

HORMONAL CORRELATES OF PARENTAL AND HELPING BEHAVIOR IN COOPERATIVELY BREEDING HARRIS' HAWKS (*PARABUTEO UNICINCTUS*)

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ABSTRACT.—We measured plasma levels of progesterone and prolactin in free-living adult breeders, adult-plumaged helpers, and juvenal-plumaged helpers of the cooperatively breeding Harris' Hawk, *Parabuteo unicinctus*, at different stages of the nesting cycle. Overall, progesterone levels did not vary significantly with sex, nest stage, or behavioral role, but they increased significantly with handling time. Progesterone levels were highest (2–4 ng/ml) in breeding females just before egg laying. Prolactin levels did not vary with handling time but were significantly elevated in breeding females during the nest-building stage (14.1 ng/ml) and in both breeding males (8.4 ng/ml) and females (25.5 ng/ml) during incubation. Both sexes of breeders incubate the eggs, but the females do the bulk of incubation and only they develop a brood patch. Prolactin levels in the breeders declined immediately after the eggs hatched, in contrast to the pattern seen in many other altricial species. Prolactin levels in the adult-plumaged male helpers rose significantly after the eggs hatched (9.1 ng/ml). At this time these birds bring more food items from group kills to the nestlings than any other group members. The elevated prolactin levels in the adult-plumaged helpers may facilitate the helping behavior that they exhibit toward the nestlings and fledglings. Received 8 August 1991, accepted 1 April 1991.

HELPING behavior conventionally refers to parentlike behavior directed toward young that are not the offspring of the bird displaying the behavior. It has been one of the main foci of studies on cooperatively breeding species because helping behavior seems to entail costs, often without clear-cut benefits (see reviews by Woolfenden and Fitzpatrick 1984, Brown 1987, Koenig and Mumme 1987). Investigators have sought to explain not only the present selective advantages of helping behavior, but also the evolutionary origins of helper systems, and it remains controversial whether helping behavior is selected for, or is simply a result of misdirected parental behavior (cf. Jamieson and Craig 1987, Jamieson 1989, Ligon and Stacy 1989). The proximate mechanisms that control such parentlike behaviors, however, have not been investigated in any cooperatively breeding species. We investigated the hormonal correlates of parental behavior in the cooperatively breeding Harris' Hawk (*Parabuteo unicinctus*). Evidence for an endocrine system that promotes helping behavior in nonbreeding birds would suggest that selection has operated at a physi-

ological level to augment the behavior. This would support the hypothesis that helping behavior is adaptive.

The social system in the Harris' Hawk is complex and has been described in detail for populations in Arizona (Dawson and Mannan 1991a) and New Mexico (Bednarz 1987). In Arizona, group size ranges from a breeding pair to 7 birds (mean group size = 3.8). The breeding male and female (or *alpha birds*) build the nest, the female lays the eggs, both male and female incubate, shade or brood the nestlings, and feed the nestlings and fledglings. Breeding males only incubate approximately one-fourth as much as females (Dawson and Mannan 1991a), and the male does not develop a brood patch (pers. obs.). The alpha female rarely leaves the nest area during the nesting season and is provided food from group kills by her mate and the other birds in the group.

We call all other birds in the group *helpers* even though the extent to which individual hawks help differs (see Dawson and Mannan 1991a for details) and some of them breed (Sheehy et al. MS). In particular, few groups (0–

11%, depending on the year studied) contain another breeding female (termed an *alpha-2* female; Dawson and Mannan 1991a), but this type was absent from the groups we studied. Two classes of helpers have been described, distinguished by behavior (Dawson and Mannan 1991a): *beta males* and *gamma birds*, who may be either males or females. Beta males are the most common, are found in approx. 62% of groups, and are always in adult plumage. Gamma birds are usually in juvenal plumage (1 yr old or less) and may be either male (66%) or female (34%). They are in adult plumage (>1 yr old) approx. 32% of the time. Gamma birds are usually, but not always, offspring of the breeders in the group, whereas beta males are not related to the breeders. We did not divide our helpers into beta and gamma types because we did not always have enough information, but classified them as either in adult plumage or in juvenal plumage. Approximately 80% of adult-plumaged males were probably beta birds, and all adult-plumaged female helpers and all juvenal-plumaged birds were probably gamma birds (see details in Mays et al. 1991).

