PRE-MIGRATORY FATTENING AND MASS GAIN IN FLAMMULATED OWLS IN CENTRAL NEW MEXICO

JOHN P. DELONG^{1,2}

ABSTRACT.—Hatching-year (HY) and presumed HY Flammulated Owls (*Otus flammeolus*) were captured during a period of pre-migratory activity in central New Mexico from 2000 to 2003. Mass gains were evident through the pre-migratory period. Fat deposition was an important component of these mass gains; muscle growth appeared to contribute to a lesser degree. Fat scores and pectoral-muscle scores were positively related to body mass and to each other, and, from first to last capture, most recaptured owls showed increases in body mass that were accompanied by fat deposition and growth in pectoral muscles. These data add to a growing body of research indicating that pre-migration increases in fat and muscle mass may be interdependent, but the magnitude of increased muscle mass may be too small to be detected at certain scales. *Received 4 February 2005, accepted 26 November 2005*.

Many migratory birds show substantial gains in body mass prior to migration (King 1972, Bairlein 2002). These gains typically represent some combination of growth in fat, muscle, and organ tissues (King 1972, Lindström and Piersma 1993, Bairlein 2002). Fat is a major component of internal energy reserves and it can be catabolized during migratory flights (King 1972). The amount of fat stored appears to vary in relation to the expected travel distance, opportunities to refuel, and predation risk en route (King 1972, Alerstam and Lindström 1990, Bairlein 2002). Increases in muscle size appear to have a twofold role: to increase the power output from the wings (specifically for pectoral muscles) and to provide a source of amino acids and water as they are catabolized during flight (Marsh 1984, Pennycuick 1998, Lindström et al. 2000, Bairlein 2002). Increases in the size of digestive organs facilitate more rapid uptake of nutrients, aiding in fat storage and the growth of pectoral and other muscles. When not in use, the digestive organs themselves may provide additional nutrient sources as they are catabolized (Karasov and Pinshow 1998, Piersma et al. 1999).

The masses of fat and non-fat tissues often are correlated with overall body mass, but it is not clear that changes in masses of fat and lean tissues are interdependent (Gosler 1991;

Selman and Houston 1996; Redfern et al. 2000, 2004). Because changes in mass are related to foraging and behavioral patterns before migration and during migration stopovers, understanding how lean and fat tissues contribute to changes in mass in migratory birds may help to elucidate important aspects of migratory bird ecology (Karasov and Pinshow 1998, Bairlein 2002). The concurrent study of fat deposition, muscle hypertrophy, and mass gain prior to migration has received little attention in field studies, probably because carcass analysis is usually required (e.g., Redfern et al. 2000). Although carcass analysis can provide precise measurements, samples sizes are often small because birds must be killed for analysis. Scoring body composition does not require killing birds and it confers the possibility of adequate sample sizes (Redfern et al. 2004).

Flammulated Owls (Otus flammeolus) are small, insectivorous birds that breed in the montane forests of western North America and Mexico (McCallum 1994). The species is believed to winter in southern Mexico and Guatemala; thus, it is considered by most sources to be a Neotropical migrant, undertaking potentially long flights between summering and wintering areas (McCallum 1994). During the falls of 2000–2003, I examined the interrelationships among mass gain, fat deposition, and the size of pectoral muscles in Flammulated Owls captured in central New Mexico. My coworkers and I captured Flammulated Owls from late August, when hatching-year (HY) birds become independent from their parents (Linkhart and Reynolds 1987),

¹ HawkWatch International, Inc., 1800 S. West Temple, Ste. 226, Salt Lake City, UT 84115, USA.

² Current address: Eagle Environmental, Inc., 2314 Hollywood Ave. NW, Albuquerque, NM 87104, USA; e-mail: jpdelong@comcast.net

through October, when birds begin their southward migration. These capture efforts were part of a larger study on the migration ecology of Flammulated Owls (DeLong 2004, DeLong et al. 2005). Based on stable hydrogen isotope analysis of feathers and the stage of the preformative molt, most of the owls had not traveled far from their natal areas (De-Long 2004, DeLong et al. 2005). During latter stages of our field seasons, we captured some migrants that had come from latitudes north of central New Mexico, but they were few in number. Hence, our sampling period was a post-independence/pre-migration period for owls that had summered in central New Mexico. Using this sample, I tested the hypothesis that fat and muscle tissue growth simultaneously contribute to overall mass gain in Flammulated Owls prior to their southward migration.

