

Short Communications

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Migration Timing of Canada Warblers Near the Northern Edge of Their Breeding Range

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ABSTRACT.—Canada Warblers (*Wilsonia canadensis*) are one of the last warblers to arrive in breeding areas in northern Alberta and one of the first to depart in autumn resulting in a condensed breeding chronology relative to other locally breeding wood warblers. Males arrived before females during spring migration, while in autumn, adult females departed prior to males. Second-year males arrived later ($P = 0.029$) than after-second year males. Adult males departed later ($P = 0.015$) than adult females. Hatch-year birds departed after adult females but prior to adult males. Female Canada Warblers remained in breeding areas for 62 days while males remained 72 days. These data provide the shortest documented breeding site occupancy estimate for any bird that shows a post-nuptial molt. The short time spent in breeding areas may impose energetic constraints that influence breeding, molt, and survival, particularly for females. Received 21 August 2006. Accepted 7 March 2007.

Migration timing can strongly influence fitness (McNamara et al. 1998) and imposes temporal constraints to completing annual activities including territory establishment, breeding, and molt. Individuals that arrive later likely have tighter time constraints in breeding activities compared to early arriving individuals. Time and energetic constraints are even more intense when populations are at the northern edge of their breeding distribution (Briskie 1995).

The Canada Warbler (*Wilsonia canadensis*) is one of the least studied warblers and information concerning its breeding ecology and population dynamics is mostly lacking (Conway 1999). The northern and most western breeding populations occur in north-central Alberta and eastern British Columbia (Semenchuk 1992, Conway 1999). Canada Warblers

are among the latest warblers to arrive and earliest to depart (Conway 1999) potentially placing time constraints on breeding ecology (Forstmeier 2002, Smith and Moore 2005).

Male neotropical wood warblers generally arrive in breeding areas before females in spring while, within gender, after-second year (ASY) birds typically precede second-year (SY) birds (Francis and Cooke 1986, Morris and Glasgow 2001, Stewart et al. 2002, Smith and Moore 2005). Studies of timing of autumn migration for a variety of wood warblers have offered contrasting results for gender and age-class patterns. Some studies found that hatch-year birds (HY) departed earlier than after hatch-year birds (AHY) (Benson and Winker 2001, Andres et al. 2005, Benson et al. 2006), while others found no difference in age and gender migration patterns in autumn (Morris and Glasgow 2001).

When spring and autumn migration dates are known for breeding areas, it is feasible to estimate the duration the breeding range is occupied (Benson and Winker 2001). For example, Alder Flycatchers (*Empidonax alnorum*) were in breeding areas for 48 days in Alaska (Benson and Winker 2001) but for 72 days in southern Ontario (Hussell 1991). Therefore, northern populations have less time to complete breeding and molt activities than southern populations. Furthermore, individuals at higher latitudes often have lower survival than their southern counterparts and have increased investment in fewer reproductive attempts (Ardia 2005). The objectives of my study were to: (1) document arrival and departure dates for male and female Canada Warblers by age-class, and (2) provide estimates of breeding range occupancy on a study area close to the northern limit of the species range.

METHODS

Study Area and Field Methods.—Migration of Canada Warblers was monitored daily be-

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tween 1994 and 2005 by staff at the Lesser Slave Lake Bird Observatory (LSLBO) on the eastern shoreline of Lesser Slave Lake, Alberta (55° 20' N, 114° 40' W) as part of the Canadian Migration Monitoring Network (Dunn et al. 2006). Birds were captured within a 0.5-ha area of willows (*Salix* spp.) bordered by continuous aspen (*Populus tremuloides*) dominated mixed-wood boreal forest. Spring and autumn migration was monitored continuously in most years between 1 May and 10 June, and between 18 July and 30 September, respectively. Birds were captured using 12 nylon mist nets (30 mm, 3 × 12 m) from 30 min prior to sunrise to 6 hrs (1994–1999) or 7 hrs (2000–2005) thereafter. Net locations have been consistent since 1996, and were not greatly different in prior years.

Captured birds were banded, classified to age and gender by plumage attributes (Rappole 1983) and the extent of skull pneumatization, and checked for breeding characteristics (Pyle 1997). Canada Warblers can be classified in spring as SY or ASY and autumn as HY or AHY. Occasionally individuals could not be reliably classified to age and gender for reasons such as the data not being recorded or intermediate plumage characteristics. Excluding unknown individuals from migration estimates could bias results if they are not a random sample of their gender and age class.

I used raw banding totals because banding effort occurred relatively uniformly throughout spring and autumn each year (Francis and Cooke 1986). Mean arrival and departure date varied between years, probably due to weather conditions, but I did not standardize capture dates to year because the effects of weather can influence both trapping efforts and population differences in migration timing. Data were pooled over the study period as sample sizes of some gender and age-classes were small.

