

Effects of nutritional restrictions during post-hatching development on adrenocortical function in western scrub-jays (*Aphelocoma californica*)

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Received 10 May 2005; revised 16 June 2005; accepted 29 June 2005

Available online 15 August 2005

Abstract

Altricial birds grow rapidly during post-hatching period and are developmentally sensitive to variations in food supply. Limited food results in elevated corticosterone levels in chicks of semi-precocial birds but it is not clear whether altricial songbirds show similar adrenocortical stress response to nutritional restrictions during early development. It is also unknown how nutritional stress during early development affects the adrenocortical function later in life in altricial birds which show tremendous variation in the magnitude of adrenocortical stress response. Using western scrub-jays (*Aphelocoma californica*), we experimentally demonstrated that moderate food restrictions (65% of ad libitum) during post-hatching development caused significant elevation of baseline corticosterone levels in nest-bound chicks. Compared to controls, 1-year-old scrub-jays that experienced nutritional deficits during post-hatching development also showed a marginally significant trend to have stronger adrenocortical stress response and significantly greater degree of fluctuating asymmetry in bone and feather measurements. Thus, our results demonstrated that developing altricial birds show adrenocortical response to nutritional deficits, which might produce long-term changes in responsiveness of the adrenal system. Our study suggests that baseline corticosterone levels are a good indicator of physiological conditions of developing birds and that individual variance in adrenocortical stress response commonly observed in many species might, at least in part, be explained by environmental conditions during early development. Considering that nutritional restrictions during early development are linked to many permanent changes including impaired cognitive abilities, corticosterone levels in developing young might be a reliable predictor of their future fitness.

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Keywords: Corticosterone; Development; Food-stress; Food restrictions; Fluctuating asymmetry; Stress response; Western scrub-jay

1. Introduction

Altricial birds experience extremely rapid growth during post-hatching development but show significant variation in growth rates both within and between the broods, most likely due to variance in food supply (Lack, 1954). While in the nest, growing young depend

entirely on their parents for food and thus parent's ability to provide food could be an important source of variation in nestling growth (Lack, 1954). An important evolutionary question is whether variation in development rates has fitness consequences for the young.

Adult animals respond to restrictions in food supply by elevating levels of glucocorticoid hormones (Wingfield et al., 1995, 1997, 1998), which in turn initiate behaviors directed toward improving chances of survival—elevated corticosterone levels facilitate increased feeding behavior (Pravosudov, 2003), fat deposition and

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sometimes migration to more favorable habitats (Breuner and Hahn, 2003; Gray et al., 1990; Silverin, 1986; Wingfield and Silverin, 1986; see also reviews in Wingfield et al., 1995, 1997, 1998). If glucocorticoid levels remain elevated over long period of time, an animal might suffer significant deleterious effects such as muscle waste, weakened immune system, and cognitive impairments (Wingfield et al., 1995, 1997, 1998). Nestlings are usually bound to their nest, they cannot escape poor foraging conditions and thus elevation of corticosterone might potentially have only harmful consequences (Sims and Holberton, 2000). For example, Sims and Holberton (2000) reported that nestling mockingbirds (*Mimus polyglottos*) did not show adrenocortical response to stress even though their adrenals were capable of producing a response similar to that of adults. Sims and Holberton (2000) concluded that adrenocortical stress response is suppressed in nestlings because it cannot facilitate appropriate behaviors at that stage.

Contrary to Sims and Holberton's (2000) conclusions, several studies reported that nestlings of other songbird species have significantly elevated corticosterone levels in poor quality habitats as well as in enlarged broods, suggesting that poor feeding conditions trigger corticosterone elevation in nest-bound young (Saino et al., 2003; Suorsa et al., 2003). Although nestlings cannot leave their nests in search of better environment they might be capable of manipulating parents' provisioning rates, mostly through begging behavior (Kitaysky et al., 2001a; Trivers, 1974). Furthermore, Kitaysky et al. (2001a) experimentally demonstrated that elevated corticosterone facilitates begging behavior which could affect parents food provisioning rates. This suggests that stress response in nest-bound young might be highly adaptive. In non-passerine bird species, it has been well established that food restrictions result in corticosterone elevation (Kitaysky et al., 1999, 2001a,b; Sockman and Schwabl, 2001) but the evidence of stress response in nestling songbirds is scarce (Saino et al., 2003; Sims and Holberton, 2000).