Helpers rarely come into direct contact with the eggs or young (Dawson and Mannan 1991a). Beta males are allowed to bring food to within 50 m of the nest before transferring it to one of the alpha birds, who delivers it to the incubating female or the nestlings. Gamma birds bring food to the nest area but transfer it to the alpha birds at least 150 m from the nest. Occasionally the beta males will incubate or bring food directly to the nest, and gamma birds will also occasionally attempt to incubate and feed the young directly, but they are usually supplanted from the nest by the breeding pair. All birds in the group detect and harass predators, defend the nesting territory from both predators and conspecifics (Dawson and Mannan 1991b), and take part in group hunting. Participation in cooperative hunting efforts (Mader 1975, Bednarz 1988, Bednarz and Ligon 1988) and delivering prey items to the nest area are probably the largest contributions that helpers make to the breeding effort.

In the accompanying paper (Mays et al. 1991), we described how testosterone, estradiol-17 β , and luteinizing hormone (LH) levels are correlated with breeder/helper status and nest stage in both males and females. Here we describe the correlation between progesterone and prolactin and parental behavior in individual birds

and, in particular, we compare hormone levels of breeders with those of helpers. We chose to examine the levels of these two hormones because they (often in synergy with estrogen and testosterone) are the hormones most often associated with parental care (incubation and care of young) in birds (reviewed in Balthazart 1983, Goldsmith 1983, Silver and Cooper 1983, Brown 1985, Buntin 1985).

METHODS

Field methods.—The study areas, animals, blood collection, field measurements, and observations were described in detail elsewhere (Mays et al. 1991). Briefly, we used bal-chatri traps (Berger and Mueller 1959) to capture 157 hawks north of Tucson, Arizona, in upland Sonoran Desert habitat between May 1985 and August 1987. Most hawks were trapped during their nesting season (February to July). Blood samples for hormonal analyses were taken from a wing vein, and each bird was banded with a unique color-band combination and weighed before release. Approx. 80% of blood samples were collected between 0530 and 1300, but because of the difficulty in trapping birds, we did some trapping in the afternoon and three samples were collected after 1800.

Most birds during the breeding season were examined for evidence of a brood patch, which was scored as 0 = absent: breast completely feathered; 1 = developing: breast beginning to lose feathers; 2 = present: breast fully defeathered, but not vascularized; 3 = functional: breast fully defeathered and vascularized; or 4 = regressing: breast defeathered, but no longer vascularized and beginning to sprout new feathers. In 1985 we noticed reddening and swelling of the outer cloaca of some females during the breeding season very similar to that described in Alpine Accentor (*Prunella collaris*) females (Nakamura 1990: fig. 2c). In 1986 and 1987 we recorded the appearance of the cloacal opening of all hawks as either dry and small, or red and swollen.

Blood samples were stored on ice in the field and centrifuged later the same day. The plasma was stored at -20°C until analyzed by radioimmunoassay. We recorded the maximum possible time the hawk was ensnared on the trap and the time taken to obtain the blood sample, and their sum is the maximum possible handling time for that bird. The mean maximum handling time was 70 min (± 61 min SD). Maximum possible handling times were high because we were forced to remain away from the traps for long periods of time to increase the probability of capturing a bird.

We identified hawks as either male or female, based on body mass, and as either in juvenal or adult plumage. Females are approx. 30% larger, and there is essentially no overlap between the sexes (Hamerstrom and Hamerstrom 1978). Birds retain the juvenal plum-

age until after the next year's breeding season. We identified the behavioral role (helper or breeder) and stage of the nesting cycle for 105 of the hawks for which we had blood samples by observing the hawks from enclosed blinds near the nests (details in Mays et al. 1991). The nest stage was calculated relative to the date of the first-laid egg. Samples collected >50 days before the first-laid egg were considered to be from the nonbreeding stage of the annual cycles (approx. August through early January), those collected during the 50 days before the first egg were from the nest-building and gamete-production stage, those collected during the next 35 days were from the incubation stage (Mader 1975), 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 after hatching (Mader 1975), and group members continued to feed the young after fledging for several months (pers. obs.). The mean date of the first-laid egg was 30 March (± 17 days SD), and the range was from 21 February through 5 May.

