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## THE ADRENOCORTICAL STRESS RESPONSE IN THREE NORTH AMERICAN ACCIPITERS DURING FALL MIGRATION

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**ABSTRACT.**—The associations among corticosterone levels, energy stores, and stress are highly relevant to bird migration physiology. Many birds maintain elevated baseline corticosterone levels during migration, yet they frequently modulate additional glucocorticoid secretion, probably to protect their flight muscles from catabolism. We report on the adrenocortical response to capture and handling stress in three *Accipiter* species, the Sharp-shinned Hawk (*Accipiter striatus*), the Cooper's Hawk (*A. cooperii*), and the Northern Goshawk (*A. gentilis*) during fall migration. We found mean baseline corticosterone levels to be similar in Sharp-shinned Hawks and Northern Goshawks, but significantly higher in Cooper's Hawks. Likewise, mean baseline levels of corticosterone did not differ in hatch-year and after-hatch-year male and female Sharp-shinned Hawks and Northern Goshawks, but they were higher in adult male Cooper's Hawks than adult females. Mean corticosterone levels did not increase significantly after 30 min of capture and handling stress in any of the three species, indicating that they modulated their adrenocortical stress responses. Fat scores were not correlated with baseline corticosterone levels, except in Sharp-shinned Hawks, in which elevated baseline corticosterone levels were associated with low fat scores.

**KEY WORDS:** *Sharp-shinned Hawk*; *Accipiter striatus*; *Cooper's Hawk*; *Accipiter cooperii*; *Northern Goshawk*; *Accipiter gentilis*; *adrenocortical stress response*, *corticosterone*, *migration*.

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### RESPUESTA ADENOCORTICAL AL ESTRÉS EN TRES ESPECIES DE ACCIPITER DE AMÉRICA DEL NORTE DURANTE LA MIGRACIÓN DE OTOÑO

**RESUMEN.**—Las asociaciones entre niveles de corticoesterona, reservas de energía y estrés son muy importantes para la fisiología de la migración de las aves. Muchas aves mantienen elevados niveles de base de corticoesterona durante la migración. Sin embargo, ellas frecuentemente modulan secreciones adicionales de glucocorticoides, probablemente para proteger sus músculos del catabolismo. Brindamos datos sobre la respuesta adenocortical al estrés de captura y manipuleo en tres especies de *Accipiter*, *Accipiter striatus*, *A. cooperii* y *A. gentilis* durante la migración de otoño. Encontramos que los niveles de base promedio de corticoesterona son similares en *A. striatus* y *A. gentilis*, pero significativamente más altos en *A. cooperii*. Del mismo modo, los niveles de base promedio de corticoesterona no difirieron entre individuos macho y hembra nacidos en el año y de más de un año de *A. striatus* y *A. gentilis*, pero fueron mayores en los machos adultos que en las hembras adultas de *A. cooperii*. Los niveles promedio de corticoesterona no aumentaron significativamente luego de 30 min de estrés producido por captura y manipuleo en ninguna de las tres especies, indicando que ellas modulan sus respuestas adenocorticales al estrés. Los niveles de grasas no estuvieron correlacionados con los niveles de base de corticoesterona, excepto para *A. striatus*, para quien los elevados niveles de base de corticoesterona estuvieron asociados con niveles bajos de grasas.

[Traducción del equipo editorial]

Migration poses numerous behavioral and physiological challenges for birds, such as accumulating and managing energy stores that fuel these seasonal movements. Lipids are the major source of energy for migration (Ramenofsky 1990, McWilliams et al. 2004), although birds also regularly catabolize protein (Lindström et al. 2000, Bauchinger and Bie-

bach 2001), especially as fat stores become depleted (Schwilch et al. 2002). However, protein catabolism must be limited because all proteins are either functional or structural, and excessive protein loss can reduce flight performance (Schwilch et al. 2002).

