.597	2
Female E	6	0.850	8.51	0.058	2	24	0.555	13.12	<0.001*	2	9	0.284	1.19	0.368	2	16	0.141	1.07	0.372	2
Male LH	5	0.500	3.00	0.182	1	15	0.286	2.40	0.133	2	12	0.253	1.53	0.269	2	16	0.101	0.73	0.502	2
Female LH	5	0.470	0.89	0.530	2	24	0.225	3.05	0.069	2	9	0.057	0.18	0.838	2	16	0.088	0.62	0.551	2

E. Two-way ANOVA—effect of role and nest stage. Model: body mass = role, nest stage.

	Combined					Role			Nest stage		
	n	r^2	F	P	df	F	P	df	F	P	df
Adult males	36	0.413	5.46	0.002*	4	0.05	0.826	1	6.87	0.001*	3
Adult females	38	0.314	3.77	0.012*	4	8.77	0.006*	1	3.42	0.029*	3

Levels of T in adult females were significantly higher than those in juvenal-plumaged females (Table 2A).

Effect of nest role in females. In females there were also significant differences in plasma T levels between nest roles and due to handling time (Table 2B). Breeding adult females had the highest T levels during the nest-building stage (Fig. 1d). We think that the higher levels of T in breeding females when compared with helper females during nest building are unlikely to be solely due to handling time because the mean handling time for the adult breeding females during this nest stage was less ($\bar{x} = 62$ min, $n = 10$) than that for the adult helper females ($\bar{x} = 90$ min, $n = 5$), and similar to that for the juvenal-plumaged helper females ($\bar{x} = 57$ min, $n = 9$).

Handling time (maximum time on trap plus processing time) significantly affected T levels in females (Table 2: A and C), but not in males. Previously, we reported that T levels increase with handling time in serially sampled Harris' Hawk males (Mays and Vleck 1987). Stress due to handling time may cause an adrenal cortical release of T as well as corticosterone. The maximum T values resulting from this stress-related release are an order of magnitude less than those in males during nest building and territorial defense, so it is not surprising that there were no statistical effects of handling time on male T, but there were effects on female T.

ESTRADIOL

Effect of season in females.—Mean plasma E levels varied significantly over the year in female Harris Hawks (Fig. 2a) and were significantly higher in adults than in juvenal-plumaged birds (Table 2A). Plasma E levels in adults rose in March just before egg laying, but not significantly so, whereas in juvenal-plumaged birds, there were no changes in levels during the months when birds were sampled.

Effect of nest role in females.—Nest role, but not handling time, had a significant effect on E levels in females (Table 2B, Fig. 2b). In adult breeders, E levels were significantly higher during the nest-building stage than during incubation and feeding of young and were lower during feeding of the young than during the non-breeding stage (BON, $t = 2.83$, $P < 0.05$, $n =$
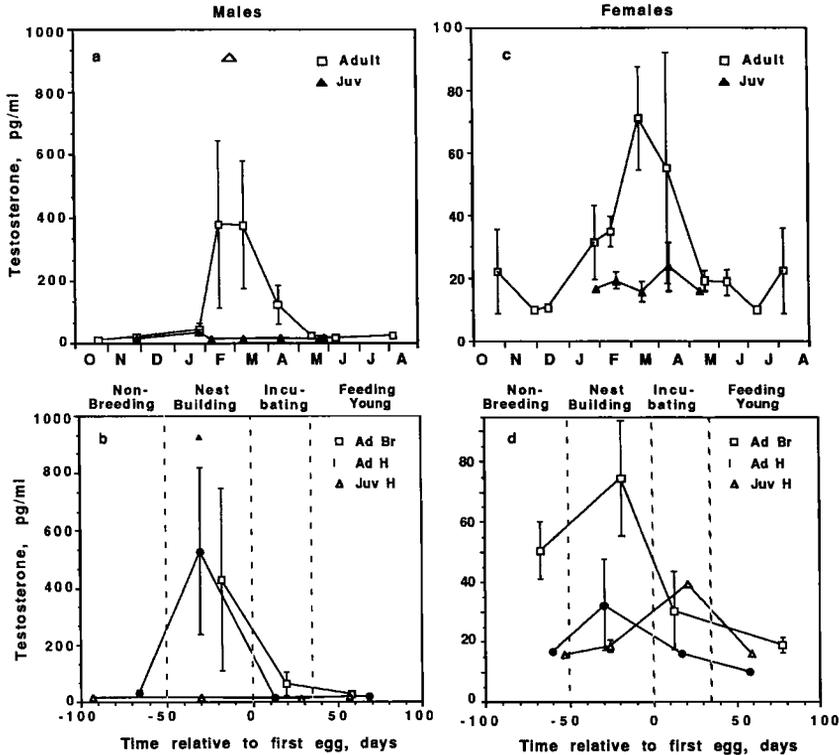
Fig. 1. Mean plasma testosterone levels in Harris' Hawk males (a and b) and females (c and d). The top panels indicate the mean level for all adult-plumaged and juvenal-plumaged birds in each month. The bottom panels plot the mean values during each nest stage for those individuals for whom nest-role is known. The nonbreeding season extends from approximately August through early January. Ad Br = adult breeder, Ad H = adult-plumaged helper, and Juv H = juvenal-plumaged helper. Error bars indicate ± 1 SE. Lack of error bars indicates no variance, sometimes because $n = 1$ (see Table 1). The open triangle (in a) and closed triangle (in b) show the testosterone value for the one juvenal-plumaged male helper who was not on his parent's territory; this value was not included in the mean for juvenal-plumaged auxiliaries for that interval. Within each nest stage the mean hormone value is plotted on the mean day on which samples were collected.