I limited all records to original bandings (92% of all captures) to reduce bias of including birds using the site as a stopover over several days. I excluded birds in spring that were developing breeding characteristics (male: cloacal protuberance, female: brood patches) potentially indicating locally breeding individuals, and those captured after 9 June when most Canada Warbler captures shifted to pre-

viously banded individuals. I limited autumn records to captures after 19 July because prior to this date few Canada Warblers were captured, most captures were already banded, and new bandings likely represented dispersing individuals rather than true migrants (Carlisle et al. 2005). I included birds with breeding characteristics as they can be protracted in autumn migration. Birds that bred locally were likely already banded at adjacent MAPS (Monitoring Avian Productivity and Survivorship) sites during the breeding season.

Statistical Analysis.—I first ascertained if excluding records of unknown age or gender would bias arrival and departure date estimates of known groups using Wilcoxon tests. I only present these results where a difference was found. Kolmogorov-Smirnov two-sample tests were used for spring and autumn migration timing comparisons (Siegel and Castellan 1988, Carlisle et al. 2005). Dates for minimum estimates of breeding range occupancy were calculated by subtracting median arrival dates from median departure dates for adult males and females separately (Benson and Winker 2001). All statistical analyses were conducted with SPSS 13.0 (SPSS 2004) with significance at $\alpha = 0.05$.

RESULTS

Collectively, males arrived earlier than females in spring with ASY individuals arriving prior to SY's of both males and females (Fig. 1). Among males, the arrival date of ASY's was earlier ($D = 1.454$, $P = 0.029$) than the arrival date of SY's. ASY females arrived earlier than SY's, but this difference was not significant ($D = 1.143$, $P = 0.15$).

Males departed later in autumn than females (Fig. 2). A large proportion of autumn HY birds could not be classified to gender and these birds departed earlier than HY males and females ($Z = -6.411$, $P < 0.001$; Fig. 2). There was no difference between classified males and females in autumn departure dates for HY's ($D = 0.879$, $P = 0.42$), but this should be inferred cautiously because unknown HY's preceded males and females. AHY females departed first while AHY males departed last ($D = 1.569$, $P = 0.015$).

Overall, males arrived by 1 June and departed by 12 August, providing an indirect estimate of time spent in breeding areas of ap-

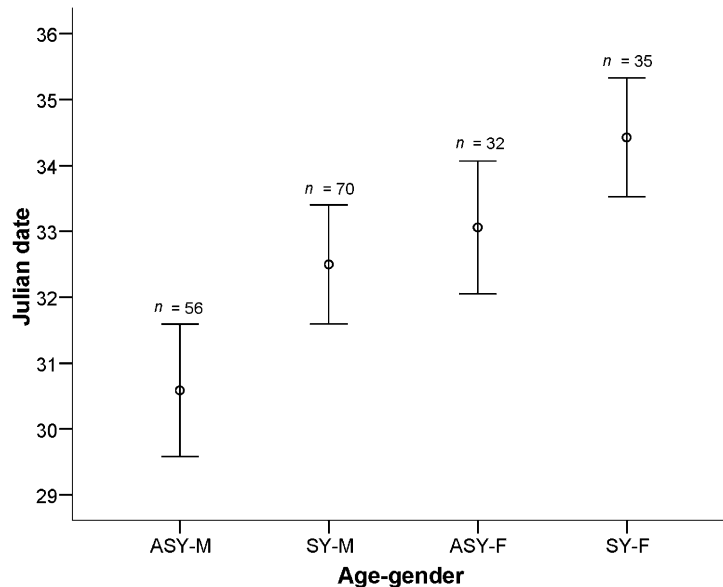


FIG. 1. Arrival of Canada Warblers in northern Alberta. Error bars represent mean and 95% CI of spring arrival date. Julian date 32 = 1 June.

proximately 72 days or 19.7% of the annual cycle. Females occupied breeding areas for approximately 62 days (17% of the annual cycle) arriving by 3 June and departing by 4 August.

DISCUSSION

Arrival and Departure.—Male Canada Warblers in northern Alberta arrived prior to females and older wood warblers arrived prior to younger individuals (Francis and Cooke 1986, Stewart et al. 2002). Males may arrive earlier to acquire better breeding territories (Smith and Moore 2005) while females may arrive later to maximize survival as food is often less available in early spring (Nilsson 1994).

I found protogynous autumn migration in adult Canada Warblers with females departing prior to males. Other studies of wood warblers have reported either that males depart after females for MacGillivray's Warbler (*Oporornis tolmiei*) (Carlisle et al. 2005), Yellow-rumped Warbler (*Dendroica coronata*), and Magnolia Warbler (*D. magnolia*) (Mills 2005) or that females depart after males as for Wilson's Warbler (*Wilsonia pusilla*) (Carlisle et al. 2005). Later departure by males is thought to offer benefits in the following breeding season

through exposure to and defense of potential breeding sites (Forstmeier 2002).

