

Testing optimal body mass theory: Evidence for cost of fat in wintering birds

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Abstract. Optimal body mass models for small wintering birds are central to animal ecology, and offer insights into maximizing individual fitness in a complex environment. Such models assume both costs and benefits of fat deposition, and consider how they affect winter survival probability. Hypothesized mass-dependent costs of elevated fat include increased wing load and subsequent reduced ability to avoid predators, as well as increased predator exposure while feeding to fatten. A likely benefit of winter fat is increased fasting capacity during resource shortages. Here I test optimal body mass theory by searching for both cost and benefits of winter fattening, utilizing interspecific variation in winter fat in natural populations. If increased predation risk is a mass-dependent cost of fattening, wintering birds occupying dense (closed) winter habitat offering low exposure to predators should show (1) higher fat reserves, and (2) higher wing load, than wintering birds occupying less dense (open) habitat offering less protection from predators. This prediction was tested in the two winters in south-central Kansas, a north temperate region with winter precipitation falling as snow and low ambient winter temperatures. The predicted patterns in wing load and winter fat reserve were observed: with phylogeny controlled, both were significantly lower in two open cover species (Dark-eyed Junco *Junco hyemalis*, American Tree Sparrow *Spizella arborea*) than in eight closed cover species (seven sparrow species in the genera *Melospiza*, *Passerella*, and *Zonotrichia*, and the Spotted Towhee *Pipilo maculatus*). Body mass increased with wing area at a greater rate in the closed than in the open cover group, indicating lower body-size specific wing load in the latter group. With phylogeny controlled, fat level varied inversely with resource predictability among three winter foraging guilds occupying a vertical gradient of snowfall probability, indicating both costs and benefits exist in the study system.

This study is the first to support the existence of fat cost with a positive fat-cover relationship in natural populations. These results serve to verify the cost-benefit approach widely taken by optimal body mass models, to studying the relationship between a surrogate fitness variable and factors affecting it in a variable winter environment.

Key words: costs and benefits of fat; *Junco hyemalis*; *Melospiza melodia*; optimal body mass; predation risk; small wintering bird; south-central Kansas, USA; winter fat reserve; winter habitat; winter survival probability; *Zonotrichia querula*.

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INTRODUCTION

A central focus in animal ecology is the study of optimality of traits (Alexander 1996). How

well do animals living in unpredictable environments allocate time and attention to conflicting demands, when different choices can strongly affect survival and reproduction? A useful and

developing example of these processes is energy (fat) storage in small-bodied wintering birds. Adaptive body mass models suggest that a given winter fat reserve reflects a trade-off, whereby winter survival probability, a surrogate fitness variable, is maximized by optimally balancing the costs and benefits of fattening (Lima 1986, McNamara and Houston 1990, Houston and McNamara 1993, Bednekoff and Houston 1994).

At least three costs of fat seem likely (Hedenström 1992, Witter and Cuthill 1993): (1) increased body fat could increase metabolic expenditure associated with movement, (2) while feeding to increase the fat reserve, birds may be increasingly exposed to avian predators; and (3) via increased wing loading, an increased fat reserve may negatively affect one or more aspects of flight performance related to take-off and/or maneuverability under predator attack. The first two may not be independent, as increased metabolism could lead to increased exposure.

Studies testing for predation risk-related costs of increased fat reserve are diverse in approach and have yielded a useful if complex picture (Brodin 2007, Lind et al. 2010). Evidence exists to suggest that increased fat (body mass) during the diel body mass cycle in winter can negatively affect (Lilliendahl 1997, 2000, Krams 2002) or not affect (Kullberg 1998, Kullberg et al. 1998, Veasey et al. 1998, Van Der Veen and Lindström 2000, Macleod 2006) flying ability. Wing loading increases with size of the fat reserve (Chandler and Mulvihill 1992), and thereby negatively affects flight performance (Hedenström 1992, Norberg 1995). European Starlings (*Sturnus vulgaris*) fitted with artificial weights showed temporary declines in flight take-off velocity (Witter et al. 1994). Clear negative effects of increased fat on flying ability have been shown during migration, when increases in this mass component can be large (Kullberg et al. 1996, Lind et al. 1999, Kullberg et al. 2000, Burns and Ydenberg 2002). When European Sparrowhawk (*Accipiter nisus*) abundance increased in a long-term study, great tit (*Parus major*) body mass decreased (Gosler et al. 1995), as it did when this species was exposed to a model hawk (Gentle and Gosler 2001). In keeping with these findings, Coal Tits (*P. ater*) decreased mass in response to simulated increased predation (Carrascal and Polo 1999).