METHODS

The study site was located near Capilla Peak in the Manzano Mountains of central New Mexico (34° 42′ N, 106° 24′ W). The Manzano Mountains are part of an important migratory corridor for many raptors and songbirds that move through New Mexico during the fall (see DeLong and Hoffman [1999] and DeLong et al. [2005] for additional details). My coworkers and I set up two mist-netting stations, spaced ~200 m apart, one on each side of the north-south trending Capilla Peak ridge. We lured owls to the stations by broadcasting the territorial breeding-season hoots of the male Flammulated Owl from within arrays of 3-6 mist nets (60-mm mesh). From 18 August to 22 October, we opened mist nets 3-7 nights/week, depending on volunteer support and weather. We typically began netting 0-30 min after sunset and continued until 15-30 min before sunrise. We closed the nets when winds exceeded ~24 km/hr or when precipitation began to fall. We checked nets for captured owls every 40-70 min.

We banded owls with federal aluminum leg bands, used an electronic scale to determine their mass to the nearest 0.1 g, and used a standard wing chord ruler to measure their unflattened wing chords to the nearest 1 mm. To determine whether body mass and other parameters of males and females differed, we obtained blood samples or feather shafts from

randomly selected HY owls and sent them to Wildlife Genetics, Inc. (Nelson, British Columbia, Canada; www.wildlifegenetics.com) for DNA analysis (CHD gene method; Griffiths et al. 1998).

Whenever possible, we aged owls as either HY or adult. We identified HY owls by the presence of retained juvenal plumage (De-Long 2004) or by uniform fault-barring (Pyle 1997). We identified adult owls by the presence of multiple generations of flight feathers. For the analyses in this paper, I excluded adults because their body mass was significantly greater (HY mean mass = 53.9 g, n =124; adult mean mass = 59.9 g, n = 13; t =4.7, P < 0.001) and adults were not captured frequently enough to analyze separately. The analyses included both confirmed and presumed HY owls. I presumed that owls of unknown age were HY birds if they were molting their contour feathers, had only a single generation of flight feathers, and weighed less than the mean weight for adults. Most adult Flammulated Owls finish molting their flight feathers by late September (Reynolds and Linkhart 1987), in which case they too would have had a single generation of flight feathers during our study period; thus, it is possible that some adult birds were misidentified as hatching-year birds. For two reasons, however, I believe the number of adults included in the analyses is small. First, most unknown-age owls were captured before October (74% of 128 unknown-age owls) and thus would likely show multiple generations of flight feathers if adult. Second, nearly all of these birds were captured before we were able to use the retained-plumage criterion for identifying hatching-year owls; therefore, these owls were labeled unknown-age only because they did not show multiple generations of flight feathers, not because they lacked retained juvenal plumage. We did not know to look for these feathers in the early years, but learned to do so as the study progressed (DeLong 2004). As the study progressed, it became clear that adult owls were rarely captured at our study site (JPD unpubl. data).

We used a 5-point scoring technique to visually assess the size of pectoral muscles. The pectoral-muscle score was based on thickness (roughly a cross-section), as follows: 1 = muscle very concave with keel of sternum

protruding sharply, 2 = muscle roughly triangle-shaped with keel protruding sharply, 3 = rounded muscle with keel still protruding just slightly above the muscle level, 4 = muscle rounded and flush with keel, and 5 = muscle depth exceeds (bulges beyond) the keel. The cross-sectional shape of pectoral muscles is positively correlated with the pectoral mass in small birds (Selman and Houston 1996); therefore, visual assessments of the cross-sectional shape of pectoral muscles should provide a suitable index of pectoral-muscle size. A similar approach has been used effectively in studies of songbirds (Gosler 1991).