The patterns in departure of age classes of Canada Warblers in autumn are of interest because HY's were intermediate of adult (AHY) males and females. Contrasting migration strategies usually occur between neotropical migrants depending on timing of autumn molt. Carlisle et al. (2005) found strong correlation with molting strategy and migration timing of age-classes; AHY birds molting flight feathers near breeding areas departed later than HY individuals. Adult Canada Warblers have a post-nuptial (basic) molt and the expected pattern is for adults to leave after HY's. Males and females departed at different times and, thus, appear to have different strategies for autumn migration departure.

Indirect Estimate of Breeding Range Occupancy.—A measure of the time spent in breeding areas may indicate temporal constraints on reproduction timing, investment, and reneesting ability. These parameters may be more critical for reproductive success at the northern limit of a breeding range compared to more southern locales. Occupancy of only 62 days for female and 72 days for male Canada Warblers in this study is shorter than documented for any other wood warbler, and is

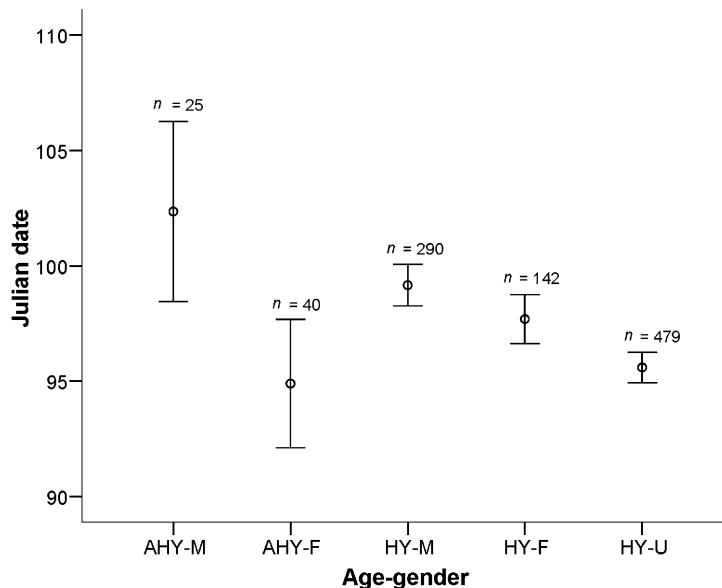


FIG. 2. Departure of Canada Warblers in northern Alberta. Error bars represent mean and 95% CI of autumn departure date. Julian date 93 = 1 August.

the shortest for any bird with a post-nuptial molt on or near breeding areas. Occupancy estimates for six species of wood warblers breeding in Alaska varied from 84 to 108 days (Benson and Winker 2001). Both late spring arrival and the need for early autumn migration offer the ability to test hypotheses concerning reproductive versus survival tradeoffs during temporally constrained periods in breeding areas that may ultimately influence conservation of the Canada Warbler. Future studies could investigate the implications of reduced occupancy time in breeding areas between northern and southern populations of Canada Warblers.

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Occurrence and Condition of Migrating Swainson's Thrushes in the British Virgin Islands

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ABSTRACT.—Swainson's Thrushes (*Catharus ustulatus*) migrate widely throughout North and Middle America. In the Caribbean, the species is known to occur only in the western-most Greater Antilles, and there only as a rare migrant. We captured and visually detected migrant Swainson's Thrushes beginning in 2000 at a banding station on Guana Island, British Virgin Islands. The majority of thrushes captured were adults (79%) and most had no (71%) or little fat (12%) reserves at time of capture; 61% were classified as being in emaciated or poor condition. The poor physiological conditions may have resulted from longer over water flights rather than island hopping. Received 8 September 2006. Accepted 8 January 2007.

The Swainson's Thrush (*Catharus ustulatus*) is a neotropical migrant passerine broadly distributed across the forested north and mountainous west of North America (Mack

and Wang 2000). Population trends across the species' breeding distribution are inconsistent and difficult to interpret (Mack and Wang 2000), but there is evidence to suggest long-term declines in eastern North America (Holmes and Sherry 1988, Hill and Hagen 1991, Buckelew and Hall 1994). Recent analysis of Breeding Bird Survey (BBS) data indicates a declining trend (-0.83 ; $P = 0.09$) in the eastern United States (Sauer et al. 2005). Site-specific factors associated with breeding habitat may be influencing population trends (Sauer et al. 1997, Mack and Wang 2000), but population declines may also be related to factors occurring outside the breeding season (Petit et al. 1995, Mack and Wang 2000, Greenberg and Marra 2005). In particular, birds encounter a host of obstacles to survival during migration (Moore et al. 2005). The ecology of *en route* migrants is poorly understood (Heglund and Skagen 2005), which has been a major obstruction to progress on conservation of neotropical migrant birds (Cochran and Wikelski 2005).