34). Estradiol-17β levels did not differ significantly between nest stages in either adult or juvenal-plumaged helpers (Table 2C).

During the nest-building stage, levels of E in breeding females were significantly higher than in either adult helpers or juvenal-plumaged helpers (Table 2D, BON, $t = 2.60$, $P < 0.05$, $n = 24$). Adult- and juvenal-plumaged helper female levels did not differ significantly from each other. This is in contrast to the pattern of T in males in which both breeder and helper adults had higher levels than juvenal-plumaged helpers. There were no significant changes in E in females of different roles during the other nest stages. Males exhibited no variation in E with time of year or nest role, and values were always low (Table 2A).

LUTEINIZING HORMONE

Effect of season in males.—Plasma LH levels in males differed from month to month (Fig. 3a, Table 2A). In adult-plumaged males, LH rose in January and fell in May (two-way ANOVA, $F = 8.54$, $P = 0.0001$, $n = 52$). In contrast to the seasonal pattern in T, LH levels remained high throughout April (during incubation). Plasma LH did not vary significantly with month in juvenal-plumaged birds, where levels were lower overall than in adults, but not significantly so (Table 2A). In March, during nest building and mate guarding, LH levels in adults were significantly higher than in juvenal-plumaged males (one-way ANOVA, $F = 8.26$, $P = 0.017$, $n = 12$).

Effect of nest role in males.—Plasma LH levels differed significantly between nest roles (Fig. 3b, Table 2B). In adult breeders, LH was significantly higher during nest building and incubation than during feeding of young (Table 2D; BON, $t = 2.64$, $P < 0.05$, $n = 22$). For adult helpers, LH was highest during nest building but not significantly so. There were no significant changes in LH levels of juvenal-plumaged helpers between nest stages. Luteinizing hormone levels in breeders and adult helpers were similar during each nest stage and higher than those in juvenal-plumaged helpers (except during feeding of young), but these differences were not statistically significant (Table 2D). Overall, LH levels were lower in males than in females (three-way ANOVA, $F = 5.26$, $P = 0.024$, $n = 98$).

Effect of season in females.—In plasma samples of females, LH levels differed significantly among months (Fig. 3c), but there were no statistically demonstrable differences due to age or handling time (Table 2A). In adult-plumaged females, LH levels differed among months (two-way ANOVA, $F = 2.16$, $P = 0.036$, $n = 62$); they rose in January and remained relatively high through April. The one female sampled during November had a high level of LH (1.68 ng/ml), which may indicate an undiscovered autumn nest (Radke and Klimosewski 1977, Bednarz 1987b). There was no statistically significant seasonal pattern detected in the plasma LH values from juvenal-plumaged females, and their levels did not differ significantly from those of adults.

Effect of nest role in females.—There were no significant differences in female plasma LH levels between nest roles or due to handling time (Fig. 3d, Table 2B). In breeding females, LH levels were significantly higher during the nest-building stage than during feeding of young (Table 2C; BON, $t = 2.83$, $P < 0.05$, $n = 34$). Adult breeders had higher levels of LH than either adult or juvenal-plumaged helpers during all nest stages, but these differences were not significant (Table 2D). The adult helper females had lower levels of LH than either adult breeder or juvenal-plumaged females during all stages except nonbreeding (Fig. 3d).