We visually assessed furcular fat deposits (i.e., the claviculo-coracoid fat body described by King and Farner 1965) using a 6-point scoring technique similar to that of Helms and Drury (1960). The furcular fat score reflected the depth of fat in the furculum: 0 = no fat, 1 =furculum 1-5% filled with fat, 2 = 5-33% filled, 3 = 34-66% filled, 4 = 67-100%filled, and 5 = fat bulging above furculum. Subcutaneous fat in this region is correlated with overall body fat in small birds—as are fat-scoring procedures, which are based at least partly upon it (Krementz and Pendleton 1990; Rogers 1991; Redfern et al. 2000, 2004). We assigned pectoral-muscle and furcular fat scores to recaptured birds without reference to original capture records.

This study incorporated data from 350 captures, including 9 birds recaptured in the same season; however, sample sizes for some analyses were <350 because we did not record all of the necessary measurements for all birds. I used t-tests and Kolmogorov-Smirnov tests to evaluate whether males and females differed in body composition variables. I used linear regression to evaluate the effect of capture date on body mass and fat and pectoral-muscle scores. I used analysis of covariance (AN-COVA) to evaluate the relationship of fat score and body mass, with wing chord length and pectoral-muscle score as covariates. I also evaluated the relationship of pectoral-muscle score and body mass, with wing-chord length and fat score as covariates. These two analyses allowed me to produce mass estimates for each level of each score, having controlled for the effects of the other tissue type and size. Statistical tests were conducted with NCSS

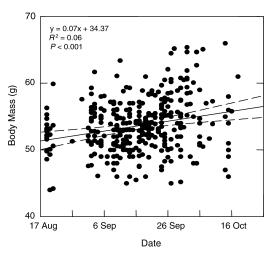


FIG. 1. Body mass (g) of hatching-year Flammulated Owls increased in relation to capture date, showing the gradual gains in body mass through the premigration season. The dashed lines represent the 95% confidence interval for the regression line (solid line). Owls were captured during fall at Capilla Peak, New Mexico, 2000–2003.

2004 (Hintze 2001) and considered significant if P < 0.05.

RESULTS

The number of owls captured varied annually—89 owls were captured in 2000, 157 in 2001, 85 in 2002, and 19 in 2003. Of these 350 owls, our first capture was on 19 August and our last capture was on 18 October, with a median capture date of 17 September.

Of the 88 owls whose sex was determined, 37 were female and 51 were male. Females and males did not differ in body mass (t = 1.04, P = 0.30, n = 88), fat score (Z = -0.66, P = 0.51, n = 85), or pectoral-muscle score (Z = 0.50, P = 0.62, n = 88). Therefore, I combined data for males and females in all further analyses.

Body mass increased through the season in all years, but capture date explained only a small proportion of the variation in body mass $(R^2 = 0.06, P < 0.001, n = 350; Fig. 1)$. Body mass was significantly lower in 2000 than in 2001-2003 ($F_{3,346} = 46.4$, P < 0.001, n = 350), but there was no body mass \times date interaction and no effect on the overall pattern of mass change. Fat scores also increased through the season ($R^2 = 0.19, P < 0.001;$ Fig. 2). There was a drop in fat scores in mid-

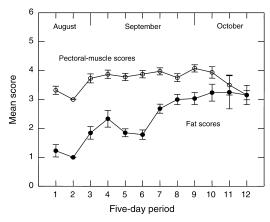


FIG. 2. Mean ± SE fat scores (filled circles) and pectoral-muscle scores (unfilled circles) in relation to capture date for Flammulated Owls captured during fall at Capilla Peak, New Mexico, 2000–2003. Fat scores increased through the season, but pectoral-muscle scores did not. Dates were grouped into 5-day periods from 18 August to 22 October.

September (Fig. 2), but fat scores continued to increase after that time. Pectoral-muscle scores did not change through the season ($R^2 = 0.0$, P = 0.34; Fig. 2).

