Heterogeneous changes in avian body size across and within species

Michael D. Collins, George E. Relyea, Erica C. Blustein & Steven M. Badami

Springer

Springer

steigende Sommertemperaturen generell in Verbindung mit kleinerer Flügellänge, aber hatten keinen Zusammenhang mit fettfreier Masse oder Fettwert. Eine geringere fettfreie Masse, nicht aber Flügellänge oder Fettwert, stand im Zusammenhang mit steigenden Temperaturen im Winter-mittel. Die Temperatureffekte unterschieden sich für keines der drei Maße signifikant zwischen Arten. Über alle nicht-ziehenden Arten hinweg war das Ausmaß der Veränderung der Körpergröße über die Zeit nicht korreliert mit dem Einfluss der mittleren Winter- oder Sommertemperatur und könnte durch andere Faktoren bedingt sein. Unsere Ergebnisse stehen im Kontrast zu denen einer nahegelegenen Beringungsstation, in der weitreichende Abnahmen in der Flügellänge und der fettfreien Körpermasse beobachtet wurden. Unsere Ergebnisse zeigen, dass Populationen einer einzigen Art über kurze Entfernungen (\ 250 km) entgegengesetzte Veränderungen in der Körpergröße aufweisen können. Wir schließen daraus, dass Veränderungen in der Körpergröße über kurze Zeiträume heterogen sind und sich innerhalb von und zwischen Arten auch über kurze Entfernungen unterscheiden können. Ständige Fortschritte im Verständnis des Zusammenhangs zwischen Veränderungen in der Körpergröße und Klimawechsel müssen die Komplexität erfassen und alternative Hypothesen ins Gespräch bringen.

Introduction

Mounting evidence continues to demonstrate that the Earth's climate is changing rapidly (Jones et al. 2001; Karl and Trenberth 2003; Hansen et al. 2006; IPCC 2014). Particularly for birds and other endotherms, climate change has been linked to changes in phenology (Cook 2004; Torti and Dunn 2005; Macmynowski et al. 2007; Miller-Rushing et al. 2008; Ve

captured in western Pennsylvania have exhibited decreasing fat-free mass (mass when fat score is zero) and wing length since 1961, and noted that this trend was consistent with a response to a warming climate. In contrast, Salewski et al. (2010) found no general trend for body size changes in response to climate change between 1972 and 2006 for 12 central European passerines. In a study of 11 bird species in Germany, Salewski et al. (2014) found that morphological changes between 1889 and 2010 were not consistent either within or across species, and that observed changes were not associated with temperature.

In addition to these inconsistent results, Goodman et al. (2012) found that body sizes of birds in California increased between 1983 and 2009, and attributed these changes to increases in primary productivity or climatic variation. Thus, although climate change has been associated with morphological responses in birds, observed changes have varied across species and across studies (Gardner et al. 2011). Given the myriad factors that can influence body size (Peters 1983; Calder 1984) and the complex interaction between climate and body size (Ozgul et al. 2009, 2010; Chown 2012; Huey et al. 2012), observed heterogeneity in the magnitude and direction of body size responses to climate change should not be surprising (Millien et al. 2006). Here, we examine whether avian body size changes also vary regionally within species and ask whether populations of the same species exhibit differing changes in body size over time. Our objectives in this exploratory analysis were to (1) examine how body sizes of resident and short-distance migratory birds have changed in Laurel, Maryland, from 1980 to 2012, (2) evaluate whether observed morphological monsebody

free mass, time of day and fat score were also included as fixed continuous variables.

For each of the 20 species included in the GLMM, we estimated the morphological change (i.e., change in wing length and change in fat-free mass over years) using the MIXED procedure in the SAS program. We included age, sex, year, and Julian day as fixed effects. For analyses of fat-free mass, we also included time of day and fat score.

We examined the influence of annual temperature variation only on resident species, because short-distance migrants might be less impacted by regional temperatures that were used as explanatory variables. We added mean summer temperature (SumTemp) and mean winter temperature (WintTemp) as continuous fixed effects to the two GLMMs (for wing length and fat-free mass) described previously. To test whether species differed in their slopes to SumTemp and WintTemp, we compared models with and without the heterogeneity in slopes with a likelihood ratio test (West et al 2006). Significance of effects was determined from F-tests (Type III SS). We estimated the influence of mean summer and mean winter temperature on each species separately by adding SumTemp and WintTemp to the MIXED models described previously.