Radioimmunoassay of hormones.—Plasma samples for progesterone analysis (150–200 μ l) were equilibrated overnight with approximately 1,000 cpm of 3 H-progesterone for determination of recovery and then extracted in 4 ml hexane : ethyl acetate (98:2). The extract was dried under nitrogen and then resuspended in phosphate buffer. Duplicate samples of the resuspension were analyzed by radioimmunoassay following the procedure of Wingfield and Farner (1975). The progesterone antiserum used was P11-192 (Endocrine Sciences). The standard curve covered the range from 1.96 to 1,000 pg and was run in triplicate. Lowest detectable concentration was 64 pg/ml plasma. Intrassay and interassay coefficients of variation (SD/mean \times 100) were 7.6% and 9.7%, respectively. Mean recovery was 49%.

Prolactin concentrations in plasma from 102 birds for which we knew the nest stage and behavioral role were measured at the University of Bristol using a heterologous radioimmunoassay system developed by McNeilly et al. (1978) and modified by Goldsmith and Hall (1980). After confirming that a plasma sample from a Harris' Hawk assayed at five doubling dilutions gave a dilution curve parallel to that of the standard (NIADDK ovine prolactin PS-12), all samples were assayed in duplicate 20 μ l volumes. Intra- and interassay coefficients of variation were 5.2% ($n = 10$) and 12.3% ($n = 10$), respectively, and the lowest detectable concentration was 2.0 ng/ml.

Statistical analysis.—For analysis we used a variable called *nest role* to group the data. This grouping variable is a composite of stage of the nest with which each bird was associated (nonbreeding, nest building, incubating eggs, or feeding young) and that individual's role and age (adult breeder, adult-plumaged helper, or juvenal-plumaged helper). This composite variable separates the values for each sex into 12 possible

categories (see Mays et al. 1991: table 1). We used three-way analysis of variance (ANOVA) on log-transformed data to test for the effects of sex, nest role, and handling time on hormone levels in each blood sample (data from all years combined). After separation by sex we used a two-way ANOVA to examine the effects of nest role and handling time (Table 1A). For the prolactin data in which there was no significant effect of handling time, we then did one-way ANOVAs on each behavioral role category, testing whether means differed between nest stages for each role (Table 1B). One-way ANOVAs were also done for each nest stage, testing whether prolactin levels differed between behavioral roles during the same nest stage (Table 1C). Each variable that showed a significant effect ($P < 0.05$) was further analyzed with Bonferroni multiple comparison tests (BON) to find which means differed. We used Spearman's coefficient of rank correlation (r_s) to analyze brood patch scores or cloacal swelling and hormone data. For these tests we used only brood patch scores between 0 and 3, indicative of progressing development.

RESULTS

Progesterone.—Progesterone levels did not differ between males and females (three-way ANOVA, $F = 1.29$, $P = 0.26$, $n = 97$). In both sexes there were significant differences in progesterone levels in different individuals, but the differences can be statistically accounted for by handling times (Fig. 1 and Table 1A). For example, an exceptionally high progesterone level in the plasma of the one juvenal-plumaged male helper sampled during the incubation period was correlated with a long handling time (180 min) for this individual. Plasma progesterone levels increase with handling time in serially bled Harris' Hawks (Mays and Vleck 1987), probably due to progesterone release from the adrenal cortex where it is produced as a precursor to corticosterone (Assenmacher 1973), a hormone released in response to stress (Harvey et al. 1984).

