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SEASONAL BODY WEIGHT VARIATION IN FIVE SPECIES OF WOODPECKERS

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Abstract. We investigated patterns of seasonal variation in body weight in six populations of five resident species of temperate-zone woodpeckers: Acorn Woodpecker (*Melanerpes formicivorus*), Red-bellied Woodpecker (*M. carolinus*), Red-cockaded Woodpecker (*Picoides borealis*), Downy Woodpecker (*P. pubescens*), and Great Spotted Woodpecker (*Dendrocopos major*). After controlling for time of day and overall body size, annual variation in body weight was small and generally not statistically significant. However, analysis revealed evidence of significant ''winter fattening,'' comparable in magnitude to other temperate-zone resident species, in three of the species. The degree of winter fattening did not correlate with either the size of the acorn crop (for the Acorn Woodpecker) or latitude, two variables potentially related to predictability of food resources. However, the smaller species exhibited significantly greater winter fattening than the larger species, as predicted by the hypothesis that energy storage should be more important for small-bodied species. Furthermore, the food-storing Acorn Woodpecker exhibited considerably less winter fattening than the nonfood-storing species, supporting the hypothesis that food storage provides an ecological alternative to winter fattening.

Key words: *body mass, body weight, fat storage, food storage, Piciformes, seasonality, woodpeckers.*

Variación Estacional en el Peso Corporal en Cuatro Especies de Pájaros Carpinteros

Resumen. Investigamos los patrones estacionales de variación en el peso corporal en seis poblaciones de cinco especies residentes de pájaros carpinteros de la zona templada: *Melanerpes formicivorus*, *M. carolinus*, *Picoides borealis*, *P. pubescens* y *Dendrocopos major*. Tras controlar por la hora del día y el tamaño corporal general, la variación anual en el peso fue pequeña y en general no significativa estadísticamente. Sin embargo, los análisis evidenciaron que tres de las especies experimentan un ''engordamiento invernal'' comparable en magnitud al documentado para otras aves residentes de la zona templada. El grado de engordamiento invernal no se correlacionó con el tamaño de la cosecha de bellotas (para *M. formicivorus*) ni con la latitud, dos variables potencialmente relacionadas con la predecibilidad de los recursos alimenticios. Sin embargo, las especies de menor tamaño engordaron significativamente más que las especies de tamaño más grande, una predicción de la hipótesis que plantea que el almacenamiento de energía debería ser más importante para las especies de cuerpo pequeño. Además, *M. formicivorus,* una especie que almacena alimentos, exhibió un engordamiento de invierno considerablemente menor que las especies que no almacenan alimentos, lo que apoya la hipótesis de que el almacenamiento de alimento representa una alternativa ecológica al engordamiento.

INTRODUCTION

Body weight of birds generally varies diurnally and seasonally due to changes in body fat content and reproductive condition. Except in arctic and antarctic areas, diurnal changes in body weight are inevitable due to the variation in activity prompted by the light-dark cycle (Lehikoinen 1987). In contrast, seasonal changes in body weight need not occur, although changes in day length and environmental conditions during the year make it likely that seasonal variation will exist. This has thus far proved to be the case for a variety of both migratory (Helms and Drury 1960, Morton et al. 1973) and resi-

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dent (Barnett 1970, Rogers and Rogers 1990) species, and even in some tropical species, where seasonality is considerably reduced (Wikelski et al. 2003). Seasonal changes in body weight are most dramatic in long-distance migrants, which may gain up to 100% of their premigration body weight prior to long flights (Clark 1979). However, many resident species also appear to follow a ‘‘winter fattening strategy’’ in which body mass increases during autumn and reaches a peak in midwinter (Baldwin and Kendeigh 1938, Haftorn 1989), presumably aiding survival during the cold, short days of winter (King 1972, Pravosudov and Grubb 1997a).

Considerable work in this area has been performed on tits (or titmice; *Parus* spp. *sensu latu*). In a study of individually marked birds, Haftorn (1989) found that most individuals of five European tit species followed the classic winter fattening strategy in which body weight increased during autumn and reached a midwinter peak around December, after which mass declined. Studying two species in this group as well as the White-breasted Nuthatch (*Sitta carolinensis*), Pravosudov et al. (1999) found that more dominant individuals (based on age and sex) carried lower fat reserves than subordinates, supporting the prediction that the more predictable food supply, presumably available to socially dominant animals, enables them to maintain lower fat reserves (Clark and Ekman 1995).

Titmice are also notable because several species are known to store food (Sherry 1989, Vander Wall 1990). However, despite the various potential advantages of storing food rather than fat (Lima 1986, Rogers 1987, Vander Wall 1990, Pravosudov and Lucas 2001), no specific differences have been detected in changes in diurnal or seasonal body weight between species that store food and those that do not. In particular, Haftorn (1989) found similar patterns of body weight change in five *Parus* species that varied in the length of time that they store food (Cowie et al. 1981, Sherry 1982). However, it remains possible that food and fat storage may interact in other taxa.

As part of independent studies of Acorn Woodpeckers (*Melanerpes formicivorus*) in central coastal California, Red-bellied Woodpeckers (*M. carolinus*) in northern Florida, Red-cockaded Woodpeckers (*Picoides borealis*) in North Carolina, Downy Woodpeckers (*P. pubescens*) in Indiana, and Great Spotted Woodpeckers (*Dendrocopos major*) near Vienna, Austria, we captured and weighed large numbers of individuals of these species throughout the year. Additional published data on Downy Woodpeckers in Pennsylvania were obtained from Clench and Leberman (1978).

We analyzed patterns of seasonal body weight in these populations in order to address two general questions. First, do resident woodpecker species exhibit the same basic winter fattening strategy that is apparently widespread among other temperate bird species? At least some woodpecker species exhibit seasonal acclimatization, but there is little indication that this involves winter fat storage (Liknes and Swanson 1996). Given the apparent lack of significant fat storage in winter, combined with the perception that food supplies on which these species depend are available year-round, we predicted that relatively little seasonal variation in body mass of these species would be found, in contrast to the standard paradigm.