CORTICOSTERONE

Effect of season.—Although most of the variance in corticosterone was due to handling time,
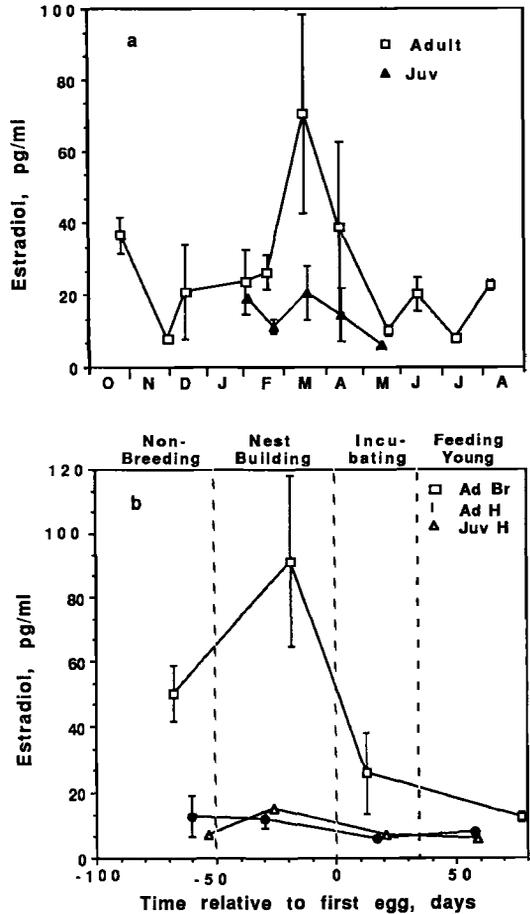

Fig. 2. Mean plasma estradiol levels in female Harris' Hawks. The (a) panel indicates the mean level for all adults and juvenal-plumaged birds in each month, whereas (b) plots the mean value during each nest stage for those individuals for whom nest role is known. Symbols and statistics as in Figure 1.

there were also significant effects of age and month of year in males (Fig. 4a, Table 2A). Corticosterone levels were generally lower in juvenal-plumaged males than in adults and were higher in adults during the breeding season than during the nonbreeding season. In females, corticosterone levels differed significantly from month to month and with handling time (Fig. 4b); however, there were no significant differences between adult- and juvenal-plumaged birds (Table 2A). As with the males, corticosterone levels in females were higher during the breeding season than during the nonbreeding season.

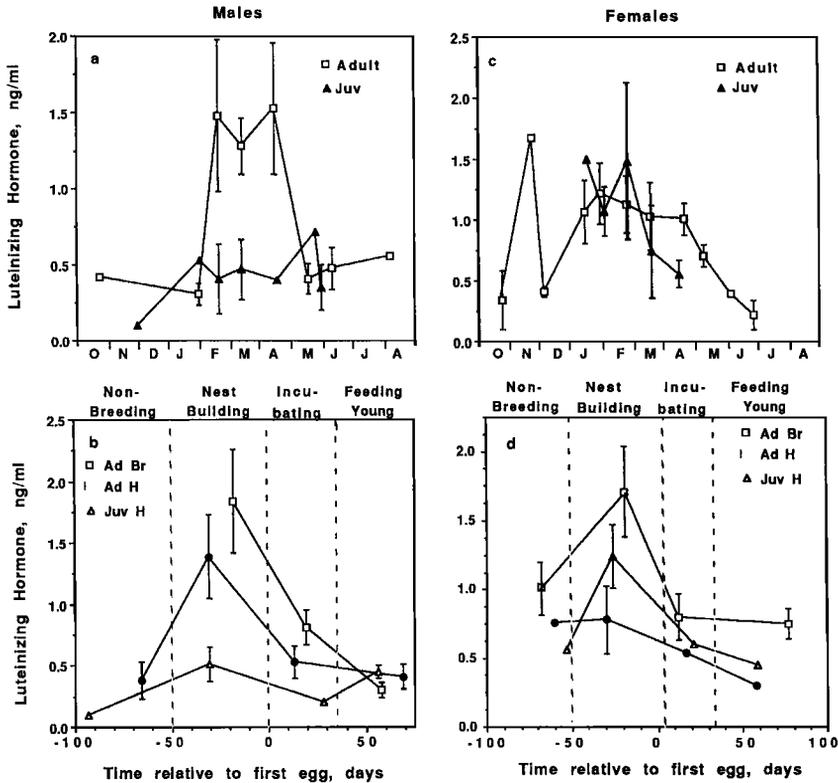*Effect of nest role.*—Average plasma cortico-

Fig. 3. Mean plasma luteinizing hormone levels in Harris' Hawk males (a and b) and females (c and d) in each month (top) or during each nest stage for those individuals for whom nest role is known (bottom). Symbols and statistics as in Figure 1.

sterone levels did not differ significantly between nest roles. The only statistically significant variation in corticosterone levels we could account for in this data set was due to handling time (Table 2B), although the effect of nest role approached significance in males ($P = 0.052$). Corticosterone is the major adrenocorticoid in birds associated with stress, and an effect of handling time has been demonstrated in several other species (reviewed in Harvey et al. 1984).