Analysis of ecological factors affecting size of the winter fat reserve suggests that increased fasting capacity during periods of potential resource curtailment is a likely main benefit of fat, as has been maintained (King and Farner 1966, Lima 1986). Thus, during the temperate winter, fat levels of small birds in natural populations can be substantially higher than in early or late winter (e.g., Helms and Drury 1960, Newton 1969, Carey et al. 1978, Cresswell 1998, Gosler 2002, MacLeod et al. 2005), and can also be much greater at higher than at lower latitudes (e.g., Blem 1973, Rogers et al. 1993) and altitudes (Rogers 1995, Smith and Metcalfe 1997). In addition, extensive interspecific differences in winter fat level have been demonstrated with winter fat level varying among different winter foraging guilds occupying a gradient of resource predictability (Lehikoinen 1987, Rogers 1987, Rogers and Smith 1993, Rogers and Heath-Coss 2003).

Further studies can serve to clarify the assumed costs, in the context of benefits, of avian winter fat deposition made by optimal body mass theory. The present report utilizes interspecific variation in winter fat level in natural wintering populations to search for both in a complete test, and was conducted in south-central Kansas, a geographic region with winter precipitation falling as snow and low ambient winter temperatures often below freezing. If increased predation risk is a cost of increased body fat, then (1) size of the winter fat reserve will be lower in bird species occupying open winter habitats compared with species occupying closed winter habitats, as the latter group will be overall less exposed to predators and should experience lower predation risk, (2) as a consequence, in the same groups, wing loading will be lower in the open than in the closed cover group (Lind 2004). A closed winter habitat is defined as any occupied habitat that by virtue of dense vegetation offers protection from aerial hunting predatory hawks. In contrast, an open habitat is a habitat offering less vegetative cover in which wintering birds might hide from such predators.

To test for fat benefit, winter fat levels are compared among ground, ground-tree, and tree winter foraging guilds. Higher fat levels reflecting increased fasting capacity are expected in the ground foraging guild, members of which exploit

Table 1. Nested analysis of variance of wing load and visible fat class for wintering bird populations in two habitat cover groups in south-central Kansas.

Factor	Wing load (g/cm ²)			Visible fat class (0–5)		
	Partial F	df	P	Partial F	df	P
cover	889.34	1	<0.01	22.44	1	<0.01
win (cover)	1.42	2	0.24	1.78	2	0.17
hmon (win cover)	4.02	13	<0.01	3.26	13	<0.01
genus (hmon win cover)	9.63	17	<0.01	5.06	17	<0.01
sp (genus hmon win cover)	3.95	10	<0.01	3.07	10	<0.01

Notes: Abbreviations are: win, winter; hmon, half month period; sp, species. Error df: 201 (wing load), 205 (fat class).

relatively unpredictable winter resources as may be covered suddenly by new snowfall. Ground-tree and tree-foraging species, are expected to show intermediate and low winter fat reserves, due to dependence on resources of intermediate and low unpredictability, respectively. Further details of winter guild classification are described by Rogers (1987, Table 1) and Rogers and Smith (1993).