Assuming that nestlings increase their corticosterone levels when they do not get sufficient amount of food, and that such an increase facilitates more begging behavior, parents should increase their provisioning rate. But what happens if parents are not capable of providing more food? It is possible that corticosterone levels in nestlings would remain chronically elevated which might produce long-lasting deleterious effects. In mammals, it has been well documented that pre- and post-natal stress produces life-long changes in adrenal function (Anisman et al., 1998; Liu et al., 1997; Meaney et al., 1996; Penke et al., 2001; Vallee et al., 1999; Weaver et al., 2000). Prenatal stress usually results in enhanced adrenal activity later in life and in stronger adrenocortical response to stress (Meaney et al., 1996; Penke et al., 2001; Vallee et al., 1999). In domestic chicken (*Gallus gallus domesticus*),

protein restrictions during early development altered adrenal steroidogenic tissue and resulted in enhanced adrenal response (Carsia and Weber, 2000). At the same time, stress during early development has also been reported to affect cognitive abilities in adult mammals (Vallee et al., 1999). In seabirds, corticosterone elevation in chicks was associated with poor learning abilities later in life (Kitaysky et al., 2003). In songbirds, food deprivation and corticosterone elevation during early post-hatching period have been reported to affect song learning abilities and song nuclei HVC volume (Buchanan et al., 2003, 2004; Nowicki et al., 2002; Spencer et al., 2003). It remains unclear, however, whether HVC volume is selectively affected by food restriction and/or elevated corticosterone levels because one study showed that the entire brain size was affected (Nowicki et al., 2002), whereas the other study did not control for the total brain volume (Buchanan et al., 2004).

Surprisingly, none of these songbird studies directly documented that nutritional stress was associated with elevated corticosterone levels. Thus, whereas there are many indications that nutritional restrictions during post-hatching development should affect corticosterone levels in altricial birds (Saino et al., 2003; Suorsa et al., 2003), direct evidence is lacking. The question of long-term effects of nutritional deprivations and corticosterone elevation during early development on adrenal function later in life is also poorly studied in altricial birds. Birds show tremendous individual variation in adrenocortical stress response (Cockrem and Silverin, 2002), but it remains unclear whether such variation might be explained, at least in part, by conditions during early development. In this study, we investigated the effects of moderate nutritional deficits on baseline corticosterone levels in western scrub-jays (*Aphelocoma californica*) during post-hatching development and whether such deficits have long-term effects on adrenocortical responsiveness later in life. Previously, we have shown that nutritional deficits during post-hatching development result in impaired spatial memory and reduced hippocampal volume with fewer neurons later in life (Pravosudov et al., in press). Here, using the same birds we specifically tested two direct predictions: (1) food restrictions should result in significant corticosterone elevation in nestlings, and (2) food restrictions during post-hatching development should result in enhanced adrenocortical response later in life (Carsia and Weber, 2000; Vallee et al., 1999).

2. Methods

Twenty-four western scrub-jay chicks were collected from 12 natural nests in April 2003 at approximately 7 days of age. Two chicks were collected from each nest; one chick was randomly assigned to the control group

while the other was added to the experimental group. Chicks were fed Roudy Bush Hand Feed Formula 3 using plastic syringes, which allowed precise measurements of the amount fed to each individual. Control chicks were fed until satiation, after which nutritionally deprived chicks received 65% of the amount of food given to the control chicks at each feeding. Hand feeding continued until all chicks started eating on their own and completely refused our feeding attempts. Jays first started eating on their own at ca. 30 days of age and became completely independent of our feeding at about two months of age (Pravosudov et al., in press). Once jays became nutritionally independent they were given food ad libitum (peanuts, Roudy Bush pellets, waxworms, and mealworms). Birds were maintained individually in cages (120 × 42 × 60 cm) on a natural photoperiod until October after which they were placed on a winter-like photoperiod (9 h light:15 h dark) for the rest of the experiment. All birds participated in memory experiments until they were 12 months old (Pravosudov et al., in press).