The mechanisms regulating energy utilization during migration are complex, involving multiple hormonal and enzymatic pathways (Wingfield et al. 1990, Bairlein 2002, McWilliams et al. 2004, Hol-

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berton and Dufty 2005). One of these hormones is the adrenocorticoid, corticosterone, which facilitates both physiological and behavioral activities associated with the regulation of daily energy use (Wingfield and Silverin 1986, Astheimer et al. 1992, Dallman et al. 1993, Sapolsky et al. 2000, Landys et al. 2005). During migration, baseline corticosterone levels often become elevated (Holberton et al. 1996, Jenni et al. 2000, Piersma et al. 2000, Landys-Ciannelli et al. 2002, Long and Holberton 2004). This increase is condition-dependent with birds with large fat stores having lower baseline corticosterone levels than those with small stores (Jenni et al. 2000, Piersma et al. 2000, Jenni-Eiermann et al. 2002, Long and Holberton 2004). Corticosterone is involved in mobilizing lipid reserves during migration (Jenni and Jenni-Eiermann 1998, Landys et al. 2004). Thus, elevated baseline corticosterone levels may help to regulate energy utilization during migration, especially as fats become depleted and protein usage increases.

The adrenocortical response to capture and handling stress also differs between migrants and nonmigrants. Typically, corticosterone levels increase with handling time in nonmigrants, although the pattern of hormonal change is affected by environmental conditions and contaminants as well as life-history stage (Wingfield and Farner 1978, Wingfield et al. 1992, 1997a, 1997b, Astheimer et al. 1994, Blas and Baos 2008, Baos and Blas 2009). In migrants, whose baseline corticosterone levels may already be elevated, increases in corticosterone secretion with capture and handling time may be dampened (Holberton et al. 1996, Jenni et al. 2000, Long and Holberton 2004; but see Romero et al. 1997, Landys-Ciannelli et al. 2002). Similarly, reduced fat stores in fasted nonmigrants also are followed by increases in corticosterone secretion, as well as by increased protein metabolism (Cherel et al. 1988). Since long-distance migration flight and fasting by nonmigrants have many similarities (Battley et al. 2001), it is likely that modulation of stress responsiveness in migrants prevents corticosterone secretion from exceeding a level above which critical protein reserves, such as flight muscles, are catabolized.

Studies on adrenocortical function during migration have mainly dealt with long-distance migrant passerines and shorebirds. In contrast, little is known about physiological changes associated with migration in raptors. Large raptors, such as hawks, have very different flight strategies during migration than most other birds for, in addition to flapping

flight, many also use a combination of soaring and gliding flight during migration (Kerlinger 1989). When compared to flapping flight, such soaring/gliding flight reduces energy requirements during migration (Hedenström 1993, Spaar et al. 1998). Because the optimum fuel composition likely varies with migration strategy (Jenni and Jenni-Eiermann 1998), the physiological mechanisms that regulate energy utilization in raptors may differ from those found in other birds. Here, we report the adrenocortical response during migration in three species of the genus *Accipiter*, the Sharp-shinned Hawk (*A. striatus*), Cooper's Hawk (*A. cooperii*), and Northern Goshawk (*A. gentilis*). In addition to determining whether or not these three raptor species modulate their adrenocortical stress response during fall migration, we also examined the effect of sex and age on corticosterone levels.

#### STUDY AREA

The *Accipiters* were captured at the Idaho Bird Observatory (IBO) located at Lucky Peak in southwestern Idaho, approximately 12 km east of the city of Boise (43°45'N, 115°17'W). Lucky Peak is the southernmost forest peak in the Boise Ridge, which runs north-south as part of the Boise Mountains. It is the northern geographic boundary of the Western Snake River Plain and it naturally concentrates migratory birds. Over 950 migratory raptors have been captured and banded annually at the trapping station since 1993. As of 2009, a total of 8498 Sharp-shinned Hawks, 3278 Cooper's Hawks, and 413 Northern Goshawks have been captured and banded during fall migration (Kaltenecker et al. 2010). Fifty-three of these Sharp-shinned Hawks and 24 Cooper's Hawks have been encountered in Arizona, California, and as far south as Guerrero, Mexico, and 20 Sharp-shinned Hawks and Cooper's Hawks have been recaptured at the migration trapping station operated by HawkWatch International at the Goshutes Mountains in northern Nevada, approximately 500 km south of Lucky Peak. Encounters north of the observatory have occurred in northern Idaho, Oregon, Washington, Montana, and British Columbia. Band recovery patterns from IBO show a similar pattern to those from other banding stations in the Intermountain West (Goodrich and Smith 2008), indicating that the Lucky Peak banding station is situated roughly in the central portion of migratory routes of these three species.

