Development of the Corticosterone Stress Response in Young Northern Mockingbirds (Mimus polyglottos)

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In birds, additional adrenocortical secretion in response to stressors often redirects an individual's ongoing activities toward immediate life-saving activities, usually by facilitating an increase in food searching and food intake needed to meet periods of increased energy demand. We asked whether young birds, who are entirely dependent on parents for food acquisition and therefore unable to manipulate their own food intake, fail to show an adult-like adrenocortical response to the acute stress of capture and handling. In 1998, plasma profiles of acute corticosterone secretion (e.g., samples taken at the time of capture and 30 min later) were compared across seven age classes of Northern Mockingbirds (Mimus polyglottos) representing various age-related stages of foraging ability and opportunity. As predicted, young birds less able, or entirely unable, to readjust their own foraging effort exhibited significantly lower stress responses compared to adults. The magnitude of the stress response (at 30 min postcapture) increased and approached that of adults as young birds approached independence. Energetic condition was not correlated with the magnitude of the stress response at any age, suggesting that variation in its expression was most likely due to age alone. We also investigated at what level within the hypothalamic–pituitary–adrenal (HPA) axis the corticosterone response may be controlled in young birds. In 1999, baseline corticosterone samples were taken in 8-day-old nestlings and were immediately followed by intrajugular injections of adrenocorticotropic hormone (ACTH) or saline. While plasma corticosterone concentrations did not change in saline-injected nestlings, ACTH-injected nestlings showed a significant increase in plasma corticosterone concentrations similar to 30-min samples taken from adults. These results indicate that, while young birds do not normally show the corticosterone response, the adrenocortical tissue has the capacity to do so, and the control appears to be within the hypothalamic–pituitary component of the HPA axis. Collectively, our results indicate that the expression of the corticosterone stress response develops in concert with a young, altricial bird's ability to utilize it as it approaches independence; the reduced corticosterone secretion may also allow young, rapidly growing birds to avoid potential deleterious exposure to elevated glucocorticosteroid concentrations.

Key Words: corticosterone; adrenocorticotropic hormone; hypothalamic–pituitary–adrenal (HPA) axis; stress response; glucocorticosteroids; avian growth; development; Northern Mockingbird (Mimus polyglottos).
Piersma and Ramenofsky, 1998; Tsipoura et al., 1999). The acute increase in corticosterone is in response to adrenocorticotropin hormone (ACTH) released from the pituitary which, in turn, is released in response to a variety of secretagogues. These may include arginine vasotocin and mesotocin, but corticotropin releasing factor (CRF) may play a primary role in ACTH secretion (Castro et al., 1986; Romero et al., 1998b). The stimulation of this hypothalamic–pituitary–adrenal (HPA) pathway is believed to shift toward behavioral and physiological processes away from ongoing activities and toward life-saving responses, such as increased food searching and increased food intake (Wingfield and Silverin, 1986; Gray et al., 1990; Astheimer et al., 1992). Currently, in birds, it is thought that corticosterone may also play a role in nonstressful situations, such as facilitation of fattening prior to migration (Holberton, 1999; Holberton et al., 1996a, 1999), preparation for fledging (Heath, 1997), and preparation for postnatal dispersal (Belthoff and Dufty, 1998).

Despite the benefits of acute corticosterone secretion during emergency situations, chronically high levels of corticosterone can have negative consequences. In adult vertebrates, chronically elevated corticosterone levels can suppress territorial and/or reproductive behavior, compromise the immune system, and deplete protein reserves through promotion of gluconeogenesis (for review see Sapolsky, 1987; Wingfield, 1994). Although there is a growing body of literature on the role of corticosterone in behavioral and physiological responses associated with energy regulation, most of it has focused on patterns found in adults (Wingfield et al., 1994a,b; Wingfield, 1994; Holberton et al., 1996a,b; Romero et al., 1998a; Marra and Holberton, 1998; Holberton, 1999), and few studies have investigated corticosterone in young birds (Dufty and Belthoff, 1997; Heath, 1997; Belthoff and Dufty, 1998; Romero et al., 1998b). 