We collected first blood sample 10 days after the treatment started when chicks were about 17 days old and the second sample 22 days since nutritional deprivation began when chicks were about 29 days old. The second sampling occurred after all birds fledged from the nest when they were about 26 days old. Both times, we collected a single blood sample from a brachial vein within 2 min after handling a bird to obtain estimates of baseline corticosterone levels. Each individual was sampled in an isolated room to avoid potential effects on other birds. We alternated experimental and control birds with the first bird determined at random each day. When all birds were about 12 months old, we collected four samples during a standard protocol of handling and restraint (Wingfield and Farner, 1975; Wingfield et al., 1992) to evaluate adrenocortical response to acute stress. Blood samples were collected at 2, 5, 20, and 50 min after initially disturbing a bird. Birds were moved into a different room for bleeding and held in cloth bags between the samplings. All birds were sampled at the same time of day between 10:00 and 13:00 h and we alternated experimental and control individuals with the first bird determined at random. Order of sampling had no significant effect on either baseline levels ($F_{1,17}=0.23$, $P=0.64$) or the entire adrenocortical stress response ($F_{1,16}=0.86$, $P=0.36$) in experimental or control scrub-jays and thus it was removed from all statistical analyses. Samples collected within 2 min after inducing handling stress represent baseline levels because it usually takes more than 3 min for corticosterone levels to increase (Pravosudov et al., 2001, 2002, 2003, 2004). Indeed, in our first sample, time had no significant effect on corticosterone levels ($F_{1,19}=0.05$, $P=0.82$). Blood samples were collected into heparinized capillary tubes, emptied into 0.3 ml vials and kept on ice. All samples were centrifuged within 1 h of collection and

frozen at -20°C until radioimmunoassay analyses (Wingfield and Farner, 1975; Wingfield et al., 1992).

We measured corticosterone concentrations after extraction of 5–20 μl samples in dichloromethane. Recovery values of the extraction averaged 94.4% (range 88.9–99.0%). All samples were analyzed in a single assay; the intra-assay variance was 1.7% and assay sensitivity was 7.8 pg/tube.

A GLM and a repeated-measures GLM were used to compare corticosterone baseline levels and the entire stress response. Two birds have died during the experiment and only 22 individuals (experimental group: 7 males and 4 females; control group: 8 males and 3 females) were available at the end of the study. For some analyses, however, we were not able to obtain reliable samples from every individual. We predicted that nutritionally deprived birds would have stronger adrenocortical stress response compared to controls (Carsia and Weber, 2000; Penke et al., 2001; Vallee et al., 1999); thus after performing repeated-measures GLM (two-tailed), we used directional one-tailed independent contrasts analyses. All other statistical tests are two-tailed.

To assess whether nutritional deficits during early development resulted in developmental instability (Palmer, 1994), we also measured fluctuating asymmetry in 12-month old jays using length of tibiotarsus, ulna, first secondary feather and allula feather. All measurements were done by the same observer using calipers with 0.01 mm precision (Clinchy et al., 2004).

3. Results

3.1. Nestlings

Scrub-jay nestlings on restricted diet had significantly elevated baseline corticosterone levels compared to birds fed ad libitum (Repeated-measures ANOVA, $F_{1,19}=10.45$, $P=0.004$; Fig. 1). There were significant differences between plasma levels sampled at 10 and 22 days after the treatment started ($F_{1,19}=0.02$) and a treatment × sampling time interaction was marginally significant ($F_{1,19}=3.33$, $P=0.08$). Independent contrasts analyses showed that baseline corticosterone levels did not change significantly between the two samplings in control scrub-jay chicks ($P>0.3$). In food restricted nestlings, on the other hand, corticosterone levels decreased significantly between 10 and 22 days after the start of food restrictions ($P<0.01$) which explains marginally significant interaction between treatment and sampling time.