In females during the nest-building stage, the mean progesterone level in the breeding birds was about twice that found in adult or juvenal-plumaged helpers (Fig. 1). We do not think these differences can be accounted for solely by differences in handling time because the mean handling time during the nest-building stage for the breeding females with high progesterone (62 min) was similar to that for the juvenal-plumaged helpers (59 min) and actually lower than that for the adult helpers (90 min), al-

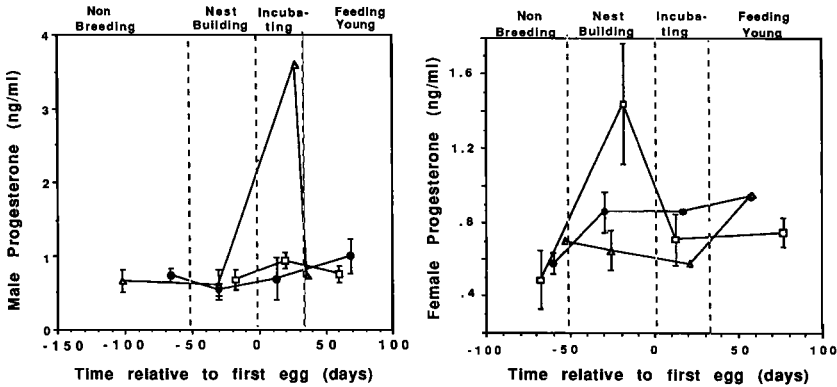


Fig. 1. Mean plasma progesterone levels in Harris' Hawk males (left panel) and females (right panel) during each nest stage. Key: \square = adult breeder, \bullet = adult-plumaged helper, and \triangle = juvenal-plumaged helper. Error bars indicate ± 1 SE. Sample sizes and statistical significance are in Table 1.

though the handling times do not differ significantly among these groups (one-way ANOVA, $F = 0.05$, $P > 0.59$).

Prolactin.—Prolactin levels varied significantly with sex and nest role in the ANOVAs, but not with handling time (Fig. 2 and Table 1A). We could detect no tendency in our data for prolactin levels to increase with handling time. A regression of prolactin levels from 97 birds plotted against maximum possible handling time for each sample (5–225 min) had a slope (0.001) not significantly different from 0 ($t = 0.14$, $P > 0.89$). Overall, values were lower in males than in females (three-way ANOVA, $F = 8.33$, $P < 0.005$, $n = 91$). In the breeding birds, prolactin levels varied with nest stage (Table 1B), and rose significantly during incubation in both males (BON, $t = 2.63$, $P < 0.05$) and females (BON, $t = 2.87$, $P < 0.05$). The mean level in female breeders during incubation was significantly higher than that in helper females at this stage (Table 1C; BON, $t = 3.53$, $P < 0.05$). Prolactin was also elevated in breeding females during the nest-building stage compared with helper females at the same stage (Table 1C; BON, $t = 2.60$, $P < 0.05$).

Levels of prolactin fell in both breeding males and females soon after hatching of the eggs, but there was a significant elevation in prolactin in the adult male helpers during care of young (Table 1B; BON, $t = 2.05$, $P < 0.05$). During this stage, the prolactin levels in the adult male helpers were significantly higher than those in the other males (Table 1C; BON, $t = 2.05$, $P < 0.05$), whereas the prolactin levels in the females did not differ from one another. There

were no significant changes in prolactin with nest stage in the juvenal-plumaged birds nor in the adult-plumaged female helpers (Table 1B). We do not think the differences in prolactin levels between the breeders and helpers during incubation or care of young are due to an undetected effect of the long handling times for the different groups because the mean handling times did not differ among the nest roles for both sexes (one-way ANOVA, $F = 0.53$, $P > 0.74$ for incubation; $F = 0.81$, $P > 0.55$ for feeding young). In addition, it seems unlikely that differences in the time of day samples were collected for the different nest roles could have biased our interpretation because all but one of 31 samples from birds in groups caring for young were collected before 1200.

