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REVIEW

Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review

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Abstract Comparative analyses of avian energetics often involve the implicit assumption that basal metabolic rate (BMR) is a fixed, taxon-specific trait. However, in most species that have been investigated, BMR exhibits phenotypic flexibility and can be reversibly adjusted over short time scales. Many non-migrants adjust BMR seasonally, with the winter BMR usually higher than the summer BMR. The data that are currently available do not, however, support the idea that the magnitude and direction of these adjustments varies consistently with body mass. Long-distance migrants often exhibit large intra-annual changes in BMR, reflecting the physiological adjustments associated with different stages of their migratory cycles. Phenotypic flexibility in BMR also represents an important component of short-term thermal acclimation under laboratory conditions, with captive birds increasing BMR when acclimated to low air temperatures and vice versa. The emerging view of avian BMR is of a highly flexible physiological trait that is continually adjusted in response to environmental factors such as temperature. The within-individual variation observed in avian BMR demands a critical re-examination of approaches used for comparisons across taxa. Several key questions concerning the shapes and other properties of avian BMR reaction norms urgently need to be addressed, and hypotheses concerning metabolic adaptation should explicitly account for phenotypic flexibility.

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Abbreviations

BMR	Basal metabolic rate
T_a	Air temperature
M_b	Body mass
M_{sum}	Summit metabolism
FMR	Field metabolic rate
MMR	Maximal metabolic rate
T_{CL}	Temperature at cold limit

Introduction

Phenotypic flexibility, one category of phenotypic plasticity, involves reversible within-individual phenotypic adjustments (Piersma and Drent 2003). Birds exhibit phenotypic flexibility in numerous physiological traits, including digestive enzyme activities (Afik et al. 1995; Karasov 1996; Levey et al. 1999; Martinez del Rio et al. 1995), cutaneous evaporation rates (Haugen et al. 2003; Hoffman and Walsberg 1999; Marder and Arieli 1988; McKechnie and Wolf 2004b), and the upper and lower limits of metabolic power (Battley et al. 2001; McKechnie et al. 2007; Piersma et al. 1995; Swanson 1990; Swanson (2007); Tieleman et al. 2003). Flexibility in physiological phenotypes has far-reaching implications for ecological and evolutionary physiologists, since many of the traits that are compared among taxa are not fixed, but fluctuate through time within individuals. The inter- and/or intraspecific variation observed in avian physiological traits thus reflects a number of sources of phenotypic variation, including body mass, phylogenetic inertia and genotypic adaptation, as well as phenotypic flexibility associated with acclimation/acclimatization history.

Basal metabolic rate (BMR) is the minimum maintenance metabolism of a normothermic resting endotherm, measured at thermoneutral environmental temperatures and in the absence of thermoregulatory, digestive, circadian or other increments in metabolic heat production (Dawson and Whittow 2000; McNab 1997). Whereas measurements of field metabolic rate (FMR; total daily energy expenditure) allow researchers to quantify total energy requirements and elucidate patterns of energy allocation in free-ranging animals (e.g., Nagy 1987; Tieleman et al. 2004; Weathers and Sullivan 1993), BMR is a standardized, baseline parameter whose long history of empirical measurements and comparative analyses has made it an extremely useful trait for comparing metabolic power output among avian taxa (Bennett and Harvey 1987; Lasiewski and Dawson 1967; McKechnie et al. 2006; McNab 1988; Tieleman and Williams 2000; Weathers 1979; White et al. 2007). Recent analyses have shown that, once body mass (M_b) effects are removed, residual interspecific variation in BMR is correlated with summit metabolism (M_{sum}, the maximum resting rate of metabolic thermogenesis) in birds (Rezende et al. 2002) and with M_{sum} and FMR in mammals (White and Seymour 2004), although Ricklefs et al. (1996) found no correlation between avian BMR and FMR. These M_b-independent correlations between BMR and ecologically-relevant measures of energy expenditure, when taken together with a number of studies reporting significant repeatabilities for avian BMR (e.g., Bech et al. 1999; Rønning et al. 2005; Tieleman et al. 2003), emphasize the validity of using BMR as a comparative metabolic parameter.