3.2. One-year-old jays

In 1-year-old scrub-jays, there were no significant differences in baseline corticosterone levels between individuals that experienced nutritional deficits during

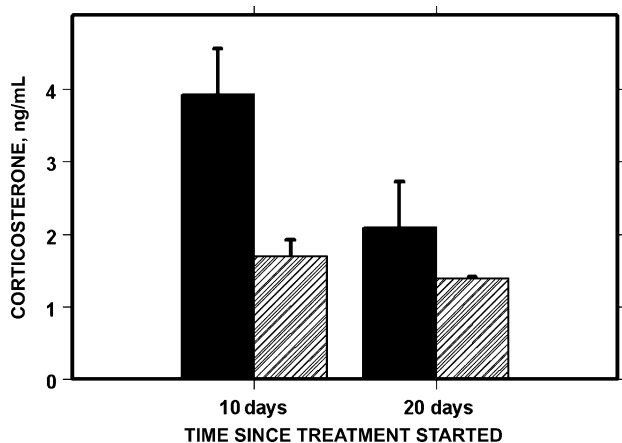


Fig. 1. Baseline corticosterone levels in nutritionally deprived (filled bars) and control (hatched bars) scrub-jay chicks after 10 and 22 days since the beginning of experimental treatment.

post-hatching development and controls ($t_{20} = -0.23$, $P = 0.82$; Fig. 2). All jays had elevated corticosterone levels in response to acute stress of handling and restraint (time since inducing handling stress: $F_{3,59} = 28.9$, $P < 0.001$, Fig. 2), but such response tended to be stronger in individuals that experienced nutritional deficits during post-hatching period ($F_{1,18} = 3.6$, $P = 0.07$; Fig. 2). Differences between the groups in the entire stress response were only marginally significant but because we predicted a priori that food-restricted birds should have stronger adrenocortical stress response compared to controls, we also employed a directional one-tailed test which resulted in a significant P value ($P = 0.035$). Directional independent contrasts analyses also showed that nutritionally deprived birds had significantly higher corticosterone levels at 20 ($P = 0.04$) and at 50 ($P = 0.03$) min after initiating handling stress (Fig. 2). There was no effect of sex ($F_{1,18} = 0.02$, $P = 0.88$) or body mass ($F_{1,59} = 0.46$, $P = 0.5$) on the adrenocortical stress

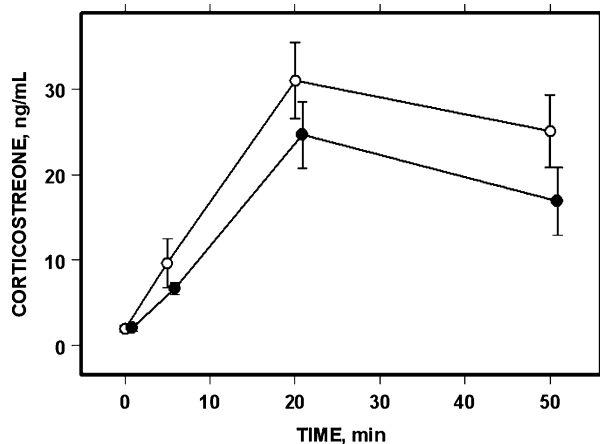


Fig. 2. Least square means (\pm SE) of corticosterone levels at 0, 5, 20, and 50 min since inducing stress of handling and restraint in 12-month old scrub-jays. Empty circles—chicks that experienced nutritional deficits during early post-hatching development; filled circles—controls.