Brood patch and cloacal swelling.—Although breeding males incubate, none of the 58 males examined showed any sign of a brood patch except one breeding male, who had slight, non-vascularized defeathering of the breast at the end of incubation (stage 1). Only breeding females developed brood patches ($n = 23$); none of the 16 female helpers examined before or during incubation had a brood patch. Breeding females began to show a developing brood patch as early as 55 days before the first egg, and most had a fully functional brood patch by the time the eggs were laid, although two incubating females showed only a stage-2 brood patch during incubation. The brood patch began to regress within a few days after hatching. In breeding females during the nest-building and incubating stages, there was a positive correlation between the extent of development of

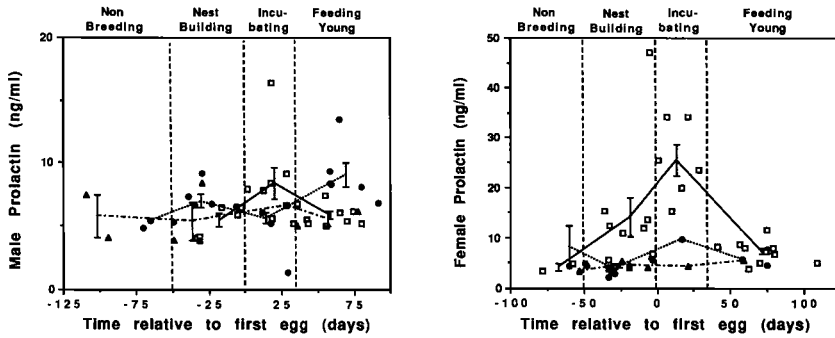


Fig. 2. Plasma prolactin levels in Harris' Hawk males (left panel) and females (right panel) during each nest stage. Symbols (see Fig. 1 legend) represent values from individuals. The mean levels for individuals with the same behavioral role during each nest stage are connected with lines (solid line for adult breeders; dotted line for adult-plumaged helpers; dashed line for juvenal-plumaged helpers); error bars indicate ± 1 SE.

the brood patch and prolactin levels ($r_s = 0.66$, $P < 0.001$, $n = 14$), although we cannot determine whether this relationship is independent of the effect of time on brood-patch development and prolactin levels over the same intervals since the partial correlation between brood patch and prolactin, holding the effect of time constant, is lower ($r = 0.47$, $P > 0.05$).

Cloacal swelling also occurred in breeding females at about the same time that the brood patch was developing. Of 13 female breeders, 10 showed cloacal swelling from 57 days before the first egg to 17 days after the first egg. None showed any cloacal swelling after the incubation period ($n = 4$). The presence of cloacal swelling was positively correlated with prolactin levels ($r_s = 0.58$, $P = 0.022$, $n = 15$), but it was not significantly correlated with nest stage or the levels of luteinizing hormone, testosterone, estradiol (data from Mays et al. 1991) or with progesterone. Only 1 of 10 adult female helpers showed any cloacal swelling, and no males did at any time ($n = 41$).

DISCUSSION

Progesterone.—In birds, progesterone is thought to be involved in ovulation. For example, in the domestic fowl (*Gallus gallus*) there is a positive feedback relationship between progesterone and LH that determines the ovulatory sequence; progesterone levels usually peak 4–6 h before ovulation (reviewed in Kamiyoshi and Tanaka 1983). A similar relationship probably exists in Harris' Hawks. All elevated levels (2–4 ng/ml) of progesterone and LH in breed-

ing female Harris' Hawks were found in the week before egg laying (LH data in Mays et al. 1991), although the effects of handling time and probable diel rhythms in hormone levels make interpretation of the data difficult. In captive-breeding American Kestrels (*Falco sparverius*), peaks in progesterone reaching 2–4 ng/ml are closely associated with egg laying (Rehder et al. 1986).

Our data indicate no correlation between plasma progesterone and parental behaviors such as incubation or care of young in Harris' Hawks. Plasma progesterone is not elevated in breeding male hawks that incubate and care for young, although a change in progesterone-receptor density, possibly mediated by the previously elevated testosterone levels (see Brown 1985), might have altered the effect of progesterone even if plasma levels did not change. There does not seem to be an important role for progesterone in incubation in domestic fowl (Bedrak et al. 1981), but it does influence the timing of incubation bouts in African Turtle Doves (*Streptopelia roseogrisea*; Silver and Norgren 1987). In the Harris' Hawk, progesterone could be involved in brood-patch formation as suggested by Jones (1971), possibly in conjunction with elevated estradiol since only the breeding females develop a brood patch, and only they have elevated estradiol (Mays et al. 1991) and progesterone before incubation begins.