ANCOVA revealed that fat scores and pectoral-muscle scores were both related positively to body mass (Table 1). Wing chord length was a strong predictor of body mass, and fat score was a stronger predictor of body mass than pectoral-muscle score (Table 1). Based on least-square means of fat scores (ANCOVA), increments in mass from one fat score to the next ranged from 1.0 to 1.8 g and spanned 7.0 g overall (difference in least-square mean mass of fat scores 0 and 5; Table 2). Mass increments from one pectoral-muscle score to the next ranged from 0.3 to 1.1 g but

TABLE 2. Least-square mean (as derived from ANCOVA, see Table 1) body mass and body mass gain from one score to the next for furcular fat and pectoral-muscle scores of Flammulated Owls at Capilla Peak, New Mexico, 2000–2003.

Scoring regime	n	Mass (g)	SE	Gain in mass (g)
Fat				
0	3	51.03	1.97	a
1	61	52.45	0.44	1.4
2	50	53.59	0.48	1.1
3	79	54.63	0.38	1.0
4	61	56.45	0.44	1.8
5	6	58.07	1.39	1.6
Muscle ^b				
2	10	53.29	1.08	
3	83	53.60	0.37	0.3
4	125	54.73	0.30	1.1
5	42	55.16	0.53	0.4

a Gain in mass not calculated for lowest fat and muscle class.

^b No birds had a pectoral-muscle score of 1.

spanned only 1.9 g overall (difference in least-square mean mass of pectoral-muscle scores 2 and 5).

Based on the mean body mass of the first 10% of captured owls and that of the last 10% captured, the overall mass gain from the beginning to the end of the season was 2.5 g, or 4.8% of initial body mass, and the mean fat score increased from 1.5 to 3.2. Using the data in Table 2, I estimated that fat mass increased by 2 g over the sampling period, or approximately 80% of the total mass increase (i.e., body mass of a bird with a fat score of 3.2 [\sim 55 g] — body mass of a bird with a fat score of 1.5 [\sim 53 g] = a 2-g increase in fat). In contrast, pectoral-muscle scores averaged

TABLE 1. Results of analyses of covariance evaluating the relationships of fat and pectoral-muscle scores versus body mass in Flammulated Owls captured during fall at Capilla Peak, New Mexico, 2000–2003.

Analysis/Factor	df	F	P
Fat score as main factor			
Fat score	5	9.45	< 0.001
Pectoral-muscle score (covariate)	1	6.82	0.009
Wing chord length (covariate)	1	33.29	< 0.001
Pectoral-muscle score as main factor			
Pectoral-muscle score	3	2.54	0.057
Fat score (covariate)	1	44.86	< 0.001
Wing chord length (covariate)	1	36.78	< 0.001

TABLE 3. Nine within-season recaptures of Flammulated Owls indicating changes in mass and body condition indices, Capilla Peak, New Mexico, 2000–2003

Year	Initial capture date	Days to next capture	Change in mass (g)	Change in fat score	Change in muscle score
2000	9 Sep	19	+5.0	+1	a
2000	10 Sep	5	+2.0	+1	
2000	9 Sep	18	0.0	_	_
2000	30 Sep	14	+5.0	_	_
2001	2 Sep	21	-2.6	0	0
2001	25 Sep	1	+0.3	0	0
2001	30 Sep	2	+1.0	+1	+1
2002	19 Aug	34	+1.7	+2	+1
2003	5 Sep	9	+2.7	+1	+1

a Data not available.

3.5 among both the first 10% and the last 10% of birds captured.

All but two of the owls recaptured later in the same season (n=9) increased in body mass between the initial and second capture, and three of the owls exhibited simultaneous increases in fat and pectoral-muscle scores (Table 3). In addition, scores for fat and pectoral muscle were positively correlated (r=0.37, P<0.001), indicating that owls with high fat scores tended to have high pectoral-muscle scores. Owls showed nearly every combination of fat and pectoral-muscle scores, except for the highest pectoral-muscle score being paired with the lowest fat score, or vice versa.