To examine overall changes in body condition between 1980 and 2012, we used GLMM to model fat score as a function of year, time of day, Julian date, age, and sex with the GLIMMIX procedure in SAS. To test whether species differed in their slopes, we compared models with and without the heterogeneity in slopes with a likelihood ratio test (West et al 2006). We examined changes in fat score for each species separately with the MIXED procedure, with year, time, Julian date, age, and sex as explanatory variables.

Long-term declines in body size could indicate deteriorating environmental conditions (Teplitsky et al 2008). Environmental degradation could reduce the quality and availability of food, resulting in smaller and less healthy individuals, which could scale up to population declines. To examine this possibility, we examined Pearson correlation coefficients between changes in body size (wing length and fat-free mass), changes in body condition (fat score), and changes in population size across species. Positive correlations could indicate environmental degradation (Van Buskirk et al 2010). Winter population density was obtained from the Christmas Bird Count (www.audubon.org/bird/cbc/index.html; we selected US ENTIRE United States for the County/Region. Breeding population density was estimated from Breeding Bird Survey data using the New England/Mid-Atlantic Coast region for local breeders. For northern breeders, we used the Atlantic Northern Forest region; when a species population trend was not found in this region, we used Boreal Hardwood Transition or consulted range maps

from Birds of North America species accounts to select a suitable region.

Results

Morphological changes over time

Mean wing length across species increased between 1980 and 2012 ($F_{1,\ 35311}$ = 13.00, $P < 0.001$, Table 1).

Table 1 Summaries of generalized linear mixed models (GLMMs) to examine morphological changes (log-transformed wing length, log-transformed fat-free mass, and fat score) for 20 resident and short-distance migrant species from 1980 to 2012

Source of variation	Estimate	SE	F value	P
Wing length				
Year	0.000129	0.000036	13.00	< 0.001
Julian day	0.000198	0.000011	328.41	< 0.001
Age				
AHY	0.01921	0.000454	1791.56	< 0.001
HY	0			
Sex				
Female	- 0.02607	0.00076	4227.10	< 0.001
Male	0.03445	0.00077		
Unknown	0			
Fat-free				
Year	- 0.000060	0.000088	0.43	0.51
Time	0.000058	0.000003	295.27	< 0.001
Julian day	0.000713	0.00002	1238.65	< 0.001
Age				
AHY	0.00858	0.00082	110.86	< 0.001
HY	0			
Sex				
Female	- 0.02976	0.00137	1554.50	< 0.001
Male	0.03619	0.00137		
Unknown	0			
Fat			1406.37	< 0.001
Fat score				
Year	- 0.00525	0.00035	224.83	< 0.001
Time	0.00029	0.00003	98.08	< 0.001
Julian day	0.00693	0.000171	1634.40	< 0.001
Age				
AHY	0.04073	0.007099	32.91	< 0.001
HY	0			
Sex				
Female	- 0.00785	0.01189	17.29	< 0.001
Male	- 0.05959	0.01194		
Unknown	0			

Estimates are coefficients; negative coefficients indicate declining size and positive coefficients indicate increasing size

SE standard error

Although significant, the mean magnitude of change in wing length was just 0.41 % over the course of the study. Change in wing length differed significantly across species (v^2 = 116,282.7, df = 1, P\ 0.001) and ranged from - 0.90 to ? 2.47 %. Of the 20 species examined, 16 exhibited an increasing trend in wing length (P = 0.012, two-tailed binomial test, Table 2). Of species with a significant trend, 10 of 11 exhibited increases in wing length (P = 0.003, two-tailed binomial test, Table 2), with only Dark-eyed Juncos (Junco hyemalis) showing a significant decrease.