An increasing number of studies reveal considerable phenotypic flexibility in avian BMR, a finding that calls for new approaches to comparative analyses, and a fundamental change in how physiologists view the ecological and evolutionary significance of intra- and interspecific BMR variation. In this paper, I review published data on phenotypic flexibility in avian BMR, and discuss the implications of within-individual variation for comparative analyses seeking to infer metabolic adaptation. I also identify key questions that need to be addressed before phenotypic flexibility in avian BMR can be conceptually integrated with other sources of metabolic variation.

Patterns of phenotypic flexibility in avian BMR

Within-individual adjustments in avian BMR have typically been examined in one of three contexts: seasonal acclimatization, the physiological adjustments associated with long-distance migration, or short-term thermal acclimation in artificial environments. I follow Piersma and Drent (2003) and numerous other authors in using the term “acclimation” to refer to responses to artificial environments and “acclimatization” to refer to responses to natural environments, although this distinction can be blurred, for instance when the aviaries that captive birds are housed in are enclosed during winter but not summer (e.g., Riddle et al. 1934).

Seasonal acclimatization

Phenotypic flexibility in BMR represents an important component of seasonal acclimatization for many Holarctic species (Table 1, also reviewed in Dawson 2003 and Swanson 2007). Seasonal metabolic adjustments have been investigated in approximately 20 species representing seven orders (Table 1). With few exceptions (Dawson et al. 1985; Pohl 1971; Rising and Hudson 1974), significant BMR adjustments occurred between seasons, ranging in magnitude from <10 to 64% for total BMR, and from <10 to 40% for mass-specific BMR (Table 1). The largest fractional seasonal adjustment in total BMR was recorded in house sparrows (*Passer domesticus*; Arens and Cooper 2005), whereas the largest mass-specific adjustment was observed in downy woodpeckers (*Picoides pubescens*; Liknes and Swanson 1996). Piersma et al. (1995) reported even larger adjustments (110% of total BMR and 55% of mass-specific BMR) in captive red knots (*Calidris canutus islandica*) that had been housed in outdoor aviaries for 2–3 years. However, it is likely that these large adjustments were at least partly associated with the birds’ annual migratory cycle, rather than solely representing seasonal acclimatization (Piersma et al. 1995).

Recent evidence suggests that the winter BMR of species resident in highly seasonal environments reflects the prevailing conditions immediately before metabolic measurements. In black-capped chickadees (*Poecile atricapillus*), dark-eyed juncos (*Junco hyemalis*) and American tree sparrows (*Spizella arborea*), BMR was most strongly correlated with short- (0–7 days preceding measurements) and medium-term (14–30 days preceding measurements) climatic variables (Swanson and Olmstead 1999). Similarly, the best multivariate model for variation in the winter BMR of great tits (*Parus major*) included average minimum air temperature (T_a) during the week preceding measurements as a predictor variable (Broggi et al. 2007).

Most studies of seasonal metabolic adjustments have involved Holarctic species and, with few exceptions, have found that BMR is up-regulated during winter (Table 1, Fig. 1b). In contrast, Maddocks and Geiser (2000) found that mass-specific BMR in Australian silvereyes (*Zosterops lateralis*) was 25% higher in summer, directionally opposite to the typical pattern for similarly sized Holarctic species. This observation highlights the need for more data on seasonal BMR adjustments in species from tropical and subtropical latitudes.

Table 1 Avian species in which phenotypic flexibility in basal metabolic rate (BMR) has been observed