An understanding of migration routes is nec-

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essary before assessing stopover habitat availability or distribution along migration routes. The known fall migration routes to wintering areas in southern Mexico, Central America, and northern South America differ between western and eastern populations of Swainson's Thrushes (Mack and Wang 2000). The eastern population appears to use different routes in autumn than in spring. The higher proportion of individuals on the eastern coast in autumn than spring may be indicative of more individuals making trans-gulf migrations during autumn, but circum-gulf migrations in spring (Child 1969, Rappole et al. 1979, Mack and Wang 2000, Reugg and Smith 2002). There also may be age-related differences in survival of Swainson's Thrushes migrating over open-water routes. Woodrey and Moore (1997) reported after-hatch-year (AHY) Swainson's Thrushes on the Alabama coast had sufficient energy stores to complete trans-gulf crossings, but hatch-year (HY) birds likely could not do so under still-air conditions.

The islands of the Caribbean have received little attention as a possible migration pathway for Swainson's Thrushes. The Swainson's Thrush within the Caribbean is considered a rare migrant in Cuba, Jamaica, the Cayman Islands, and northern Bahamas (Arendt 1992, Raffaele et al. 2003). This species was not listed in Raffaele's (1989) guide to birds of Puerto Rico and the Virgin Islands. Boal et al. (2006) reported capturing and banding the first Swainson's Thrushes reported for the Virgin Islands, approximately 1,300 km east of Jamaica. The objectives of this paper are to: (1) report the age and physical condition of autumn-migrating Swainson's Thrushes in the eastern Caribbean, and (2) examine the possible relevance of the increasing number of Swainson's Thrushes detected at our banding station.

METHODS

Our study site was on Guana Island (18° 30' N, 64° 30' W), immediately north of Tortola, the largest of the British Virgin Islands (BVI). The BVI, along with the U.S. Virgin Islands (USVI), are a chain of approximately 76 islands and cays. Guana Island is relatively small (3 km²) compared to other inhabited islands such as Tortola (54 km²) and Virgin Gorda (21 km²). The British Virgin Islands have a subtropical climate tempered by north-

easterly trade winds with temperatures ranging from 28 to 33° C and humidity levels ~78% throughout the year (Lazell 2005). The annual mean rainfall for Guana Island is estimated at 92 cm (Lazell 2005).

Guana Island is topographically rugged with elevations ranging from sea level to 246 m. Approximately 90% of the island is subtropical dry forest with mesic 'ghut' forests (5%) present in some drainages, and lesser amounts of human-altered areas (3%), mangroves (*Laguncularia* spp.) (1%), and beach (1%) (Lazell 1996). The primary native vegetation on Guana Island is tabebuia (*Tabebuia heterophylla*), gumbo-limbo (*Bursera simaruba*), loblolly (*Pisonia subcordata*), buttonwood (*Conocarpus erectus*), frangipani (*Plumeria alba*), acacia (*Acacia muricata*), and sea grape (*Coccoloba uvifera*). Tam-tam (*Leucaera leucocephala*) is common in disturbed areas. Introduced species include coconut (*Cocos nucifera*), tamarind (*Tamarindus indica*), and royal poinciana (*Delonix regia*) (Lazell 1996).

A banding station has been in operation on Guana Island each October from 1994 through 2006. Net locations were primarily along a northeast-southwest ridge and the southeast-facing slope of a mountain on the west side of the island. The majority of nets were in subtropical dry forest areas, but each year 2-3 nets were in human-altered areas along the ridge, all at approximately 70 m elevation. Duration of mist-netting operations and number of nets operated were subject to local meteorological conditions, an adequate number of individuals to assist with net monitoring, and the time we were allowed access to the island. Our nets were 12 m long with a mesh size of 32 mm; we typically monitored 12 nets, although the number was variable in earlier years of the banding station. Nets were opened at 0630 hrs and closed at 1100 hrs. However, nets were opened and operated during all daylight hours during migrant fallouts. We identified all birds captured to species and, when possible, gender and age (Raffaele 1989, Pyle 1997, Raffaele et al. 2003). We recorded wing chord and mass, estimated fat reserves, physiological condition, and banded each bird with an aluminum leg band provided by the U.S. Geological Survey, Bird Banding Laboratory. We measured mass with an electronic scale accurate to 0.1 g. Our fat esti-

mates were based on the five categories presented by the North American Banding Council (2001). We used four categories to assess physiological condition of the breast muscle: emaciated, poor, fair, and good. Fat amounts and physiological condition were assessed by the same person for all but one thrush.

