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Corticosterone Levels During Nest Departure of Juvenile American Kestrels

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mine selection pressures responsible for sexual dimorphism in this and other species.

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CORTICOSTERONE LEVELS DURING NEST DEPARTURE OF JUVENILE AMERICAN KESTRELS[1]

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Abstract. Many avian behavior patterns, such as breeding, migration and territoriality, are correlated with changes in hormone levels. Elevated levels of corticosterone, an adrenal steroid hormone, are associated with increased foraging and increased activity levels in birds. Young birds about to take their first flight may benefit from elevated plasma corticosterone levels that facilitate locomotor activity and foraging behavior while they are developing flight and hunting skills. I examined the relationship between corticosterone levels and the timing of nest departure in nestling American Kestrels (*Falco sparverius*). American Kestrels are cavity nesters and typically depart from the nest between 25–30 days of age, when they take their first flight. I collected blood from 21–25-day-old kestrels and monitored nest boxes to determine date of nest departure. Consistent with my prediction, as birds prepared to depart from the nest their plasma corticosterone levels increased significantly. The relationship between corticosterone levels and nest departure may

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be particularly important in those cavity nesters that must make a quick transition from inactivity to full-flight at the time of nest departure.

Key words: corticosterone, nest departure, Falco sparverius, *American Kestrel, cavity nester, stress response, fledging.*

Changes in hormone levels correlate with many events during a bird's life, such as breeding, nesting and molting (Rehder et al. 1986). Increases in plasma levels of corticosterone (B), a steroid hormone released by the adrenal glands, correlate with increases in locomotor activity (Astheimer et al. 1992, Smith et al. 1994) and foraging behavior (Bray 1993). Corticosterone can be associated with behavior and metabolic patterns during ephemeral stressful situations, such as poor weather conditions that result in reduced food availability (Wingfield 1994). In this situation, corticosterone levels may increase to promote movement away from a storm (Smith et al. 1994) and stimulate gluconeogensis via protein catabolism (Siegel 1980). Corticosterone also may be involved with transitional periods during a bird's life, such as natal dispersal (Belthoff and Dufty 1995, Heath, unpubl. data) and migration (O'Reilly and Wingfield 1995). During these transitional periods, increasing corticosterone levels may increase a bird's restlessness (e.g., *Zugunruhe* during migration) and stimulate movement or flight (Gray et al. 1990). Similarly, high levels of corticosterone that facilitate locomotor activity, foraging activity and increased energy availability may be beneficial to young birds as they leave the nest and take their first flight.

Previous studies on the timing of nest departure have focused on factors related to the external environment, such as reduced food provisioning to offspring by parents (Trivers 1974, Viñuela and Bustamante 1992), sibling competition (Lindén et al. 1992, Nilsson and Svensson 1993), or size of nestlings (Kersten and Brenninkmeijer 1995). The reduced provisioning and sibling competition hypotheses predict that birds leave the nest to approach parents for food (Viñuela and Bustamante 1992), whereas the size hypothesis predicts that birds depart from the nest once they reach a certain threshold size (Lindén et al. 1992). These hypotheses are not mutually exclusive and are based primarily on food availability. Such external factors may influence the timing of nest departure by affecting plasma corticosterone levels. For example, if nestlings experience sibling competition, then they may be stressed as a result of aggressive interactions. This stressful situation may stimulate adrenal activity and increase plasma corticosterone levels, thus stimulating locomotor activity and flight, resulting in fledging.

I examined the relationship between plasma corticosterone levels and nest departure in the American Kestrel (*Falco sparverius*), a cavity-nesting bird common to many parts of North America (del Hoyo 1994). I tested the hypothesis that corticosterone levels increase prior to fledging, and predicted that birds about to leave the nest would have higher B levels than those not about to fledge. However, because confounding factors such as reduced food access (Siegel 1980) and handling stress (Wingfield et al. 1992) also can cause increased B levels, I also evaluated the relationships between food availability and corticosterone levels, and between handling stress-response and time of fledging.

