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PRESS

Corticosterone levels during post-natal development in captive American kestrels (*Falco sparverius*)

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Abstract

We investigated post-natal development of the adrenocortical stress-response system in captive American kestrels (*Falco sparverius*) by measurements of baseline and stress-induced levels of corticosterone at ages 10, 16, 22, and 28 days post-hatching. Baseline levels of corticosterone increased significantly during post-natal development and although chicks aged 10- and 16-days old exhibited comparable baseline corticosterone levels, those of 22-day-old chicks were significantly higher and those of 28-day-old chicks close to fledging were higher than all younger groups. Chicks in this study exhibited low levels of stress-induced corticosterone early in development and did not exhibit adult-type stress-induced levels of corticosterone until 22 days of age post-hatching. Finally, although baseline and stress-induced levels of 28-day-old birds were significantly higher than one-year-old adults, there was no relationship between baseline corticosterone concentrations and time to nest departure. The fact that baseline levels of corticosterone are low during early development and then increase during later development may be an adaptation to the negative effects of chronically elevated corticosterone levels and as previously noted in other studies may minimize these negative effects on rapid growth and development in young birds, potentially maximizing normal growth. The ability of even young kestrel chicks to elevate corticosterone levels in response to stress suggests that they may be able to physiologically cope with food shortages associated with unpredictable food resources which wild kestrels often face.
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1. Introduction

The adrenocortical response in birds is characterized by short-term, temporary increases of corticosterone, a hormone messenger that initiates several important physiological changes in birds, including effects on intermediary metabolism and growth (Wingfield, 1994). Elevated plasma concentrations of corticosterone stimulate alternative metabolic pathways and behavior patterns in response to unpredictable environmental conditions such as severe weather or restricted food availability. Behavioral and metabolic responses include increased locomotory activity (Astheimer et al., 1992), decreased nocturnal oxygen consumption (Astheimer et al., 1992), lipogenesis (Gray et al., 1990; Harvey et al., 1984), increased food intake (Bray, 1993), and increased energy availability resulting from protein catabolism (Gray et al., 1990; Wingfield et al., 1995).

Although there has been investigation into the role of the adrenocortical response in adult birds in relation to unpredictable events such as food shortage and severe storms (Smith et al., 1994; Wingfield, 1994), energetic condition (Kern et al., 2001; Marra and Holberton, 1998; Sockman and Schwabl, 2001) and predictable life-history events such as wintering, migration, and breeding (Marra and Holberton, 1998; Piersma and Ramenofsky, 1998; Romero, 2002; Romero et al., 1997; Landys-Ciannelli et al., 2002; Silverin, 1998), the role of this response system during early life is less understood. Mammalian

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studies indicate that adrenocortical activity increases near term, possibly in combination with the maturation of fetal organ systems (Dalle and Delost, 1976; Dupouy et al., 1975; O'Malee and Marotta, 1982; Rose et al., 1982). Additionally, the function of the hypothalamic-pituitary-adrenal (HPA) axis (responsible for adreno-cortical activity) has been shown to be organizationally influenced by neonatal sex steroid hormones in male rats (McCormick et al., 1998). Studies of ontological adrenal steroidogenic function in birds are mostly limited to precocial species which show well-developed adrenocor-tical responses at hatching (Carsia et al., 1987; Kallich-aran and Hall, 1976; Tanabe et al., 1986; Wise and Frye, 1973). Schwabl (1999) found that post-natal baseline corticosterone levels in the altricial canary (*Serinus canaria*) increase during post-natal development and reach adult levels near fledging. Sims and Holberton (2000) reported that 10-day-old northern mockingbirds (*Mimus polyglottos*) show little stress-induced cortico-sterone secretion, with the highest levels seen in fledglings nearing parental independence. A study of wild Ameri-can kestrel (*Falco sparverius*) chicks where the authors removed the entire brood and sampled each individual once, in sequential order, found that chicks as young as 10 days exhibited a response to handling during removal from the nest box, with the absence of a response at 20 and 25 days post-hatching (Sockman and Schwabl, 2001).