Prolactin.—The roles of prolactin in avian reproduction and the mechanisms that control its secretion are not well understood and appear to vary among species. Prolactin has been im-

plicated in the development of the brood patch (Jones 1971), the development of photorefractoriness (Ebling et al. 1982, Goldsmith and Nicholls 1984), migration, molt, and fat deposition (Meier 1975) as well as parental behavior (Balthazart 1983, Goldsmith 1983, Silver and Cooper 1983, Brown 1985, Buntin 1985). Elevations in prolactin have been correlated with incubation and brooding in many species, as well as with feeding of young in the European Starling (*Sturnus vulgaris*; Dawson and Goldsmith 1982) and columbiform birds that produce crop milk (Goldsmith et al. 1981), and with the display of antipredatory behavior in Willow Ptarmigan (*Lagopus l. lagopus*; Pedersen 1989).

Elevated prolactin is clearly associated with incubation behavior in birds. Whether or not prolactin initiates parental behavior or simply maintains it, however, has been of interest. In addition, whether elevated prolactin levels are the cause or the result of incubation behavior is not always clear. In some species, artificial extension or termination of the incubation period affects prolactin levels, which suggests that the act of incubation influences prolactin secretion (Silverin and Goldsmith 1984, Oring et al. 1988). Similarly, manipulation of chick ages can influence prolactin levels in brooding Pied Flycatchers (*Ficedula hypoleuca*; Silverin and Goldsmith 1990). In other species, prolactin levels seem to be determined by an endogenous schedule or by day length, relatively independently of the bird's exposure to nest and eggs (Ebling et al. 1982, Hector and Goldsmith 1985). Usually levels of prolactin are higher in females than in males, whether or not the male participates in incubation (Dawson and Goldsmith 1982, Hiatt et al. 1987). Prolactin levels are higher in males than in females in species in which the male incubates more than the female, e.g. the Spotted Sandpiper (*Actitis macularia*; Oring et al. 1986) and Wilson's Phalarope (*Phalaropus tricolor*; Oring et al. 1988). On the other hand, prolactin levels need not necessarily be elevated for incubation behavior to be expressed. Turkeys (*Meleagris gallopavo*) deprived of their nest show a decline in prolactin levels, but will incubate as soon as returned to their nest, even though prolactin levels do not become elevated until later (Zadworny et al. 1985).

In Harris' Hawks, prolactin levels are elevated in breeding females before egg laying and during incubation in a manner similar to other birds. Presumably, high levels of prolactin are

involved in development of a functional brood patch and incubation in this species. Prolactin is also elevated in breeding male Harris' Hawks during incubation, although not as much as in females. The significant elevation in prolactin we detected in all incubating hawks implies that our methods allow us to detect functional changes in plasma prolactin levels associated with the breeding cycles, even though the long handling times for many of these birds might be expected to have changed prolactin levels independently of the breeding cycle. Elevated prolactin levels may also be involved in the development of the swelling and reddening of the cloacal region in the females, but the functional significance of this in Harris' Hawks is unknown. Nakamura (1990) suggested a display of cloacal swelling was used by female Alpine Accentors to solicit copulations from the male.

Prolactin levels in the breeding Harris' Hawks decrease immediately after incubation to levels not different from those found in the nonbreeding season. In other altricial and semiprecocial species, prolactin levels usually remain relatively elevated as long as the birds are brooding nonthermoregulating young (Dawson and Goldsmith 1982; Goldsmith 1982; Hector and Goldsmith 1985; Oring et al. 1986, 1988; Myers et al. 1989; Ketterson et al. 1990). Levels may decrease at about the same time that the chicks begin to thermoregulate and no longer require extensive brooding by the parent (Silverin and Goldsmith 1984, 1990; Oring et al. 1986, 1988), but prolactin levels often remain elevated compared with nonbreeding levels as long as the parents are caring for young. Prolactin levels remain elevated between broods in multiple-brooded White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*; Hiatt et al. 1987) and Song Sparrows (*Melospiza melodia*; Wingfield and Goldsmith 1990), although not in multiple-brooded canaries (*Serinus canaria*; Goldsmith 1982). The pattern of prolactin changes we observed in breeding Harris' Hawks resembles that in precocial galliform and anseriform species (reviewed in Goldsmith 1983) in which the young can thermoregulate and leave the nest soon after hatching. In these species, prolactin usually falls to nonbreeding levels as soon as the young are hatched.