DISCUSSION

Body mass of Flammulated Owls increased significantly as the migration season approached. This result is consistent with data showing that migratory birds often increase their total body mass prior to migration (Bairlein 2002). Such patterns have been shown for songbirds, shorebirds, and even some diurnal raptors, but little information is available on pre-migration gain in mass among owls (Gessaman 1979, Bairlein 2002). In Colorado, Linkhart and Reynolds (1987) found mass gain in one radio-tracked adult Flammulated Owl during the month of September. In the present study, I confirmed this pattern for a large number of owls, but I also found that capture date explained only a small amount of variation in the mass of captured owls. This

latter pattern is not surprising given the expected variation in hatching dates and that owls of different ages likely gain mass at different rates

I evaluated the relationship of pectoralmuscle size and fat stores to the seasonal increase in body mass in three ways. First, using recapture data, I found that there were concurrent increases in fat scores, muscle scores, and body mass for most individuals. Second, scores of furcular fat and pectoral muscles were closely tied to body mass, but fat scores were better predictors of body mass than pectoral-muscle scores. Third, fat scores increased through the season along with total body mass, but pectoral-muscle scores did not. Taken together, these three results indicate that fat stores are an important component of the overall mass gain in Flammulated Owls prior to migration, but pectoral-muscle size is not as important.

Recently, the question of whether fat stores and muscle tissues develop independently has been raised. For example, Redfern et al. (2000, 2004) found a general interdependence in fat stores and muscle mass for Sedge Warblers (*Acrocephalus schoenobaenus*) and Redwings (*Turdus iliacus*). My data also support the hypothesis that fat and pectoral-muscle scores are interdependent because (1) there were concurrent increases in fat scores, muscle scores, and body mass for most recaptured birds; (2) there was a positive correlation between the variables; and (3) there were no owls having high scores for one parameter without also having high scores for the other.

There appeared to be a non-fat component to the season-long mass gain that was unrelated to pectoral-muscle size. About 20% of the season-long mass gain was not explained by increases in fat mass or pectoral muscle. These increases in mass may have been related to increased sizes of internal organs, which may have been necessary to facilitate the observed accumulation of muscle and fat reserves. Such changes have been observed in other migratory birds as fat reserves were replenished. For example, Karasov and Pinshow (1998) found that internal organ size increased and contributed to gains in body mass among foraging Blackcaps (Sylvia atricapilla) captured at a stopover site in Israel during northbound-migration.

These data add to the growing body of work showing that both fat deposition and muscle growth are associated with migration-related mass gains and that the two processes are somewhat interdependent. The implication of these studies is that birds getting ready to migrate or already migrating may have specific nutrient needs when foraging. This work may help to improve our understanding of foraging ecology and site selection before and during migration—two concerns becoming increasingly important for the conservation of migratory birds.

ACKNOWLEDGMENTS

Primary financial support was provided by the USDA Forest Service (Cibola National Forest and Region 3), the New Mexico Game and Fish Department (Share with Wildlife Program), Public Service Company of New Mexico, and the New Mexico Ornithological Society. Additional funds for the project came from J. and J. Humber. I gratefully thank all of our supporters for their generosity. B. G. deGruyter, H. P. Gross, and J. P. Smith were instrumental in arranging funding and logistical support for this project. I benefited greatly from working with S. L. Stock, who introduced me to, and trained me in, fat- and musclescoring techniques for owls. The company and assistance of the Manzano Mountains' field crew and volunteers from both HawkWatch International and Rio Grande Bird Research were greatly appreciated. In particular, W. L. Beard, Z. M. Hurst, W. M. King, and E. A. Snyder made significant contributions to the field effort. I appreciate discussions with J. F. Kelly about migration ecology and analytical techniques. Thanks to J. V. Jewell for support in so many ways. This manuscript benefited from thoughtful reviews by J. F. Kelly, J. P. Smith, and three anonymous reviewers.

