

FAT STORES OF MIGRANT SHARP-SHINNED AND COOPER'S HAWKS IN NEW MEXICO

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Birds use stored fats to supply energy during times when foraging is limited or not possible (King 1970, Blem 1980). During migration, stored fat allows birds to make uninterrupted flights between places and times when foraging can occur and fat stores can be replenished (King 1970, Blem 1980). The amount of fat that birds store during and leading up to migration varies widely (Blem 1980). Fat stores ranged from 4% of total body mass in Common Buzzards (*Buteo buteo vulpinus*) migrating through Israel (Gorney and Yom-Tov 1994) to

32% of total body mass in Pacific Golden-Plovers (*Pluvialis fulva*) preparing to cross the Pacific (Johnson et al. 1989). Presumably, the amount of fat stored is adaptive and relates to the amount of energy needed to fuel flights between predicted stopover sites where fat stores can be replenished (King 1970, Blem 1980, 1990). Although many studies have investigated fat stores in migrating songbirds and shorebirds (Blem 1980), only a few have examined the fat stores of migrating raptors (Gessaman 1979, Smith et al. 1986, Harden 1993, Gorney and Yom-Tov 1994).

Sharp-shinned (*Accipiter striatus*) and Cooper's hawks (*A. cooperii*) are medium-range-partial migrants often observed migrating along mountain ridges and coastlines across much of North America (Kerlinger 1989). We captured Sharp-shinned and Cooper's hawks during spring and fall migration in central New Mexico and used equations developed by DeLong and Gessaman (2001) to estimate their fat stores. In this paper, we describe fat stores in these migrating hawks and examine differences by migration season, species, age, and sex.

METHODS

We captured hawks at two sites in central New Mexico where HawkWatch International, Inc., conducts long-term raptor migration studies (Hoffman et al. 2002). The spring study site is located at the south end of the Sandia Mountains in the Cibola National Forest, ca. 18 km east of Albuquerque (35°05'N, 106°26'W). The spring banding season generally began on 10 March and lasted through late April, and we used data collected from 1994–96. The fall study site is located in the Manzano Mountains in the Cibola National Forest, ca. 56 km south-southeast of Albuquerque (34°42'N, 106°24'W) and 34 km south of the Sandia site. The fall banding season generally began on 1 September and lasted through late October, with peak flights occurring in late September and early October (DeLong and Hoffman 1999). We used data collected from 1992–96. Sharp-shinned and Cooper's hawks migrating through these sites are using the Rocky Mountain Flyway described in Hoffman et al. (2002). Birds captured at these sites appear to breed from New Mexico north to Alberta and winter primarily in southwestern Mexico (Hoffman et al. 2002).

We captured hawks as described in Hoffman et al. (2002). We used plumage characters to determine age (adult and immature; Mueller et al. 1979, 1981) and size to determine sex (Hoffman et al. 1990). We measured mass to the nearest 1 g (using an electronic balance) and tarsus length (Hoffman et al. 1990) to the nearest 0.1 mm (using calipers). We examined birds for the presence of food in their crop (esophageal pouch) and hereafter refer to "cropped" birds (with food detectable in the crop) and "uncropped" birds (with no food detectable). We assigned fat scores to birds using the subalar fat pad located under the wing on the bird's right side with the 4-point (0–3) classification system described in DeLong and Gessaman (2001). Scores were assigned as follows: 0 for birds with no visible fat, 1 for birds with a shallow streak of fat, 2 for birds with fat that was approximately flush with surrounding muscle tissue, and 3 for

birds with fat that exceeded the depth of the surrounding muscle tissue. Birds were released promptly after processing.

We estimated the fat stores for each bird using a model with body mass and tarsus length as predictor variables (DeLong and Gessaman 2001). These models were based on fat extraction techniques that allowed known fat stores to be regressed against structural size measurements and mass. The four models were specific to species and sex classes:

$$\ln(Y)_{\text{Cooper's Hawk, female}} = 3.1380 + 0.0149 \times M - 0.0881 \times T \quad (1)$$

$$\ln(Y)_{\text{Cooper's Hawk, male}} = 9.9095 + 0.0149 \times M - 0.1868 \times T \quad (2)$$

$$\ln(Y)_{\text{Sharp-shinned Hawk, female}} = -0.1362 + 0.0437 \times M - 0.0881 \times T \quad (3)$$

$$\ln(Y)_{\text{Sharp-shinned Hawk, male}} = 6.6353 + 0.0437 \times M - 0.1868 \times T \quad (4),$$

where M = mass in g, T = tarsus length in mm, and Y = fat stores in g. We took the antilog of the values produced by these equations (e to the power of the equation output) to get an estimate of the total grams of fat stored by each bird.