In young vertebrates, elevated corticosterone concentrations may be detrimental to growth and development (for review see Martin, 1985; Sapolsky, 1987). Studies on juvenile alligators (Alligator mississippiensis) implanted with exogenous corticosterone have shown that elevated plasma corticosterone concentrations inhibited growth over a 3-month period of treatment (Morici et al., 1997). Similarly, Leile and Scanes (1998) found that synthetic glucocorticosteroids significantly inhibited growth in young domestic chicks (Gallus gallus). A possible mechanism for this response may be through the negative impact that glucocorticoids can have on the secretion of thyroid and growth hormones (for review see Martin, 1985; Kühn et al., 1998). The effect of elevated endogenous glucocorticosteroid levels on the rapid growth and development of free-living birds is unknown.

The Northern Mockingbird (Mimus polyglottos) displays an altricial developmental strategy in which nestlings and postfledging juveniles depend on both parents for food and protection until they leave the natal territory. The altricial strategy is believed to have evolved from the precocial developmental strategy, in which juveniles can move about and forage more independently immediately following hatching (Rickels, 1983). It is hypothesized that, as birds evolved more specialized foraging strategies, young of altricial species needed to process more information about food identification and techniques of acquiring food prior to becoming independent (Starck, 1993). As a consequence of this pattern, compared to precocial species, in altricial birds significant differentiation of the brain and associated neural pathways occurs after hatching to coordinate neural development with the learning processes associated with foraging (Starck, 1993). Young birds may follow a pattern of neural development, particularly that of the HPA axis, that reflects the degree of parental dependence (e.g., altricial vs precocial) after hatching.

Mammals, such as sheep and rats, have advanced prenatal neural development and can exhibit an endocrine response to stress prior to birth (Sapolsky and Meaney, 1986; Naumenko, 1991; Matthews and Challis, 1996). Whereas the ability to mount an endocrine response to stress is initially present in young rats, they fail to display it during a period beginning 1 week after birth and lasting into the 2nd week after birth, a time in which critical development of the neonate may be occurring (Sapolsky and Meaney, 1986; Naumenko, 1991). Similarly, Romero et al. (1998b) found that young Redpolls (Carduelis flammea) did not show a stress response for 1–2 weeks following fledging. This “stress hyporesponsive period” (SHRP) may be due to delayed maturation of the brain’s ability to regulate the HPA axis (Sapolsky and Meaney, 1986; Naumenko, 1991). In rats, a complex interaction of reduced receptor density, continuing development of the pituitary, and low hypothalamic
and pituitary CRF and ACTH, as well as regression of the adrenal cortex, results in the reduced ability of young to secrete corticosterone in response to stress during the SHRP (for review see Sapolsky and Meaney, 1986). In Redpolls, it has been shown that the missing link in the HPA axis is found in the pituitary’s ability to release ACTH and not in delayed adrenal cortical tissue development (Romero et al., 1998b). In birds and mammals, the inability to respond to stress at a young age may be an adaptation to reduce the possible negative effects of chronically elevated glucocorticoid concentrations.

If the corticosterone stress response is an evolutionary adaptation that enables individuals to evade predators, increase food searching and food intake, and redirect energy utilization during stressful periods, then dependent offspring that are unable to leave the nest or adjust their own provisioning rate may have little need and, therefore, little ability to secrete corticosterone in response to short-term stress. The benefit of this strategy would be that rapidly growing young birds could avoid the potential deleterious effects of high glucocorticosteroid levels on rapid growth and development. It follows that, if the strength of the corticosterone stress response represents its capacity to aid the individual, it is likely to develop in parallel with increasing independence from the parents (e.g., development of more efficient foraging and predator detection abilities) and decreasing risk to growth and development. In this study we examined the possibility that the HPA axis may be less developed in newly hatched birds and that it develops with age and experience in altricial species as the time of independence approaches.