In the present study, we wished to investigate post-natal adrenocortical stress responses in captive American kestrels as in Sockman and Schwabl (2001), however, using a repeated sampling procedure (Wingfield, 1994). The objectives were (1) to investigate the dynamics of chick adrenocortical function through measures of baseline and stress-induced corticosterone during post-natal development and (2) to determine if chicks exhibit adrenocortical responses comparable with adults at the time of fledging. These aims were accomplished by evaluating the ability of American kestrels at four suc-cessive developmental stages to respond to a standard-ized stressor of capture and handling. The ability of the birds to respond to the stressor was inferred from the measurement of immuno-detectable levels of circulating corticosterone. The "capture-stress" protocol employed to measure this response has been applied to a wide spectrum of species under a number of variable envi-ronmental and ecological conditions (see Schwabl et al., 1991; Wingfield, 1994; Wingfield et al., 1992 for details).

2. Materials and methods

2.1. Breeding procedures and species

The study was conducted at the Avian Science and Conservation Centre of McGill University from April to July 1999 using captive birds reared from captive-raised adults. Twenty-two pairs of adult banded kestrels were removed from same-sex communal flight pens and placed in outdoor breeding pens measuring $3.5 \times 5.5 \times 3.0$ m (l × w × h). Depending on pairs, egg-laying began within 10–13 days following pairing. Eggs were individually marked in order to keep track of laying and hatching order of chicks, and once chicks hatched they were individually marked with non-toxic colored felt markers each day. Parents were fed a daily diet of three, day-old cockerels each until hatching, at which time they were fed this plus an additional 1.5-day-old cockerels for each nestling present. All birds were supplied with water for drinking and bathing. Captive-hatched chicks hatch after 28–30 days of incubation and depend on adults for the delivery of prey and feeding. Their eyes are partially open by the first or second day (Bird and Palmer, 1988; Roest, 1957) and chicks are able to thermoregulate by age 8–10 days (Bird and Palmer, 1988). By seven days they begin to show stereotypical defense behavior of rolling on their backs and presenting talons, and are fully able to defend against nest-box intruders by 16–18 days of age. They reach adult body mass by 22 days, fledge between 26–28 days in captivity and in the wild are dependent on parents for food for about 12–14 days (Bird and Palmer, 1988; Varland et al., 1991).

2.2. Blood sampling and general procedure

Blood samples were taken from chicks at the ages of 10, 16, 22, and 28 days post-hatching between 10:00 and 15:00 to minimize time of day effects on circulating plasma corticosterone levels (Wingfield et al., 1992). These ages were chosen in an attempt to cover the span of post-natal development sufficiently, as well as focus on major stages of muscular and behavioral develop-ment. An individual bird was blood sampled from one age class only and this study therefore, involved a total of 40 chicks split equally ($n = 10$/age class) among the four age sampling groups. First- and second-hatched chicks of each nest were sampled during this experiment and these were randomly distributed among age classes. Sockman and Schwabl (2001) found no relationship between hatching order and corticosterone levels in kestrels. Birds underwent a standardized capture, han-dling and restraint protocol known to elicit an increase in the circulating hormone, corticosterone (Wingfield et al., 1992). Birds were removed from their nest boxes and a stopwatch was used to record the time of first contact when the nest box door was opened. Birds were transported from outdoor breeding pens to an indoor laboratory in $45 \times 35 \times 40$ cm (l × d × h) insulated plastic coolers with 10 mm holes drilled for ventilation. Ten-day-old chicks were kept warm with the use of a hot-water bottle covered with a towel placed at the bottom of the cooler. Opaque mesh tops were used on

the coolers after chicks had been brought in from the breeding pens to facilitate capture of the bird for subsequent blood samples.

Individual birds were first weighed and then between 25 and 75 µl (depending on the age of the chick) of whole blood was collected from the brachial vein as soon as possible after removal of the bird from its pen (∼1–2 min) using a heparinized 27-guage needle and 1cc syringe. Additional samples were collected at 5, 10, 30, and 45 min after capture from the same bird. All initial samples were taken in under 2 min following capture and linear regression analyses showed no effect of time after capture (within 0–2 min interval) on plasma levels of corticosterone in initial blood samples ($R^2 = 0.048$, $F_{1,16} = 0.804$, $P = 0.38$). Thus, initial blood samples were considered to reflect baseline levels of corticosterone. Whole blood samples were centrifuged at 10,000 rpm for 10 min. The plasma was removed and stored frozen at −30 °C for radioimmunoassay analysis.