BODY MASS

In adult male Harris' Hawks, there were no differences between the body masses of the helpers and breeders, but nest stage had a significant effect (Table 2E). Males were heaviest during the nonbreeding season and mass decreased throughout the nesting season in both helpers and breeders (Fig. 5a). In adult females, both behavioral role and nest stage statistically

affected body mass. Breeding adults were significantly heavier than adult helpers (BON, $t = 2.03$, $P < 0.05$). During the nonbreeding and nest-building stages, breeding females had a mean mass of 1,100 g ($n = 10$, range: 975–1,225 g), but the helper females averaged only 990 g ($n = 7$, range: 925–1,050 g). As with males, body mass decreased though the breeding season in the adult breeding females (Fig. 5b).

DISCUSSION

INTERSPECIFIC COMPARISONS

Plasma LH levels in breeding male and female Harris' Hawks are generally lower than levels in breeding members of the same sex in most other species studied (e.g. Lincoln et al. 1980, Silverin and Wingfield 1982, Dufty and Wingfield 1986, Hiatt et al. 1987). In addition, T levels in breeding male Harris' Hawks were lower than those in breeding males during the
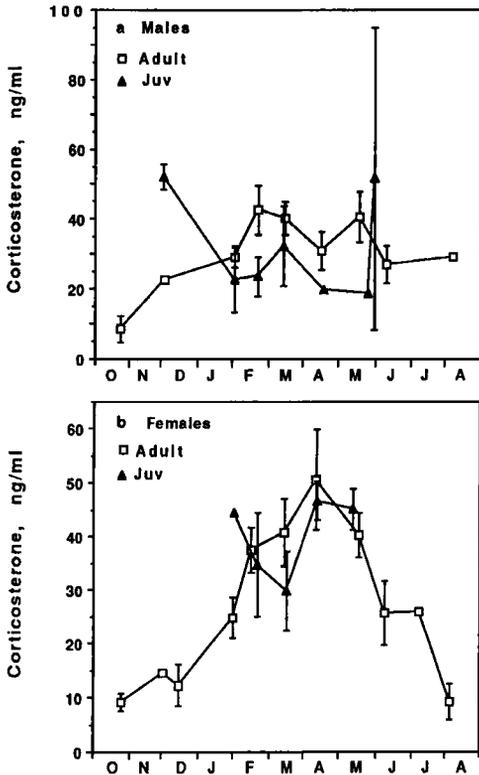
Fig. 4. Mean plasma corticosterone levels in male (a) and female (b) Harris' Hawks in each month. Values for adult-plumaged and juvenal-plumaged birds are plotted separately. Symbols and statistics as in Figure 1.
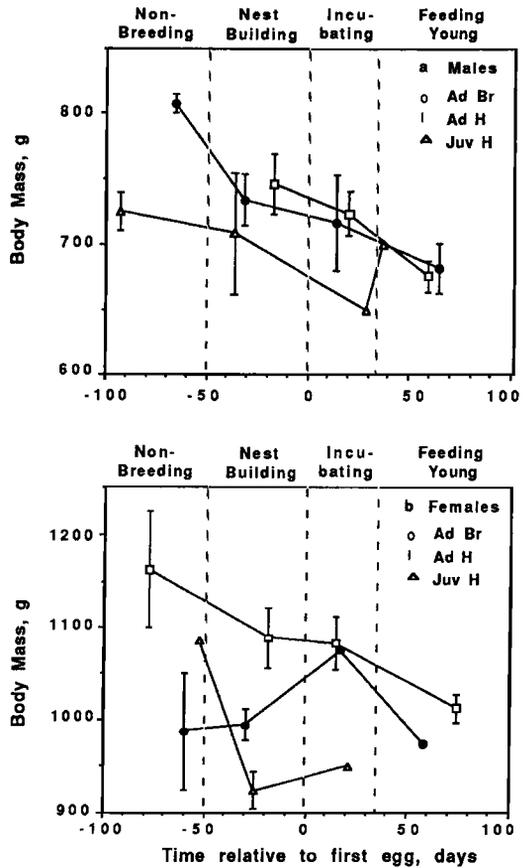

Fig. 5. Mean body mass in male (a) and female (b) Harris' Hawks during each nest stage for those individuals for whom nest role is known. Symbols and statistics as in Figure 1.