We limited our dataset in three ways. First, the estimated fat stores for migrating hawks produced by equations 1–4 exceeded the range of fat stores in the calibration sample (up to about 70 g fat in the calibration sample; DeLong and Gessaman 2001). Although the calibrated model was linear, we felt that only modest use of data beyond the calibration range was justified. An examination of a histogram of fat stores for migrants indicated that an appropriate upper cutoff to use in this study was a fat store of 100 g, and we excluded from all analyses captured birds with estimated fat stores that exceeded this level (55 individuals excluded). Second, we excluded cropped birds from these analyses because equations 1–4 were derived using birds that were uncropped or from which crop contents were removed. Including cropped birds in the analysis would allow the extra mass of the crop contents to inflate the estimates of fat stores.

To determine whether cropped birds carried different amounts of body fat than uncropped birds, we compared fat scores of cropped and uncropped birds for each species, age, and sex class captured during each migration season using chi-square tests. We made 16 comparisons and used a Bonferroni-adjusted significance value of 0.003 for these tests (0.05/16). Third, we included data only if collected by a bander that participated significantly in the study (i.e., had processed more than 100 birds during the study period) and excluded all other data.

To simplify comparing groups of birds that differed widely in body mass (i.e., species and sex classes), we calculated percent total body fat: (fat stores/body mass) $\times$ 100. We square-root-transformed the resulting values to remove the positive skew in the data. We used 3-way ANOVA for each species to examine season, age, and sex differences in fat stores, using transformed percent total body fat as the dependent variable. We conducted analyses using SYSTAT v. 7.01 (SPSS Inc. 1997).

Table 1. Estimated percent total body fat for Sharp-shinned and Cooper's hawks captured during fall (Manzano Mountains, 1992–96) and spring (Sandia Mountains, 1994–96) migration with empty crops in central New Mexico.

SPECIES	AGE AND SEX	FALL			SPRING		
		$\bar{x}$	SE	N	$\bar{x}$	SE	N
Sharp-shinned Hawk	Adult female	6.75	0.18	389	9.95	0.74	71
	Adult male	5.25	0.12	202	6.05	0.39	24
	Immature female	4.18	0.1	347	6.79	0.6	28
	Immature male	4.74	0.12	264	4.87	0.47	6
Cooper's Hawk	Adult female	9.45	0.2	314	10.62	0.24	224
	Adult male	4.64	0.13	245	4.62	0.12	230
	Immature female	5.52	0.16	238	9.07	0.57	28
	Immature male	3.69	0.11	188	4.15	1.05	3

RESULTS

Fat stores in Sharp-shinned and Cooper's hawks migrating in central New Mexico were generally low, averaging 3–12% of total body mass (Table 1, Fig. 1). Fat scores of cropped and uncropped birds did not differ by species, age, or sex during either season ($\chi^2_{3 \text{ or } 2} < 7.7$, $P > 0.025$). This indicates our use of only uncropped birds to estimate fat stores was justified and resulted in a representative sample.

Fat stores of Sharp-shinned Hawks varied significantly

across season, age, and sex (Table 1, Fig. 1). Overall, percent total body fat was higher in spring than in fall, higher for adults than for immatures, and higher for females than for males; however, significant interactions modified all of these main effects (Table 2). The differences in percent total body fat by season were large for females, and this difference was greater in immature females than in adult females. In contrast, males showed relatively little seasonal variation, with only adult males having more fat in spring than in fall. The difference in percent total body fat by age occurred primarily for females, with males showing little age-related differences.