METHODS

STUDY SPECIES

This study was conducted in southwest Idaho where kestrels breed from early April until July (Steenhof 1994, Heath, pers. observ.). Both sexes incubate the eggs, which hatch after 28–30 days (Willoughby and Cade 1964, Kellner 1988). The sex ratio in broods is typically 1:1 (Bird 1985). During the first week after young hatch, adult males deliver the majority of food to the nest, whereas during the following three to four weeks both parents provision the young (Heath, pers. observ.) By 22 days of age, nestlings have lost most of their down feathers (Griggs and Steenhof 1993) and have almost achieved adult mass (males 80–110 g; females 110–140 g). Chicks fledge when they are between 25–30 days of age (Bird 1985). Fledglings depend almost entirely on parental feeding during their first week postfledging (Varland et al. 1991). In the second and third weeks postfledging, young kestrels refine their hunting techniques by imitating adults and other young kestrels (Varland et al. 1991, Heath 1994). In southern Idaho, juvenile kestrels from the same brood typically disperse within one day of each other, approximately three weeks after they fledge (Heath 1994).

FIELD STUDY

I monitored American Kestrel nest boxes from April to June in 1994 and 1995. Nest boxes were located 70 km southwest of Boise, Idaho in Ada and Canyon counties (elevation 950 m, 43° 30′N, 116° 20′W). Once eggs were present I made up to five attempts (mode = 2) to capture the adults in the box and mark them with U.S. Fish and Wildlife Service aluminum leg bands. Approximately 85% of adults were marked. All attempts to trap adults occurred during the egg stage, except for two attempts in 1994. I returned 30 days after banding the last adult and used a photographic aging guide (Griggs and Steenhof 1993) to age nestlings. When the nestlings were 22–25 days old, I marked the young with colored leg jesses (modified from Varland and Loughin 1992), and collected blood samples. Jesses were made from colored herculite and attached in the traditional falconer-style (Young and Kochert 1987). Jesses were made 1-cm wide around the leg with a 3 × 3 cm trailing tab. The time period between the visit to age birds and blood collection was typically greater than two weeks. Whereas the majority of blood samples were collected before 12:00, five samples were collected between 13:00 and 16:00. To collect blood for hormone assays, I punctured the brachial vein with a 26-gauge needle and collected 0.4 ml of whole blood in a heparinized caraway collecting tube. Sampling time began when the clutch was removed from the nest box and ended when the individual sample was obtained. Each bird was bled only once. Blood was transferred to plastic 1.5-ml microcentrifuge tubes and transported (approximately 1 hr) from the field to the laboratory in an ice chest. Within

3 hr of blood collection, I centrifuged the blood for 9–10 min at 2,100 rpm and separated the plasma from the cellular fraction. Plasma was stored at −20°C until analyzed one month later.

After obtaining blood samples, I returned to the nest box daily to determine date of nest departure. In doing so, I attempted not to disturb the nest to prevent the young from fledging prematurely. I determined when young fledged by the parents' location and behavior and through visual identification of the young outside the nest box.

The reduced-food provisioning and sibling competition hypotheses predict that, prior to fledging, young birds may be fasting or undergoing mild food deprivation because of decreased parental care or increased competition. Consequently, high corticosterone levels prior to fledging may be the result of restricted food availability. To examine this possibility, I randomly selected six nests to be used in a supplemental-feeding experiment in 1995. If nestlings were experiencing food restriction prior to fledging, then their corticosterone levels would be higher than those of nestlings that were supplementally fed. At three boxes I provided 12–20 g laboratory mice per nestling per day, beginning when nestlings were 13–16 days of age and continuing until they fledged. Mice were placed in the nest box through the entrance hole so that birds in the box did not see me. Occasionally adult birds saw me approach the box, but they did not change activity or exhibit alarm behavior. I made similar daily visits to the three control boxes but did not provide food. For both groups of boxes, I returned when the young were 22–25 days old to process nestlings as described above.