Fat-free mass showed a negative but non-significant trend across years ($F_{(1, 33481)}$ = 0.43, P = 0.51, Table 1), but species varied significantly in change in fat-free mass (v^2 = 145,264.4, df = 1, P\ 0.001), ranging from - 4.11 to ? 5.22 % between 1980 and 2012. Fat-free mass of Blue Jays (Cyanocitta cristata, - 4.11 %), Ruby-crowned Kinglets (Regulus calendula, - 1.18 %), and White-throated Sparrows (Zonotrichia albicollis, - 0.73 %) decreased significantly, and fat-free mass of three species (Eastern Phoebe, Sayornis phoebe, 5.22 %; Gray Catbird, Dumetella carolinensis, 0.66 %; and Tufted Titmouse,

Table 2 Changes in log-transformed wing length and log-transformed fat-free mass (9 10,000) and change in fat score on a 0–4 scale (9 10,000) 1980–2012

Family Common name	Species code	Scientific name	Wing		Fat-free mass		Fat score	
			Est.	SE	Est.	SE	Est.	SE
Cardinalidae								
Northern Cardinal	NOCA	Cardinalis cardinalis	7.63	1.63	4.71	3.41	- 1.7	6.9
Corvidae								
Blue Jay	BLJA	Cyanocitta cristata	- 2.80	2.39	- 13.10	5.37	- 27.8	17.9
Emberizidae								
Dark-eyed Junco	SCJU	Junco hyemalis	- 2.00	0.36	- 1.60	0.86	- 27.8	7.5
Swamp Sparrow	SWSP	Melospiza georgiana	- 0.01	1.41	1.17	2.79	- 80.6	22.2
Song Sparrow	SOSP	Melospiza melodia	0.11	1.12	- 1.90	2.04	- 56.2	14.7
Fox Sparrow	FOSP	Passerella iliaca	0.40	2.07	- 7.10	3.69	4.1	32.3
Eastern Towhee	EATO	Pipilo erythrophthalmus	1.78	2.01	0.27	1.91	- 67.7	16.0
Field Sparrow	FISP	Spizella pusilla	4.39	1.78	2.00	2.75	3.6	22.2
White-throated Sparrow	WTSP	Zonotrichia albicollis	- 0.20	0.43	- 2.30	0.97	- 65.7	8.8
Mimidae								
Gray Catbird	GRCA	Dumetella carolinensis	2.71	0.55	2.05	0.84	- 57.0	7.5
Paridae								
Tufted Titmouse	TUTI	Baeolophus bicolor	6.64	1.63	8.48	3.47	- 11.6	6.3
Carolina Chickadee	CACH	Poecile carolinensis	3.84	1.75	4.61	3.42	- 22.1	8.8
Parulidae								
Yellow-rumped Warbler	MYWA	Setophaga coronata	7.02	0.83	3.31	2.11	14.0	17.8
Regulidae								
Ruby-crowned Kinglet	RCKI	Regulus calendula	1.32	0.63	- 3.70	1.39	- 45.9	16.4
Golden-crowned Kinglet	GCKI	Regulus satrapa	0.72	0.80	- 0.30	2.01	- 111.1	23.7
Troglodytidae								
Carolina Wren	CARW							

Baeolophus bicolor 2.75 %) increased significantly, from 1980 (Table 2). Across species, change in wing length and change in fat-free mass were positively correlated (r = 0.82, N = 20, P \ 0.001, Fig. 1).

Across all species, fat scores decreased between 1980 and 2012 ($F_{1, 35272}$ = 224.83, P \ 0.001, Table 1), with a decrease of 0.17 (on a 0–4 scale) over the course of the study. Species exhibited significant variation in fat score change over time (χ^2 = 3704.65, df = 1, P \ 0.001, Table 2), ranging from - 0.36 to ? 0.04 over 32 years. Eleven of the 20 species exhibited a significant decline in fat score, and none showed a significant increase (P \ 0.001, two-tailed binomial test, Table 2).

did not differ significantly across species (χ^2 = 3.9, df = 1, P = 0.10, Table 4). Eastern Towhees (*Pipilo erythrophthalmus*) and Northern Cardinals (*Cardinalis cardinalis*) exhibited significantly shorter wings with increases in mean summer temperature, and no species had significantly longer wings (Table 4). Increasing mean winter temperatures were not related to wing lengths of residents ($F_{1, 6654}$ = 0.03,

Body size changes and annual temperature variation

Wing length

Across resident species, increasing mean summer temperatures were associated with shorter wing lengths ($F_{1, 6654}$ = 5.77, P = 0.016, Table 3). Although significant, the magnitude of wing change was small (0.26 %/ C). The association between mean summer temperature and wing length ranged from - 0.63 % to ? 0.15 %/ C but

Table 3 Summaries of generalized linear mixed models (GLMMs) for log-transformed wing length, log-transformed fat-free body mass and fat score for 9 resident species from 1980–2012