METHODS

Study site

This study was conducted primarily at the Wichita State University Biological Field Station, Ninescah Reserve (hereafter, field station). The field station includes 133 ha in a habitat mosaic of dense riparian, shrubland and oldfield habitats bordering open fields and tall grasslands, along the Ninescah River in southwestern Sedgwick County, Kansas (37°32' N 97°41' W). Woody vegetation occurring as trees is mostly osage orange (*Maclura*), Siberian elm (*Ulmus*), honeysuckle (*Lonicera*) and box elder (*Acer*). Red cedar (*Juniperus*) occurs as scattered individuals and several dense patches, offering significant roost sites for wintering birds. Frequent dense shrubby patches are composed mainly of sumac and poison ivy (*Rhus*), grape (*Vitis*) and other less common species. Many areas between woody patches are filled in by mixtures of dense grasses and forbs.

Cover comparison and study species

All species in both cover groups forage on the ground in winter (Rogers 1987, Rogers and Smith 1993). The open cover group (two species) consists of the Dark-eyed Junco (*Junco hyemalis*) and American Tree Sparrow (*Spizella arborea*).

Open cover birds often feed in open areas such as edges and middle of fields, and spend a considerable amount of time moving visibly through trees and shrubs between feeding areas as they choose foraging circuits on winter days (Naugler 1993, Nolan et al. 2002, respectively). The closed cover group consists of the Harris's Sparrow (*Zonotrichia querula*), the White-throated Sparrow (*Z. albicollis*), the Lincoln's Sparrow (*M. lincolni*), the White-crowned Sparrow (*Z. leucophrys*), the Spotted Towhee (*Pipilo maculata*), the Swamp Sparrow (*M. georgiana*), the Fox Sparrow (*Passerella iliaca*), and the Song Sparrow (*Melospiza melodia*). In winter these closed cover birds feed in dense cover and are rarely or never seen on obvious foraging circuits (Norment and Shackelton 1993, Falls and Kopachena 1994, Ammon 1995, Chilton et al. 1995, Greenlaw 1996, Mowbray 1997, Weckstein et al. 2002, Arcese et al. 2004, respectively).

The open and closed cover groups are considered to occupy a gradient of predation risk based on a literature review of the winter behavior of relevant predators. The main predator on small wintering birds at the study site is the Cooper's Hawk (*Accipiter cooperi*), a medium-sized accipiter that hunts in the open, primarily by surprising prey from a perch, and by engaging in low transect flights several feet over the ground (Palmer 1988, Rosenfield and Bielfeldt 1993, Ferguson-Lees and Christie 2001). This hawk may pursue prey into cover, but despite frequent observations of its hunting behavior, there are no records of this species directly hunting inside cover to locate wintering songbird prey. Given this hawk species' hunting behavior, all small-bodied wintering birds experience predation risk at the study site (and at other locations in its wintering range), but open cover

species very likely experience greater predation risk than closed cover species. A smaller accipiter, the Sharp-shinned Hawk (*A. striatus*) is rare at the study site, and is not present in most winters.

In the winters of 2008–2009 and 2009–2010, six winter feeding stations were established at the field station and provided continuously with wild bird seed mix from late December through late February. All sites were cleared by shoveling the day of any new snowfall, hence were continuously available to wintering birds. Birds were captured after 15:00 in mist nets set at feeding stations, banded with an individually USGS numbered aluminum leg band, and species, total body mass (Pesola scale, nearest 0.1 g) and visible subcutaneous fat class (0–5 scale, Rogers 1991) were determined. Sample dates were from 22 Dec to 20 Feb 2008–2009, and 15 Jan to 17 Feb 2009–2010. All average capture times by species fell into a 1.3 hr and 1.8 hr range in the two winters, respectively. Therefore capture time is not considered further.

To measure wing area, each bird was held in a standard position in the left hand and the extended right wing was traced onto a sheet of paper. Wing span was measured to the nearest mm with the bird dorsal side down with both wings outstretched. Wing area was measured in the laboratory after Pennycuik (1989), with standardized area in cm² of the traced right wing determined on a computer using Image J, a software program for measuring area of uneven two-dimensional shapes. Total wing loading is right wing area \times 2; wing loading is expressed as g/cm². A random sample of each species' winter fattening strategy is assumed in interspecific comparisons.

