Corticosterone and Dispersal in Western Screech-Owls (*Otus kennicottii*)

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Abstract.—Belthoff and Dufty (in press) posed a model for dispersal in screech-owls and similar nonmigratory birds. The model is based on interactions among hormonal changes, body condition, and locomotor activity patterns. It predicts that corticosterone increases in blood plasma prior to dispersal under endogenous and exogenous influences, and this increase mediates the locomotor activity that underlies dispersal. Juveniles in good body condition (i.e., those with sufficient fat reserves) will disperse at that time, while birds in poor body condition will not. The latter will increase their foraging activity under the influence of corticosterone and disperse later. This paper presents preliminary data that show that locomotor activity levels are reduced in captive Western Screech-owls at the time of dispersal under the influence of a corticosterone-blocking drug.

The objectives of this paper are to (1) review briefly a recent model that explains natal dispersal in birds, and (2) present results from a preliminary experiment that examines an important prediction of this model. Belthoff and Dufty (in press) proposed a theoretical model based upon interactions among hormonal changes, body condition, and locomotor activity patterns to explain dispersal in screech-owls and similar nonmigratory species of birds. Briefly, this model for dispersal predicts that corticosterone, an adrenal hormone known to stimulate locomotor activity and hyperphagia, increases in blood plasma prior to dispersal through endogenous and/or exogenous events. This increase in corticosterone mediates the locomotor activity that underlies dispersal, but it interacts with body condition such that juveniles in good body condition disperse first. Previous studies on Western and Eastern Screech-owls (*Otus kennicottii* and *O. asio*, respectively) have produced results that are consistent with the model, and these results are reviewed below. We also present results from a hormone manipulation study that examined the effect of a corticosterone blocker on locomotor activity in young Western Screech-owls at the time of dispersal.

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NATAL DISPERSAL IN BIRDS

Dispersal is the movement of individuals from their point of origin (natal area) to where they reproduce or would have reproduced had they survived and mated (Howard 1960). Because these movements are characteristic of individuals in the juvenile age class and they represent departures from the natal area, Greenwood (1980) later coined the term *natal dispersal* to describe them. Virtually all species of birds make a dispersal movement at some stage of the life cycle, and juveniles of both sexes usually disperse from parental territories soon after they achieve independence during the post-fledging period (e.g., Belthoff and Ritchison 1989).

Several aspects of the dispersal process are of interest to students of the ecology of animal movement. These include the initiation of dispersal and its timing, distance, duration, rate, and direction of movements, and the effectiveness of the movement (i.e., whether the bird survived dispersal and successfully reproduced in the new area). Certainly, each of these components of dispersal could come under selection, but the dispersal model developed by Belthoff and Dufty (in press) relates primarily to the first of these, the initiation of dispersal and its timing.

Beyond achieving independence from adults, the proximate factors that stimulate young to initiate dispersal are poorly understood. Some factors that may be important are parental aggression toward young, aggression of young toward each other, and resource depletion within the natal area (e.g., De Laet 1985, Kenward and others 1993, Wiggett and Boag 1993). Despite evidence that such exogenous factors are important in driving dispersal, some birds disperse even though their parents have been removed and they have unlimited access to food (Nilsson 1990). In these cases, dispersal must have been initiated by some endogenous mechanism. Endogenous mechanisms likely involve hormones, they appear to be influenced by the body condition of the individual, and ontogenetic effects are most certainly involved, such that the movement occurs at the biologically appropriate time (Belthoff and Dufty in press, Holekamp 1986, Holekamp *et al*. 1984).

At least for many nonmigratory species, one factor appears relatively clear: selection has operated for dispersal to occur early so that it is usually initiated and completed before winter (Morton 1992). If territories are at a premium, selection might also operate on young to disperse as early as they can, and this may be particularly important in resident species that defend territories the year round. Many migratory species do not establish territories until the subsequent breeding season; therefore they may not be under identical selection pressures, and this is why the dispersal model is specific to nonmigratory species. However, it probably has important applications to dispersal in migratory species of birds as well (Belthoff and Dufty in press).