Fat stores of Cooper's Hawks also varied significantly across season, age, and sex (Table 1, Fig. 1). The pattern of differences was very similar to that of Sharp-shinned Hawks. However, female Cooper's Hawks showed higher percent total body fat than female Sharp-shinned Hawks and male Sharp-shinned Hawks showed marginally higher percent total body fat than male Cooper's Hawks. Otherwise, variation by site, age, and sex mirrored closely the variation of Sharp-shinned Hawks with one notable exception: adult male Cooper's Hawks showed the same percent total body fat in spring and fall (Table 1).

DISCUSSION

Average fat stores in migrating raptors have been estimated at 4–5% of body mass for Common Buzzards in Israel (Gorney and Yom-Tov 1994), 6–9% for American Kestrels (*Falco sparverius*), 6–11% for Sharp-shinned Hawks, and 14–18% for Merlins (*F. columbarius*) in New Jersey (Harden 1993). Our results, in combination with these previous estimates, indicate that many raptors migrate with fat stores in the range of 4–18% of body mass.

Migration season was an important source of variability in fat stores. In females of both species, fat stores were higher in spring than in fall (Table 1, Fig. 1). These differences were not seen in males, except for adult male Sharp-shinned Hawks. One possible adaptive advantage of females having high spring fat stores is that they may

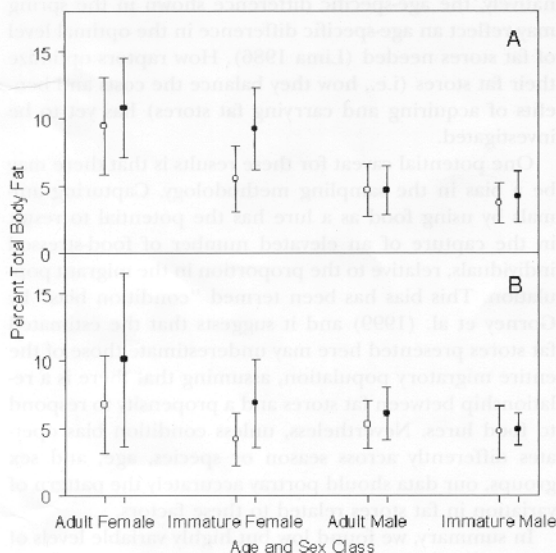


Figure 1. Estimated mean ($\pm$ SD) percent total body fat for (A) Cooper's Hawks and (B) Sharp-shinned Hawks captured with empty crops during spring (solid circles, 1994–96; Sandia Mountains) and fall (open circles, 1992–96; Manzano Mountains) migration in central New Mexico.

Table 2. Three-way analyses of variance examining variation in transformed (square-root) percent total body fat by season, age, and sex for 1331 Sharp-shinned Hawks and 1470 Cooper's Hawks captured during spring (Sandia Mountains, 1994–96) and fall (Manzano Mountains, 1992–96) migration in central New Mexico.

FACTOR	SHARP-SHINNED HAWK		COOPER'S HAWK	
	$F_{1, 1323}$	P	$F_{1, 1462}$	P
Season	23.4	<0.001	10.6	0.001
Age	27.0	<0.001	18.3	<0.001
Sex	16.6	<0.001	125.1	<0.001
Season $\times$ age	0.1	0.79	4.0	0.046
Season $\times$ sex	9.9	0.002	6.1	0.013
Age $\times$ sex	6.2	0.013	4.3	0.039
Season $\times$ age $\times$ sex	0.4	0.552	1.4	0.241

use those fat stores to aid in developing eggs when spring migration ends and they enter the breeding period. Newton (1979) found that female European Sparrow Hawks (*A. nisus*) that did not reach a minimum body mass during courtship failed to lay eggs; this failure to lay eggs could potentially be avoided by accumulating fat stores before or during spring migration. In both Sharp-shinned and Cooper's hawks, adult females showed higher spring fat stores than immatures. This difference may be related to the higher likelihood of adults breeding compared to immatures; however, some female Sharp-shinned and Cooper's hawks breed in their first yr (Rosenfield and Bielefeldt 1993, Bildstein and Meyer 2000, Boal 2001). Nevertheless, Boal (2001) found that females that breed in their first yr (immatures) have later, smaller, and less successful nests than adults. Boal (2001) cited the possibility of physiological constraints as one possible reason for these differences, a constraint that may be reflected in this study as relatively low percent total body fat during spring migration.