We predicted that the most dependent age group (nestlings) would be least likely to express the corticosterone stress response as compared to adults and young birds that have left the nest. We also predicted that, as young birds gained independence from their parents and developed greater ability to forage and evade predators on their own, the stress response exhibited by them would become more similar to that of adults. Because the strength of the stress response is often correlated with energy reserves (Wingfield et al., 1994a; Marra and Holberton, 1998; Holberton et al., 1999), we investigated relationships between energetic condition and baseline corticosterone concentration, as well as those between energetic condition and magnitude of the stress response throughout the stages of development in young birds and in adults.

Previous studies have shown that the absence or reduction of a corticosterone stress response during certain periods of the avian annual cycle is due to the absence of the pituitary secretion of ACTH (Astheimer et al., 1994; Romero et al., 1998a). If, in our study, young birds do not show the same capacity as adults in their ability to exhibit the corticosterone stress response, it may be the result of delayed neural development of the hypothalamus, pituitary, and/or lower capacity of adrenocortical tissue to secrete hormone. In addition to measuring the stress response as a function of age in young mockingbirds, we investigated the level of activity within the HPA axis at which the ability to secrete corticosterone might be controlled in young birds. Specifically, we administered exogenous ACTH to nestlings, the age class of young birds that we predicted would be least likely to exhibit the corticosterone stress response.

**METHODS**

Our study site was located on the University of Mississippi campus, in Lafayette County, Mississippi. In 1998, nestling, fledgling, independent young, and adult mockingbirds were captured on their breeding/natal territories using potter traps baited with meal worms or using mist nets. In this species, incubation lasts 12–13 days (Laskey, 1962; Doughty, 1988). Nestlings remain in the nest approximately 12 days, and after fledging, young birds gradually become less dependent on their parents for another 21–28 days before leaving the natal territory (Laskey, 1962; Doughty, 1988). Nestlings were captured daily to determine hatch and fledging date. Seven age classes were established *a priori* in this study: nestlings 5–7 days posthatch (early stage, NE), nestlings at least 8–9 days old but still in the nest (mid stage, NM), nestlings at least 10 days old but still in the nest (late stage, NL), fledglings that were out of the nest but captured within the first 5 days of leaving the nest (early stage, FE), fledglings 18–28 days out of the nest but still on the natal territory (late stage, FL), independent juveniles that were captured on a territory known not to be their natal territory (IND), and adults born previous to 1998 and...
determined to be actively breeding or to be a resident on a territory at the time of sampling (ADULT). All birds were captured and sampled between 0500 and 1200 h CST. All nestlings and FE were captured by hand or with a dip net (approx 2.5 m long with 0.75-mm mesh). Blood samples were taken only if they could be collected within 5 min of initial disturbance (Holberton, 1999). After sampling, each bird was marked with a USFWS band and a unique set of plastic color bands. The presence or absence of a brood patch was used to determine sex in adult birds (Pyle et al., 1987).

To measure the acute stress response, a blood sample (100–150 μL) was obtained from the brachial vein, using a 26-gauge needle, within the first 5 min after the initial disturbance (referred to as baseline or “T0” in the text, tables, and analyses) and again 30 min later (referred to as “T30” in the text, tables, and analyses). Birds were held in cloth bags during the 30-min sampling period. Measurements of body size (tarsus length, ± 0.1 mm) (Pyle et al., 1987) and body mass (± 0.5 g) were recorded. To look for relationships between energetic condition and baseline corticosterone concentration (T0) within each age group, we used the residuals from the regression of tarsus length on the cubed root of body mass as an indicator of energetic condition (Cash et al., 1997; Bradshaw, 1986). We also looked for correlation between energetic condition and the magnitude of the stress response over the 30-min (T30) period.