Gravimetric and Image J estimates of right wing area from $n = 19$ birds in nine small-bodied species (10–28 g; passerine, piciform) wintering at the field station are related in linear fashion (C. M. Rogers, unpublished data; $R^2 = 0.99$; gravimetric wing area is mass of the cut out wing tracing multiplied by paper density).

Guild comparison

In the winters of 2000–2001 through 2009–2010, birds in the ground, ground-tree, and tree foraging guilds wintering at the field station and one nearby site (in adjacent Butler County, 62 km

northwest of the field station) were captured in mist nets at winter feeding stations similar to those described above and fat classed. Many were captured outside the time interval in which fat class and wing loading were measured in the present study (above stated winters) and these individuals are excluded. Only the winters of 2000–2001, 2001–2002, 2006–2007, 2008–2009, and 2009–2010 are used in this comparison. The sampling period includes birds captured after 15:00 from 22 Dec to 20 Feb (extreme dates for all winters).

Statistical analysis

Statistical analyses were carried out with SAS release 9.2 (SAS Institute 2008) with all tests two-tailed and statistical significance accepted at $P < 0.05$. Recaptured birds were not used in any statistical analysis.

In the cover comparison, nested analyses of variance used cover (open vs. closed) as a fixed factor, and winter, two-week period of capture (half-month), and genus and species as random factors. Thus potential effects of phylogeny (Losos 2011) and lack of data independence were controlled by modelling correlation among individuals in the same level of each factor. Nested analysis of variance makes a test of a fixed factor (here, cover group) more powerful (Zar 2010). Taxonomic designation follows the American Ornithologists' Union Checklist (AOU 2014). Half-month period has been shown to capture meaningful temporal variation in fat reserves and body mass of wintering birds (Rogers and Rogers 1990). Type III sums of squares were used, which structure F-tests with effects of all other factors controlled. Open and closed groups differ in body size, thus body size was included in the analysis as follows. Total body mass was regressed versus wing area for different cover groups and compared with analysis of covariance.

In the guild comparison, nested analyses of variance (Type III sums of squares) use guild as a fixed factor and winter, two-week period, and taxonomic order through species as random factors. In this latter analysis, multiple comparisons (Tukey) adjusted for experiment-wise error rate at $P = 0.05$ are reported.