nesting season in most monogamous and polygamous species (e.g. Wingfield and Farner 1978b, 1980; Lincoln et al. 1980; Silverin and Wingfield 1982; Wingfield 1984a, b; Fivizzani et al. 1986; Fivizzani and Oring 1986; Hegner and Wingfield 1986a, b; Ball and Wingfield 1987). Low LH levels, similar to those in Harris' Hawks, are found in breeding polyandrous male Spotted Sandpipers (*Actitis macularia*; Rissman and Wingfield 1984) and in Pied Flycatcher females (*Ficedula hypoleuca*; Silverin and Wingfield 1982). Levels of T in Harris' Hawks are only slightly lower than concentrations in the Spotted Sandpiper and are similar to levels reported in the Mallard (*Anas platyrhynchos*; Donham 1979) and male Western Gulls (*Larus occidentalis wymani*; Wingfield, Newman, Hunt, and Farner 1982). Plasma T and E levels are lower in breeding Harris' Hawks than in the captive-breeding American Kestrel (*Falco sparverius*; Rehder et al. 1986, 1988).

Relatively low lvels of LH and sex steroids seem to be found in those species that are not strongly territorial such as the Spotted Sandpiper and Mallard or those that pair for life or return to the same territory year after year, such as the Western Gull. For instance, Wingfield et al. (1987) correlated the low T levels found in male Western Gulls with low levels of competition between males for mates and nest sites. Relatively low levels of LH and sex steroids are also found in some tropical species (e.g. Dittami and Gwinner 1985, Dittami 1986, Reyer et al. 1986). Several of these characteristics apply also to the Harris' Hawk, such as their generally tropical distribution (southwestern United States to Argentina and Chile), year-round residency, and long-term pair bonds between birds. Bednarz (1987a) described the Harris' Hawk

in New Mexico as not obviously territorial. In contrast, Dawson and Mannan (1991b) reported that groups in Arizona reside on nesting territories all year and continuously defend at least a portion of their territory, and that all group members participate in this defense to some degree. Aggressive encounters (attacking, chasing, and foot grabbing) occur between members of different groups during the winter (Dawson and Mannan 1991b) but to a lesser degree than in intraspecific territorial disputes in other raptors (de Vries 1975, Newton 1979). Members from more than one group may hunt, feed, and perch together during the winter (Mader 1975b, Whaley 1986, Dawson and Mannan 1991b). The relatively low amplitude of T cycles in male breeding Harris' Hawks compared with other species may partly reflect the relatively low level of conflict present in territorial disputes. The rise in T during the nest-building stage is presumably associated primarily with nest defense, sperm production and copulatory behavior.

Among female Harris' Hawks, T levels are elevated only in alpha females and only during the nest-building stage. In other species, females show elevated T levels only when they participate in territorial defense (Wingfield and Farner 1978b, Rissman and Wingfield 1984). Harris' Hawk breeding females participate in territorial defense and are especially likely to exhibit aggressive behavior toward other breeding females or nest predators (Dawson and Mannan 1991b). Unlike Western Gulls, in which females have levels of T equivalent to those of the males, T levels in Harris' Hawk females, although elevated, are significantly lower than those of the males. Levels of T in female helpers are not elevated during nest building, and female helpers are much less likely to defend the nest (Dawson and Mannan 1991b).

As in most monogamous species studied, steroid levels fell in breeding Harris' Hawks of both sexes at the onset of incubation. Elevated T levels are thought to be incompatible with parental care in males (Silverin and Wingfield 1982; Hegner and Wingfield 1986a, 1987a; Wingfield and Moore 1987). Estradiol-17β levels decrease following egg laying in the American Kestrel (Rehder et al. 1986), as they do in breeding female Harris' Hawks, although E does not necessarily decrease at the onset of incubation in all species (Donham 1979, Schwabl et al. 1980, Wingfield 1984a).

ENDOCRINE DIFFERENCES BETWEEN HELPERS AND BREEDERS

Understanding why (both mechanistically and functionally) helpers do not breed is central to understanding the evolution of cooperative breeding systems, because the lack of breeding would seem to produce a heavy cost in terms of direct fitness (Woolfenden and Fitzpatrick 1977, Brown 1978, Emlen 1984). We first examine several alternative, but not mutually exclusive, hypotheses that could account for the lack of breeding in helper Harris' Hawks and then discuss our interpretation of our hormonal data from breeding and helping Harris' Hawks in the light of these hypotheses. We propose that the proximate and ultimate causes for the lack of breeding in Harris' Hawks are not the same for all helpers in the group.