However, to the extent that any winter fattening occurs, do intra- and interspecific patterns support the findings of prior theoretical work that the degree of fattening is directly related to the predictability of food available to individuals (Ekman and Hake 1990, Pravosudov and Grubb 1997a, 1997b)? If so, we predict (a) small-bodied species, (b) high-latitude populations, and (c) nonstoring species should all show greater winter fattening than their respective counterparts because these groups encounter more restricted access to food, higher energy demands, less capacity to store energy supplies, or greater environmental variation in food supply relative to other populations. We further predict that (d) winter fattening should be greater in years when food supply is poor compared to years when it is plentiful.

With respect to food storage (prediction c), there is a clear difference among the species considered here, with food storage being by far the most important in the Acorn Woodpecker. Not only does this species store insects on a short-term basis, it also regularly stores acorns, often by the thousands, in holes drilled expressly for this purpose in specialized storage trees, or granaries (MacRoberts and MacRoberts 1976, Koenig et al. 1995). Although stored acorns make up a relatively modest proportion of their total diet during the winter (Koenig 1991), storing nonetheless ensures the availability of food throughout most winters and is thus likely to affect the pattern of seasonal body weight changes in this species.

In contrast, none of the other populations considered here regularly stores food. Of the four species, food caching is best documented in the Red-bellied Woodpecker (Kilham 1963, Shackelford et al. 2000); however, this species does not appear to store food in south Florida (Breitwisch 1977), nor has food storage been observed in the more northerly Florida population studied here (ELW and MSS, pers. obs.). Despite extensive study throughout North America, the Downy Woodpecker has been recorded potentially caching berries only once (Burchsted 1987). Red-cockaded Woodpeckers have not been recorded storing food of any sort, although a record exists of this species caching bone fragments (Repasky et al. 1991). Finally, no records of food storage in Great Spotted Woodpeckers are known (Michalek and Miettinen 2003). Thus, to the extent that food storage provides an ecological alternative to body fat storage, we predicted that Acorn Woodpeckers should exhibit less seasonal variation in body weight than the other four species.

METHODS

Individuals of the five species were captured and measured as part of independent ecological and behavioral studies. All species are permanent residents in the areas studied; two (Acorn and Red-cockaded Woodpeckers) are cooperative breeders living in groups that frequently contain nonbreeding helpers, while the other three live exclusively as pairs. All are socially monogamous except for the Acorn Woodpecker which, in addition to having nonbreeding helpers, is opportunistically polygynandrous, with groups containing anything from a simple breeding pair of birds to up to seven cobreeding males that compete for matings with one to three joint-nesting females (Koenig et al. 1995). Birds in their first calendar year of life (1Y) were excluded from all analyses. Sample sizes for all species are generally smaller than the total number of birds captured due to missing data.

In general, the mean number of captures per individual was small in all of the studies, ranging from only one capture in the Red-bellied Woodpecker study to 2.1 among Downy Woodpeckers studied in Indiana. Time between recaptures was often fairly long, ranging from a mean of 0.4 years in the Downy Woodpecker study to 2.0 years in the Red-cockaded Woodpecker study. However, in order to reduce pseudoreplication stemming from multiple captures of the same individual, recaptures within one month (30 days) were excluded from the analyses.

ACORN WOODPECKERS

Birds were captured between 1975 and 2003 as part of long-term work on their social behavior at Hastings Reservation in central coastal California. Methods varied, but most frequently involved capturing birds at nest and roost cavities (Stanback and Koenig 1994).

A total of 1753 captures of 1176 individuals was analyzed (mean of 1.5 captures per individual with recaptures an average of 1.5 years apart). Ages of birds (2Y: second calendar year; 3Y+: third calendar year or older) were known for individuals banded as nestlings or juveniles. Otherwise, birds included were aged 2Y or AHY (after hatch year; on or after 1 January of a bird's second calendar year) based on criteria summarized in Koenig (1980).

Beginning in 1980, the overall size of the acorn crop for each year was estimated from visual surveys conducted in September or early October on 250 individual trees spread throughout the study area and among all five species of oaks (genus *Quercus*) present (Koenig, Knops et al. 1994, Koenig, Mumme et al. 1994). In order to test for the effect of the acorn crop on winter fattening, we correlated the mean log-transformed number of acorns counted in 30 sec across all trees in a particular year with the first measure of winter fattening (variable 1) described below, calculated among birds captured during that year only.

RED-BELLIED WOODPECKERS

Red-bellied Woodpeckers were captured and released as part of one study examining their haematozoan parasites (Schrader et al. 2003), and captured and collected as part of a second study examining their interactions with Red-cockaded Woodpeckers (Walters 2004) in the Apalachicola National Forest in northern Florida between January 1997 and July 2001. Although some birds were captured during the day, the majority were collected at night in their roost holes; we used data from 593 individuals in the analyses.

The majority of birds were collected and there were no recaptures.

There were two noteworthy differences between the Red-bellied Woodpecker data and that from the other species. First, an independent index of body size (wing length or tarsus) was available for only a small fraction of birds, and thus analyses were performed without controlling for body size. Second, body weight was measured at the time of capture for only 320 (54%) of the birds. Others were not measured when captured, but were instead frozen and weighed after a variable amount of time (1.4 to 6.5 years). Using a sample of 108 birds for which both fresh and frozen weights were available, the ability to accurately estimate fresh weight from a regression using frozen weight and the length of time birds were frozen was very high (fresh weight = 0.978 [frozen weight] + 0.730 [years frozen] + 0.421; R^2 = 0.98). Thus, for the 160 birds for which only frozen weights were available, we estimated fresh weight based on this regression.

RED-COCKADED WOODPECKERS

Red-cockaded Woodpeckers are cooperative breeders, but in contrast to Acorn Woodpeckers, groups consist of a single breeding pair along with one or a small number of male nonbreeding helpers. Birds were captured between 1980 and 2002 in the Sandhills region of south-central North Carolina and Camp Lejeune Marine Base in southeastern North Carolina as part of a long-term study of social behavior and population ecology (Pasinelli and Walters 2002, Schiegg et al. 2002). Most birds were captured in their roost holes prior to dusk, and were divided into breeders, helpers, and floaters that were not currently part of an established group. A total of 2265 captures of 1700 individuals was available for analysis (mean of 1.3 captures per individual with recaptures an average of 2.0 years apart).