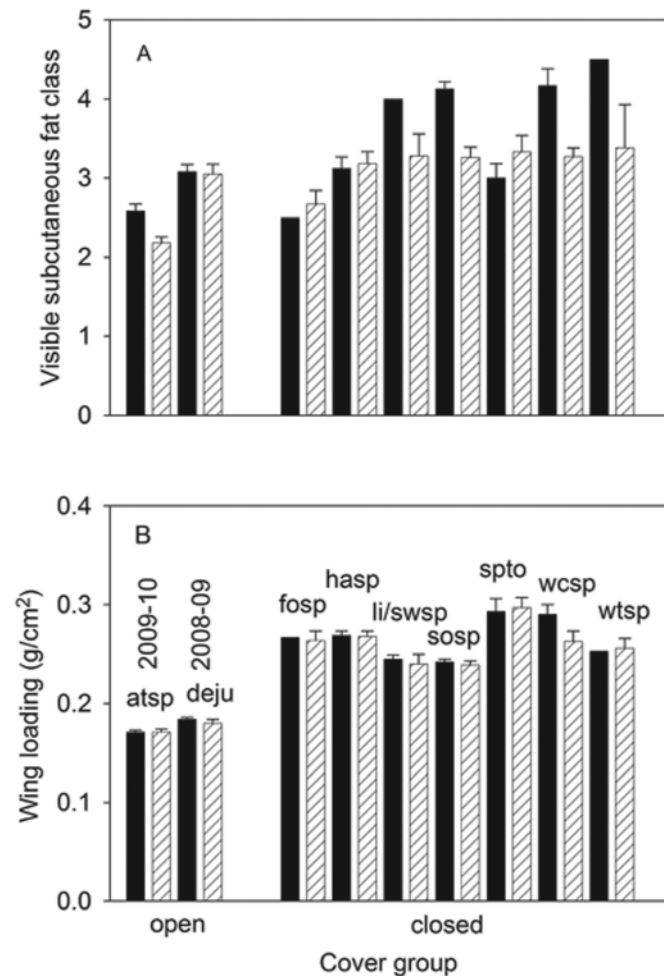


Fig. 1. (A) Visible subcutaneous fat class in the open and closed cover ground-feeding species in the two study winters. Values are mean + 1 SE. Species abbreviations: atsp, American Tree Sparrow ($n = 56$; subsequent numbers also refer to n); deju, Dark-eyed Junco (67); fosp, Fox Sparrow (4); hasp, Harris' Sparrow (46); swsp, Swamp Sparrow (9; first winter only); lisp, Lincoln's Sparrow (2; second winter only); sosp, Song Sparrow (31); spto, Spotted Towhee (8); wcsp, White-crowned Sparrow (17); wtsp, White-throated Sparrow (5). (B) Wing load values for the same species. Values are mean + 1 SE.

RESULTS

Cover comparison

Visible subcutaneous fat class and wing load are shown by species within cover group in Fig. 1A and B, respectively. Nested by winter, two-week period and phylogeny, the data showed a highly significant cover effect on wing load and visible fat class, with both variables being higher in the closed than in the open cover species (Table 1). In both analyses, winter was nonsignificant, and two-week period, genus, and

species were significant if minor factors. A few species had low sample sizes for wing load and fat class; when analyses were repeated using sample size as a weighting factor, results were unchanged except half-month $P = 0.07$ and species $P = 0.13$ (wing load), and half-month $P = 0.22$ and species $P = 0.57$ (fat class) in weighted analyses.

Analysis of covariance showed a significant relationship between wing area and total body mass that varied with cover group: body mass increased with wing area at a greater rate in the

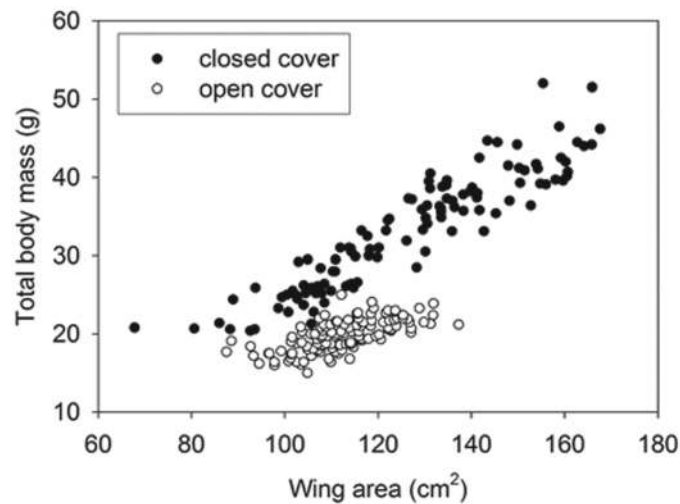


Fig. 2. Total body mass versus wing area in the closed and open cover groups. Associated analysis of covariance in *Results*.

closed than in the open cover group (Fig. 2). Wing area ($F_{1,245} = 416.8$, $P < 0.01$) and cover ($F_{1,245} = 14.5$, $P < 0.01$) were both significantly and positively related to total body mass, but this relationship was steeper in the closed than in the open cover group (Fig. 2; area \times cover group interaction $F_{1,245} = 55.5$, $P < 0.01$). Thus wing load was lower in the open than in the closed cover group, and a cover-specific body size effect existed but was controlled in the cover comparison.

A significant relationship existed between wing area and wing span, and the relationship was quadratic (stepwise regression: wing area = $63.73 + 0.0028$ (wing span²), $F_{1,248} = 3111.4$, $P < 0.01$; wing span $P = 0.09$; $R^2 = 0.93$ without wing span; Fig. 3). The positive quadratic term indicated that among bird species, as wing span increased, wing area increased at a lesser rate.