Reproductive maturity.—Absence of breeding by helpers could be due to incomplete maturation and not a particular social factor. Lack of breeding and low reproductive-hormone levels found in most juvenal-plumaged helpers could be simply due to their age. Both sexes of Harris' Hawks, however, have been reported to breed while still in juvenal plumage (Mader 1975a, Whaley 1986, Dawson and Mannan 1991a, Lett pers. comm.), and one juvenal-plumaged male we sampled had a T level higher than the mean value for breeding males (Fig. 1). Clearly possession of juvenal plumage does not necessarily mean that a bird is sexually immature.

Reyer et al. (1986) rejected the hypothesis that the low T levels in (usually younger) primary helpers of the cooperatively breeding Pied Kingfisher (*Ceryle rudis*) were due to incomplete maturation. They found that T levels did not necessarily correlate with age but with helper status. In addition, some primary helpers are failed breeders that have returned to their natal territories. In other cooperatively breeding species that previously were thought to exhibit delayed maturation, it is now known that first-year individuals can and do breed under appropriate circumstances (Stallcup and Woolfenden 1978, Koenig and Mumme 1987).

Behavioral suppression.—Helpers may not breed because of behavioral interactions with the breeders (e.g. mate guarding) even though they are physiologically ready to do so. The ultimate reason for this may be that dominant breeders have an interest in protecting their genetic in-

vestment by interfering with, or not cooperating in, mating attempts by helpers. Most, but not all, adult-plumaged male Harris' Hawks—whether breeders or helpers—have elevated LH and T during the nest-building stage. Thus, most adult male helpers appear reproductively ready, based on LH and T levels indistinguishable from those in breeders at the same time. In fact, adult helper males often attempt to copulate with the alpha female, and their apparent lack of success is due mainly to her lack of cooperation. In 46 observations of mounting of the alpha female by the alpha male, copulation was completed in 44, whereas only 1 in 22 observed mountings by beta males appeared to be successful (Dawson and Mannan 1991a, pers. obs.). Females will occasionally copulate with more than one male, which results in some polyandrous mating groups (Mader 1979, Whaley 1986, Sheehy et al. MS).

Physiological suppression. —Alternatively, helpers may be sexually mature but not physiologically ready to breed (i.e. with inactive gonads and low levels of reproductive hormones). In Harris' Hawks, all helper females and most juvenal-plumaged male helpers appear to be physiologically unprepared for breeding, based on very low levels of LH, T, and E. At the same time, these hormones were elevated in breeders and adult-plumaged male helpers. Physiological readiness to breed could be constrained by factors such as poor body condition, or it could be the result of social interactions between birds. For instance, physiological inhibition could result from stress due to domination by the breeder of the *same* sex to assure its genetic parentage (Reyer et al. 1986). For example, an alpha female might dominate a potentially competing female, causing hormonal suppression in the helper and preventing breeding. On the other hand, physiological inhibition could occur due to the presence of the parent of the *opposite* sex, presumably as a result of selection to avoid inbreeding. Under this hypothesis, physiological readiness to breed would depend primarily on the relatedness between helpers and breeders, rather than on age or status within the dominance hierarchy. Of course, physiological suppression of reproduction could be due to a combination of these factors.

Behavioral vs. physiological suppression.—We suggest that whether behavioral or physiological suppression of breeding occurs is likely to

vary with the relatedness of the helper to the breeders because relatedness affects the probability that a helper can become a breeder in a nonconsanguineous mating. In monogamous groups, a helper unrelated to the breeder of the opposite sex could ascend to breeding status on the departure of the alpha bird of the same sex. A helper related to the breeder of the opposite sex should not ascend to breeding status because doing so would risk inbreeding and potentially reduce the inclusive fitness of both birds (although the adverse effects of inbreeding in birds are controversial; cf. Greenwood et al. 1978, Craig and Jamieson 1988). If inbreeding is avoided, ascent of a related helper to breeding status would require the loss of both breeders from the group: loss of one to free a breeding slot and loss of the other to avoid inbreeding. Thus, while the energetic costs of becoming physiologically ready to reproduce would be the same for both related and unrelated helpers, the probability of receiving any benefit from this readiness would be much lower for a helper related to the breeder of the opposite sex. This leads to a prediction: if we assume that opportunities to breed outside the breeding unit are few, helpers that are related to the breeder of the opposite sex should be less likely to invest in reproductive readiness (gonad growth, gamete production, costs of carrying and maintaining reproductive tissues, etc.) than helpers that are unrelated to the breeders. (This energetic argument is analogous to that which was been used to explain the regression of gonads in seasonal breeders during the nonbreeding season when chances of successful reproduction are slim).