RESULTS

A Swainson's Thrush was first captured on Guana Island on 9 October 2000; we captured another and observed a second, unbanded individual on 16 October 2003. A fallout of Swainson's Thrushes occurred on Guana Island on 13 October 2005 and we captured 26 individuals between 13 and 15 October. Twenty-two (79%) of the 28 thrushes captured between 9 October 2000 and 15 October 2005 were AHY and 6 (21%) were HY birds. The average (\pm SD) mass of AHY birds (24.6 ± 2.2 g) was slightly lower than that of HY birds (26.4 ± 1.8 g). The difference approached statistical significance ($t_{26} = -1.85$, $P = 0.07$), but we suspect any difference may be related to a small sample of HY individuals. Seventeen (71%) of 24 thrushes examined had no fat reserves at time of capture, 4 (17%) had a trace of fat, 2 (8%) had a little fat built up, and 1 (4%) had a moderate amount of fat visible. We classified 1 (5%) thrush as emaciated, 12 (57%) as poor, 6 as fair (29%), and 2 (10%) of the 21 individuals as in good condition.

One AHY thrush captured at 1000 hrs on 13 October was recaptured at 0830 hrs on 14 October, 1400 hrs on 16 October, and 0650 hrs on 17 October. When originally captured, the thrush weighed 24.9 g, had no fat reserves, and was considered in poor condition. On 14 October the thrush weighed 26.0 g; it weighed 29.9 g on 16 October, and was evaluated as in fair condition with a moderate amount of fat visible. Thus it had gained 5.0 g in 3 days. It weighed 28.5 g on 17 October, possibly due to being captured before sunrise and, hence, after a nocturnal fast.

We did not conduct systematic surveys during the Swainson's Thrush fallout in October 2005 and estimates of the number arriving on Guana are subjective. We are confident that we captured only a small proportion of the Swainson's Thrushes in our immediate netting area during the fallout. We believe an estimate of 300 to 500 individuals in the area of our

banding station is reasonable and probably conservative. A far greater number of Swainson's Thrushes likely made landfall on the island during the fallout.

DISCUSSION

Few studies of neotropical migrants have been undertaken in the eastern Caribbean (Wiley 2000). Ours is the only current and consistently operated autumn-migrant banding station east of Puerto Rico. This may explain our detection of previously unreported neotropical migrant species in the BVI, including Swainson's Thrush (Boal et al. 2006). The species is fairly cryptic and our observations may be evidence of a regular, if previously undocumented, migration route. However, during the fallout on Guana Island in 2005, we easily observed numerous individuals and groups moving about our study area; we doubt such a fallout would go unnoticed by ornithologists or experienced bird-watchers in the region.

If Swainson's Thrushes recently arrived in the east Caribbean, it may be due to anomalous weather events. The normal wind flow over the extreme southeastern United States and Gulf of Mexico in October is from northeast to southwest (Gauthreaux et al. 2005), resulting in crosswind displacement for which Swainson's Thrushes exhibit little or no compensation (Cochran and Kjos 1985). The storm track of most hurricanes and storms in the Caribbean would likely increase such a crossing wind. An east-to-west crossing wind would result in displacement to the west, and does not explain an approximate 1,300-km displacement east of the more commonly (yet still infrequently) used route over Jamaica (Raffaele et al. 2003).

Our data suggest at least some Swainson's Thrushes may use, or be shifting to use, the Atlantic Coast Migration Route identified by Lincoln (1935). Birds using this route "island-hop" through the Bahama Islands to the Dominican Republic, across the Greater Antilles, and south along the Lesser Antilles to South America (Lincoln 1935). Habitat loss has been identified as a possible force resulting in changes in some migration routes (Arendt 1992, Askins et al. 1992), and we may be witnessing early indications of a change in migration behavior of some Swainson's Thrushes. Alternatively, the poor condition and great-

er proportion of AHY thrushes arriving on Guana could be indicative of a longer open-water migration. Woodrey and Moore (1997) reported AHY Swainson's Thrushes had sufficient energy stores to complete a trans-gulf crossing, whereas HY birds likely could not under still-air conditions. Whether intentional or forced by weather conditions, fewer HY thrushes may have been able to survive if an extensive open-water crossing was undertaken. Additional data are needed on migration routes, specific stop-over site conditions, and habitats used by this species during migration before we can further speculate on associations between stop-over habitats and potential shifts in migratory routes.

Our observations have supplanted DeGraaf and Rappole's (1995) assertion that Swainson's Thrushes are absent from the Caribbean and expanded the ranges reported in Raffaele (1989), Arendt (1992), and Raffaele et al. (2003). Continued and increased monitoring effort for neotropical migrant bird presence and habitat use in the eastern Greater Antilles and the Lesser Antilles will be necessary to verify migration route use, changes in migration patterns, and development of an understanding of why such changes may be occurring.