Source of variation	Estimate	SE	F value	P
Wing length				
Year	0.000372	0.000082	20.55	\ 0.001
Julian day	0.000207	0.000022	89.93	\ 0.001
Age				
AHY	0.02201	0.001468	224.64	\ 0.001
HY	0			
Sex				
Female	- 0.01659	0.00474	223.98	\ 0.001
Male	0.02731	0.00486		
Unknown	0			
SumTemp	- 0.00257	0.00107	5.77	0.016
WintTemp	0.000091	0.000548	0.03	0.87
Fat-free mass				
Year	0.00023	0.000158	2.11	0.15
Time	0.000057	0.000008	50.90	\ 0.001
Julian day	0.000509	0.000034	229.09	\ 0.001
Age				
AHY	0.01898	0.002209	73.87	\ 0.001
HY	0			
Sex				
Female	- 0.02288	0.00715	219.73	\ 0.001
Male	0.04268	0.00733		
Unknown	0			
Fat			49.53	\ 0.001
SumTemp	- 0.00227	0.001293	3.08	0.079
WintTemp	- 0.00188	0.000639	8.63	0.003
Fat score				
Year	- 0.00343	0.000617	30.92	\ 0.001
Time	0.000182	0.000047	15.23	\ 0.001
Julian day	0.001442	0.000194	55.00	\ 0.001
Age				
AHY	0.02982	0.01286	5.38	0.020
HY	0			
Sex				
Female	- 0.02176	0.03860	2.81	0.061
Male	- 0.06121	0.03959		
Unknown	0			
SumTemp	0.000068	0.006282	0.00	0.99
WintTemp	- 0.00911	0.004775	3.64	0.056

Estimates are coefficients, and SE is standard error

Fat score

Fat score of residents was not associated with increasing mean summer temperature ($F_{1, 6629} = 0.00$, P = 0.99, Table 3) and did not vary significantly across species ($v^2 = 0.08$, df = 1, P = 0.87). Fat score did not vary with mean winter temperature ($F_{1, 6629} = 3.64$, P = 0.06), and the relationship with mean winter temperature did not vary significantly across species ($v^2 = 1.95$, df = 1, P = 0.27). Fat score of Song Sparrows (*Melospiza melodia*) decreased with increasing mean winter temperature (Table 3).

Correlated morphological changes and annual temperature variation

Across resident species, the effects of mean summer temperature on wing length and on fat-free mass were not correlated ($r = 0.44$, N = 9, P = 0.24, Fig. 2). The effects of mean winter temperature on wing length and fat-free mass were positively correlated ($r = 0.80$, N = 9, P = 0.01, Fig. 3). Wing responses to increasing summer temperature and to increasing winter temperature were not correlated ($r = 0.04$, N = 9, P = 0.93). Change in fat-free mass with increasing summer temperature was also not correlated with change in fat-free mass with increasing winter temperature ($r = 0.44$, N = 9, P = 0.24).

Body size changes over time and annual temperature variation

Across resident species, change in wing length over time was not correlated with response to mean summer temperature ($r = - 0.60$, N = 9, P = 0.09) or to mean winter temperature ($r = - 0.27$, N = 9, P = 0.48). Change in fat-free mass over time was not correlated with response to mean summer temperature ($r = 0.26$, N = 9, P = 0.50) or to mean winter temperature ($r = - 0.60$, N = 9, P = 0.09).

Assessment of deteriorating environmental conditions

Changes in wing length and fat score over time were weakly positively correlated across species ($r = 0.45$, N = 20, P = 0.045, Fig. 4), but these morphological responses were not correlated with any measure of population change (N = 20, P [0.07 for all tests, Table 5). Change in mass over time was weakly correlated with change in breeding population density since 1980 (r = 0.45, N = 20, P = 0.049, Fig. 5; Table 5), but not with change in winter population density ($r = 0.26$, N = 20, P = 0.27, Table 5).