The fall in prolactin in breeding Harris' Hawks after the eggs hatch, even though the altricial young remain in the nest approximately 45 days, suggests that the high levels of pro-

lactin associated with incubation need not be maintained to ensure brooding and feeding of the young. The chicks are altricial and the parents will brood the young in the nest at night, but relatively little brooding occurs during the day because ambient temperatures in May and June (the normal months for hatchlings to be in the nest) are relatively high compared with higher-latitude species. In fact, the chicks are often shaded by the parents rather than brooded, presumably to keep chicks from overheating. In addition, because food items brought to the nestlings are large (e.g. parts of rabbits), adults make relatively few feeding trips to the nest per day (Dawson and Mannan 1991a, references therein). Consequently the intensity of parental behavior displayed by an individual Harris' Hawk (in terms of time spent in the nest and feeding trips to the nest) may be low compared with altricial species in general, especially those without helpers, and could account for the relatively low levels of prolactin found in the parents at this time.

The contribution that the helpers make toward provisioning the young may decrease the effort the breeding pair must expend to raise the young. In a survey of feeding rates of young in 15 cooperatively breeding species, Reyer (1990) found that in species that make few feeding trips (<10 per hour), the contribution the parents make to feeding young is reduced when helpers are present. In species that make >20 feeding trips per hour, parents do not reduce their effort when helpers are present. If Harris' Hawk breeders provide less care for young when helpers are present, one might expect an inverse relationship between group size and prolactin levels in the breeders during the nestling/fledgling stage. We could not demonstrate such a relationship (Fig. 3). In Pied Flycatchers (Silverin and Goldsmith 1984) and Dark-eyed Juncos (*Junco hyemalis*; Ketterson et al. 1990), there is also no discernable difference in prolactin levels in females that raise young alone and those that are aided by a mate. Thus the level of prolactin secretion does not seem to be modulated in any precise way by the level of parental effort expended.

The most surprising thing that we found was that prolactin levels rose significantly in the adult male helpers during the nestling/fledgling stage; at the same time prolactin decreased in the breeding birds (Fig. 2). In fact, the mean level at this time in the adult male helpers (9.1

ng/ml) was higher than that in either male (5.6 ng/ml) or female (7.3 ng/ml) breeders at the same time. This increase occurs at a time when the male beta helpers, if present in a group, actually provide more food for the nestlings than either of the breeding birds. For example, Dawson and Mannan (1991a) determined which individuals brought food to the nest area in four Harris' Hawk groups of five individuals matched for group composition (a breeding pair, a beta male, and a male and female gamma bird). In 136 food deliveries, the adult beta male transported the food 37% of the time, whereas the breeding male performed this task only approximately 30% of the time, the breeding female only 3% of the time, and the two other gamma helpers combined, >30% of the time.

We have few samples from adult female helpers during incubation and care of young, but their prolactin levels do not seem to be elevated as in adult male helpers. This may not be surprising because female gamma helpers spend the least amount of time of any group member near the nest or feeding young, although they participate in group hunting (Dawson and Mannan 1991a).

The rise in prolactin in the adult-plumaged male helper Harris' Hawks indicates that elevation in prolactin associated with care of young can be uncoupled from the earlier prolactin elevation associated with nest building and incubation in this cooperatively breeding species. We cannot rule out a relation between previously elevated sex steroids and the subsequent elevation in prolactin (see Goldsmith 1983 and Buntin 1985), because these adult-plumaged helpers have elevated LH and testosterone earlier in the nesting cycle (Mays et al. 1991). Luteinizing hormones and testosterone decrease in both the adult male helpers and the breeders during the incubation stage. This seems to follow the pattern described by Brown (1985) for many species in which both sexes show parental behavior. Elevated testosterone in males is probably associated with defense and courtship early in the nesting season, and it possibly acts as a primer for parental behavior; but later as the level of prolactin rises (possibly stimulated by the presence of eggs or young), the testosterone level falls. The effects of exogenous prolactin on behavior in nonbreeding individuals have been demonstrated before (reviewed in Goldsmith 1983, Buntin 1985), but we are aware of no previous report of a correlation between