Between blood collections, birds were placed back in their individual coolers, which were then placed in a quiet and dark location. Wing chord and tarsus length were measured following the sampling period to provide a measure, when combined with mass, of body condition. Body mass to wing chord ratios are commonly used to assess body condition in birds (e.g., Chastel et al., 1995). Therefore, to estimate body condition, a ratio of body mass (g) to tarsus length (mm) was calculated. The sex of each bird was identified using dimorphic plumage, which is clearly visible by the age of 12 days (Bird and Palmer, 1988). The size of 15 clutches used in this study ranged between four and six. For comparison with juvenile levels, ten non-breeding adult male kestrels underwent the same capture and restraint protocol as the chicks and were sampled during mid-June to July 1999.

2.3. Corticosterone radioimmunoassay analysis

Plasma levels of corticosterone were measured using a specific radioimmunoassay (RIA) at the National Wildlife Research Centre, Hull, Quebec. Plasma samples were thawed, vortexed, and diluted at a 1:10 ratio of plasma to steroid diluent using RIA kits (ICN Biomedicals, Costa Mesa, CA, cat. no. 07-120103) designed for mouse and rat corticosterone analysis (validated in-house for avian plasma). One hundred microliter of each sample were added in duplicate to labeled assay tubes. Next 200 µl each of ^{125}I-labeled corticosterone and then corticosterone anti-serum were added to each tube, vortexed and allowed to incubate for 2 h. Then 500 µl of steroid precipitant were added, vortexed and centrifuged for 15 min at 2300 rpm. The supernatant was removed and analyzed with a Packard Cobra II Auto Gamma-counter (model number E5002). Each day standard concentrations of corticosterone were used to develop a standard binding curve. Recovery values ranged from

85–90% and were used to adjust assayed concentrations of corticosterone. Quality control samples were run with every set and intra- and inter-assay coefficients of variation were 9.4% and 11.6%, respectively.

2.4. Statistical treatment

The experimental design was a two-factor mixed factorial, where age was a between-groups factor and time (1–45 min) was a within-subjects factor or repeated-measure. During statistical analyses, initial data were tested for homoscedasticity required by a parametric statistical test according to Sokal and Rohlf (1995). At no time were any of these assumptions violated, and therefore, data transformation was not necessary. Where necessary, data were transformed to meet the assumptions of a particular parametric test (i.e., body condition mass:size ratios).

Temporal corticosterone patterns for the two groups were performed using a two-way (age × time) repeated-measures ANCOVA, where age and sex were used as factors, body condition was used as a covariate and serial sampling of the same bird during the stress protocol was used as the repeated-measure. Baseline corticosterone levels were examined between the age groups using ANOVA and differences between age classes were examined using Fisher's protected LSD post-hoc parametric test. Since baseline corticosterone levels in this study were significantly different between the age classes, we used the difference between actual corticosterone levels at 10 min (T10) during the stress response and baseline levels for a particular bird as a measure of corrected T10 corticosterone levels. These are simply referred to as T10 corticosterone levels.

3. Results

Baseline (T0) corticosterone levels (with all age groups pooled) were not affected by either sex ($F_{1.32} = 0.44$, $P = 0.50$), body condition ($F_{1.32} = 0.19$, $P = 0.39$), time of day ($F_{1.32} = 0.92$, $P = 0.71$), season ($F_{1.32} = 0.67$, $P = 0.54$) nor hatch order ($F_{1.32} = 0.96$, $P = 0.69$). Furthermore, there were also no interactions between these factors.