## METHODS

**Trapping and Blood Collection.** We trapped *Accipiters* from late August through October. Trapping occurred between 11:00–18:00 H. We used a combination of mist nets, bow nets, and dho-gaza nets for trapping (Bloom et al. 2007). Rock Pigeons (*Columba livia*), Ring-necked Turtle Doves (*Streptopelia risoria*) and House Sparrows (*Passer domesticus*) were used to lure hawks into the nets. Only those hawks that flew directly into traps were used for sampling. Because corticosterone levels can rise very rapidly after stress (Romero and Reed 2005), we collected ~100  $\mu$ L of blood from the brachial vein in 50  $\mu$ L heparinized capillary tubes as quickly as possible (average time of first blood draw after capture = 1 min; all baseline samples were collected within 3 min of capture). After being handled and held in a metal can for 30 min, a second sample of ~100  $\mu$ L was taken from the other wing. Thirty minutes was used because it is the standard time interval used in corticosterone stress tests in birds (Holberton et al. 1996). Blood samples were kept on ice until the end of the day (<7 hr), when the plasma and blood cells were separated by centrifugation. The plasma was stored at  $-20^{\circ}\text{C}$  until the end of the trapping season, when the hormonal analyses were done. After the initial blood draw, we banded each bird with a United States Geological Survey (USGS) aluminum leg band, determined its age and sex, and collected morphometric measurements. Morphometric measures consisted of wing chord (mm), length of longest tail feather (mm), body mass (g), and fat scores. We assessed fat levels in the abdominal and furcular regions using a scale from 0 to 5, with 0 denoting no visible fat and 5 indicating bulging fat (Wingfield and Farner 1978, Wingfield et al. 1997).

**Analysis of Plasma Corticosterone.** We analyzed plasma corticosterone levels in a single radioimmunoassay as described by Wingfield et al. (1992). All samples were aliquoted into test tubes with distilled water to a volume of 400  $\mu$ L. To determine recovery values, 20  $\mu$ L (approximately 2000 cpm) of tritium-labeled corticosterone was added to each sample. After equilibrating, the lipid fraction was extracted using 4 ml of distilled dichloromethane. The organic phase was collected and dried under nitrogen gas at  $40^{\circ}\text{C}$  and resuspended in 550  $\mu$ L of phosphate-buffered saline. For the recovery values, we pipetted 100  $\mu$ L of this into scintillation vials and added 4 ml of scintillant. After mixing, the vials were allowed to equilibrate overnight before being counted. Ali-

quots of 200  $\mu$ L were placed in duplicate assay tubes for the radioimmunoassay. Into each assay tube we aliquoted 100  $\mu$ L of labeled corticosterone and 100  $\mu$ L of corticosterone antiserum, and the solution equilibrated overnight. Bound and free hormone was separated by adding 0.5 ml of a dextran-coated charcoal solution for 10 min, and then centrifuged. The supernatant was decanted into a scintillation vial into which 4.0 ml of scintillant was added. After equilibrating overnight, the samples were counted to 2% accuracy or 10 min on a liquid scintillation counter.

**Statistical Analysis.** We analyzed the adrenocortical response to capture and handling stress for each species using a multifactorial ANOVA with repeated measures on the last factor (time) with the factors being sex, age, and time. For Sharp-shinned and Cooper's Hawks, baseline corticosterone levels were analyzed for differences between sexes and ages using two-way ANOVAs. The relationship between fat and corticosterone levels was analyzed by Pearson Rank Correlation (Zar 1996). All statistical analyses were done using the SAS statistical program (Hatcher and Stepanski 1994). Data are presented as means  $\pm$  SE.

## RESULTS

The mean baseline corticosterone levels in Sharp-shinned Hawks and Northern Goshawks were similar at approximately 29 ng/ml, but it was significantly higher in Cooper's Hawks at 49 ng/ml ( $F_{2,234} = 18.65$ ,  $P = 0.0001$ ; Table 1). Mean corticosterone levels did not change significantly after 30 min of capture and handling stress in any of the three species (Sharp-shinned Hawk:  $F_{1,286} = 0.00$ ,  $P = 0.973$ ; Cooper's Hawk:  $F_{1,144} = 0.03$ ,  $P = 0.868$ ; Northern Goshawk:  $F_{1,17} = 0.03$ ,  $P = 0.852$ ; Table 1).