Guild comparison

Using the same fat class data in Fig. 1 (2008–09 and 2009–10 winters) compared with the tree and ground-tree foraging guilds measured in these same winters in addition to those of 2000–01, 2001–02, fat level varied inversely with resource predictability, being highest among bird species that feed on ground-borne food that may be covered unexpectedly with snow, and lower among bird species that never (tree guild) or infrequently (ground-tree guild) face a possible

resource shortage (Fig. 4, Table 2). Guild was a significant ecological factor, winter and two-week period were significant temporal factors, and genus and species were significant phylogenetic factors. Virtually similar results were obtained when data from all three winter foraging guilds were restricted to the 2008–2009, 2009–2010 winters [guild $F_{2,227} = 122.0$, $P < 0.01$; winter (guild) factor $P = 0.06$; order and family nested within other factors, both $P > 0.18$; all other nested factors significant at $P < 0.01$]. Tukey multiple comparison tests showed all three guilds to differ from one another at $P < 0.05$ in both analyses.

DISCUSSION

Background theory

Among small-bodied wintering birds, two strategic body mass responses to increased predation risk are currently recognized. When birds decrease mass in response to a perceived increase in predation risk (Lima 1986, McNamara and Houston 1990, Bednekoff and Houston 1994), the response is formalized as the “mass-dependent predation risk response”, and is expected under unfavorable resource conditions, e.g., temperate winter environmental conditions (MacLeod et al. 2007). Alternatively, during the “interrupted foraging response”, increased predation risk leading to foraging interruptions may

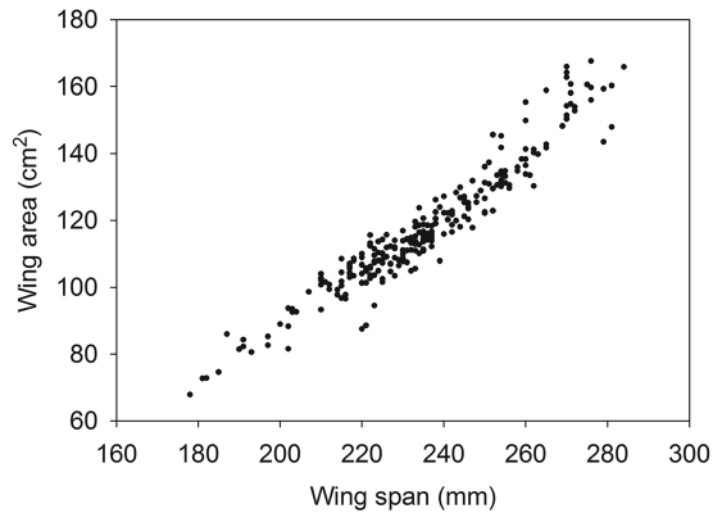


Fig. 3. Total wing area versus wing span in the open and closed cover groups. Regression equation in *Results*.