THE BELTHOFF AND DUFTY DISPERSAL MODEL

Belthoff and Dufty (in press) hypothesized that avian dispersal is influenced by the adrenal hormone corticosterone. The model argues that as the post-fledging period progresses, parents reduce their provisioning of young and/or competition increases among siblings. Any resulting reduction in food intake by juveniles causes stress, or endogenous pathways are triggered at the biologically appropriate time, and either or both increase adrenal activity, leading to increased secretion of corticosterone. Increased plasma corticosterone levels stimulate or are accompanied by increased locomotor activity. The model suggests further that corticosterone levels interact with body condition to induce dispersal. When corticosterone secretion increases, activity levels increase, and this eventually leads young to disperse. However, only those juveniles that are in good physical condition are prepared for immediate dispersal. That is, only juveniles with the necessary fat stores will survive the rigors of territory establishment, territory defense and independent foraging. Good physical condition includes adequate lipid reserves, and this provides a buffer against possible corticosterone-induced depletion of muscle tissue. On the other hand, juveniles in poor condition at the time that plasma corticosterone levels increase will require more time to forage in the natal area to attain the physical condition necessary to disperse successfully. The model predicts that corticosterone levels remain elevated in these birds, stimulating increased foraging behavior that improves body condition and, eventually, promotes dispersal. Following dispersal of their siblings in better condition, the remaining juveniles undergo reduced competition for food, they experience less aggression from siblings, and they have the exclusive attention of the parents. This improves their physical condition and eventually leads to natal dispersal. Thus, the model predicts a relationship between physical condition, the extent to which corticosterone levels remain elevated, and the timing of natal dispersal, such that birds in good physical condition leave the natal area first.

STUDY SPECIES

The dispersal model (Belthoff and Dufty in press) is based upon the biology of two representative species of nonmigratory birds: Eastern and Western Screech-owls. These owls are common to eastern and western North America, respectively, and sufficient data are now available from both field and laboratory studies to begin to understand factors affecting their dispersal behavior. The post-fledging behavior and dispersal of radio-tagged Eastern Screech-owls in Kentucky was described by Belthoff and Ritchison (1989, 1990), Ritchison *et al*. (1992), Belthoff *et al*. (1993), and Sparks *et al*. (1994). Briefly, young screech-owls fledge in mid-May and spend roughly the next 5 weeks in close association with adults. After this time, young increase their independence from adults by roosting farther away, increasing the sizes of their home ranges, and wandering outside the nightly ranges of their parents more frequently. Dur-ing this same time period, locomotor activity levels of both captive and free-living owls are high. Young owls of both sexes initiate dis-persal approximately 8 weeks after fledging, usually in mid-July, although the timing of dispersal within and among broods varies. Many of the dispersing owls settle in overwinter sites between 1 and 17 km from the natal area. The number of birds for which suitable data are available is small, but individuals settle an average of approximately 6 days after initiating dispersal, and some individuals breed in or near these overwinter sites. Studies by Belthoff and Dufty (1995, in press) and Ellsworth and Belthoff (unpubl. data) suggest that the post-fledging behavior and dispersal of Western Screech-owls is similar to that of their eastern counterpart. Because of these similarities, Belthoff and Dufty (in press) believe that their model is applicable to both species of screech-owls, as well as to other similar species of birds.

SUPPORTIVE DATA

Body Condition and Dispersal

Initial results have been consistent with the dispersal model (Belthoff and Dufty in press). For example, one prediction of the model is that individuals in adequate body condition will disperse when corticosterone levels increase. Individuals in poorer body condition will continue to forage on the natal area and disperse later. There have been no direct tests of the effects of body condition on the dispersal of screech-owls. However, Ellsworth and Belthoff (unpubl. data) have examined effects of social dominance on the timing of dispersal in young Western Screech-owls. This study used video cameras to record dominance interactions among nestlings, and followed radio-tagged young during the post-fledging period and as they dispersed. Individuals scored as dominant were the first to disperse in six of the seven broods. Moreover, the most subordinate juvenile dispersed last in five of seven broods. Finally, in four broods, the order of dispersal correlated perfectly with dominance status, even in a brood with as many as five young. If dominance status is a predictor of body condition in these young, and assuming dominant birds have the best body condition, then these data indicate that young in good condition dispersed earlier, and they provide at least indirect support for the body condition prediction of the model (Belthoff and Dufty in press).

Locomotor Activity and Dispersal

The model also predicts that locomotor activity levels should be high or peak near the time of dispersal, and this prediction has been supported in studies by Ritchison *et al*. (1992) and Belthoff and Dufty (1995). For example, both captive and free-living screech-owls show increased locomotor activity at the time of dispersal, and they exhibit much lower activity thereafter (Ritchison *et al*. 1992, Belthoff and Dufty 1995).