DOWNY WOODPECKERS

Downy Woodpeckers were captured in manually operated traps during daylight hours as part of a study of pair interactions and endocrinology at the Ross Biological Reserve in West Lafayette, Indiana, between 1997 and 2002 (Kellam et al. 2004). Experimental birds carrying radio transmitters or hormonal implants were excluded from the analyses. Once this was done, a total of 224 captures of 107 individuals was available for analysis (mean of 2.1 captures per individual with recaptures an average of 0.4 years apart). As a second, independent set of data on this species, body weights were taken from a more comprehensive mist-netting study conducted at Powdermill Nature Reserve in Westmoreland County, Pennsylvania, between 1961 and 1974 (Clench and Leberman 1978). This latter study provided monthly means and standard deviations, but not weight, body size, or time of day that individual birds were captured; thus, general linear models comparable to those done on the other populations could not be performed. Consequently, in all analyses below that were based on estimated marginal mean values, for this population, raw mean monthly values were used instead.

GREAT SPOTTED WOODPECKERS

Parentage and parental care of this species were studied in the Vienna Woods on the outskirts of Vienna, Austria, from spring 1994 through summer 1996. The population was socially and genetically monogamous despite a very high breeding density in the study area (Michalek and Winkler 2001). Males and females were caught using mist nets at feeders and at nest and roost cavities. Many males were also captured with mist nets in spring using a mounted male woodpecker and a drumming playback. Birds captured in their hatching year were excluded. A total of 220 captures of 140 individuals was analyzed (mean of 1.6 captures per individual with recaptures an average of 0.6 years apart).

GENERAL

Body weights were normally distributed for four of the five species (Kolmogorov-Smirnov test, all $P > 0.3$); however, for Red-cockaded Woodpeckers, body weights were significantly nonnormal (Kolmogorov-Smirnov test, $z = 3.3$, $P \leq 0.001$). Thus, we used nonparametric tests for univariate analyses. General linear models (SPSS 1997) were used for multivariate analyses, which were generally performed for each species. In order to keep the results tractable, three-way and higher interactions were not included in these analyses.

Sample sizes for the studies are summarized in Table 1. Winter fattening was quantified in three ways, all based on the estimated marginal monthly mean values derived from general linear models controlling for hour of capture and

TABLE 1. Sample sizes (number of captures) and overall significance of annual variation from general linear models incorporating month, time of capture, and (except for Red-bellied Woodpeckers) wing chord for the woodpecker populations used in this study. Analyses were not performed on the Pennsylvania Downy Woodpecker data, for which individual body weight data were not available.

Sex and species	Month												F-value[a] (df)	
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Males														
Acorn Woodpecker	53	28	60	167	126	89	48	25	26	52	45	26	1.4	(11, 688)
Red-bellied Woodpecker	18	14	5	25	35	32	16	15	8	15	30	4	0.9	(11, 170)
Red-cockaded Woodpecker	35	57	65	46	29	77	227	197	196	121	77	33	1.7	(11, 1112)
Downy Woodpecker, IN[b]	13	18	20	9	7	11	2	1	1	7	12	4	0.7	(11, 75)
Downy Woodpecker, PA[b]	3	2	25	44	34	7	0	6	7	18	10	0	–	
Great Spotted Woodpecker	17	10	10	32	2	6	3	0	0	0	0	5	2.9**	(7, 68)
Females														
Acorn Woodpecker	38	14	108	125	102	75	31	28	24	40	49	16	0.7	(11, 593)
Red-bellied Woodpecker	18	4	3	7	7	10	23	5	1	3	16	0	1.7	(10, 64)
Red-cockaded Woodpecker	24	30	37	23	19	56	184	168	115	68	41	18	2.5**	(11, 745)
Downy Woodpecker, IN[b]	15	25	20	3	8	13	2	1	4	10	11	5	1.1	(11, 87)
Downy Woodpecker, PA[b]	6	2	18	38	15	2	2	4	4	11	12	3	–	
Great Spotted Woodpecker	15	20	17	11	5	4	3	0	1	0	0	9	4.3***	(8, 64)

[a] Asterisks indicate level of significance such that ** = $P \leq 0.01$, *** = $P \leq 0.001$, other $P > 0.05$.
[b] Study sites for Downy Woodpeckers were in Indiana (IN) and Pennsylvania (PA).

wing chord (except where noted). First, assuming that winter fattening consists of a general increase in body weight from summer or autumn to midwinter, we calculated the percent increase (or decrease) in mean body weight between the two time periods, determined by averaging the monthly mean values from June to October and November to January (variable 1). Second, we determined the percent increase from the overall mean body weight to the winter peak, defined as the highest mean monthly value occurring between November and March, inclusive (variable 2). Third, following Haftorn (1989), we determined the percent increase from the mean September value to the winter peak (variable 3). For female Great Spotted Woodpeckers, no individuals with complete data were captured between August and November and thus we used the value for July in this analysis. Values for the two populations of Downy Woodpeckers were averaged for interspecific comparisons. These values are subsequently referred to as ''winter fattening values.''

Statistical testing of the winter fattening values was conducted by randomization tests. For each species $\times$ sex combination, 2500 trials were performed by randomizing mean monthly body weight values, after which the winter fattening variables were calculated, using the above criteria. Significance was based on the proportion of trials yielding values of winter fattening that were less than the observed value; these proportions are subsequently referred to as ''winter fattening *P*-values.'' Winter fattening *P*-values provide an alternative index of winter fattening (with smaller values indicating greater winter fattening) that, unlike the winter fattening values themselves, take into consideration the distribution of monthly mean weight values for the particular set of birds being analyzed.

Comparative analyses were performed with two general linear models that combined sexes and the three different measures of winter fattening. These analyses thus included sex and variable number (1, 2, or 3) as factors and overall mean body weight and latitude as covariates. Dependent variables included the actual winter fattening values (the values of variables 1, 2, and 3) and the winter fattening *P*-values from the randomization tests. With only a single food-storing population, it was not possible to statistically test for differences between food-storing and nonfood-storing species; instead, mean values were calculated and compared.