There was a significant effect of AGE class and TIME on the corticosterone-stress response (AGE: $F_{3.28} = 5.40$, $P < 0.005$; TIME: $F_{4.28} = 19.7$, $P < 0.0001$; AGE × TIME interaction: $F_{12.20} = 12.3$, $P < 0.01$; Fig. 1, Table 1). There was also a significant effect of AGE class on baseline (T0) corticosterone (AGE: $F_{3.36} = 11.4$, $P = 0.025$, Fig. 2, Table 1). The T0 and T10 corticosterone levels were indistinguishable between chicks aged 10 and 16 days (Fisher's protected LSD test, $P = 0.64$ and $P = 0.35$, respectively). However, the T0 and T10 corticosterone levels of 28-day-old fledglings
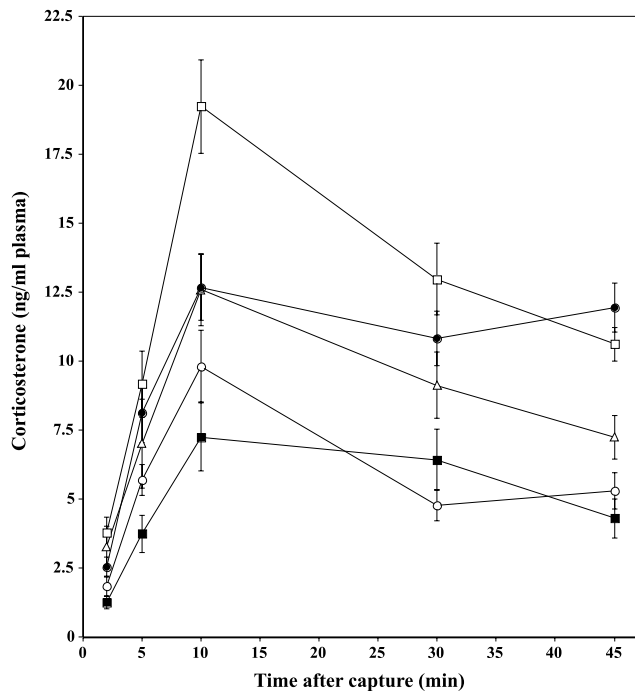
Fig. 1. Adrenocortical responses of American kestrel chicks during post-natal development and one-year-old adult birds (Means (± SE)). 10-day-old chicks (■), 16-day-old chicks (○), 22-day-old chicks (●), 28-day-old chicks (□), and adult birds (△), $N = 10$ for each group.

Fig. 2. Baseline and stress-induced levels of corticosterone in post-natally developing chicks and one-year-old adults (Mean (± SE)).

Table 1
Mean (± SE) plasma concentrations of corticosterone (ng/ml) at the time of capture (T0) and 10 min later (T10) in five age classes of captive american kestrels

Age class	T0	T10
10 days	1.24 ± 0.21	7.42 ± 1.89
16 days	1.84 ± 0.19	9.81 ± 2.04
22 days	2.55 ± 0.15	12.68 ± 1.95
28 days	3.78 ± 0.52	19.23 ± 4.05
Adult	3.29 ± 0.44	12.56 ± 2.23

Note. Days refers to days post-hatching, adults are one-year-old adults. $N = 10$ for each group.

were higher than those of 22-day-old (Fisher's protected LSD test, $P < 0.05$ and $P = 0.05$, respectively), 16-day-old (Fisher's protected LSD test, $P < 0.01$ and $P < 0.05$, respectively) and 10-day-old chicks (Fisher's protected LSD test, $P < 0.01$ and $P = 0.01$, respectively). In addition, the T0 and T10 corticosterone levels were significantly higher in 22-day-old chicks than in 16-day-old (Fisher's protected LSD test, $P < 0.05$ for both) and 10-day-old chicks (Fisher's protected LSD test, $P < 0.01$ and $P < 0.05$, respectively). Furthermore, T0 and T10 in chicks aged 22 days were not significantly different from those of one-year-old adults (Fisher's protected LSD test, $P = 0.55$ and $P = 0.68$, respectively; Fig. 2, Table 1). In addition, although T0 levels for 28-day-old chicks were not significantly higher than those of one-year-old adult birds (Fisher's protected LSD test, $P = 0.82$),
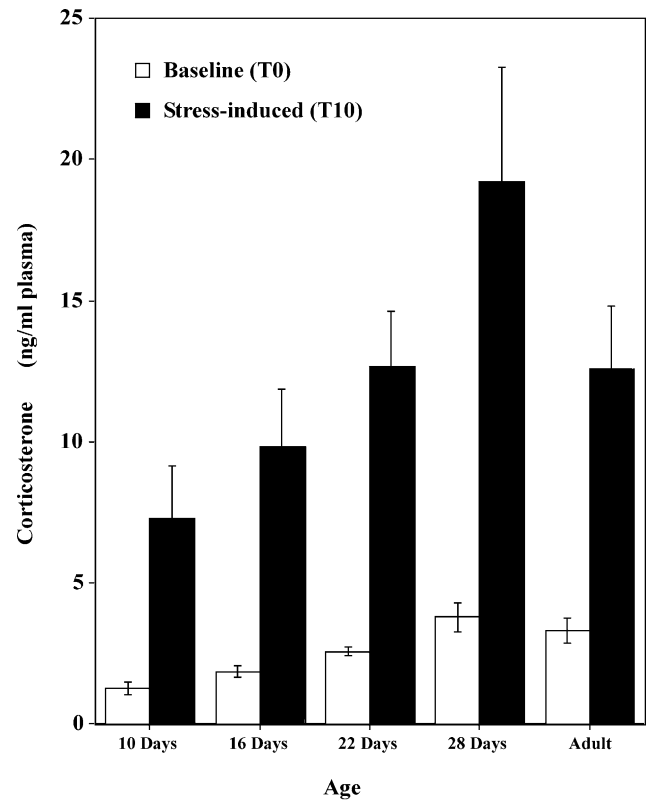
T10 levels were higher (Fisher's protected LSD test, $P < 0.05$). In order to control for elevated stress-induced corticosterone levels induced by the act of fledging itself, we also compared T10 levels between nest-bound and already-fledged chicks at 28 days. There was no significant difference in these levels between birds, which had already fledged and those which were about to ($F_{1,9} = 0.35$, $P = 0.76$) and there was no relationship between baseline corticosterone concentrations and time to nest departure in fledging birds ($R^2 = 0.01$, $P = 0.67$).