Discussion

We document widespread increases in wing length, but not in fat-free mass, across 20 resident and short-distance migrant species between 1980 and 2012. Annual

temperature variation was associated with some changes in body size, but the magnitude and direction of change depended on the trait examined. In contrast, Van Buskirk et al. (2010) found that wing length and fat-free mass of passerines had decreased since 1961 in western Pennsylvania, and McCoy (2012) found that mean wing length of three of six resident species in Connecticut declined between two sampling periods, 1874–1952 and 1958–2010. These results suggest that changes in avian body size can exhibit different patterns over regional spatial scales, and

were small: - 0.13 to ? 0.16 %/year in our study, - 0.08 to ? 0.02 %/year in Van Buskirk et al. (2010), and - 0.03 to ? 0.08 %/year in Goodman et al. (2012). In our study, 16 of 20 species showed a trend of increasing wing length, and 10 of these trends were statistically signi cant. Van Buskirk et al. (2010) analyzed 19 of the 20 species in our study (all except Carolina Chickadee [Poecile carolinensis]) and found that wing length decreased signi cantly in 12 species and did not increase signi cantly in any species. Dark-eyed Juncos, the only species that showed signi cantly shorter wing length in our study, did not show a signi cant trend in theirs. McCoy's (2012) ndings also show that species can exhibit differing body size changes. Wing lengths of Blue Jays, the only species in common with our study, decreased

signi cantly in Connecticut, but did not change signi - cantly in our study. Van Buskirk et al. (2010) analyzed all six species examined by McCoy (2012). Only Purple Fin- ches (Haemorhous purpureus), which decreased in both locations, and White-breasted Nuthatches (Sitta caroli- nensis), which showed no signi cant trend, exhibited consistent patterns. Some species showed signi cant decreases in western Pennsylvania, but no signi cant change in Connecticut, and these discrepancies might be

associated with wet-bulb temperature, a measure that incorporates temperature and humidity, than with temperature alone. We found that annual variation in mean summer and mean winter temperatures was related to some measures of body size of residents. Increasing mean summer temperatures were associated with shorter wing

References

Acquarone C, Cucco M, Malacarne G, Silvano F (2004) Temporary shift of body size in hooded crow *Corvus corone cornix* of NW Italy. Folia Zool 53:379–384

Arnett AE, Gotelli NJ (1999) Bergmann's rule in the ant lion *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae): geographic variation in body size and heterozygosity. J Biogeogr 26:275–283. doi:10.1046/j.1365-2699.1999.00271.x

Ashton KG (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Glob Ecol Biogeogr 11:505–523. doi:10.1046/j.1466-822X.2002.00313.x

Atkinson D (1994) Temperature and organism size—a biological law for ectotherms? Adv Ecol Res 25:1–58

Bergmann C (1847) Ueber die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse. Gottinger Stud 3:595–708

Blackburn TM, Gaston KJ (1996) Spatial patterns in the body sizes of bird species in the new World. Oikos 77:436–446

Blackburn TM, Gaston KJ, Loder N (1999) Geographic gradients in body size: a clarification of Bergmann's rule. Divers Distrib 5:165–174

Brown CR, Brown MB (1999) Intense natural selection on tail and bill morphology in Barn Swallows *Hirundo rustica* during severe weather. Ibis (Lond 1859) 141:52–659

Bumpus HC (1899) Biology lectures. Mar Biol Lab Woods Hole 11:209

Calder WA (1984) Size, function and life history. Harvard University Press, Cambridge

Caruso NM, Sears MW, Adams DC, Lips KR (2014) Widespread rapid reductions in body size of adult salamanders in response to climate change. Glob Chang Biol 20:1751–1759. doi:10.1111/gcb.12550

Chown SL (2012) Trait-based approaches to conservation physiology: forecasting environmental change risks from the bottom up. Philos Trans R Soc B Biol Sci 367:1615–1627. doi:10.1098/rstb.2011.0422

Crick HQP (2004) The impact of climate change on birds. Ibis (Lond 1859) 146:48–56

Cushman JH, Lawton JH, Manly BFJ (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. Oecologia 95:30–37. doi:10.1007/BF00649503

Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. Proc Natl Acad Sci USA 106:12788–12793. doi:10.1073/pnas.0902080106

Davis S (1981) The effects of temperature change and domestication on the body size of Late Pleistocene to Holocene mammals of Israel. Paleobiology 7:101–114

Desrochers A (2010) Morphological response of songbirds to 100 years of landscape change in North America. Ecology 91:1577–1582. doi:10.1890/09-2202.1

Easterling DR, Evans JL, Groisman PY et al (2000) Observed variability and trends in extreme climate events: a brief review. Bull Am Meteorol Soc 81:417–425. doi:10.1175/1520-0477(2000)081<0417:OVATIE>2.3.CO;2