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Daily and Seasonal Variation in Body Mass and Visible Fat in Mountain Chickadees and Juniper Titmice

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ABSTRACT.—Diurnal variations in body mass and visible fat scores were measured for seasonally acclimatized Mountain Chickadees (*Poecile gambeli*) and Juniper Titmice (*Baeolophus ridgwayi*) to examine if they undergo winter fattening. Body mass varied with time of day and was highest in evening for both species in summer and winter. Body mass, expressed as percent mass increase from morning to evening, was 7.3% for summer chickadees, 7.6% for summer titmice, 9.1% for winter chickadees, and 6.1% for winter titmice. Body mass was not significantly higher in winter-acclimatized birds compared to summer-acclimatized birds. Visible fat scores were significantly elevated in winter-acclimatized Mountain Chickadees relative to summer. Mountain Chickadees and Juniper Titmice appear to have seasonally constant body mass rather than undergoing winter fattening. These data are similar to other North American species in the family

Paridae but contrast with data on European parids. *Received 26 December 2006. Accepted 1 April 2007.*

Increased body mass and fat levels are a common pattern of many cold-temperate wintering passerines, enabling these birds to meet thermoregulatory demands and buffer against temporary foraging restrictions due to inclement weather (King 1972, Dawson and Marsh 1986, Swanson 1991, O'Connor 1995). Although fat reserves may lower the risk of starvation, they may also increase predation risk (Blem 1990, Witter and Cuthill 1993, Lillien-dahl et al. 1996). Body mass and fat levels of tree-foraging birds typically change little seasonally compared with ground-foraging birds. This is associated with more predictable food supplies for tree-foraging birds than for ground-foraging birds (Rogers 1987, Rogers and Smith 1993).

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Lehikoinen (1987) presented four graphical models to illustrate the possible relationship between seasonal and daily variation in body mass. Two models appear most probable for small tree-foraging birds (Haftorn 1989). The first is the "constant morning weight strategy" and the second the "winter fattening strategy". The constant morning mass model is characterized by seasonally constant mass recorded during the early morning, but a significant increase in evening body mass in winter compared to summer. The winter fattening model is characterized by both increased morning and evening body mass in winter-acclimatized birds relative to summer-acclimatized birds. Both seasonality of daily mass amplitude and daily minimum mass must be measured to separate between the two models (Lehikoinen 1987).

Body mass and fat data for birds in the family Paridae are equivocal. In addition to being tree-foraging species, many parids also cache food throughout the fall and winter (Bent 1946, Haftorn 1956) which might reduce the need for increased morning body fat in these birds. Body mass of five species of European parids followed the winter fattening strategy (Haftorn 1989) whereas Black-capped Chickadees (*Poecile atricapillus*) from New York, South Dakota, and New Jersey appear to have constant morning body mass with daily increases in body mass that do not vary seasonally (Chaplin 1974, Cooper and Swanson 1994, Graedel and Loveland 1995). They do not appear to follow the constant morning mass model since their average body mass in winter is not higher than in summer. Morning body mass and lipids do not vary seasonally in Mountain Chickadees (*Poecile gambeli*) or Juniper Titmice (*Baeolophus ridgwayi*), but diurnal changes in mass and lipids were not measured by Cooper (2002). Chaplin (1974) recorded both morning and evening body mass and lipid mass for Black-capped Chickadees during fall, winter, and spring. Body mass increased throughout the day, but seasonal differences in morning or evening body mass were not evident. Lipid mass also increased throughout the day and was significantly higher in evening in winter compared to fall or spring. North American parids do not appear to undergo true winter fattening and it is also unclear if they fit the constant

morning mass model or use some other strategy regarding regulation of body mass.

My objectives were to measure seasonal and diurnal patterns of body mass and visible fat stores in Mountain Chickadees and Juniper Titmice to examine if they undergo winter fattening. These two species are small, largely non-migratory parids that occupy regions of western North America. They have behavioral adaptations, including food caching and cavity roosting (Bent 1946), and use regulated bouts of nocturnal hypothermia (Cooper and Gessaman 2005), which reduce costs associated with temperate overwintering. Since behavioral adaptations and nocturnal hypothermia reduce energetic costs, and because chickadees and titmice are tree-foraging birds, they may not have marked seasonal winter fattening.

METHODS

I captured Mountain Chickadees and Juniper Titmice in mist nets in Box Elder and Cache counties, Utah in summer and winter from 1995 to 1997. I used birds captured within 1 hr of sunrise in the present study. Timing of sunrise was obtained from U.S. Naval Observatory data. I measured body mass upon capture to the nearest 0.1 g with a portable electronic balance (Ohaus CT-1200), along with visible fat scores in abdominal and furcular regions using a scale of 0–5 (Helms and Drury 1960). I followed the recommendations of Rogers (1991) to reduce sources of error associated with scoring visible fat. Birds were transported following capture to the laboratory where they were housed individually in 30 × 25 × 30 cm cages inside a 3 × 3 × 2.5 m temperature-controlled environmental chamber. The chamber temperature and photoperiod followed a cycle that approximated the season and study site at which the birds had been captured. Birds were provided free access to water, grit, and food (*Tenebrio* larvae and black-oil sunflower seeds). Body mass and visible fat scores were obtained for all individuals within 15 min of sunset and again the morning after capture (within 15 min of sunrise). Thus, body masses and visible fat scores were recorded at three separate times during the day; at capture, sunset or evening, and the following or second morning. Birds measured from 15 July to 30 August were designated "summer birds" and those measured from 20

TABLE 1. Seasonal values (mean \pm SD) of body mass and visible fat scores for Mountain Chickadees and Juniper Titmice. Sample sizes are in parentheses.