4. Discussion

We assessed the post-natal development of adrenocortical function in captive nestling American kestrels through measures of plasma baseline and stress-induced corticosterone levels. Baseline levels of corticosterone increased significantly during post-natal development in the captive birds in our study. Although young chicks aged 10–16 days were responsive to the stimuli of a capture and handling protocol, chicks did not exhibit adult-type stress-induced levels of corticosterone until 22 days of age post-hatching. Captive chicks in this study exhibited low levels of stress-induced corticosterone early in development and this increased significantly until fledging, when levels were significantly

higher than those of one-year-old adults. Three studies to date have examined post-natal development of adrenocortical function in altricial species. Schwabl (1999) reported that baseline levels of corticosterone in canaries increased through development from 5 to 23 days of age. Baseline levels at 10–15 days of age were indistinguishable from those of adult birds. Sims and Holberton (2000) reported that 10-day-old northern mockingbirds show little stress-induced corticosterone secretion, with the highest levels seen in fledglings nearing parental independence. A study of wild American kestrel chicks relating corticosterone levels with handling stress found that chicks as young as 10 days exhibited a response to handling during removal from the nest box, but there was no response at 20 and 25 days post-hatching (Sockman and Schwabl, 2001). Since the sampling protocol of these wild kestrel chicks involved (1) a single sample after removal from the nest and resulted in (2) low sample sizes at 10+ min, it is not unusual to see that some of these results contrast those of the present study. However, results of the present study concur with those of Sockman and Schwabl (2001) in that even birds at 10 days of age exhibited a significant rise in corticosterone after handling. The absence of a detectable response in the wild chicks aged 20 and 25 days in the study by Sockman and Schwabl (2001), may simply be due to low sample sizes at the point at which corticosterone levels are rising, which were detectable in the present study because of continued sampling of the same bird during a stress response. Since captive kestrel chicks were only sampled once during development and they are isolated within a nest cavity, we do not believe that the differences in corticosterone levels stem from captive chicks exhibiting the effects of habituatuation to handling and blood sampling sometimes observed in captive adult kestrels (Love et al., unpublished data).

As seen in other studies of altricial young, the rate and timing of development of the adrenocortical response system in captive kestrel chicks may be dependent on the degree of development of the chick at hatching, the degree of parental care and the type of nest structure used by the species. Schwabl (1999) investigated post-natal baseline corticosterone levels in the altricial canary, which shows the typical altricial developmental patterns of passerines. Levels of corticosterone of 5-, 10-, or 15-day-old chicks were lower than those of adults. Levels of 23-day-old chicks were intermediate between adult baseline and adult stress-induced levels, possibly indicating an adaptive mechanism for elevated corticosterone levels just prior to fledging. In addition, Sims and Holberton (2000) found that baseline corticosterone levels in altricial northern mockingbird nestlings did not vary significantly during post-natal development. Although comparable studies of species with varying reproductive modes are very few at this time, in canaries, which fledge after 16–17 days,