Plasma Corticosterone and Dispersal

Finally, Belthoff and Dufty (in press) reported that circulating corticosterone levels in captive Western Screech-owls were elevated before or during the time when locomotor activity was greatest. Plasma corticosterone levels were high or peaked during the period of greatest locomotor activity, and corticosterone levels were almost always lower outside of this period (Belthoff and Dufty in press). One interesting result was that corticosterone often peaked around 35-40 ng/ml, which is equivalent to maximum circulating corticosterone levels exhibited by many passerines during the migration period (e.g., see Holberton *et al*. 1996). This is of particular interest because it indicates that some of the physiological mechanisms underlying dispersal and migration may be similar.

While these results illustrate an association between corticosterone and locomotor activity at the time of dispersal in Western Screech-owls, they do not allow confirmation of cause-effect relationships between these two variables. Experiments that manipulate either or both of these variables are required before such relationships can be understood completely.

HORMONE MANIPULATION EXPERIMENT

To begin to understand the cause-effect relationships between corticosterone and locomotor activity at the time of dispersal, we performed a hormone manipulation study on captive Western Screech-owls using metyrapone, an 11*B*-hydroxylase inhibitor that reduces the production of adrenal corticosteroid hormones, including corticosterone (Jain *et al*. 1993, Zulkifli *et al.* 1993). If corticosterone is important in the initiation or maintenance of locomotor activity at the time of dispersal, birds exposed to metyrapone are expected to show reduced locomotor activity compared to control owls which receive only a placebo, or metyrapone-treated owls should fail to show the typical peak in activity that occurs in captive owls near the time of dispersal.

In July 1996, which corresponds to the dispersal period for Western Screech-owls in Idaho (Ellsworth and Belthoff, unpubl. data), we treated four young Western Screech-owls with subcutaneous implants of metyrapone (90-day release, 10 mg total dosage capsule, Innovative Research of America, Toledo, OH) and monitored the owls' locomotor activity for the next 5 weeks. These birds had been collected from the wild as nestlings (approximately 1 week prior to fledging) and maintained in captivity in wire mesh cages and isolation chambers similar to those described by Belthoff and Dufty (1995) and Dufty and Belthoff (1997). Four other birds were housed in a similar fashion but were treated with a placebo rather than the drug, and they served as controls. Locomotor activity in relation to the hormone manipulation was monitored using digital pedometers (Micronta Mini Jog-Mate pedometers, Cat. No. 63-667, Radio Shack, Fort Worth, TX) attached to the backs of owls which registered the number of hops each owl made over a 24 hour period (see Ritchison *et al.* 1992, Belthoff and Dufty 1995, in press for specifics on pedometers and their attachment). Complete packages, i.e., pedometers plus nylon cord, weighed approximately 9 g, which was equivalent to approximately 5 percent of each individual's body weight. Activity levels were recorded daily at 1600 h, and individual activity levels were averaged to obtain weekly scores. Using repeated measures analysis of variance (2 x 5 mixed factorial design), these weekly averages were analyzed to assess the null hypothesis that activity levels of treatment and control owls did not differ. Separate analyses were performed on activity levels (hops registered from pedometers) and percentage change from activity levels during the week prior to the treatment (percentage difference in average activity level).

Figure 1 shows the activity data from the metyrapone-treated and control birds as a function of weeks after they received the implant. Activity levels differed by week ($F_{4,24}$ = 5.97, P = 0.002), but there also was an effect of the treatment; birds treated with metyrapone had lower activity levels than control birds ($F_{1,6}$ = 5.17, P = 0.063). Finally, there was no treatment by week interaction ($F_{4,24}$ = 1.14, P = 0.360). The lack of a significant interaction indicates that birds treated with metyrapone had lower activity levels than control birds across all weeks of the experiment (fig. 1). Birds in the control group also exhibited a highly significant increase (P = 0.0097) in average activity levels between week one and two following the treatment (fig. 1); this increase resembles the peak in activity at the time of dispersal observed in previous experiments with screech-owls (e.g., Ritchison *et al.* 1992, Belthoff and Dufty 1995). There was a much smaller increase (P = 0.0618) in average activity levels between weeks one and two after the treatment for owls in the metyrapone group (fig. 1). These results are consistent with the notion that metyrapone dampened increases in activity levels at the time of dispersal.