I also examined the relationship between corticosterone levels and uric acid. Uric acid is a waste product of gluconeogenesis and protein metabolism. If corticosterone levels in nestlings about to leave the nest were elevated because of reduced food availability, resulting in a breakdown of protein reserves, then uric acid levels also should be high. Thus, high uric acid levels at the time of nest departure would indicate that corticosterone levels were elevated to facilitate gluconeogenesis for food deprived nestlings, not necessarily to stimulate nest departure.

HORMONE AND URIC ACID ANALYSES

In 1994 and 1995, corticosterone levels were analyzed in a single radioimmunoassay (RIA) as described by Wingfield et al. (1992) and Smith et al. (1994). I placed 500 pg/ml of standard corticosterone in two test tubes as accuracy controls. Final readings on these in 1994 were 553 pg/ml and 569 pg/ml, and in 1995 they were 582 pg/ml and 496 pg/ml.

I analyzed uric acid levels using a dry chemistry analyzer (Kodak Ektachem DT60II). I diluted plasma samples 1:1 with water prior to analysis to ensure that uric acid concentrations would be within the range of the analyzer (0.1–20.0 mg/μl). Results were then doubled to obtain true uric acid levels.

STATISTICAL ANALYSES

Because plasma corticosterone levels increase over time in response to capture stress (Wingfield et al. 1992), I performed a polynomial regression (Freund and Littell 1991) to determine if handling time had an effect on B levels (Heath and Dufty, unpubl. data). I found a significant relationship between time and B levels ($y = 5.76 + 1.14x^2 - 0.04x$, $r = 0.219$, $P < 0.05$). Because of the time required to collect the nestlings and climb back to the ground, I had no samples collected under 3 min. Thus, I used this equation to correct for the effects of time by adjusting all samples to the 3-min period, which represented the first time period for which I had accurate data. I used these estimated corticosterone levels to examine the relationship between B and nest departure.

To ensure that birds about to leave the nest did not have a faster adrenal response to capture stress than younger birds, I performed an analysis of covariance with unadjusted corticosterone levels and duration of capture as continuous variables dependent on the categorical variable "time to fledge" (Zar 1984). I categorized time to fledge as "soon" (bird left the nest in 2 days or less) and "late" (bird left the nest after 5 or more days). These data were log transformed prior to analysis to meet the homoscedastic requirement of an ANCOVA test.

To avoid the possibility of nonindependent data from young of the same nest, I used each nest's mean corticosterone value (Massot et al. 1994). At five broods I was unable to collect blood from all nestlings because of vasoconstriction. I used a polynomial regression analysis (Freund and Littell 1991) to examine the relationship between corticosterone and time to nest departure. The best fit model was a second-order polynomial regression indicating a curvilinear relationship between B levels and time to nest departure.

Because corticosterone levels can be affected by factors such as decreased food, I examined an alternative hypothesis to explain increased corticosterone. I compared B levels in control and supplementally-fed birds. To account for effect of brood, I performed a nested one-way analysis of variance with treatment (supplemental feeding or not) as the independent variable and circulating corticosterone level as the dependent variable nested within brood. I used a Spearman rank correlation test to evaluate the relationship between corticosterone and uric acid levels (Zar 1984). Data are reported as means ± SE.

RESULTS

Kestrels fledged from nest boxes at 25–32 days of age. Plasma corticosterone levels increased significantly as nest departure approached ($y = 10.64 - 3.28x + 0.43x^2$, $r = 0.48$, $P < 0.005$; Fig. 1). This result is consistent with the hypothesis that high levels of plasma corticosterone in nestlings stimulate fledging and subsequent locomotor activity and foraging behavior. Corticosterone may start increasing approximately two days prior to fledging, peak when the birds leave the nest (Fig. 1) and decrease during the later part of the postfledging period (Heath, unpubl. data). Indeed, I caught one group of birds (box # 68, $n = 3$, handling time = 4, 6, 7 min) as they were jumping from the nest box (day = 0). I feel confident that I did not cause early fledging because two of their siblings fledged before my arrival. The mean plasma corticosterone level of these birds was more than twice as high as