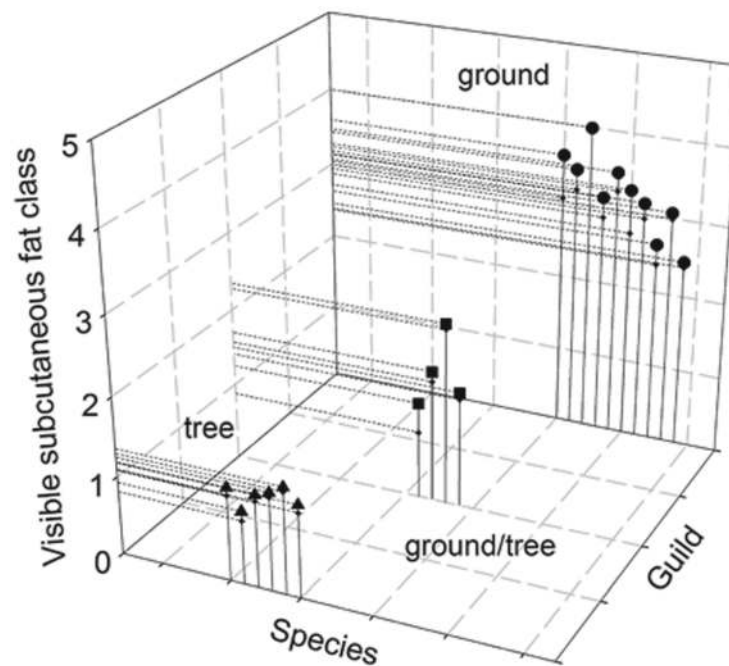


Fig. 4. Visible subcutaneous fat class in the ground, ground-tree, and tree feeding guilds. Means are symbols, crosses are 1 SE, sometimes obscured by symbols. Ground guild (circles; n in Fig. 1), right to left for: American Tree Sparrow, Dark-eyed Junco, Fox Sparrow, Harris' Sparrow, Swamp Sparrow, Song Sparrow, Spotted Towhee, Lincoln's Sparrow, White-crowned Sparrow, White-throated Sparrow. Ground-tree guild (squares), right to left for: Northern Cardinal (*Cardinalis cardinalis*, $n = 32$; subsequent numbers also refer to n), American Goldfinch (*Spinus tristis*, 36), Purple Finch (*Haemorhous purpureus*, 22), American Robin (*Turdus migratorius*, 6). Tree guild (triangles), right to left for: Carolina Chickadee (*Poecile carolinensis*, 11), Black-capped Chickadee (*Poecile atricapilla*, 48), Tufted Titmouse (*Baeolophus bicolor*, 22), Downy Woodpecker (*Picoides pubescens*, 11), Red-bellied Woodpecker (*Melanerpes carolinus*, 14), White-breasted Nuthatch (*Sitta carolinensis*, 8).

Table 2. Nested analysis of variance of visible subcutaneous fat class (0–5) for wintering bird populations in three foraging guilds in south-central Kansas.

Factor	Partial <i>F</i>	df	<i>P</i>
guild	274.4	1	<0.01
win (guild)	3.35	9	<0.01
hmon (win guild)	2.68	25	<0.01
order (hmon win guild)	1.20	7	0.30
fam (order hmon win guild)	1.02	6	0.41
genus (fam order hmon win guild)	6.00	42	<0.01
sp (genus fam order hmon win guild)	3.27	12	<0.01

Notes: Abbreviations in Table 1, except: fam, family. Error df: 351. Sample sizes by guild and species are in Fig. 4.

stimulate the bird to increase fat reserves in the newly unpredictable foraging environment (McNamara et al. 1994, Rands and Cuthill 2001). Fat has increased in response to measures of increased predation risk (Fransson and Weber 1997, Lilliendahl 1998, Pravosudov and Grubb 1998, Bautista and Lane 2000). This body mass response is expected under favorable resource conditions (MacLeod et al. 2007). In the present study, open and closed cover ground-foraging species were studied during winter in south-central Kansas, a geographic region with a harsh interior climate featuring low temperatures, snowfall and short days. Therefore the present data are interpreted within the context of hypothesized mass-dependent predation risk.

Costs and benefits of winter fattening

The present results suggest the existence of mass-dependent costs of winter fattening in small-bodied wintering birds. When winter fat reserves varied between open cover and closed cover groups, so did wing loading, and in the same direction (Fig. 1A, B). Both variables were adjusted for statistically significant but weak phylogenetic effects. This interpretation is further supported by the cover specific body mass - wing area relationship in Fig. 2. In a post hoc analysis, the same relationship was found within 3 hours of dawn in midwinter winter in central Iowa, a more northern geographic location with fewer wintering bird species (C. M. Rogers, unpublished data). Therefore the observed cover difference in wing loading, here controlling for body size, is a robust result having been obtained in widely separated geographic regions with temperate climate.

These findings together suggest a consistent pattern for temperate regions where *Accipiter*

hawks are the dominant predator on small wintering birds. Interspecific differences in exposure to predators based partly on habitat choice have been reported for breeding birds in a geographic region where another *Accipiter* species (*niseus*) is an important predator on small birds (Göttmark and Post 1996). The significance of the increase in fat reserve and wing loading with body size among both open and closed cover species is unclear. Any hypothesis must be consistent with the observation that among flying birds, induced power decreases with body size (Pennycuik 1989).