Adult females had the highest fat stores among both spring and fall migrants (Table 1, Fig. 1). Sex-specific differences in the fall were less consistent. In the fall, immature female Cooper's Hawks showed higher fat stores than immature male Cooper's Hawks, but the reverse was true for Sharp-shinned Hawks. There may be advantages for females to maintain higher fat stores. Aside from the benefit of carrying extra fat stores prior to the breeding period, females may maintain higher fat stores than males for reasons relating to migration strategies, prey preferences, foraging efficiency, or metabolism.

In all cases except for male Cooper's Hawks in the spring, adults showed higher fat stores than immatures. A similar but more modest difference was observed in spring migrant Common Buzzards in Israel (4% for immatures versus 5% for adults; Gorney and Yom-Tov 1994), and many migrating passerines show a pattern of higher fat stores in adults than immatures (Woodrey and Moore 1997). For raptors, one clear difference between adults and immatures is hunting experience. It is possible

that the net energy gained from prey captures is lower for immatures than adults because of the time spent or the number of attempts made prior to acquiring prey. Such a difference would make capturing prey more expensive, thereby reducing the energy stores gained per prey item. Under such a scenario, the age difference should be reduced during spring migration because of the additional hunting experience acquired by immatures during the winter. A reduction was observed only for female Cooper's Hawks (Table 1), suggesting that the factors that constrain immatures to lower fat stores than adults are maintained through spring migration. Alternatively, the age-specific difference shown in the spring may reflect an age-specific difference in the optimal level of fat stores needed (Lima 1986). How raptors optimize their fat stores (i.e., how they balance the costs and benefits of acquiring and carrying fat stores) has yet to be investigated.

One potential caveat for these results is that there may be a bias in the sampling methodology. Capturing animals by using food as a lure has the potential to result in the capture of an elevated number of food-stressed individuals, relative to the proportion in the migrant population. This bias has been termed "condition bias" by Gorney et al. (1999) and it suggests that the estimated fat stores presented here may underestimate those of the entire migratory population, assuming that there is a relationship between fat stores and a propensity to respond to food lures. Nevertheless, unless condition bias operates differently across season or species, age, and sex groups, our data should portray accurately the pattern of variation in fat stores related to these factors.

In summary, we found low but highly variable levels of fat stores in Sharp-shinned and Cooper's hawks migrating through central New Mexico. These complex patterns merit further investigation, especially because most work investigating fat stores in migrating birds has focused on passerines and shorebirds. Given the variable migration distances (Kerlinger 1989), flight strategies (Kerlinger 1989, Spaar 1997), and foraging behaviors

(Kirkley 1991, Candler and Kennedy 1995, Yosef 1996) of migrating raptors, there may be considerable variation in the need for internal energy storage. The actual relationships between fat stores and the flight strategies, foraging patterns, and metabolic energy needs of migrating hawks have yet to be described.

RESUMEN.—Las reservas de grasa son un sustrato de energía importante para las aves migratorias, sin embargo aun existe poca información sobre los depósitos de grasa que llevan las rapaces migratorias. Estimamos los depósitos de grasa de los gavilanes listados (*Accipiter striatus*) y los gavilanes de Cooper (*A. cooperii*) que migraron durante la primavera (1994–96) y el otoño (1992–96) en Nuevo México. Los depósitos de grasa promediaron 3–12% de la masa corporal total. Hubo una variación significativa en los depósitos de grasa por estación, edad, y sexo, y ocurrieron interacciones significativas entre estos efectos. Tres patrones fueron reconocidos: depósitos de grasa más grandes para las hembras en la primavera que para los machos en otoño, y depósitos de grasa más grandes para los adultos que para los inmaduros. Los gavilanes que tenían comida en su bolsa esofágica (buche) no tuvieron grados de grasa diferentes (grasa subcutánea visible) que los gavilanes sin comida en sus buches. Estos resultados sugieren que la variación en los patrones de depósito de grasa en aves rapaces migratorias son complejas y ameritan mayores estudios.

[Traducción de César Márquez]

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