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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.*

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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, Lilliendahl 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).

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 nonmigratory 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 $\times$ 25 $\times$ 30 cm cages inside a 3 $\times$ 3 $\times$ 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 ± SD) of body mass and visible fat scores for Mountain Chickadees and Juniper Titmice. Sample sizes are in parentheses.

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

	Body mass			Visible fat scores: Furcular		Visible fat scores: Abdominal	
Season	df	*F*	*P*	*F*	*P*	*F*	*P*
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. However, 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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