RESULTS

We first examined six variables as potentially important factors affecting body weight: body size, time of capture, age, social status, sexual dimorphism, and the size of the acorn crop. After assessing the need to include these variables in further analyses, we tested for significant annual variation in body weight and calculated the three measures of winter fattening. Finally, we performed interspecific comparisons in the degree of winter fattening based on body size, latitude, and food storage.

BODY SIZE

No independent measure of body size for a majority of individuals was available for Red-bellied Woodpeckers. For the other four species, body weight and body size as measured by wing chord were significantly correlated ($0.19 \leq r_s \leq 0.33$; all $P \leq 0.005$). Thus, wing chord was included as a covariate in all general linear models whenever possible.

TIME OF CAPTURE

Analyses generally revealed marked diurnal changes in body weight related to time of day birds were captured. Figure 1 gives an example using Acorn Woodpeckers, for which birds were captured at all times of day. Thus in all analyses where these data were available, diurnal variation was included as a factor by dividing the day into four-hour intervals.

AGE

We investigated age-related body weight changes between 2Y and older (3Y+) individuals in Acorn and Red-cockaded Woodpeckers, the two species for which detailed information on age was known. In univariate tests, there was no significant age difference in Red-cockaded Woodpeckers for either sex (Mann-Whitney *U* tests, both $P > 0.15$), but highly significant differences in Acorn Woodpeckers (Mann-Whitney *U* tests, both $P \leq 0.001$). However, in general linear models controlling for body size (wing chord), time of capture, month, and sex, age was not significant ($P > 0.09$) in the analyses for either species. Thus, relative to overall body size, 2Y birds were as heavy as older birds. Age was therefore not considered in subsequent anal-

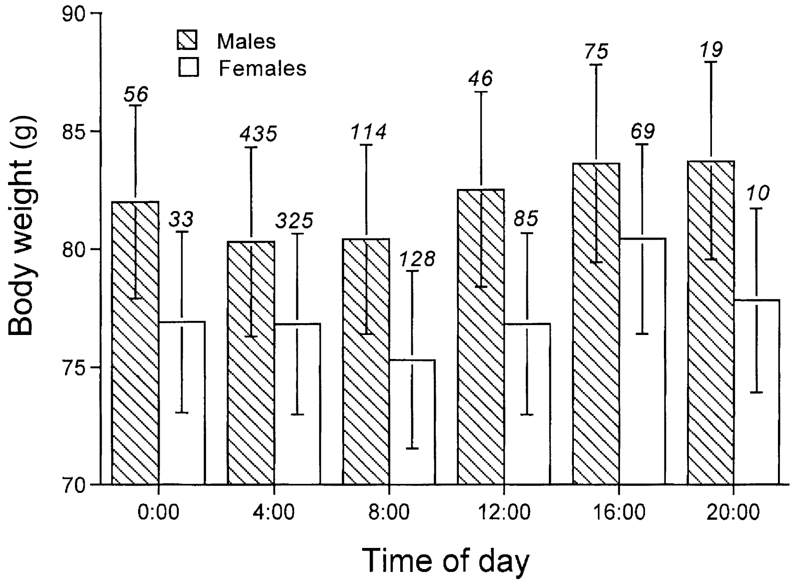

FIGURE 1. Mean (± SE) body weight of male and female Acorn Woodpeckers in relation to time of day they were captured. Time of day is divided into 4-hour intervals, such that 8:00 includes birds captured between 8:00 and 12:00. Samples sizes are listed above the bars.

yses, which included all AHY birds for all populations.

SOCIAL STATUS

The species for which this variable was potentially relevant were Acorn and Red-cockaded Woodpeckers, the two cooperative breeders. In univariate tests, there were highly significant differences for both males and females in body weight between helper and breeder Acorn Woodpeckers (Mann-Whitney *U* tests, both $P \leq 0.001$), but no significant differences between helper, breeder, and floater Red-cockaded Woodpeckers (Mann-Whitney *U* tests, all $P > 0.3$). However, in general linear models controlling for wing chord, time of capture, month, and sex, status was not significant for either species (both $P > 0.2$). Thus, status was not included in further analyses.

SEXUAL DIMORPHISM

Univariate tests indicated significant sexual dimorphism in body weight for all species (Mann-Whitney *U* tests, all $P \leq 0.001$) except the Downy Woodpecker (Mann-Whitney *U* tests, $z = 1.5$, $P = 0.12$). After controlling for time of capture, month, and (except for the Red-bellied Woodpecker) wing chord, results remained the same except for the Great Spotted Woodpecker, where there was no longer significant sexual dimorphism in body weight (Table 2). For consistency, combined with the potential for the sexes to exhibit different degrees of winter fattening, we performed separate analyses of the sexes for all five species.

SIZE OF THE ACORN CROP

This variable was only relevant to the Acorn Woodpecker population, where the size of the acorn crop is a critical determinant of annual reproductive success and survivorship (Koenig and Mumme 1987). Because of ongoing studies of acorn production, we were able to compare the mean degree of winter fattening (measured by variable 1) with estimates of the overall size of the acorn crop.

Analyzing males and females separately, the correlation between winter fattening and the acorn crop was significantly positive for males ($r_s = 0.47$, $n = 20$, $P = 0.04$), but not for females ($r_s = -0.20$, $n = 20$, $P = 0.39$). Thus to the extent that the acorn crop influenced winter fattening, birds tended to undergo more, not less, winter fattening in years when the acorn crop was good.

TABLE 2. Sexual dimorphism in body weight of woodpecker populations used in the analyses. Data are estimated marginal means ± SE (*n*) calculated from general linear models controlling for time of capture, month, and (except for Red-bellied Woodpeckers) wing chord.

Species	Males	Females	Percent difference	*P*-value
Acorn Woodpecker	81.8 ± 0.3 (745)	77.5 ± 0.4 (650)	5.5	≤ 0.001
Red-bellied Woodpecker	73.2 ± 0.5 (391)	66.0 ± 0.8 (203)	10.9	≤ 0.001
Red-cockaded Woodpecker	48.6 ± 0.2 (1160)	47.4 ± 0.3 (783)	2.5	≤ 0.001
Downy Woodpecker (IN)[a]	27.6 ± 0.3 (107)	27.7 ± 0.3 (117)	–0.4	0.78
Downy Woodpecker (PA)[a]	26.8 (156)	27.1 (117)	–1.1	–
Great Spotted Woodpecker	81.1 ± 1.0 (85)	78.8 ± 0.8 (85)	2.9	0.82

[a] Study sites for Downy Woodpeckers were in Indiana (IN) and Pennsylvania (PA). Standard errors could not be calculated from the Pennsylvania data.