LITERATURE CITED

- ALERSTAM, T. AND Å. LINDSTRÖM. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331–351 *in* Bird migration: the physiology and ecophysiology (E. Gwinner, Ed.). Springer-Verlag, Berlin, Germany.
- BAIRLEIN, F. 2002. How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory songbirds. Naturwissenshaften 89:1–10.
- DELONG, J. P. 2004. Age determination and preformative molt in hatch-year Flammulated Owls during the fall. North American Bird Bander 29:111–115.
- DELONG, J. P., S. W. Cox, AND N. S. Cox. 2005. A comparison of avian use of high and low elevation sites during autumn migration in central New Mexico. Journal of Field Ornithology 76:326– 333.
- DELONG, J. P. AND S. W. HOFFMAN. 1999. Differential

- autumn migration of Sharp-shinned and Cooper's hawks in western North America. Condor 101: 674–678
- DELONG, J. P., T. D. MEEHAN, AND R. B. SMITH. 2005. Investigating fall movements of hatch-year Flammulated Owls (*Otus flammeolus*) in central New Mexico using stable hydrogen isotopes. Journal of Raptor Research 39:19–25.
- GESSAMAN, J. A. 1979. Premigratory fat in the American Kestrel. Wilson Bulletin 91:625–626.
- GOSLER, A. G. 1991. On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the Great Tit *Parus major*. Bird Study 38:1–9.
- GRIFFITHS, R., M. C. DOUBLE, K. ORR, AND R. J. G. DAWSON. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.
- Helms, C. W. And W. H. Drury, Jr. 1960. Winter and migratory weight and fat field studies on some North American buntings. Bird-banding 31:1–40.
- HINTZE, J. 2001. NCSS and PASS: Number Cruncher Statistical Systems. Kaysville, Utah.
- KARASOV, W. H. AND B. PINSHOW. 1998. Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological Zoology 71:435– 448.
- KING, J. R. 1972. Adaptive periodic fat storage by birds. Proceedings of the International Ornithological Congress 15:200–217.
- KING, J. R. AND D. S. FARNER. 1965. Studies of fat deposition in migratory birds. Annals of the New York Academy of Science 131:422–440.
- KREMENTZ, D. G. AND G. W. PENDLETON. 1990. Fat scoring: sources of variability. Condor 92:500– 507
- 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.
- LINDSTRÖM, Å. AND T. PIERSMA. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. Ibis 135:70–78.
- LINKHART, B. D. AND R. T. REYNOLDS. 1987. Brood division and postnesting behavior of Flammulated Owls. Wilson Bulletin 99:240–243.
- MARSH, R. L. 1984. Adaptations of the Gray Catbird Dumetella carolinensis to long-distance migration: flight muscle hypertrophy associated with elevated body mass. Physiological Zoology 57:105– 117.
- McCallum, D. A. 1994. Flammulated Owl (*Otus flam-meolus*). The Birds of North America, no. 93.
- PENNYCUICK, C. J. 1998. Computer simulation of fat and muscle burn in long-distance bird migration. Journal of Theoretical Biology 191:47–61.
- PIERSMA, T., G. A. GUDMUNDSSON, AND K. LILLIEN-DAHL. 1999. Rapid changes in the size of different functional organ and muscle groups during refu-

- eling in a long-distance migrating shorebird. Physiological and Biochemical Zoology 72:405–415.
- PYLE, P. 1997. Identification guide to North American birds, part I. Slate Creek Press, Bolinas, California.
- REDFERN, C. P. F., A. E. J. SLOUGH, B. DEAN, J. L. BRICE, AND P. H. JONES. 2000. Fat and body condition in migrating Redwings *Turdus iliacus*. Journal of Avian Biology 31:197–205.
- REDFERN, C. P. F., V. J. TOPP, AND P. JONES. 2004. Fat and pectoral muscle in migrating Sedge Warblers *Acrocephalus schoenobaenus*. Ringing and Migration 22:24–34.
- REYNOLDS, R. T. AND B. D. LINKHART. 1987. The nest-
- ing biology of Flammulated Owls in Colorado. Pages 239–248 *in* Biology and conservation of northern forest owls (R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, Eds.). General Technical Report RM-142, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- ROGERS, C. M. 1991. An evaluation of the method of estimating body fat in birds by quantifying visible subcutaneous fat. Journal of Field Ornithology 62: 349–356.
- Selman, R. G. and D. C. Houston. 1996. A technique for measuring lean pectoral muscle mass in live small birds. Ibis 138:348–350.