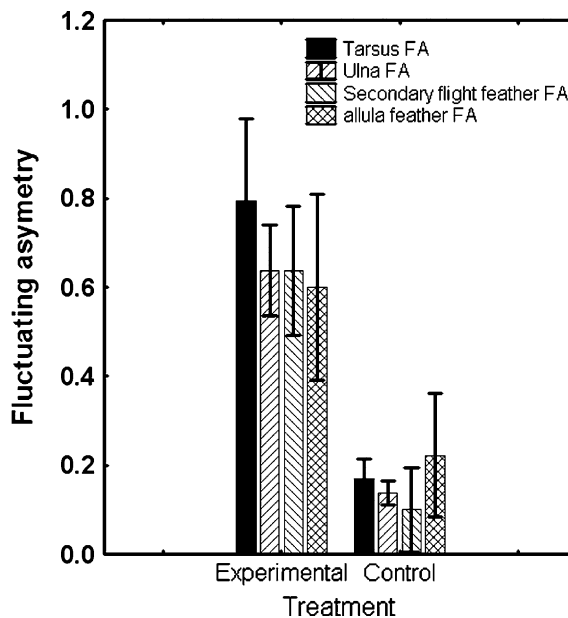


Fig. 3. Effects of nutritional stress during early development on fluctuating asymmetry in 12-month old scrub-jays.

response and none of the interactions were significant ($P > 0.3$).

3.3. Fluctuating asymmetry

There were no significant differences between experimental and control birds in directional asymmetry in any of the parameters we measured (t test, tarsus— $t_{19} = 0.06$, $P = 0.95$; ulna— $t_{20} = -0.07$, $P = 0.95$; secondary flight feather— $t_{19} = 1.39$, $P = 0.18$; allula feather— $t_{17} = -0.64$, $P = 0.53$). Fluctuating asymmetry, on the other hand, was significantly higher in scrub-jays that experienced nutritional deficits during post-hatching development than in control birds, at least in three of four measured parameters (tarsus— $t_{19} = 3.28$, $P < 0.01$; ulna— $t_{20} = 4.47$, $P < 0.001$; secondary flight feather— $t_{19} = 2.88$, $P < 0.01$; Fig. 3). Only allula feather showed similar fluctuating asymmetry between experimental and control scrub-jays ($t_{17} = 1.39$, $P = 0.18$; Fig. 3).

4. Discussion

Our study demonstrated that compared to birds fed ad libitum, western scrub-jays that experienced nutritional deficits during post-hatching development (a) had significantly elevated baseline corticosterone levels, (b) tended to have stronger adrenocortical stress response later in life whereas their baseline corticosterone levels were similar to those of controls, and (c) had higher degree of fluctuating asymmetry in bone and feather measurements.

Our results supported our prediction that altricial nestlings experience adrenocortical stress response when

they are nest-bound and that inadequate food supply triggers corticosterone elevation during development in nest-bound songbirds. Adrenocortical response to food shortages appears to be highly adaptive as it facilitates more begging which, in turn, should stimulate parents to increase their provisioning rates (Kitaysky et al., 2001a).

Spencer et al. (2003) failed to detect changes in corticosterone levels as a result of food availability manipulations in zebra finches (*Taeniopigia guttata*). However, Spencer et al. (2003) sampled corticosterone levels only once when chicks were 18 days of age, 15 days after the treatment began. Our study showed that baseline corticosterone levels were elevated at 10 days after chicks started receiving restricted diet, but these levels were decreased after 22 days. Thus, it is possible that zebra finches in Spencer et al. (2003) study did have elevated corticosterone levels at the beginning of treatment but these levels decreased by the time of sampling which occurred quite late. For example, Suorsa et al. (2003) was able to detect differences in corticosterone levels in nestling Eurasian treecreepers (*Certhia familiaris*) at 9 days of age. Thus, it may be important to either measure corticosterone levels more than once or sample them reasonably close to the beginning of treatment.

If parents are incapable of adjusting their foraging behavior, nestlings might maintain elevated corticosterone levels which appears to be responsible for numerous developmental disorders relating to fluctuating asymmetry and impaired cognition (Buchanan et al., 2004, 2003; Clinchy et al., 2004; Kitaysky et al., 2003; Pravosudov et al., in press; Spencer et al., 2003). Scrub-jays that experienced nutritional deficits during post-hatching development in this study suffered impaired spatial memory and had significantly reduced hippocampal volume with fewer neurons compared to birds raised on ad libitum food (Pravosudov et al., in press). Studies that directly manipulated corticosterone levels in growing songbird chicks also suggested that elevated corticosterone levels are likely to be a key factor in developing brain disorders related to song nuclei later in life (Buchanan et al., 2003, 2004).