ANNUAL VARIATION AND WINTER FATTENING

In general linear models controlling for time of day and (except for Red-bellied Woodpeckers) wing chord, and performed separately for the two sexes, significant annual variation in body weight was found only in both sexes of Great Spotted Woodpeckers and for female Red-cockaded Woodpeckers (Table 1). Mean estimated marginal monthly body weights for the populations are presented in Figure 2.

Winter fattening values were generally modest, ranging from −6.2% to +8.1%, with an overall mean of 2.3% (Table 3). Of the 30 values (5 species × 2 sexes × 3 variables) tested, six (20%) among three of the species were significant by means of the randomization tests, three being highly significant ($P \leq 0.001$; Table 3).

COMPARATIVE ANALYSES

In a general linear model including sex, variable number (1, 2, or 3), mean body weight, and latitude with winter fattening value as the dependent variable, only mean body weight verged on significance (Table 4). With winter fattening *P*-value (arcsine-transformed) as the dependent variable, mean body weight was highly significant ($P = 0.002$), while none of the other variables was significant (Table 4). Simple correlations between mean overall body weight and winter fattening were also significant (Fig. 3). Thus, smaller birds exhibited greater winter fattening than larger birds, but there was no apparent relationship between winter fattening and latitude.

Although it was not possible to statistically compare winter fattening in the single food-storing species compared to the other populations, all estimates indicated a lower degree of winter fattening for the food-storing Acorn Woodpecker than the nonstoring species (Table 5).

DISCUSSION

In general, resident species of woodpeckers do not exhibit much seasonal variation in body weight. Of the 10 categories of birds tested statistically (five species of two sexes each), only three exhibited significant variation in monthly mean body weight after controlling for wing chord and time of capture. This indicates that, at least statistically, annual variation in body weight is significant in only some resident woodpecker populations. However, as pointed out by Johnson (1999), such statistical tests reveal more about the sample sizes involved than whether differences are biologically meaningful. Furthermore, significant winter fattening could still be occurring even though the annual pattern is not significant when analyzed on a monthly basis.

The randomization tests indicated significant winter fattening, quantified by at least one of the three variables, for three of the five species and four of the 10 species × sex combinations (male Red-bellied and Red-cockaded Woodpeckers, and both male and female Downy Woodpeckers). The amount of winter fattening in these four populations ranged from 2.8% to 4.8% (mean of variables 1–3).

We therefore conclude that significant winter fattening occurs in at least some resident species of woodpeckers. Although, in general, the degree of fattening was small, at least compared to that observed in migratory species, it is comparable to that observed in other resident species. For example, Haftorn (1989) found that

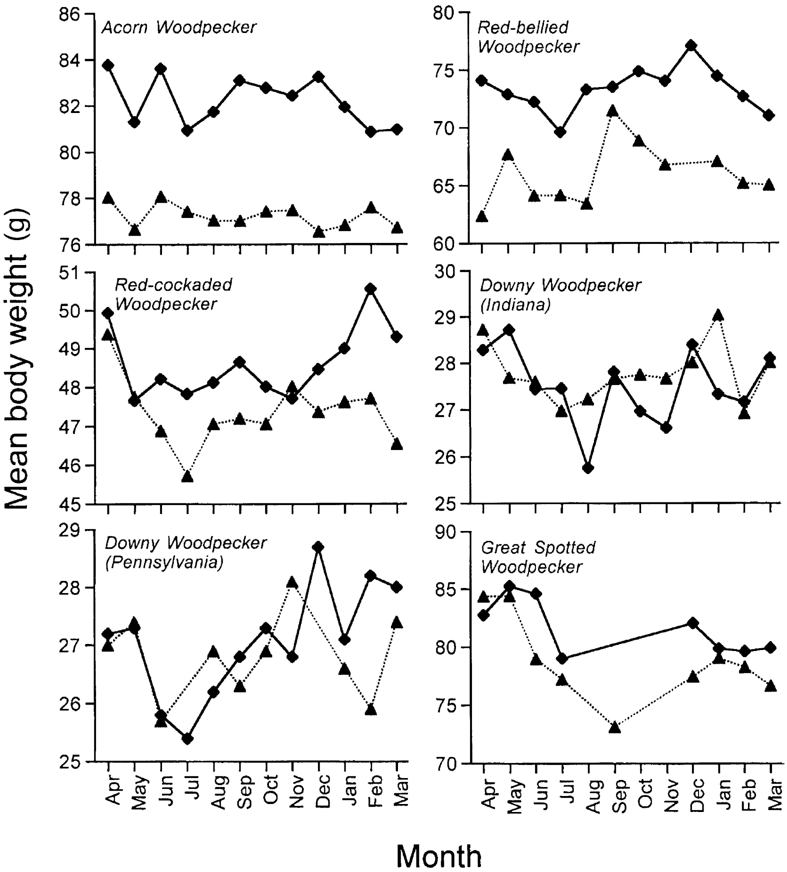

FIGURE 2. Mean body weight estimated from general linear models controlling for time of day and (except for Red-bellied Woodpeckers) wing chord divided by month (starting in April) and sex (diamonds = males, triangles = females) for the populations used in the analyses.

most individuals in his study of five species of European tits gained 2%–8% of their body weight between September and the winter peak. Such increases in body weight are potentially of biological significance, as indicated by the changes in behavior associated with radio packages as light as only 3%–4% of body weight (Hooge 1991).

Are the intra- and interspecific patterns of winter fattening consistent with the presumed or known degree of predictability of food resources? We addressed four predictions of this hypothesis.

(a) Winter fattening should be greater when the food supply is poor. The acorn crop varies considerably among years (Koenig, Mumme, et al. 1994) and significantly influences reproduction, survival, and residency of Acorn Woodpeckers (Koenig and Mumme 1987, Hannon et al. 1987, Koenig et al. 1995). However, contrary to the prediction, correlations indicate that winter fattening is either not significantly correlated (females), or positively correlated (males) with the acorn crop.