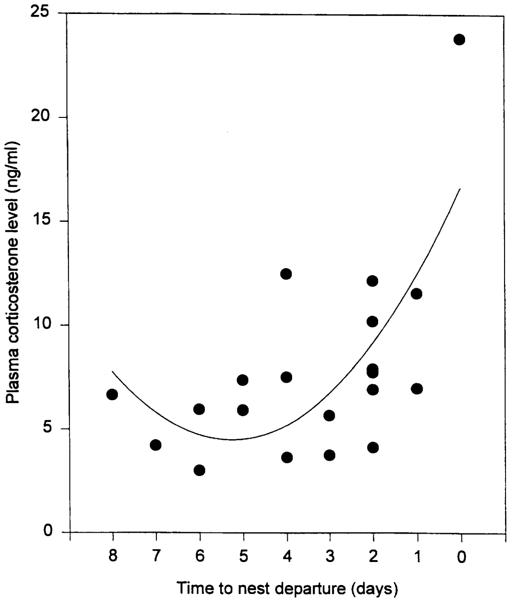

FIGURE 1. The relationship between plasma corticosterone levels and time to nest departure ($r = 0.48$, $P < 0.005$) for American Kestrels in southwestern Idaho. Solid circles represent individual nests.

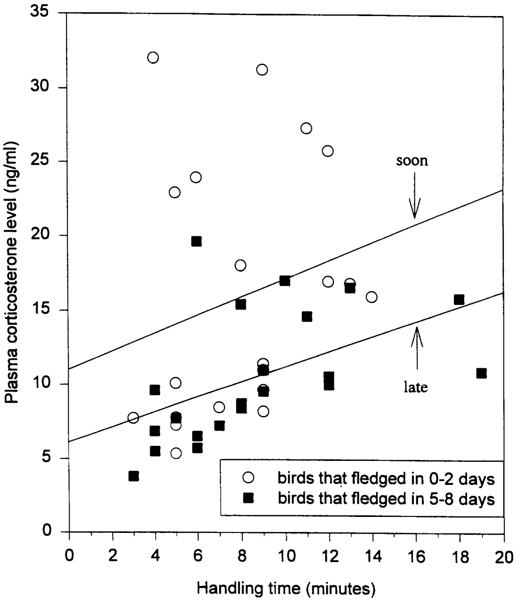

FIGURE 2. The relationship among plasma corticosterone levels, time to nest departure and handling time for American Kestrels in southwestern Idaho. There was no significant difference in rate of corticosterone increase between birds that left soon (0–2 days) and birds that left later (5–8 days, $P > 0.9$). Data shown are not log-transformed.

that of any other nest. The slow increase in plasma corticosterone levels over time may up-regulate B receptors (Baileau and Kelly 1990). Thus, on the day of fledging, birds would be sensitive to a sudden increase in plasma corticosterone levels such as the birds from box 68 experienced. These elevated levels of B may then stimulate the actual jump from the nest or the first flights.

There are two possible alternative interpretations for this result. First, birds that are about to fledge may be food-restricted because of decreased parental feeding (Viñuela and Bustamante 1992) resulting in elevated corticosterone levels that stimulate gluconeogenesis (Siegel 1980). Data from the feeding experiment are useful for evaluating this hypothesis. If control birds were food-restricted, then their plasma B levels would be higher than the supplementally-fed birds. Conversely, if control birds were not food-restricted, or if corticosterone levels were elevated regardless of food consumption, then corticosterone levels would be similar in control birds and supplementally-fed birds. There was no significant difference between B levels in control ($n = 3$) and supplementally-fed broods ($n = 3$) (control = 6.9 ± 0.6 ng/ml; fed = 9.6 ± 1.3 ng/ml; $F_{1,4} = 2.84$, $P = 0.17$). If anything, the data values were in the opposite direction from what would be expected. Therefore, it seems unlikely that corticosterone levels were high at the time of fledging because of reduced food availability.