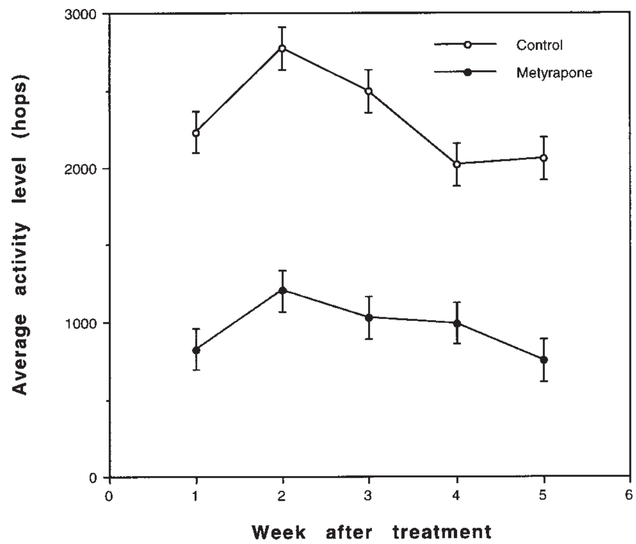

Figure 1.—*Average (± SE) locomotor activity levels at the typical time for dispersal in young Western Screech-owls exposed to metyrapone (N = 4) to reduce circulating corticosterone and control owls (N = 4) that received a placebo.*

One difficulty with examining only raw activity levels is that there can be inter-bird variation in initial activity levels that may account for some of the differences observed after application of the treatment. One way to control for such variation is to examine each owl's activity only in relation to its pre-treatment activity levels, which in effect standardizes the following activity readings to the initial ones. Thus, in a second analysis (fig. 2), we assessed the percentage change in activity following treatment as a function of the activity in the week before the treatment (e.g., [week before minus each week after]*100). Just as in the analysis of raw scores above, these measures differed significantly by week ($F_{4,24}$ = 11.88, P = 0.0001), and the metyrapone group had lower average values than the control birds ($F_{1,6}$ = 4.96, P = 0.068). There was no treatment by week interaction ($F_{4,24}$ = 1.70, P = 0.182). However, most of the difference between treatment groups was accounted for in weeks one and five after the treatment (fig. 2).

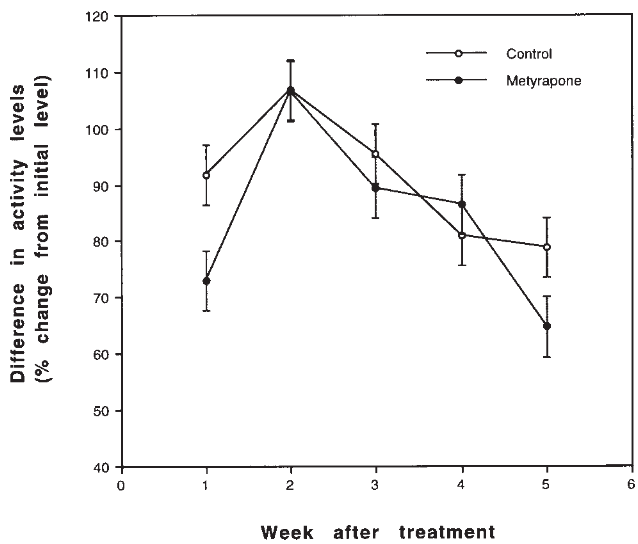

Figure 2.—*Locomotor activity levels expressed as average percentage change (± SE) from initial activity levels for Western Screech-owls that received metyrapone (N = 4) and control owls (N = 4) that received a placebo.*

The data from this initial experiment, at least in part, appear to be consistent with the predictions of the dispersal model. We predicted that if corticosterone stimulates locomotor activity, then treatment with a corticosterone blocker should reduce locomotor activity. The results suggest that activity levels of young birds at the time of dispersal may be affected by hormone manipulations, as birds that received metyrapone had lower activity levels than control owls.

SUMMARY AND CONCLUSIONS

In summary, we have proposed a model that examines the interplay between endogenous and exogenous factors that regulate natal dispersal in screech-owls and similar species of birds (Belthoff and Dufty in press). Initial results are generally in agreement with the model. Owls increase locomotor activity in the weeks leading up to dispersal, and this is accompanied by high circulating corticosterone in most cases. Also, owls in better body condition appear to be dispersing earlier. Results from an initial hormone manipulation experiment designed to reduce circulating corticosterone indicate that activity levels were significantly lower when owls received the drug treatment, and metyrapone may have dampened the peaks in activity levels normally seen in captive owls at the time of dispersal.

The model remains to be fully tested because cause-effect relationships between corticosterone and locomotor activity are only now being examined, and several variants of the model remain tenable (Belthoff and Dufty in press). Although it will be refined with future work, we believe that this model is an important first step in understanding the physiological ecology of dispersal in screech-owls and other non-migratory species of birds. Additional experiments that manipulate body condition, plasma corticosterone, and activity levels are underway as the next step in testing the model, and these should allow us to understand more fully the physiological ecology of dispersal.

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