Female *Accipiters* we captured were 1.20 to 1.76 times larger than males (female:male ratio: Sharp-shinned Hawk:  $172.0 \pm 2.1$  g vs.  $97.8 \pm 1.3$  g; Cooper's Hawk:  $439.1 \pm 6.1$  g vs.  $290.4 \pm 4.5$  g; Northern Goshawk:  $910$  g vs.  $761.5 \pm 15.2$  g). Despite this, mean baseline corticosterone levels did not differ between male and female Sharp-shinned Hawks ( $F_{1,144} = 0.32$ ,  $P = 0.571$ , Table 2). We captured no hatch-year Northern Goshawks and only one after-hatch-year female. Its baseline corticosterone level was similar to the mean we obtained for both after-hatch-year female Sharp-shinned Hawks and after-hatch-year male goshawks. Only Cooper's Hawks showed a sex difference in baseline corticosterone levels, with after-hatch-year males having

Table 1. Mean baseline and stressed levels of corticosterone in Sharp-shinned Hawks (SSHA), Cooper's Hawks (COHA), and Northern Goshawks (NOGO) captured during fall migration in southern Idaho. Sample sizes are shown in parentheses.

	TIME 0 MIN ng/ml $\pm$ SE	TIME 30 MIN ng/ml $\pm$ SE
SSHA	28.09 $\pm$ 1.68 (148)	34.04 $\pm$ 1.73 (148)
COHA	49.01 $\pm$ 3.74 (79)	56.69 $\pm$ 3.75 (79)
NOGO	29.57 $\pm$ 4.30 (10)	30.80 $\pm$ 4.84 (10)

significantly higher levels (mean = 66.44  $\pm$  10.88 ng/ml) than after-hatch-year females (mean = 41.12  $\pm$  8.21 ng/ml,  $F_{1,75} = 6.33$ ,  $P = 0.014$ ). Corticosterone levels did not differ between hatch-year and after-hatch-year Sharp-shinned Hawks ( $F_{1,144} = 0.00$ ,  $P = 0.980$ ) and there was no interaction between sex and age ( $F_{1,44} = 0.20$ ,  $P = 0.657$ ). Likewise, there were no age-dependent differences ( $F_{1,75} = 1.14$ ,  $P = 0.290$ ) or sex- and age-based ( $F_{1,75} = 0.41$ ,  $P = 0.524$ ) interactions in Cooper's Hawks.

Fat scores ranged from 1 to 4 in Sharp-shinned Hawks (mean = 2.7). In Cooper's Hawks, except for one individual with a score of 1, all fat scores ranged from 2 to 4 (mean = 3.0). All Northern Goshawks had fat scores of 3 to 4 (mean = 3.3), and almost all of the birds had medium to high levels of fat in their abdominal and furcular regions. There was no significant relationship between fat score and baseline corticosterone level in Northern Goshawks ( $\rho = -0.442$ ,  $P = 0.201$ ) but it was marginally higher in fat than lean Cooper's Hawks ( $\rho = 0.622$ ,  $P = 0.057$ ). Sharp-shinned Hawks did exhibit a significant correlation between fat score and baseline corticosterone level ( $\rho = -0.109$ ,  $P = 0.022$ ), with low fat scores associated with higher baseline corticosterone levels.

Table 2. Mean baseline levels of corticosterone (ng/ml) in hatch-year (HY) and after-hatch-year (AHY) male and female Sharp-shinned Hawks (SSHA), Cooper's Hawks (COHA), and Northern Goshawks (NOGO) captured during fall migration in southern Idaho. Sample sizes are shown in parentheses.

	MALE		FEMALE	
	HY	AHY	HY	AHY
SSHA	31.61 $\pm$ 4.94 (37)	29.65 $\pm$ 4.09 (9)	25.72 $\pm$ 1.86 (73)	29.07 $\pm$ 1.86 (29)
COHA	55.77 $\pm$ 7.59 (28)	66.44 $\pm$ 10.88 (9)	40.62 $\pm$ 4.55 (29)	41.12 $\pm$ 8.21 (13)
NOGO	—	29.67 $\pm$ 4.81 (9)	—	28.67 (1)

## DISCUSSION

Avian migration is a dangerous activity, and mortality rates during migration may exceed those occurring during any other part of a bird's annual cycle (Sillet and Holmes 2002). Moving long distances, either nonstop or with frequent foraging bouts through relatively unfamiliar habitats, puts a premium on the effective acquisition, maintenance, and utilization of energy resources.