To determine at what level, within the HPA axis, the corticosterone stress response can be regulated in young birds, 20 nestlings (8 days posthatch, NM) were captured in the nest and challenged with exogenous ACTH during the summer of 1999. Immediately (within 1–2 min) following collection of the initial (T0) blood sample, 11 control nestlings were given 10-μL intrajugular injections of physiological saline (0.9% NaCl). Nine other individuals were given 10-μL intrajugular injections of porcine ACTH (Sigma Chemical No. A-6303) in saline solution at a concentration of 0.2 IU ACTH/g body mass, a dose previously used to stimulate adrenocortical secretion in adult birds (Romero et al., 1998a). A second blood sample was taken 30 min after capture to determine whether exogenous ACTH could stimulate endogenous corticosterone secretion in nestlings, the age group that we believe to be least likely to show an endogenous stress response.

All blood samples were kept on ice in the field until centrifuged in the laboratory (Holberton, 1999). Plasma was collected with a 50-μL Hamilton syringe and kept frozen (−5°) until assayed for corticosterone concentration by radioimmunoassay at the University of Mississippi, following Wingfield et al. (1992) and described in Cash and Holberton (1999). All hormone concentrations were log transformed to correct for heteroscedacity due to unequal sample sizes. A two-factor repeated-measures analysis of variance (ANOVA) was used to detect effects of age class (AGE) and time after capture (TIME, the repeated-measures component) on the expression of the stress response. A single-factor ANOVA, using Fisher’s protected least squares difference (PLSD) as a post hoc test, was used to determine whether initial baseline (T0) corticosterone concentration differed across all groups at the time of capture as well as from plasma corticosterone 30 min later (T30). Similarly, a two-factor repeated-measures ANOVA and Fisher’s protected least squares difference were used to look for differences in the stress response between ACTH-injected and control saline-injected nestlings.

RESULTS

Samples from 1998 were spread across three assays in which a pooled avian plasma sample and a standard were used to measure intra- and interassay variation (intraassay coefficient of variation based on plasma pool = 11%, standard = 14%; interassay coefficient of variation based on plasma pool = 13%, standard = 9%). Twenty-eight NE, 28 NM, 21 NL, 17 FE, 13 FL, 9 IND, and 21 adults were sampled for the stress response. In adults, data from both sexes were pooled, as there was no effect of gender on the stress response. In adults, data from both sexes were pooled, as there was no effect of gender on the stress response. In adults, data from both sexes were pooled, as there was no effect of gender on the stress response. In adults, data from both sexes were pooled, as there was no effect of gender on the stress response.
Plasma profiles of corticosterone secretion (mean ± SE) in response to capture and handling in multiple age classes of Northern Mockingbird. NE, early stage nestlings; NM, mid-stage nestlings; NL, late-stage nestlings; FE, early stage fledglings; FL, late-stage fledglings; IND, independent young no longer on the natal territory; ADULT, adult. (See text for age details.)

on baseline corticosterone concentration (F_{6,130} = 1.861, P = 0.0922; Table 1, Fig. 1), with IND individuals being the only nonadult group to differ significantly from adults (P < 0.05, Fisher’s PLSD). In all comparisons, each bird was treated as an independent sample, as only 20 of the 117 young birds were represented in more than one age class; less than ½ of the these were likely to be represented in statistical comparisons between individual age classes. When these individuals were removed from the analyses, the effect of age on the stress response was the same (AGE: F_{6,81} = 3.100, P < 0.05; TIME: F_{1,81} = 75.653, P < 0.0001; AGE × TIME interaction: F_{6,81} = 6.495, P < 0.0001). We also found that there was no effect of brood (e.g., the putative relatedness among same-age cohorts) on T30 corticosterone concentration (single-factor ANOVA: NE, F_{7,20} = 2.221, P = 0.07; NM, F_{5,19} = 1.517, P = 0.22; NL, F_{5,14} = 2.731, P = 0.06; FE, F_{6,7} = 1.098, P = 0.46; FL, F_{7,6} = 1.735, P = 0.26; ADULT, F_{15,5} = 0.795, P = 0.67).