Measurement	Mountain Chickadee		Juniper Titmouse	
	Summer	Winter	Summer	Winter
Body mass (g)				
At capture	10.9 \pm 0.5 (13)	11.0 \pm 0.8 (19)	17.0 \pm 1.2 (16)	16.4 \pm 0.8 (10)
Evening	11.7 \pm 0.5 (13)	12.0 \pm 1.0 (19)	18.3 \pm 1.2 (16)	17.4 \pm 1.0 (10)
2nd morning	10.8 \pm 0.5 (13)	11.0 \pm 0.9 (19)	17.2 \pm 1.3 (16)	16.1 \pm 1.0 (10) ^a
Visible fat score				
Furcular				
At capture	0.46 \pm 0.52 (13)	0.74 \pm 0.81 (19)	0.25 \pm 0.45 (16)	0.20 \pm 0.42 (10)
Evening	1.85 \pm 0.69 (13)	2.53 \pm 1.07 (19) ^a	1.38 \pm 0.50 (16)	1.50 \pm 0.71 (10)
2nd morning	0.62 \pm 0.51 (13)	1.11 \pm 0.87 (19)	0.63 \pm 0.50 (16)	0.20 \pm 0.42 (10)
Abdominal				
At capture	0.38 \pm 0.51 (13)	0.37 \pm 0.50 (19)	0.06 \pm 0.25 (16)	0.10 \pm 0.32 (10)
Evening	1.23 \pm 0.44 (13)	1.89 \pm 0.81 (19) ^a	1.25 \pm 0.45 (16)	1.50 \pm 0.71 (10)
2nd morning	0.08 \pm 0.28 (13)	0.37 \pm 0.60 (19)	0.25 \pm 0.45 (16)	0.20 \pm 0.42 (10)

^a Significant difference in seasonal intraspecific comparisons ($P < 0.05$).

November to 20 February were designated “winter birds.”

All data are presented as means \pm SD. Seasonal means of body mass and visible fat scores were compared by two-way ANOVA using season and time of day as independent variables. Student's *t*-tests were used for pairwise comparisons if significant seasonal effects were detected. Repeated-measures ANOVA was used to test for time of day effects as body mass and visible fat scores were recorded at three times during the day for each individual. Bonferroni's test was used to identify where differences occurred where a significant time of day effect was noted. Sequential Bonferroni alpha values were calculated according to the number of variables to establish statistical significance for the entire anal-

ysis (Rice 1989). Statistical significance was accepted at $P < 0.05$. All statistics were computed with SPSS 13.0 (SPSS Institute 2004).

RESULTS

There were no seasonal differences ($F_{1,90} = 1.77$, $P = 0.19$) (Table 1) in body mass data of chickadees but there were diurnal differences ($F_{2,90} = 15.41$, $P < 0.001$). Analysis of body mass data for titmice revealed seasonal ($F_{1,72} = 10.02$, $P < 0.01$) and diurnal differences ($F_{2,72} = 8.90$, $P < 0.001$). Visible fat scores in chickadees varied by season (abdominal fat: $F_{1,90} = 6.95$, $P = 0.01$; furcular fat: $F_{1,90} = 8.31$, $P = 0.01$) and time of day (abdominal fat: $F_{2,90} = 50.41$, $P < 0.001$; furcular fat: $F_{2,90} = 34.57$, $P < 0.001$). Visible fat scores varied only with time of day in titmice (abdominal fat: $F_{2,72} =$

TABLE 2. Repeated measures analysis of variance for time of day effects on body mass and visible fat scores for seasonally acclimatized Mountain Chickadees and Juniper Titmice.