The physiological mechanisms underlying migration have received considerable attention recently, including the role of corticosterone secretion (e.g., Ramenofsky et al. 1995, Holberton et al. 1996, Romero et al. 1997, Jenni et al. 2000, Piersma et al. 2000, Landys-Ciannelli et al. 2002, Long and Holberton 2004). Several investigations have focused on the hormone's role in regulating metabolism. Birds primarily use lipids to fuel migratory activity (Ramenofsky 1990, Bairlein 2002). Despite the functional nature of proteins, some organs undergo hypertrophy prior to migration and proteins in these organs are catabolized to provide a modest, yet important, source of energy (Piersma 1998, Lindström et al. 2000). Nonetheless, birds must manage their energy supplies so as not to delete important proteins, such as those involved in flight muscles, beyond some critical level (Schwilch et al. 2002).

Some migrants exhibit elevated levels of corticosterone compared to nonmigrants (Ramenofsky et al. 1995, Holberton et al. 1996, Holberton 1999, Jenni et al. 2000, Landys-Ciannelli et al. 2002), although migrants with ample fat reserves have lower baseline corticosterone levels than do migrants that are relatively lean (Jenni et al. 2000, Long and Holberton 2004, Piersma et al. 2000, but also see Romero et al. 1997). Furthermore, lean migrants with elevated corticosterone levels dampen their adrenocortical stress response more so than do individuals with ample fat reserves (Jenni et al. 2000, Long and Holberton 2004), while migrants faced with critical-

ly low energy reserves allow their elevated circulating corticosterone levels to go even higher (Holberton et al. 1999, Jenni et al. 2000).

Our findings indicate that, like migrating songbirds, migrating *Accipiters* modulate their adrenocorticosterone response to stress and do not produce a significant increase in corticosterone secretion when subjected to capture and handling stress. It is possible that our sampling method, which involved luring birds with potential prey items, generated a biased sample of hungry birds in poor body condition (Weatherhead and Greenwood 1981). However, if this were so, then we should have seen an increase in plasma corticosterone levels with handling time, as has been found in other species in poor condition (Holberton et al. 1999, Jenni et al. 2000). Tests of such a trapping bias in *Accipiters* have produced mixed results (Gorney et al. 1999), and most of the *Accipiters* we captured appeared to be in relatively good body condition with moderate to high fat scores. Thus, our findings of modulation of adrenoresponsiveness occurred despite using a capture technique that may be biased against producing such a result.

We found no age- or sex-related differences in baseline corticosterone levels in either Sharp-shinned Hawks or Northern Goshawks, but adult male Cooper's Hawks had significantly higher baseline levels than adult females. Cooper's Hawks show a high degree of sexual dimorphism with females having a body mass 1.5 times larger than males. It is unclear why males maintain a higher corticosterone level but it may indicate that they experience higher stress levels during migration than their female counterparts.

Sharp-shinned Hawks exhibited the widest range of fat scores and also demonstrated a significant inverse relationship between fat scores and baseline corticosterone levels. This was consistent with earlier findings that baseline corticosterone levels increase as energy reserves decline (Holberton et al. 1999, Jenni et al. 2000, Piersma et al. 2000). In contrast, we found no relationship between fat score and baseline corticosterone level in Northern Goshawks and Cooper's Hawks, but this may have been due to low variability in their fat scores.

The relationship we found between baseline corticosterone levels and fat reserves in Northern Goshawks and Cooper's Hawks contrasts with some earlier findings where elevated corticosterone titers were characteristic of lean birds (Jenni et al. 2000, Long and Holberton 2004, Piersma et al. 2000).