In general, whereas baseline corticosterone levels did not vary with age, the magnitude of corticosterone secretion over the 30-min period did (Fig. 1, Table 1). T30 corticosterone concentrations of all nestling and fledgling age classes were significantly lower than that of adults (AGE: F_{6,130} = 12.524, P < 0.0001, P < 0.05 for all comparisons, Fisher’s PLSD). However, the T30 concentration of corticosterone in the IND age class was not significantly lower than that of the adult age group (P > 0.05, Fisher’s PLSD). The T30 corticosterone concentrations in the FL and IND groups were not significantly different from each other (P > 0.05, Fisher’s PLSD). The T30 corticosterone concentrations in the IND group was significantly higher than all age classes younger than FL (P < 0.05, Fisher’s PLSD), and the same pattern is true for the FL group, with the exception of the FL and NL comparison for which no difference was found.

Variation in baseline corticosterone concentration was not correlated with energetic condition within any age class (P > 0.05, for all groups, NE, r = 0.196, r_{crit} = 0.413; NM, r = 0.206, r_{crit} = 0.396; NL, r = 0.063, r_{crit} = 0.482; FE, r = 0.250, r_{crit} = 0.602; FL, r = 0.441, r_{crit} = 0.553; IND, r = 0.117, r_{crit} = 0.632; ADULT, r = 0.101, r_{crit} = 0.444). Similarly, the T30 corticosterone concentration was not correlated with energetic condition within any age class (P > 0.05, for all groups, NE, r = 0.370, r_{crit} = 0.413; NM, r = 0.202, r_{crit} = 0.396; NL, r = 0.195, r_{crit} = 0.482; FE, r = 0.023, r_{crit} = 0.602; FL, r = 0.392, r_{crit} = 0.553; IND, r = 0.032, r_{crit} = 0.666; ADULT, r = 0.370, r_{crit} = 0.413).

Nestlings injected with exogenous ACTH differed significantly in the secretion of corticosterone from that of birds injected with physiological saline (TREATMENT × TIME interaction: F_{1,18} = 10.393, P = 0.0047, Fig. 2) during the 30-min sampling period. Whereas baseline concentrations did not differ between the two groups (control mean = 0.37 ng/mL at the Time of Capture (T0) and 30 min Later (T30)) in Six Age Classes of Northern Mockingbirds

<table>
<thead>
<tr>
<th>Age class</th>
<th>T0</th>
<th>T30</th>
</tr>
</thead>
<tbody>
<tr>
<td>NE</td>
<td>3.17 ± 0.42</td>
<td>6.73 ± 1.03</td>
</tr>
<tr>
<td>NM</td>
<td>3.82 ± 0.59</td>
<td>8.00 ± 1.09</td>
</tr>
<tr>
<td>NL</td>
<td>4.89 ± 0.59</td>
<td>10.56 ± 2.29</td>
</tr>
<tr>
<td>FE</td>
<td>4.49 ± 0.77</td>
<td>8.87 ± 2.43</td>
</tr>
<tr>
<td>FL</td>
<td>2.92 ± 1.15</td>
<td>13.81 ± 1.92</td>
</tr>
<tr>
<td>IND</td>
<td>6.71 ± 2.32</td>
<td>25.05 ± 5.05</td>
</tr>
<tr>
<td>ADULT</td>
<td>4.02 ± 0.67</td>
<td>29.38 ± 2.40</td>
</tr>
</tbody>
</table>