(b) Populations at higher latitudes should exhibit greater winter fattening than those at lower latitudes. The general linear models including sex, mean body weight, latitude, and variable number indicated no significant effect of latitude.

(c) Smaller species should exhibit greater winter fattening than larger species. General linear models including sex, mean body weight, latitude, and variable number indicated that smaller species exhibited greater winter fattening, particularly when measured by the winter fattening *P*-value. This pattern was also evident in the randomization tests, which indicated sig-

TABLE 3. Measures quantifying winter fattening, ordered from largest to smallest in body size. Values are the winter fattening value followed (in parentheses) by the winter fattening *P*-value, except for Downy Woodpeckers, where the combined winter fattening *P*-value is listed on the first line in parentheses followed by the winter fattening values for each of the two populations.

Species	Variable 1[a]		Variable 2[b]		Variable 3[c]	
	Males	Females	Males	Females	Males	Females
Great Spotted Woodpecker	–1.0 (0.64)	2.4 (0.31)	0.7 (0.99)	0.3 (0.85)	3.9 (0.52)	8.1 (0.36)
Acorn Woodpecker	0.1 (0.47)	–0.6 (0.87)	2.8 (0.84)	0.5 (0.81)	0.2 (0.79)	0.7 (0.65)
Red-bellied Woodpecker	3.4 (0.03)	0.7 (0.39)	6.2 (≤ 0.001)	2.0 (0.88)	4.9 (0.31)	–6.2 (0.99)
Red-cockaded Woodpecker	0.5 (0.38)	1.9 (0.09)	4.0 (≤ 0.001)	2.0 (0.56)	3.9 (0.39)	1.7 (0.60)
Downy Woodpecker	(0.03)	(0.01)	(0.21)	(≤ 0.001)	(0.41)	(0.11)
Indiana (IN)[d]	1.3	2.9	2.8	3.9	2.1	5.0
Pennsylvania (PA)[d]	4.7	3.4	5.9	3.1	7.1	6.8

[a] Percent increase in body weight from mean in June–October to mean in November–January.
[b] Percent increase in body weight from overall mean to winter peak (largest mean monthly value between November and March, inclusive).
[c] Percent increase in body weight from September mean to winter peak (largest mean monthly value between November and March, inclusive). July value used for male Great Spotted Woodpeckers.
[d] Study sites for Downy Woodpeckers were in Indiana (IN) and Pennsylvania (PA).

nificant winter fattening assessed by at least one of the three measures among the three smaller species but in neither of the larger species of woodpeckers examined.

(d) Winter fattening should be less in food-storing species. Although it was not possible to statistically test this prediction, results were consistent with it. First, the randomization tests indicated no significant winter fattening in the food-storing Acorn Woodpecker. In contrast, they suggested significant winter fattening of at least one measure for three of the four nonfood-storing species. Second, both winter fattening values and winter fattening *P*-values were consistently lower in the Acorn Woodpecker than the mean of the other four species, or even of the mean of the other two relatively large species. Overall, the mean winter fattening value across all estimates for the food-storing Acorn Woodpecker was 0.6% compared to 2.7% for the nonfood-storing species and 2.2% for the two large nonfood-storing species, while the mean winter fattening *P*-value was 0.74 compared to only 0.38 for the nonfood-storing populations and 0.53 for the two large nonfood-storing species.

We conclude that the degree of intraspecific winter fattening does not correlate with apparent or presumed predictability of food resources as estimated by the annually varying acorn crop, at

TABLE 4. Results of general linear models testing the variables potentially influencing interspecific variation in winter fattening.

Dependent variable	Model term	df	Mean square	*F*-value	*P*-value
Winter fattening value	Sex	1, 22	9.7	1.4	0.25
	Variable number[a]	2, 22	6.0	0.9	0.44
	Latitude	1, 22	6.9	1.0	0.33
	Body weight	1, 22	24.8	3.6	0.07
	Sex × variable	2, 22	3.6	0.5	0.60
Winter fattening *P*-value	Sex	1, 22	0.1	1.3	0.27
	Variable number[a]	2, 22	0.1	1.3	0.31
	Latitude	1, 22	0.1	0.1	0.76
	Body weight	1, 22	1.2	12.9	0.002
	Sex × variable	2, 22	0.1	0.4	0.71

[a] Refers to whether winter fattening was estimated using variable 1, 2, or 3, as described in Table 3.

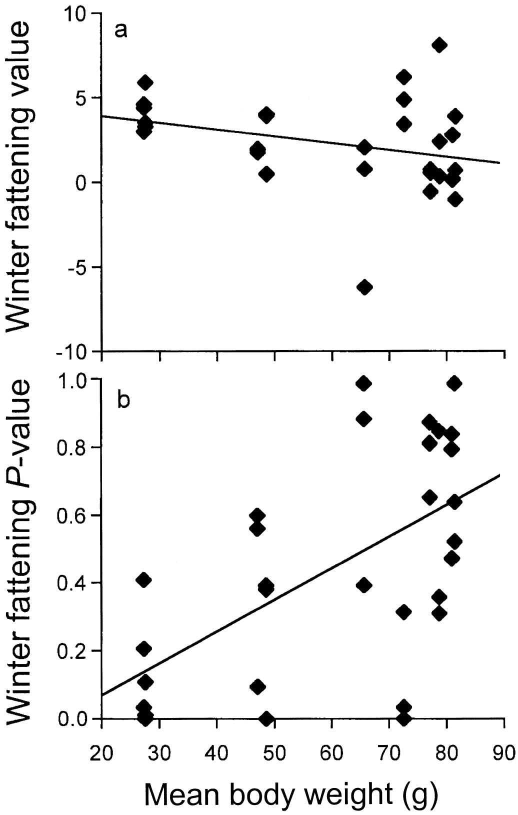

FIGURE 3. Mean overall body weight plotted against (a) winter fattening values ($r_s = -0.40$, $n = 30$, $P = 0.03$) and (b) winter fattening P-values ($r_s = 0.53$, $n = 30$, $P = 0.003$). The two Downy Woodpecker populations were combined, but otherwise all species × sex × variable combinations were included.

least in the Acorn Woodpecker, or interspecifically by latitude. However, there is a reasonably strong interspecific relationship between winter fattening and body size, with small-bodied species exhibiting greater winter fattening than large-bodied species. Also, food storage appears to affect winter fattening, with the food-storing Acorn Woodpecker exhibiting slightly less than one-quarter the winter fattening of the nonfood-storing species. These latter two results are consistent with the hypothesis that winter fattening is related to the predictability of food resources insofar as such predictability is inherently lower for smaller-bodied species and greater for species that cache food.