only 30, 67, and 72% of 5-, 10-, and 15-day-old chicks, respectively, had detectable levels of circulating corticosterone. In contrast, precocial chicks, which hatch well developed and are able to locomote and feed themselves independent from their parents, exhibit adult-type adrenocortical function before or at hatching (Carsia et al., 1987; Kallicharan and Hall, 1976; Tanabe et al., 1986; Wise and Frye, 1973). In chickens (*Gallus domesticus*) and mallard ducks (*Anus platyrynchos*) embryonic corticosteroidogenesis has been shown to increase during mid-incubation and peak at hatching (Carsia et al., 1987; Kallicharan and Hall, 1976; Tanabe et al., 1986; Wise and Frye, 1973). After hatching, baseline corticosterone levels decline (Carsia et al., 1987; Holmes and Kelley, 1976; Wentworth and Hussein, 1985); however, mild restraint stress can induce corticosterone secretion in newly hatched chicks (Holmes et al., 1992). Recent work has also shown that herring gull (*Larus argentatus*) embryos exhibit significantly elevated adrenocortical responses compared with baseline corticosterone levels when challenged by a heat stress (Lorenzen, unpublished data). Adrenocortical development in chicks of the semi-altricial, cavity-nesting American kestrel apparently fall somewhere between that of an altricial and a precocial species. As Schwabl (1999) suggests, since the hypothalamo-pituitary-thyroidal and hypothalamic-pituitary gonadal axes become functional later in altricial than in precocial species, it is not surprising to find the HPA axis matures later as well. In kestrels the cavity itself likely provides some measure of buffering for chicks from drastic changes in weather and ambient temperature, as well as increased protection from nest-predators compared with an open nesting species. This may allow for a delayed maturation of the adrenocortical response.

The fact that baseline levels of corticosterone are low during early development and then increase during later development may be an adaptation to the negative effects of chronically elevated corticosterone levels, such as catabolism of skeletal muscle and inhibition of thyroid and growth hormones (Kühn et al., 1998; Martin, 1985; Morici et al., 1997; Wingfield, 1994). As noted by Sims and Holberton (2000), this may minimize these negative effects on rapid growth and development in young birds, potentially maximizing normal growth. The fact that young American kestrel chicks exhibit immuno-detectable levels of stress-induced corticosterone early in post-natal development suggests the ability of even young chicks to potentially cope with food shortages associated with unpredictable food resources wild kestrels often face (Wiebe and Bortolotti, 1994). This response is probably especially important for these chicks after 10 days of age when the female no longer broods during the day, forcing chicks to thermoregulate on their own (Bird and Palmer, 1988). Sufficient maturation of the stress response as a means of providing

alternative energy may be especially important during the latter half of post-natal development in kestrels when nestling energetic demands increase due to size and development, potentially forcing parents to forage for less profitable food items (Wiebe and Bortolotti, 1994). This is consistent with the fact that in our study kestrel chicks develop adult-type stress-induced corticosterone levels between the ages of 16 and 22 days. The combination of reasonably low baseline levels through development coupled with the ability to respond to stressful situations, even at a young age, may allow this cavity nester to maximize growth and be able to respond to shortages in food as well.

The greatest values observed at T10 in young birds were seen at 28 days, at or near fledging when chicks would have to survive on their own. The highest baseline corticosterone concentrations were also observed in this group. As noted by Sims and Holberton (2000) in relation to dispersal behavior in northern mockingbirds, these elevated baseline concentrations of corticosterone may facilitate behaviors related to dispersal in kestrels (Bird and Palmer, 1988) in much the same way as reported for owls (Dufty and Belthoff, 1997). Heath (1997) reported that as young kestrels prepared to depart from the nest during the fledging stage, their baseline corticosterone levels increased significantly. In the present study, there was no relationship between baseline corticosterone concentrations and time to nest departure. Heath (1997) also noted that after growing up in a confined space, young kestrels are required to take full flight during the fledging period, a period when there is a significant increase in activity. Temporary increases in corticosterone levels facilitate locomotor (Astheimer et al., 1992) and foraging behavior (Bray, 1993) and an enhanced adrenocortical response system may stimulate not only fledging, but also foraging behavior once they are exposed to an environment where they are more likely to be preyed upon (Varland et al., 1993). It is possible that elevated baseline corticosterone levels may be an adaptive physiological mechanism facilitating such rapid transitions in young birds. Young Snowy owls (Nytec scandiaca) did not show an increase in baseline corticosterone levels (Romero, personal communication cited in Heath, 1997). The young of this species go through a more gradual process of learning to fly which may not necessitate such a strong physiological stimulus as in kestrels. Young of open-nesting raptorial species may exhibit earlier developing response systems than the cavity-nesting kestrels. Within raptors therefore, one might expect that kestrels fall at the late-developing end of a continuum of HPA axis development. This variation remains to be investigated, as does determining what varied roles adrenocortical function can play in brain development and learning during different periods of post-natal development in birds.

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