Note. NE, Early stage nestlings, n = 28; NM, middle stage nestlings, n = 28; NL, late stage nestlings, n = 21; FE, early stage fledglings, n = 17; FL, late stage fledglings, n = 14; IND, independent juveniles, n = 9; ADULT, n = 21.
mL ± 0.13 SE, ACTH mean = 0.41 ng/mL ± 0.19 SE; 
$F_{1,18} = 0.035, P = 0.8544$), ACTH-injected nestlings  
had significantly higher concentrations of corticosterone at T30 (control mean = 8.23 ng/mL ± 3.18 SE,  
ACTH mean = 30.20 ng/mL ± 3.31 SE; $F_{1,18} = 12.068, 
P = 0.0027$). Nestlings in the 1999 ACTH experiment  
had a significantly lower baseline concentration of  
corticosterone than adults from the 1998 sample group  
(ADULT mean baseline = 4.02 ng/mL ± 0.67 SE,  
nestling mean baseline = 0.39 ng/mL ± 0.11 SE; 
$F_{1,30} = 77.48, P < 0.0001$) and NM from the 1998  
sample group (NM mean baseline (1998) = 3.28 ng/  
mL ± 0.57 SE, nestlings mean baseline (1999) = 0.39  
ng/mL ± 0.11 SE; $F_{1,33} = 47.55, P < 0.0001$). There  
was no significant difference in T30 corticosterone  
concentrations in adult birds (1998) and ACTH-injected  
nestlings (ADULT mean T30 = 28.51 ng/mL ± 2.72 SE,  
nestling mean T30 = 30.19 ng/mL ± 3.31 SE; 
$F_{1,26} = 0.363, P = 0.552$).

**DISCUSSION**

Like many other passerines, adult mockingbirds  
show a significant increase in plasma corticosterone  
concentrations within 30 min following capture (Daw- 
son and Howe, 1983; Schwabl et al., 1991; Astheimer et  
al., 1994; Wingfield, 1994; Wingfield et al., 1992,  
1994a,b, 1995; Holberton et al., 1996a, 1999; Marra and  
Holberton, 1998; Romero et al., 1998a,b). However, our  
results demonstrate that the corticosterone response to  
capture and handling stress changes significantly dur- 
ing development in this species, and young birds ap- 
pear to acquire an adult-like stress response as they  
approach independence. The youngest birds, particu- 
larly those 10 days old or less, show very little, if any,  
corticosterone secretion, even after experiencing the  
same exposure to capture and handling as adults, with  
maximum plasma values rarely approaching 5 ng/mL. These findings support earlier work by Romero et al. (1998b) in Redpolls, but our study provides greater resolution of the time course of HPA axis develop- 
ment in altricial young. The greatest values observed  
at T30 in young birds were seen in fledglings reaching  
the point at which they would have to survive on their  
own (FL) and in independent juveniles already caring  
for themselves (IND). The highest baseline corticoste- 
rone concentrations were observed in the IND group.  
These elevated baseline concentrations of corticoste- 
rone may facilitate behaviors related to dispersal movement in mockingbirds (C. Sims, unpublished  
manuscript) in much the same way as reported for  
owls (Belthoff and Dufty, 1998).

The adult stress response is thought to facilitate  
behavioral and physiological responses that help in- 
dividuals escape or survive stressful perturbations  
(Wingfield and Silverin, 1986; Gray et al., 1990; Asthei- 
mer et al., 1992; Wingfield, 1994). However, due to  
their inexperience and their dependence on parental  
 provisioning, young birds may have little need for the  
benefits of an adult-like stress response that may be  
detrimental to growth and development. Our results  
support this hypothesis in that, during the time that  
young mockingbirds remain in the nest (approx 12  
days after hatching), they have a reduced corticoste- 
rone stress response. During the 3–4 weeks leading up  
to independence, the corticosterone stress response  
appears to develop in concert with the young birds’  
increasing ability to be independent.

Another explanation for the absence of a stress re- 
sponse in young naïve birds could be that they are not  
able to recognize the risk of a potential predator (the  
researcher) at the nest and therefore do not respond in  
the same way as older birds do to capture and han- 
dling. We have no evidence that young nestlings do  
perceive disturbance as stressful. However, the fact  
that older nestlings often attempt to escape when dis-
turbed, yet still show no corticosterone stress response, suggests that failure to perceive the stimulus as stressful can be discounted as an explanation for our results with nestlings of all ages. As stated earlier, young rats (1 week postbirth) lack an endocrine stress response during a potential critical period in early postnatal development (Sapolsky and Meaney, 1986; Naumenko, 1991). The same may be true for young birds that may be able to recognize potential dangers, but the neuroendocrine mechanisms associated with adult-like responses are not yet fully developed.