The pattern of LH and sex steroid levels we observed in Harris' Hawk helpers is consistent with the hypothesis that inbreeding avoidance is an important ultimate selective factor determining their reproductive readiness (except in adult female helpers, see below). Most juvenal-plumaged Harris' Hawks (~75%) are helping their own parents and are not hormonally ready to breed with the opposite-sex parent even if the same-sex breeder disappeared. In contrast, most adult-plumaged male helpers are not helping their own parents (~80%). We suggest that, for these birds, the cost of becoming reproductively ready during the breeding season is more than offset by the potential benefits to be derived from either occasional successful copu-

lations with the breeding female or attainment of alpha status. Those adult helpers whose LH and T levels were not elevated during the nest-building stage were presumably not reproductively ready, and they were possibly related gamma helpers rather than unrelated beta helpers. For instance, one of the six adult-plumaged male helpers we sampled during the nest-building stage had a T value in the same range (<15 pg/ml) as all the juvenal-plumaged male helpers on their natal territories. The other adult-plumaged males, whether helpers or breeders, had T values 2–70 times higher than related juvenal-plumaged helpers. We do not know the relatedness of this adult-plumaged helper whose T value was low. We do know that the only juvenal-plumaged helper who was known not to be helping on its parents' territory was the only such bird with high sex steroid levels (T > 900 pg/ml).

MECHANISMS FOR PHYSIOLOGICAL SUPPRESSION OF REPRODUCTION

Poor body condition.—Adult female helpers do not appear to be reproductively ready to breed even though they are unlikely to be on their natal territory. These birds also weigh significantly less than breeding females. In contrast, male adult helpers and breeders do not differ in mass. In fact, these female helpers weigh ~10% less than the breeding females during the 6–7 weeks before the first egg, when gonadal development is probably occurring in those females that become breeders. The greater mass in the female breeders compared with female helpers is not likely to be simply due to having eggs in the oviduct. Body masses of laying American Kestrels exhibited distinct peaks relative to nonlaying females, but only for approximately 1 week before and 1 week after egg laying (Rehder et al. 1986). The low hormone levels in the adult female helpers during the early nesting stages may be due to poor body condition rather than to any social suppression. Adult-plumaged female helpers do not usually remain with a group for >1 yr, and have never been observed to replace an alpha female (Dawson and Mannan 1991a). It may be that they join a group primarily to benefit from group hunting (Bednarz and Ligon 1988) rather than to actively participate in reproduction.

The cost/benefit ratio of becoming reproductively ready in female helpers is probably great-

er than that for the male helpers in Harris' Hawks. The cost of recrudescence in a 1,000 g female bird (growth of oviduct and functional but nonovulating ovary) is probably ca. 100–150% of a single day's basal energy expenditure, whereas estimates of the costs of testicular recrudescence in male birds range from only 7% to 40% (based on data *in* Walsberg 1983). Helpers in other cooperatively breeding species may be constrained to help rather than breed because they are energetically incapable of attaining breeding condition (Brown 1983). Unsuccessful breeding has been attributed to a less than adequate weight gain in females for many wild and captive species including raptors (Newton 1979, Hardy et al. 1981, Rehder et al. 1986), and reduced food intake has dramatic antigonadal effects (see Wingfield 1983 for review) or results in lower reproductive output (Drent and Daan 1980) in all avian species investigated. For instance, poor body condition (i.e. low fat deposits and body mass) results in low circulating levels of T in male Song Sparrows (*Melospiza melodia*; Wingfield 1985).

Dominance suppression.—On the other hand, dominance behavior by alpha females could result in physiological suppression of reproduction in adult female helpers either directly or indirectly. For instance, subordinate females may have low access to resources due to their low rank in the dominance hierarchy. An adult female helper that is capable of reproducing may pose a greater threat to the alpha female or to group stability than a reproductively ready adult male helper, possibly because two or more laying females would increase the number of chicks to be raised. One normal-sized brood may be all a Harris' Hawk group can care for (Faaborg and Bednarz 1990). In the Acorn Woodpecker (*Melanerpes formicivorous*), competition among communally nesting females is greater than that among males and decreases the reproduction of groups significantly more than does male-male competition in the group (Koening et al. 1983). Dominant females in a group can suppress reproductive output in birds (e.g. Jamieson and Craig 1987), and a similar phenomenon is seen in some mammals (Wasser and Barash 1983 and references therein).

Mechanisms by which breeding females might suppress reproduction in adult female helpers are not clear. One might predict that the mechanism of (or a correlate of) dominance-induced hormonal suppression would involve

the adrenocorticoids, which are normally elevated with stress (Deviche 1983). Corticosterone levels in females did not differ between breeders and helpers, however, and thus levels were not correlated with the subordinate status and reproductive hormone suppression of adult female helpers. If reproductive-hormone levels are suppressed in helpers because of their subordinate status it must work via some mechanism other than adrenocorticoid-induced inhibition.