In addition, I found no correlation between uric acid and B ($r_s = -0.079$, $n = 68$, $P = 0.75$). Unfortunately, uric acid may be a poor indicator of gluconeogensis in raptors. Although uric acid increases during food restriction because of elevated corticosterone levels (Jeffrey et al. 1985), raptors, including nestling American Kestrels (Varland et al. 1992), eat a high protein diet, and elevated uric acid concentrations in the blood can indicate a recent meal (Lumeij and Remple 1991) rather than catabolism of protein reserves.

A second interpretation for high corticosterone at fledging is that birds about to fledge have a faster adrenal response to handling stress than birds that remain in the nest longer. Previous studies have demonstrated that acute stress (e.g., handling) causes an increase in plasma corticosterone levels (Smith et al. 1992, Wingfield et al. 1995). A comparison of the rate of corticosterone increase between young kestrels two days or less from fledging and those five days or more from fledging showed no significant differences ($F_{1,37} = 0.01$, $P = 0.93$, Fig. 2) Thus, the adrenal response of birds in the two age groups was similar, indicating that birds about to fledge did not have a faster rate of B secretion during handling. In addition, this ANCOVA comparison revealed a significant difference between y-intercepts of birds leaving "early" (y-intercept = 10.9 pg/ml) and birds leaving "late" (y-intercept = 6.1 pg/ml) ($F_{1,38} = 7.85$, $P = 0.008$). This is consistent with the hypothesis that birds about to leave the nest have higher corticosterone levels.

DISCUSSION

Hormonal changes are associated with many aspects of a bird's behavior, such as reproduction (Dufty and

Wingfield 1986) and territoriality (Wingfield et al. 1987). Species may have different hormonal changes depending on their life history (Wingfield et al. 1995). These are the first data to suggest a hormonal correlate of fledging. American Kestrels are cavity nesters and spend their first month of life in a confined space with little opportunity for movement. At fledging they must quickly change from being relatively inactive to being full-flighted. Proximate factors for nest departure must stimulate young kestrels to move from an enclosed structure, where they are relatively safe, to an exposed environment where they are more likely to be preyed upon (Varland et al. 1993). Increased B levels may be a physiological mechanism that facilitates this rapid transition in such young birds.

However, like other hormonal and behavior relationships this one may depend on species-specific characteristics. The relationship between corticosterone and nest departure may not be as strong in species that nest in open structures. Birds that nest in trees or on the ground may not have such a strong physiological stimulus because they can go through a more gradual "branching" period to practice flapping and other movements. Therefore, their behavioral transition at fledging is less abrupt. For example, in Snowy Owls (*Nyteca scandiaca*), which nest on the ground, young do not show increasing corticosterone levels prior to nest departure (M. Romero, pers. comm.). In addition, nest departure in these birds occurs six weeks before first flight (M. Romero, pers. comm.). Young Snowy Owls walk from the nest, whereas young kestrels must take their first flight from the nest. Therefore, the relationship between plasma corticosterone levels and nest departure may be affected by nest type, or activity transition. Furthermore, if high B levels are stimulated by the stress of leaving the nest, then young kestrels may experience more stress attempting flight activity from high above the ground than Snowy Owls that walk over a small mound of nest material.

The present study indicates a relationship between corticosterone levels and nest departure in nestling American Kestrels and suggests that high circulating corticosterone levels could trigger movement from the nest. Two alternative hypotheses, that food deprivation stimulates high B levels and that sensitivity to handling stress causes B levels to be higher in birds about to fledge, were not supported. Further research examining the relationship between B levels and fledging among birds that nest in open versus closed (cavity) structures is required to determine whether this relationship is affected by type of nest structure. Finally, additional work is needed to determine the extent to which the relationship between corticosterone and nest departure depends upon external factors, such as stress resulting from competition, an internal mechanism, or both.

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