In addition to the behavioral aspects, as birds approach independence, the physiological consequences of corticosterone may also be changing. If chronically elevated corticosterone levels can result in catabolism of skeletal muscle and inhibition of thyroid and growth hormones (Martin 1985; Wingfield, 1994; Morici et al., 1997; Kühn et al., 1998), young birds may be seriously impacted during the period of rapid growth and development. In mammals, elevated maternal stress hormone levels result in reduced stress sensitivity in offspring once they reach adulthood (Naumenko, 1991). This is believed to be an adaptation allowing offspring to survive under the same conditions experienced by their parents without detrimental effects to growth and development. The patterns of corticosterone secretion observed in our young mockingbirds suggest that the reduced corticosterone stress response may, in addition to its possible ineffectual nature regarding emergency behaviors, be an evolutionary strategy that minimizes skeletal muscle catabolism and negative effects on rapid growth and development in young birds. In this way, a reduced stress response in young animals may help maximize normal development under possibly suboptimal conditions.

In contrast to other studies in which either the baseline corticosterone concentration or the magnitude of the stress response has been found to correlate with energy reserves (Schwabl et al., 1991; Gwinner et al., 1992; Wingfield et al., 1994a; Ramenofsky et al., 1995; Marra and Holberton, 1998; Holberton et al., 1999), our mockingbirds, regardless of age, failed to show these relationships. Our data suggest that changes in the corticosterone stress response during the growth and development of young birds are more a function of ontogenic changes in the HPA axis and are not the result of age-related changes in energetic condition. In our study we were not able to make between-age group comparisons of energetic condition (often based on body mass corrected for tarsus length) in the younger age groups because tarsus length increases dramatically and not in proportion to the rapid increase in body mass early in development. However, the tarsus length of late-stage fledglings was similar to that of adults (FL mean tarsus = 32.66 mm ± 0.16 SE vs ADULT mean tarsus = 32.79 mm ± 0.25 SE; two-tailed t test, P > 0.05), and we found no difference in energetic condition in these two age groups (C. Sims, unpublished manuscript). This suggests that the change in the corticosterone stress response in young birds as they approach independence may be due to age alone.

In general, the difference in the strength of the stress response across age groups was the result of an ontogenic increase in the strength of its expression and not in changes in baseline corticosterone concentrations. Late-stage nestlings however, showed an elevated baseline corticosterone concentration at a time when they would soon be fledging from the nest (C. Sims, unpublished manuscript). This is similar to the pattern found by Heath (1997) in a bird of prey, the American Kestrel (Falco sparverius), in which an ephemeral increase in baseline corticosterone concentration is believed to facilitate the impetus to leave the nest. When considered with the results of this study, the data suggest that changes in baseline corticosterone concentration that occur at the time of fledging may be ubiquitous among birds.

The results of the ACTH challenge experiment clearly demonstrate that, in response to exogenous ACTH, the adrenocortical tissue of young mockingbirds has the ability to secrete significant concentrations of corticosterone into the plasma. At least for the dose of ACTH used in this study, nestlings appeared to have the capacity to secrete corticosterone equivalent to that of adults, suggesting that adequate development of adrenocortical tissue occurs early in ontogeny. These results show that the ability to respond physiologically to stress in developing birds, like mammals, is limited not by adrenocortical development, but rather by that of the hypothalamic–pituitary component of the HPA axis. The results also support the hypothesis that development of the HPA axis in species with altricial young occurs in parallel with the rate of behavioral abilities leading to independence.
Baseline corticosterone concentrations in the ACTH-experiment birds (1999) and the NM birds (1998) differed significantly. It is not known why this annual difference occurred, yet it is known that the difference is not due to assay variation between years. In summary, the ability of young birds to respond to acute stress may be acquired when (1) the individual is able to utilize such a mechanism to facilitate appropriate changes in its own behavior and (2) the physiological consequence of high glucocorticosteroid activity on growth and development is minimized. Corresponding age-related patterns of glucocorticosteroid secretion in precocial young who may be able to adjust their own feeding behaviors early in life are not, as yet, known.

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REFERENCES