In juvenal-plumaged helpers, we suggest that the breeding birds do not directly cause hormonal suppression via dominance. Rather, we believe that related juvenal-plumaged helpers remain reproductively inactive to avoid inbreeding. Lack of evidence for dominance suppression is of two types. First, corticosterone levels in the juvenal-plumaged males were lower, not higher, than those in the adults, which again does not support their involvement in hormonal suppression. Second, most studies that correlate hormone levels with degree of dominance have indicated that subordinate individuals do not differ from dominant individuals in sex-steroid levels once social relationships between birds have become well established, although they can differ in corticosteroid levels (Balthazart et al. 1979, Tsutsui and Ishii 1981, Rohwer and Wingfield 1981). Similar conditions have been found in free-ranging olive baboons (*Papio anubis;* Sapolsky 1987). Levels of testosterone can play an important role in determining status in the first place (Ramenofsky 1984, Hegner and Wingfield 1987b) and T levels increase in male birds following repeated intense aggressive interactions with other males (Searcy and Wingfield 1980, Wingfield and Moore 1987). Harris' Hawk group hierarchies, however, are well established and stable by the nesting season in March with little aggression displayed between members (Dawson and Mannan 1991b).

Inbreeding avoidance.—If low T levels in birds helping on their natal territories are related to inbreeding avoidance, it should be possible to identify a link between kin recognition and reproductive inhibition, but little is known about how birds recognize relatives or how this affects physiological processes. In Harris' Hawks, LH concentrations in different types of helpers parallel concentrations of T, thus the mechanism is presumably central and acts above the anterior pituitary/hypothalamic axis. Acorn Wood-

peckers (Koenig and Pitelka 1979, Koenig et al. 1983) and Florida Scrub Jays (*Aphelocoma coerulescens;* Woolfenden and Fitzpatrick 1978) show well-developed behavioral patterns to avoid close consanguineous matings, but nothing is known of the hormonal status of the nonbreeders in these species. The likelihood that other males will cuckold the alpha male, or other females will parasitize the alpha female, should be greater when the individuals involved are unrelated (Koenig 1981, Faaborg and Bednarz 1990). Whether this results from a hormonal suppression in related birds is unknown.

Hormone data for Pied Kingfisher helpers are also consistent with inbreeding avoidance. The Pied Kingfisher has two types of helpers: primary and secondary (Reyer 1980). Primary helpers are offspring of the breeding pair from a previous year, whereas secondary helpers are not related to the breeders (Reyer 1986). Primary helpers are associated with the breeders throughout the entire nesting cycle. In contrast, secondary helpers are tolerated by the breeders only after the young hatch and then only when the parents' feeding capacities are exceeded (Reyer 1984, Reyer and Westerterp 1985). Reyer et al. (1986) found that before egg laying, secondary helpers have T levels similar to the breeders, whereas primary helpers have T levels significantly lower. They attributed the low levels of T in the primary helpers to dominance suppression by the breeding males. Their hormone data are also consistent with the hypothesis that reproductive hormones are suppressed in the primary helpers because the potential mate is also a parent. Primary helpers are, of course, also subordinate to their parents, so these two hypotheses cannot be distinguished in this case.

Reyer's (1986) behavioral data provide additional support for inbreeding avoidance. In 7 cases secondary helpers had an opportunity to breed in a slot vacated by the male breeder they helped. In each of the 7 cases the secondary male helper moved into the vacated slot and bred with the widowed female that was not his mother. In 6 cases primary helpers had an opportunity to move into a slot vacated by a breeder. In 4 of the 6 cases the primary helper dispersed and ultimately bred with another female, and in 2 cases he moved into the vacated position. In the 4 cases of dispersal, if the helper had assumed the vacated slot, he would have mated with his mother; in the 2 cases where

the primary helper bred with the widowed female, she was not his mother. The hormone levels of these individuals are not known, but it may be that primary helpers have high T levels, similar to the secondary helpers, if they are not helping their own mothers.

In Harris' Hawks, physiological suppression of reproductive readiness in helpers on their natal territories and the lack of such suppression in helpers not on their natal territories are consistent with the hypothesis of inbreeding avoidance. Physiological readiness is necessary but not sufficient for a helper to breed. Reproductively ready male helpers are presumably not often able to breed because of behavioral interactions with the breeders (Dawson and Mannan 1991a). In our study, the one juvenal-plumaged male with high T did not breed after leaving his natal territory, presumably because of his low social status in his new group. Inbreeding avoidance also does not account for the low hormone levels in adult female helpers because they are unlikely to be related to the breeders in the group. Either poor body condition, behavioral interactions with other birds in the group, or both could be proximate causes for their hormonal suppression.

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