Freeman S, Jackson WM (1990) Univariate metrics are not adequate to measure avian body size. Auk 107:69–74

Gardner JL, Peters A, Kearney MR et al (2011) Declining body size: a third universal response to warming? Trends Ecol Evol 26:285–291. doi:10.1016/j.tree.2011.03.005

Gardner JL, Amano T, Backwell PRY et al (2014a) Temporal patterns of avian body size reflect linear size responses to broadscale environmental change over the last 50 years. J Avian Biol 45:1–7. doi:10.1111/jav.00431

Gardner JL, Amano T, Mackey BG et al (2014b) Dynamic size responses to climate change: prevailing effects of rising temperature drive long-term body size increases in a semi-arid passerine. Glob Chang Biol 20:2062–2075. doi:10.1111/gcb.12507

Geist V (1987) Bergmann's rule is invalid. Can J Zool 65:1035–1038

Goodman RE, Lebuhn G, Seavy NE et al (2012) Avian body size changes and climate change: warming or increasing variability? Glob Chang Biol 18:63–73. doi:10.1111/j.1365-2486.2011.02538.x

Gosler AG, Greenwood JJD, Baker JK, Davidson NC (1998) The field determination of body size and condition in passerines: a report to the British Ringing Committee. Bird Study 45:92–103. doi:10.1080/00063659809461082

Graves GR (1991) Bergmann's rule near the equator: latitudinal clines in body size of an Andean passerine bird. Proc Natl Acad Sci USA 88:2322–2325

Hansen J, Sato M, Ruedy R et al (2006) Global temperature change. Proc Natl Acad Sci USA 103:14288–14293. doi:10.1073/pnas.0606291103

Huey RB, Kearney MR, Krockenberger A et al (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos Trans R Soc B Biol Sci 367:1665–1679. doi:10.1098/rstb.2012.0005

IPCC (2014) Climate change 2014: Impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press,

Meiri S, Dayan T (2003) On the validity of Bergmann's rule. J Biogeogr 30:331–351

Miller-Rushing AJ, Lloyd-Evans TL, Primack RB, Satzinger P (2008) Bird migration times, climate change, and changing population sizes. Glob Chang Biol 14:1959–1972. doi:10.1111/j.1365-2486.2008.01619.x

Millien V, Kathleen Lyons S, Olson L et al (2006) Ecotypic variation in the context of global climate change: revisiting the rules. Ecol Lett 9:853–869. doi:10.1111/j.1461-0248.2006.00928.x

Min SK, Zhang X, Zwiers FW, Hegerl GC (2011) Human contribution to more-intense precipitation extremes. Nature 470:378–381. doi:10.1038/nature09763

Olalla-Tárraga MÁ, Rodríguez MÁ, Hawkins BA (2006) Broad-scale patterns of body size in squamate reptiles of Europe and North America. J Biogeogr 33:781–793. doi:10.1111/j.1365-2699.2006.01435.x

Olson VA, Davies RG, Orme CDL et al (2009) Global biogeography and ecology of body size in birds. Ecol Lett 12:249–259. doi:10.1111/j.1461-0248.2009.01281.x

Ozgul A, Tuljapurkar S, Benton TG, et al (2009) The dynamics of phenotypic change and the shrinking sheep of St. Kilda. Science (80-) 325:464–7

Ozgul A, Childs DZ, Oli MK et al (2010) Coupled dynamics of body mass and population growth in response to environmental change. Nature 466:482–485. doi:10.1038/nature09210

Parmesan C, Yohe G (2003) A globally coherent ngerprint of climate change impacts across natural systems. Nature 421:37–42

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Pyle P (1997) Identi cation guide to North American birds. Part 1. Slate Creek Press, Bolinas

Ray C (2005) The application of Bergmann's and Allen's rules to the poikilotherms. J Morphol 106:85–108. doi:10.1002/jmor.1051060104

Rising JD, Somers KM (1989) The measurment of overall body size in birds. Auk 106:666–674

Rosenzweig ML (1968) The strategy of body size in mammalian carnivores. Am Midl Nat 80:299–315

Salewski V, Hochachka WM, Fiedler W (2010) Global warming and Bergmann's rule: do central European passerines adjust their