Whether the observed increase in winter body weight that occurs in woodpeckers is due to increased body fat or some other change in body composition is unknown. Liknes and Swanson (1996) found no difference in fat scores of Downy Woodpeckers captured during the summer and winter, while a study of body fat in 50 Red-bellied Woodpeckers found no seasonal variation in fat scores, 33 (66%) of which were categorized as having no fat or trace fat while only 2 (4%) achieved the highest category of moderate fat levels (ELW and MSS, unpubl. data). These data suggest that body fat is generally low and fails to track seasonal variation in body weight in woodpeckers, and thus may not be the proximate cause of the winter fattening observed here. However, given the generally small magnitude of the weight increases, even in the populations where it was statistically significant, the degree to which fat or some other body component is involved will be difficult to determine.

TABLE 5. Comparison of estimates of winter fattening for the food-storing species (Acorn Woodpecker), all four nonfood-storing woodpecker species, and the two relatively large species of nonfood-storing woodpeckers (Red-bellied and Great Spotted Woodpeckers).

	Variable 1[a]		Variable 2[a]		Variable 3[a]	
Group	Males	Females	Males	Females	Males	Females
Mean winter fattening						
Storing species	0.1	–0.6	2.8	0.5	0.2	0.7
Nonstoring species	1.5	2.0	3.8	2.0	4.3	2.4
Large nonstoring species	1.2	1.6	3.5	1.2	4.4	1.0
Mean winter fattening *P*-values						
Storing species	0.47	0.87	0.84	0.81	0.79	0.65
Nonstoring species	0.27	0.20	0.30	0.57	0.41	0.51
Large nonstoring species	0.33	0.35	0.50	0.87	0.42	0.68

[a] Variables 1–3 as described in Table 3.

Two conclusions can be drawn from this study. First, a modest pattern of winter fattening on the order of 3%–5% is evident in the populations of the smaller, but not the larger, species of temperate-zone woodpeckers studied here. Comparably small degrees of winter fattening have been observed in other resident species, including not only European tits (Haftorn 1989) but also House Sparrows (*Passer domesticus*) in Illinois (Barnett 1970) and Black-capped Chickadees (*Poecile atricapillus*) in central Ontario (Lawrence 1958). Zebra Finches (*Taeniopygia guttata*) in Australia actually lose, rather than gain, weight during the colder nonbreeding season, thus exhibiting a pattern of body-weight change opposite to the winter fattening characteristic of many north-temperate species (Rozman et al. 2003). The extent of the widely accepted pattern of winter fattening among temperate-zone resident species remains to be determined, but it does not appear to be universal, and in any case generally appears to involve relatively small differences well below 10% of body weight.

Second, although differences in winter fattening in this group did not correlate with all factors presumed to covary with food predictability, two key predictions of this hypothesis were upheld: smaller species exhibited significantly greater winter fattening than larger species and the food-storing Acorn Woodpeckers exhibited considerably less winter fattening than the nonfood-storing species. Thus, in contrast to Haftorn's (1989) finding in European tits, food storage does appear to provide an ecological alternative to the winter fattening that might otherwise be expected in this species.

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LITERATURE CITED

BALDWIN, S. P., AND S. C. KENDEIGH. 1938. Variations in the weight of birds. Auk 55:416–467.

BARNETT, L. B. 1970. Seasonal changes in temperature acclimatization of the House Sparrow *Passer domesticus*. Comparative Biochemistry and Physiology 33:559–578.

BREITWISCH, R. J. 1977. The ecology and behavior of the Red-bellied Woodpecker, *Centurus carolinus* (Linnaeus; Aves: Picidae), in south Florida. M.Sc. thesis, University of Miami, Coral Gables, FL.

BURCHSTED, A. E. 1987. Downy Woodpecker caches food. Wilson Bulletin 99:136–137.

CLARK, C. W., AND J. EKMAN. 1995. Dominant and subordinate fattening strategies: a dynamic game. Oikos 72:205–212.

CLARK, G. A., JR. 1979. Body weights of birds: a review. Condor 81:193–202.

CLENCH, M. H., AND R. C. LEBERMAN. 1978. Weights of 151 species of Pennsylvania birds analyzed by month, age and sex. Bulletin of the Carnegie Museum of Natural History No. 5. Pittsburgh, PA.

COWIE, R. J., J. R. KREBS, AND D. F. SHERRY. 1981. Food storing in Marsh Tits. Animal Behaviour 29: 1252–1259.

EKMAN, J. B., AND M. K. HAKE. 1990. Monitoring starvation risk: adjustments of body reserves in Greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. Behavioral Ecology 1:62–67.

HAFTORN, S. 1989. Seasonal and diurnal body weight variations in titmice, based on analyses of individual birds. Wilson Bulletin 101:217–235.

HANNON, S. J., R. L. MUMME, W. D. KOENIG, S. SPON, AND F. A. PITELKA. 1987. Poor acorn crop, dominance, and decline in numbers of Acorn Woodpeckers. Journal of Animal Ecology 56:197–207.

HELMS, C. W., AND W. H. J. DRURY. 1960. Winter and migratory weight and fat field studies on some North American buntings. Bird-Banding 31:1–40.

HOOGE, P. N. 1991. The effects of radio weight and harnesses on time budgets and movements of Acorn Woodpeckers. Journal of Field Ornithology 62:230–238.

JOHNSON, D. S. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763–772.

KELLAM, J. S., J. C. WINGFIELD, AND J. R. LUCAS. 2004. Non-breeding season pairing behavior and the annual cycle of testosterone in male and female Downy Woodpeckers *Picoides pubescens*. Hormones and Behavior 46:703–714.