These differences may arise from differences in migration strategies in *Accipiters*, compared to most other species. Foremost among these is the well-known soaring/gliding flight behavior of migrating raptors. Flapping flight becomes disproportionately expensive as avian body size increases (Klaassen 1996), and all three *Accipiter* species we studied use soaring/gliding flight during migration, especially the two larger species, the Cooper's Hawk and Northern Goshawk (Kerlinger 1989). Although the effect of transporting large fuel reserves may not be as expensive as initially thought (Kvist et al. 2001), large birds like *Accipiters* do not accumulate large fat reserves that are seen in songbirds. Instead, they store relatively less fat and often feed during migration (Kerlinger 1989). Jenni and Jenni-Eiermann (1998) suggested that birds flying short, nonstop flights may not optimize lipid utilization and may use relatively more protein than long-distance migrants. Furthermore, Gannes (2001) noted that birds on high-protein diets use more protein to fuel their migratory movements than omnivorous birds. Therefore, migrating *Accipiters*, which have high-protein diets and feed during migration, might be expected to rely more heavily on protein than do long-distance migrants. Elevated baseline corticosterone levels during migration could facilitate proteolytic (and lipolytic) activity through interactions with low-affinity glucocorticoid receptors, which are stimulated to activate catabolic processes when corticosterone levels increase (Tempel and Leibowitz 1994). Modulation of adrenocortical responsiveness would prevent this process from tapping into protein stores too deeply. While these ideas are highly speculative, they point to the need for a broad, comparative approach to the study of migration physiology, one that incorporates the wide range of avian migration strategies.

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#### LITERATURE CITED

- ASTHEIMER, L.B., W.A. BUTTEMER, AND J.C. WINGFIELD. 1992. Interactions of corticosterone with feeding, activity, and metabolism in passerine birds. *Ornis Scandinavica* 23:355-365.