As has been observed in previous studies of North American (e.g., Rogers 1987) and European (e.g., Lehikoinen 1987) wintering birds, fat varied inversely with resource predictability, being highest among bird species that feed on ground-borne food that may be covered unexpectedly with snow, and lowest among bird species that never face such a resource shortage (Fig. 4). The trend of significantly different fat reserves in all pair-wise combinations of the three winter foraging guilds (Tukey multiple comparisons) suggests fasting capacity is inversely correlated with a vertical gradient of resource unpredictability in the temperate winter of south-central Kansas. Thus both benefits and costs of fat storage exist in the study system.

Several caveats are appropriate. Fat reserve and wing loading were shown to covary at least on a broad interspecific scale, suggesting variation in size of the fat reserve affects wing loading and flight performance to significant degree. This adaptation may be superimposed on adaptation of different flight-related body mass components in the two habitats under study, but addressing this aspect requires detailed body composition analysis. Slight evidence existed for adaptation in

wing shape, with closed cover species showing relatively broader wings to a slight but significant extent (Fig. 3). Thus unaccounted selective factors could independently affect wing area, hence wing loading, but were not identified and studied. Migratory status might lead to enhanced pectoralis size, causing error in the present study, but all species measured are migratory, and were studied in the nonmigratory winter period.

Open cover species were observed to show significantly lower fat reserves than closed cover species. An alternative explanation is that if found, lower fat reserves in the former group are due to greater exposure to harsh weather. This is not likely to be a useful explanation of why fat and wing loading were lower in the open cover group. Temperate-wintering bird species are well-known to fatten under harsh winter weather conditions (King and Farner 1966, Dawson et al. 1983, Haftorn 1989), including Dark-eyed Juncos (Rogers et al. 1993, 1994, Rogers and Reed 2003). In keeping with these observations, at the present study site, from 2000 to 2013 both the junco and tree sparrow showed higher fat in midwinter (colder on average) than in early or late winter (warmer on average) winter (C. M. Rogers, *unpublished data*). A second possibly uncontrolled ecological factor, variation in food supply between the two cover groups, was likely not an important factor independently affecting fat reserves. The primary winter foods of the study species are seeds of forbs and grasses (Rogers 1987), which grow abundantly throughout the study site. Indeed, such foods are almost certainly more abundant in open areas, where productivity is higher and the preferred winter foods of the study species (grass and weed seeds) accumulate. Finally, open cover species show a higher degree of social flocking behavior than closed cover species, possibly reducing predation risk among the former group. No data currently exist to evaluate this interesting possibility.

Conclusion: Species-specific cost-benefit fattening trade-offs

The present study is the first to suggest the existence of fat cost with a positive fat-cover relationship in natural populations, and serves to verify the cost-benefit theoretical approach widely taken by optimal body mass models. These results are consistent with those of Witter et al.

(1994), who showed that fat levels and cover were positively related in aviary-held starlings, and Lind (2004) who modelled general cover effects on fat reserves. The demonstrated costs and benefits of winter fat can be formalized into microhabitat-specific cost-benefit trade-offs varying between the closed and open cover species groups. Open cover birds may feed less at higher vigilance, leading to reduced fat reserves and lower fasting capacity, in a habitat with a higher predator attack rate. In addition, by virtue of reduced wing loading they are capable of greater flight performance in relatively dangerous habitat. The latter is crucial, as capture rate by avian predators goes down once small prey birds are in flight and chased (Lindström 1989, Cresswell 1993). Closed cover species may feed more under reduced vigilance, and maintain higher fat levels, higher wing loading and reduced flight performance in a relatively safe habitat in which these features can be tolerated without reduced survivorship. Optimal body mass models are a primary element of behavioral ecology, and by adopting a cost-benefit approach to winter energy storage are providing clear insight into nonbreeding fitness maximization in a variable environment.

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