KILHAM, L. 1963. Food storing of Red-bellied Woodpeckers. Wilson Bulletin 75:227–234.

KING, J. R. 1972. Adaptive periodic fat storage by birds. Proceedings of the International Ornithological Congress 15:200–217.

KOENIG, W. D. 1980. Variation and age determination in a population of Acorn Woodpeckers. Journal of Field Ornithology 51:10–16.

KOENIG, W. D. 1991. The effects of tannins and lipids on the digestibility of acorns by Acorn Woodpeckers. Auk 108:79–88.

KOENIG, W. D., J. M. H. KNOPS, W. J. CARMEN, M. T. STANBACK, AND R. L. MUMME. 1994. Estimating acorn crops using visual surveys. Canadian Journal of Forest Research 24:2105–2112.

KOENIG, W. D., AND R. L. MUMME. 1987. Population ecology of the cooperative breeding Acorn Woodpecker. Princeton University Press, Princeton, NJ.

KOENIG, W. D., R. L. MUMME, W. J. CARMEN, AND M. T. STANBACK. 1994. Acorn production by oaks in central coastal California: variation within and among years. Ecology 75:99–109.

KOENIG, W. D., P. B. STACEY, M. T. STANBACK, AND R. L. MUMME. 1995. Acorn Woodpecker (*Melanerpes formicivorus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 194. The Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, DC.

LAWRENCE, L. K. 1958. On regional movements and body weight of Black-capped Chickadees in winter. Auk 75:415–443.

LEHIKOINEN, E. 1987. Seasonality of daily weight cycle in wintering passerines and its consequences. Ornis Scandinavica 18:216–226.

LIKNES, E. T., AND D. L. SWANSON. 1996. Seasonal variation in cold tolerance, basal metabolic rate, and maximal capacity for thermogenesis in White-breasted Nuthatches *Sitta carolinensis* and Downy Woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. Journal of Avian Biology 27:279–288.

LIMA, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology 67:377–385.

MACROBERTS, M. H., AND B. R. MACROBERTS. 1976. Social organization and behavior of the Acorn Woodpecker in central coastal California. Ornithological Mongraphs 21:1–115.

MICHALEK, K. G., AND J. MIETTINEN. 2003. *Dendrocopos major* Great Spotted Woodpecker. BWP Update 5:101–184.

MICHALEK, K. G., AND H. WINKLER. 2001. Parental care and parentage in monogamous Great Spotted Woodpeckers (*Picoides major*) and Middle Spotted Woodpeckers (*Picoides medius*). Behaviour 138:1259–1285.

MORTON, M. L., J. L. HORSTMANN, AND C. CAREY. 1973. Body weights and lipids of summering mountain White-crowned Sparrows in California. Auk 90:83–93.

PASINELLI, G., AND J. R. WALTERS. 2002. Social and environmental factors affect natal dispersal and philopatry of male Red-cockaded Woodpeckers. Ecology 83:2229–2239.

PRAVOSUDOV, V. V., AND T. C. GRUBB JR. 1997a. Energy management in passerine birds during the non-breeding season. Current Ornithology 14: 189–234.

PRAVOSUDOV, V. V., AND T. C. GRUBB JR. 1997b. Management of fat reserves and food caches in Tufted Titmice (*Parus bicolor*) in relation to unpredictable food supply. Behavioral Ecology 8:332–339.

PRAVOSUDOV, V. V., T. C. GRUBB JR., P. F. DOHERTY JR., C. L. BRONSON, E. V. PRAVOSUDOVA, AND A. S. DOLBY. 1999. Social dominance and energy reserves in wintering woodland birds. Condor 101: 880–884.

PRAVOSUDOV, V. V., AND J. R. LUCAS. 2001. A dynamic model of short-term energy management in small food-caching and non-caching birds. Behavioral Ecology 12:207–218.

REPASKY, R. R., R. J. BLUE, AND P. D. DOERR. 1991. Laying Red-cockaded Woodpeckers cache bone fragments. Condor 93:458–461.

ROGERS, C. M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? Ecology 68:1051–1061.

ROGERS, C. M., AND C. J. ROGERS. 1990. Seasonal variation in daily mass amplitude and minimum body mass: a test of a recent model. Ornis Scandinavica 21:105–114.

ROZMAN, J., C. RUNCIMAN, AND R. A. ZANN. 2003. Seasonal variation in body mass and fat of Zebra Finches in south-eastern Australia. Emu 103:11–19.

SCHEIGG, K., G. PASINELLI, J. R. WALTERS, AND S. J. DANIELS. 2002. Inbreeding and experience affect response to climate change by endangered woodpeckers. Proceedings of the Royal Society of London Series B 269:1153–1159.

SCHRADER, M. S., E. L. WALTERS, F. C. JAMES, AND E. C. GREINER. 2003. Seasonal prevalence of a haematozoan parasite of Red-bellied Woodpeckers (*Melanerpes carolinus*) and its association with host condition and overwinter survival. Auk 120: 130–137.

SHACKELFORD, C. E., R. E. BROWN, AND R. N. CONNER. 2000. Red-bellied Woodpecker (*Melanerpes carolinus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 500. The Birds of North America, Inc., Philadelphia, PA.

SHERRY, D. F. 1982. Food storage, memory, and Marsh Tits. Animal Behaviour 30:631–633.

SHERRY, D. F. 1989. Food storing in the Paridae. Wilson Bulletin 101:289–304.

SPSS. 1997. SPSS 8.0 for Windows. SPSS Inc., Chicago.

STANBACK, M. T., AND W. D. KOENIG. 1994. Techniques for capturing birds inside natural cavities. Journal of Field Ornithology 65:70–75.

VANDER WALL, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago.

WALTERS, E. L. 2004. Estimating species interactions in a woodpecker tree-hole community at the individual, population, and community levels. Ph.D. dissertation, Florida State University, Tallahassee, FL.

WIKELSKI, M., M. HAU, W. D. ROBINSON, AND J. C. WINGFIELD. 2003. Reproductive seasonality of seven Neotropical passerine species. Condor 105: 683–695.