- , ———, AND ———. 1994. Gender and seasonal differences in the adrenocortical response to ACTH challenge in an arctic passerine, *Zonotrichia leucophrys gambelii*. *General and Comparative Endocrinology* 94:33–43.
- BAIRLEIN, F. 2002. How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory birds. *Naturwissenschaften* 89:1–10.
- BAOS, R. AND J. BLAS. 2009. Adrenocortical toxicology in birds: environmental contaminants and the avian response to stress. Pages 257–293 in P.W. Harvey, D. Everett, and C. Springall [Eds.], *Adrenal toxicology*, Vol. 26. Informa Healthcare, New York, NY U.S.A.
- BATTLE, P.F., M.W. DIETZ, T. PIERSMA, A. DEKINGA, S. TANG, AND K. HURLSMAN. 2001. Is long-distance bird flight equivalent to a high-energy fast? Body composition changes in freely migrating and captive fasting Great Knots. *Physiological and Biochemical Zoology* 74:435–449.
- BAUCHINGER, U. AND M. BIEBACH. 2001. Differential metabolism of muscle protein in Garden Warblers (*Sylvia borin*): flight and leg muscles act as a protein source during long-distance migration. *Journal of Comparative Physiology B* 171:293–301.
- BLAS, J. AND R. BAOS. 2008. Stress in the nest: causes and consequences of adrenocortical secretion in developing birds. Pages 89–128 in A. Capaldo [Ed.], *Recent advances in non-mammalian adrenal gland research*. Research Signpost, Thiruvananthapuram, Kerala, India.
- BLOOM, P.H., W.S. CLARK, AND J.W. KIDD. 2007. Capture techniques. Pages 193–220 in D.M. Bird and K.L. Bildstein [Eds.], *Raptor research and management techniques*. Hancock House Publishers, Surrey, B.C., Canada.
- CHEREL, Y., J. LELOUP, AND Y. LE MAHO. 1988. Fasting in King Penguin. II. Hormonal and metabolic changes during molt. *American Journal of Physiology* 23: R178–184.
- DALLMAN, M.F., A.M. STRACK, S.F. AKANA, M.J. BRADBURY, E.S. HANSON, K.A. SCRIBNER, AND M. SMITH. 1993. Feast and famine: critical role of glucocorticoids with insulin in daily energy flow. *Frontiers of Neuroendocrinology* 14:303–347.
- GANNES, L.Z. 2001. Comparative fuel use of migrating passerines: effects of fat stores, migration distance, and diet. *Auk* 118:665–677.
- GOODRICH, L.J. AND J.P. SMITH. 2008. Raptor migration in North America. Pages 37–149 in K.L. Bildstein, J.P. Smith, E.R. Inzunza, and R.R. Veit [Eds.], *State of North America's birds of prey*. Nuttall Ornithological Club, Cambridge, MA, U.S.A. and the American Ornithologists' Union, Washington, DC, U.S.A.
- GORNEY, E., W.S. CLARK, AND Y. YOM-TOV. 1999. A test of the condition-bias hypothesis yields different results for two species of sparrowhawks (*Accipiter*). *Wilson Bulletin* 111:181–182.
- HATCHER, L. AND E.J. STEPANSKI. 1994. A step-by-step approach to using SAS system for univariate and multivariate statistics. SAS Institute Inc., Cary, NC U.S.A.
- HEDENSTRÖM, A. 1993. Scaling migration speed in animals that run, swim, and fly. *Journal of Zoology* 259: 155–160.
- HOLBERTON, R.L. 1999. Changes in patterns of corticosterone secretion concurrent with migratory fattening in a neotropical migratory bird. *General and Comparative Endocrinology* 116:49–58.
- AND A.M. DUFTY, JR. 2005. Hormones and variation in life history strategies of migratory and non-migratory birds. Pages 290–302 in R. Greenberg and P. Marra [Eds.], *Birds of two worlds: ecology and evolution of migratory birds*. Johns Hopkins Univ. Press, Baltimore, MD U.S.A.
- , P.P. MARRA, AND F.R. MOORE. 1999. Endocrine aspects of physiological condition, weather and habitat quality in landbird migrants during the non-breeding period. Pages 847–866 in N. Adams and R. Slotow [Eds.], *Proceedings of the 22nd International Ornithological Congress*. University of Natal, Durban, South Africa, and BirdLife South Africa, Johannesburg, South Africa.
- , J.D. PARRISH, AND J.C. WINGFIELD. 1996. Modulation of the adrenocortical stress response in neotropical migrants during autumn migration. *Auk* 113: 558–564.
- JENNI, L. AND S. JENNI-EIERMANN. 1998. Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology* 29:521–528.
- , ———, F. SPINA, AND H. SCHWABL. 2000. Regulation of protein breakdown and adrenocortical response to stress in birds during migratory flight. *American Journal of Physiology* 278:R1182–R1189.
- JENNI-EIERMANN, S., L. JENNI, A. KVIST, Å. LINDSTRÖM, T. PIERSMA, AND G.H. VISSER. 2002. Fuel use and metabolic response to endurance exercise: a wind tunnel study of a long-distance migrant shorebird. *Journal of Experimental Biology* 205:2453–2460.
- KALTENECKER, G.S., J.D. KARLISLE, J. KAUFMANN, P. ALDEN, D. RANKIN, S. POEDL, J. SLAWSON, AND M.J. BECHARD. 2010. Idaho Bird Observatory fall migration monitoring of raptors and songbirds, Boise Ridge, Idaho. 2009 Annual Report. Boise State University, Boise, ID U.S.A.
- KERLINGER, P. 1989. Flight strategies of migrating hawks. University of Chicago Press, Chicago, IL U.S.A.
- KLAASSEN, M. 1996. Metabolic constraints on long-distance migration in birds. *Journal of Experimental Biology* 199:57–64.
- KVIST, A., Å. LINDSTRÖM, M. GREEN, T. PIERSMA, AND G.H. VISSER. 2001. Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature* 413:730–732.
- LANDYS, M.M., T. PIERSMA, M. RAMENOFSKY, AND J.C. WINGFIELD. 2004. Role of the low-affinity glucocorticoid receptor in the regulation of behavior and energy metabolism in the migratory Red Knot *Calidris canutus islandica*. *Physiological and Biochemical Zoology* 77:658–668.