Season	Visible fat scores						
	Body mass			Furcular		Abdominal	
	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Summer							
Chickadees	2, 24	89.45	<0.001	48.67	<0.001	27.49	<0.001
Titmice	2, 30	108.76	<0.001	32.59	<0.001	66.13	<0.001
Winter							
Chickadees	2, 36	149.50	<0.001	100.61	<0.001	81.83	<0.001
Titmice	2, 18	79.48	<0.001	49.06	<0.001	28.89	<0.001

63.94, $P < 0.001$; furcular fat $F_{2,72} = 41.48$, $P < 0.001$). Body mass in titmice was lower ($t_{24} = -2.20$, $P = 0.038$) on the second morning in winter compared to summer. Body mass did not vary for titmice at capture ($t_{24} = -1.42$, $P = 0.17$) or during the evening ($t_{24} = -1.83$, $P = 0.080$) (Table 1). Visible fat scores were higher in the evening for winter chickadees compared to summer (abdominal: $t_{30} = -2.69$, $P = 0.012$; furcular: $t_{30} = -2.182$, $P = 0.037$). Visible fat scores did not vary in chickadees at capture ($t_{30} = -1.08$, $P = 0.29$) or recorded on the second morning ($t_{30} = -1.81$, $P = 0.080$) (Table 1).

Body mass and visible fat scores varied significantly due to time of day in chickadees and titmice in summer and winter (Table 2). Body mass expressed as percent mass increase from morning to evening was 7.3% for summer chickadees, 7.6% for summer titmice, 9.1% for winter chickadees, and 6.1% for winter titmice. Evening body mass was higher than mass at capture (Bonferroni, $P < 0.001$) and the second morning (Bonferroni, $P < 0.001$) for summer and winter chickadees. Body mass at capture did not vary significantly compared to the second morning body mass in summer or winter chickadees. Evening body mass for titmice was higher than mass at capture (Bonferroni, $P < 0.001$) and the second morning (Bonferroni, $P < 0.001$) in both summer and winter. Body mass at capture did not vary significantly compared to the second morning body mass in summer or winter titmice. Winter chickadees and titmice, relative to their summer counterparts, had significantly higher evening abdominal and furcular fat scores than fat scores at capture (Bonferroni, $P < 0.001$) and from the second morning (Bonferroni, $P < 0.001$). Fat scores at capture did not vary compared to the second morning in summer or winter for either chickadees or titmice.

DISCUSSION

Mountain Chickadees and Juniper Titmice do not appear to follow the constant morning mass or winter fattening models of Lehikoinen (1987). Mean body mass at capture and in the evening did not vary seasonally in either chickadees or titmice. In addition, mean body mass for titmice was significantly lower on the second morning in winter compared to summer. This decreased second morning body mass of winter-acclimatized titmice may be

due to increased length of overnight fasting compared to summer. It may also be due to reduced eating by captive titmice in winter relative to summer. If this occurred, the evening body mass of winter titmice may have been underestimated. However, this does not affect the initial capture mass which did not show any seasonal variation. The body mass at capture data agree with that from other studies of North American parids (Chaplin 1974, Cooper and Swanson 1994, Graedel and Loveland 1995, Cooper 2002). Daily mass gains ranged from 6.1 to 9.1% in Mountain Chickadees and Juniper Titmice. These increases in evening body mass agree closely with data from Black-capped Chickadees (Chaplin 1974) and for several species of European parids (Haftorn 1992). Diurnal variation in body mass and visible fat scores was clearly evident in both chickadees and titmice. Visible fat stores for winter-acclimatized chickadees were significantly higher in evening compared to summer despite not having a significant increase in maximum evening mass. Higher evening fat without differences in body mass for winter birds has also been reported in Black-capped Chickadees (Chaplin 1974). Thus, increased amounts of fat may not be detected by measuring mass of birds. This has also been observed for Golden-crowned Kinglets (*Regulus satrapa*) (Blem and Pagels 1984).

Body mass at capture data from the present study conflicts with data from five European species of parids measured in Norway, which appear to follow a winter fattening strategy (Haftorn 1989). One possible difference is that Haftorn (1989) recorded body mass of individuals that landed on an electronic balance that served as a feeder. Birds in my study were held in captivity in individual cages which may have impacted their normal feeding behavior. However, Black-capped Chickadees recorded in the same manner as European parids also failed to show winter fattening (Graedel and Loveland 1995).

What other factors differ between North American and European parids that may explain the apparent differences in body mass strategies? Increased morning body mass and corresponding fat reserves benefit winter birds by providing more energy reserves that can be used when foraging is not possible. How-

ever, a generally assumed cost of elevated body mass and fat is an increased risk of predation (Lima 1986, Witter and Cuthill 1993, Lilliendahl et al. 1996). In Greenfinches (*Carduelis chloris*) from Sweden, the daily gain in body mass was lower for birds exposed to a stuffed flying hawk three times per day compared to no exposure to the perceived predator (Lilliendahl 2000). Thus, predation risks may vary by location in parids, which could change the daily mass strategy used by these birds. Another factor that may affect results of the North American studies compared to those of Haftorn (1989, 1992) is latitude. European parids that have been measured were in Norway at much higher latitudes than any North American parids. Thus, European parids that have been measured may have been exposed to harsher winter climates than their North American counterparts. However, chickadees and titmice used in my study were from altitudes of 1,700–2,300 m and were exposed to low ambient temperatures (Cooper 2002).

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