Second important finding of our study concerns the fact that scrub-jays that experienced nutritional deficits during post-hatching development tended to have a stronger adrenocortical response to stress later in life even though they had ad libitum food since the time they learned to eat on their own. Our results using more conservative non-directional GLM were only marginally significant but it is likely that larger sample size would have resulted in significant differences. Our prediction, however, was directional because we expected to find that nutritionally deprived birds would show stronger adrenocortical stress response than controls (e.g., Penke et al., 2001; Vallee et al., 1999). The differences between the groups became significant when a directional one-tailed test was employed. These results parallel findings

of many mammalian studies which showed that stress during early development results in permanent changes in adrenal function later in life (Anisman et al., 1998; Liu et al., 1997; Meaney et al., 1996; Penke et al., 2001; Vallee et al., 1999; Weaver et al., 2000). Our study does not differentiate between the effects of nutritional restrictions and elevated corticosterone during early development. It remains possible that either of these two factors could be responsible for changes in adrenocortical responsiveness later in life.

The finding that conditions during development might affect adrenocortical function later in life is particularly interesting because birds show tremendous variation in their adrenocortical stress response both within and between species (Cockrem and Silverin, 2002; Wingfield et al., 1995, 1997, 1998). Much avian research has been focused on the relationship between ecological conditions and adrenocortical stress response (Wingfield et al., 1995, 1997, 1998). It has been suggested that stress response reflects ecological conditions preceding the time of sampling and thus the magnitude of stress response has been used as an indicator of past conditions (Clinchy et al., 2004; Wingfield et al., 1997, 1998). Our findings suggest that conditions during early development might also be responsible for at least some variation in adrenocortical stress responses in adult birds, in addition to environmental conditions preceding sampling. Our data indicated that in identical favorable conditions, birds that experienced malnutrition during post-hatching development tended to have stronger adrenocortical response to acute stress. It is not well known, however, how developmental history would affect stress response in animals which live in less favorable environments after becoming nutritionally independent, assuming that individuals survive. It is clear, however, that environment during early development need to be taken into consideration.

Finally, our study showed that scrub-jays that experienced nutritional deficits during early development had stronger fluctuating asymmetry. Fluctuating asymmetry has been suggested to reflect developmental instability resulting from both genetic differences and environmental conditions (Palmer, 1994) and it has been used to compare quality of individuals. For example, Clinchy et al. (2004) showed that nestling song sparrows (*Melospiza melodia*) living in conditions with higher predation risk, which was likely to have an effect on parents' provisioning rates, had greater fluctuating asymmetry than nestlings growing in conditions of lower predation risk. Searcy et al. (2004), on the other hand, manipulated food abundance in nestling song sparrows and found no significant differences in fluctuating asymmetry between nutritionally restricted and unrestricted birds. Similar treatment in our study, however, resulted in significantly greater fluctuating asymmetry in food-restricted scrub-jays suggesting that malnutrition during early development may indeed increase fluctuating asymmetry. In our

study, malnutrition correlated with elevated corticosterone levels but it remains to be investigated whether corticosterone may directly affect fluctuating asymmetry in identical environmental conditions.

In conclusion, our study showed that corticosterone plays an important role in nest-bound altricial young and it can be used as an indicator of developmental conditions and future fitness for both inter- and intra-brood comparisons. Environmental conditions during early development also appear to alter adrenocortical function later in life and thus might be responsible for some variation in stress response commonly seen in adult birds. More research is needed to establish a direct link between elevated corticosterone during early development and heightened stress response later in life.

Acknowledgments

We thank Tom Hahn for providing animal space to conduct the experiments, Selvino de Kort for help collecting scrub-jays and Alicja Omanska and Christina Tuk for help with bird care. Zhenya Kitaiskaia performed the assay, supported by EPSCoR, University of Alaska Fairbanks. Comments from two anonymous reviewers greatly improved the manuscript. This work was supported by NIH/NIMH career award to V.V.P. Birds were collected under California State and Federal Scientific Collecting Permit 801080-01 and all experiments were performed in accordance with University of California Davis animal care protocol 9788.

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