- , ——, C.G. GUGLIELMO, J. JUKEMA, M. RAMENOFKY, AND J.C. WINGFIELD. 2005. Metabolic profile of long-distance migratory flight and stopover in a shorebird. *Proceedings of the Royal Society B* 272:295–302.
- LANDYS-CIANNELLI, M.M., M. RAMENOFKY, T. PIERSMA, J. JUKEMA, CASTRICUM RINGING GROUP, AND J.C. WINGFIELD. 2002. Baseline and stress-induced plasma corticosterone during long-distance migration in the Bar-tailed Godwit, *Limosa lapponica*. *Physiological and Biochemical Zoology* 75:101–110.
- LINDSTRÖM, Å., A. KVIST, T. PIERSMA, A. DEKINGA, AND M.W. DIETZ. 2000. Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting, and fuelling. *Journal of Experimental Biology* 203:913–919.
- LONG, J.A. AND R.L. HOLBERTON. 2004. Corticosterone secretion, energetic condition, and a test of the migration modulation hypothesis in the Hermit Thrush. *Auk* 121:1094–1102.
- MCWILLIAMS, S.R., C. GUGLIELMO, B. PIERCE, AND M. KLAASSEN. 2004. Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology* 35:377–393.
- PIERSMA, T. 1998. Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight? *Journal of Avian Biology* 29:511–520.
- , J. RENERKENS, AND M. RAMENOFKY. 2000. Baseline corticosterone peaks in shorebirds with maximal energy stores for migration: a general preparatory mechanism for rapid behavioral and metabolic transitions? *General and Comparative Endocrinology* 120:118–126.
- RAMENOFKY, M. 1990. Fat storage and fat metabolism in relation to migration. Pages 215–231 in E. Gwinner [Ed.], *Bird migration*. Springer-Verlag, New York, NY U.S.A.
- , T. PIERSMA, AND J. JUKEMA. 1995. Plasma corticosterone in Bar-tailed Godwits at a major stop-over site during spring migration. *Condor* 97:580–585.
- ROMERO, L.M., M. RAMENOFKY, AND J.C. WINGFIELD. 1997. Season and migration alters the corticosterone response to capture and handling in an Arctic migrant, the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). *Comparative Biochemistry and Physiology* 116C:171–177.
- AND J.M. REED. 2005. Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comparative Biochemistry and Physiology A* 140:73–79.
- SAPOLSKY, R.M., L.M. ROMERO, AND A.U. MUNCK. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews* 21:55–89.
- SCHWILCH, R., A. GRATTAROLA, F. SPINA, AND L. JENNI. 2002. Protein loss during long-distance migratory flight in passerine birds: adaptation and constraint. *Journal of Experimental Biology* 205:687–695.
- SILLET, T.S. AND R.T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- SPAAR, R., H. STARK, AND F. LIECHTI. 1998. Migratory flight strategies of Levant Sparrowhawks: time or energy minimization? *Animal Behaviour* 56:1185–1197.
- TEMPEL, D.L. AND S.F. LEIBOWITZ. 1994. Adrenal steroid receptors: interactions with brain neuropeptide systems in relation to nutrient uptake and metabolism. *Journal of Neuroendocrinology* 6:479–501.
- WEATHERHEAD, P.J. AND H. GREENWOOD. 1981. Age and condition bias of decoy-trapped birds. *Journal of Field Ornithology* 52:10–15.
- WINGFIELD, J.C., C. BREUNER, AND J. JACOBS. 1997a. Corticosterone and behavioral responses to unpredictable events. Pages 267–278 in S. Harvey and R.J. Etches [Eds.], *Perspectives in avian endocrinology*. Journal of Endocrinology Ltd., Bristol, U.K.
- AND D.S. FARNER. 1978. The endocrinology of a naturally breeding population of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). *Physiological Zoology* 51:188–205.
- , T.P. HAHN, M. WADA, AND S.J. SCHOECH. 1997b. Effects of day length and temperature on gonadal development, body mass, and fat deposits in White-crowned Sparrows, *Zonotrichia leucophrys pugetensis*. *General and Comparative Endocrinology* 107:44–62.
- , H. SCHWABL, AND P.W. MATTOCKS, JR. 1990. Endocrine mechanisms of migration. Pages 232–256 in E. Gwinner [Ed.], *Bird migration*. Springer-Verlag, Berlin, Germany.
- AND B. SILVERIN. 1986. Effects of corticosterone on territorial behavior of free-living male Song Sparrows *Melospiza melodia*. *Hormones and Behavior* 20:405–417.
- , C.M. VLECK, AND M.C. MOORE. 1992. Seasonal changes of the adrenocortical response to stress in birds of the Sonoran Desert. *Journal of Experimental Zoology* 264:419–428.
- ZAR, J.H. 1996. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, NJ U.S.A.

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