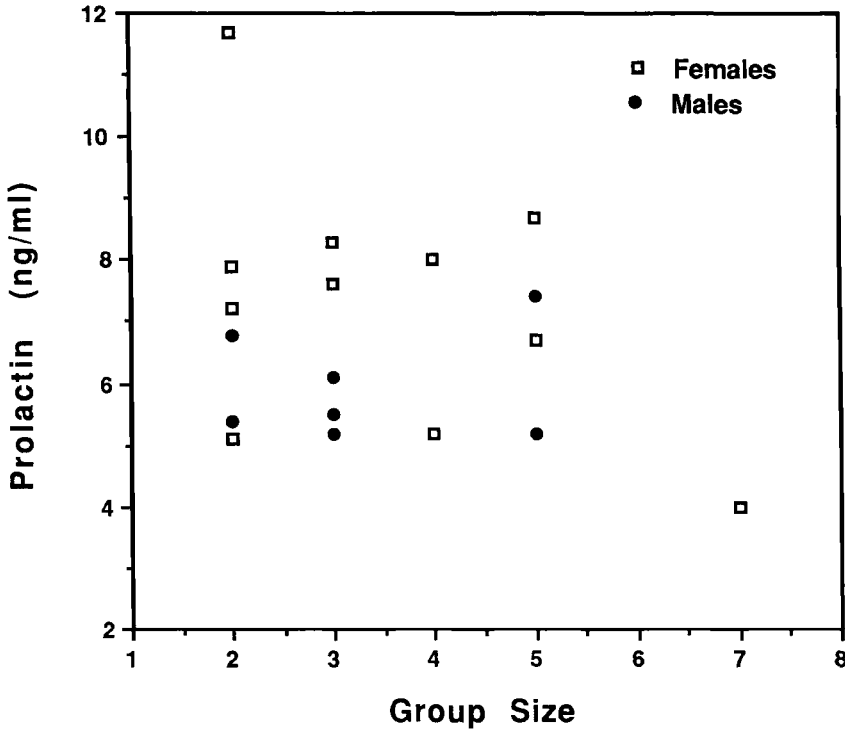


Fig. 3. Plasma prolactin levels in breeding male and female Harris' Hawks during the stage when groups are caring for their young (36–100 days after the first-laid egg) plotted in relation to group sizes. Symbols represent values from individuals.

endogenous prolactin levels and parentlike behavior in a free-living, nonbreeding bird. Ketterson et al. (1990) measured prolactin in Dark-eyed Juncos during the nestling stage in natural fathers and in males who had replaced the original male in a pair after the young hatched. They reported that prolactin levels in two replacement males that were helping the female raise young were not different from those in replacement males that were not feeding adopted young. The natural fathers who fed their own young had levels of prolactin higher than those of the replacement males. Interpretation of the data was confounded by seasonal effects on prolactin levels.

If prolactin functions to facilitate provisioning of the hatchlings and fledglings in Harris' Hawks, we suggest that there is a physiological basis for helping behavior in this cooperatively breeding bird. Although we don't know what the environmental stimulus is for the rise in prolactin in adult male helpers (it may be the

sight or sound of young birds in the nest as suggested by Woolfenden and Fitzpatrick 1984), the elevated prolactin may increase the probability that these helpers will exhibit parentlike behaviors even though they are not likely to be closely related to the young they help. It would be interesting to know whether helpers display this rise in prolactin when caring for young in cooperatively breeding species in general, and if this differs from the response of nonbreeding individuals to eggs or young in noncooperatively breeding species. If this were the case, it is likely that selection has acted at a physiological level to alter behavior in cooperatively breeding species, although this does not allow us to say with certainty whether care of young by helpers is a uniquely evolved characteristic of cooperative breeders, nor specifically why helping behavior is adaptive. Experimental manipulation of prolactin levels in helpers may provide a tool to alter helping behavior and thereby allow direct testing of hy-

potheses concerning costs and benefits of helping behavior.

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