		M_b (g)	BMR 1 (W)	BMR 2 (W)	Magnitude (%)		Increase direction	W/S	Reference	Comments
Acclimation										
Rock dove	*Columba livia*	265	1.248	1.328	6.4	MS	Summer		1	Enclosed in winter
Laughing dove	*Streptopela senegalensis*	92.6	0.546	0.665	21.8	T	Cold		2	
Red knot	*Calidris canutus islandica*	127	0.820	1.025	26.0	T*	Cold		3	
Skylark	*Alauda arvensis*	31.6			25.3	T	Cold		4	
Woodlark	*Lullula arborea*	25.6			4.7	T*	Cold		4	
Hoopoe lark	*Alaemon alaudipes*	36.5			18.0	T	Cold		4	
Hoopoe lark	*Alaemon alaudipes*	40.4	0.381	0.542	42.2	T	Cold		5	
Dunn's lark	*Eremalauda dunni*	20.5			29.1	T	Cold		4	
Spike-heeled lark	*Chersomanes albofasciata*	24.7			12.2	T	Cold		4	
Garden warbler	*Sylvia borin*	24.5	0.382	0.452	18.5	T	Cold		6	
Yellowhammer	*Emberiza citrinella*	28.7	0.501	0.522	4.2	MS	Winter		7	
Acclimatization										
Northern Bobwhite	*Colinus virginianus*	218	1.155	1.259	9.0	T	Winter	1.090	8	Captive-raised
Downy woodpecker	*Picoides pubescens*	24.1	0.330	0.491	39.8	MS	Winter	1.398	9	Wild-caught
Puerto Rican tody	*Todus mexicanus*	6.5	0.018	0.021	15.7	MS	Breeding		10	
Monk parakeet	*Myiopsitta monachus*	83.1	0.515	0.681	27.9	MS	Summer	0.756	11	Captive-raised
Long-eared owl	*Asio otus*	244	1.314	1.408	8.0	MS	Winter	1.072	12	Captivity, 1–5 years
Red knot	*Calidris canutus islandica*	160			55	MS			13	Captivity, 2–3 years
Australian silver-eye	*Zosterops lateralis*	11.1	0.013	0.016	25.2	MS	Summer	0.799	14	Captivity, 2–6 months
Black-capped chickadee	*Parus atricapillus*	11.9	0.025	0.025	0.0	MS		1.000	15	Captivity, 0–4 weeks
Black-capped chickadee	*Parus atricapillus*	12.4	0.264	0.298	12.8	T	Variable		16	Captivity, 4 months
Black-capped chickadee	*Parus atricapillus*	12.4	0.264	0.338	27.8	T	1994		16	Captivity, 4 months
Black-capped chickadee	*Parus atricapillus*	13.1	0.020	0.023	14.4	MS	Winter	1.144	17	Captivity, 2–4 weeks
Black-capped chickadee	*Parus atricapillus*	12.5	0.020	0.025	22.2	MS	Outdoor		15	Winter indoor vs. outdoors
Black-capped chickadee	*Parus atricapillus*	12.5	0.288	0.365	26.7	T	1994		18	Wild-caught
Mountain chickadee	*Poecile gambeli*	11.1	0.231	0.271	17.4	T	Winter	1.174	19	Wild-caught
Juniper titmouse	*Baeolophus griseus*	16.6	0.271	0.331	22.2	T	Winter	1.222	19	Wild-caught
Dark-eyed junco	*Junco hyemalis*	18.6	0.018	0.019	9.2	MS	Winter	1.092	20	Wild-caught
Dark-eyed junco	*Junco hyemalis*	18.6	0.365	0.476	30.2	T	1994		18	Wild-caught
White-breasted nuthatch	*Sitta carolinensis*	19.4	0.288	0.428	33.3	MS	Winter	1.333	9	Wild-caught
White-crowned sparrow	*Zonotrichia leucophrys*	26.3	0.016	0.021	32.6	MS	Winter	1.326	21	Captivity, 2–10 months
House finch	*Carpodacus mexicanus*		0.017	0.018	4.5	MS	Summer	0.957	22	Wild-caught
House finch	*Carpodacus mexicanus*	20.1	0.016	0.016	1.4	MS	Winter		23	Wild-caught, winter vs. spring
House sparrow	*Passer domesticus*	27.9	0.328	0.539	64.0	T	Winter	1.640	24	Wild-caught
American tree sparrow	*Spizella arborea*		0.352	0.405	15.2	T	1994		18	Wild-caught
American goldfinch	*Carduelis tristis*	13.1	0.238	0.348	46.0	T	Winter	1.460	25	Wild-caught
American goldfinch	*Carduelis tristis*	13.7	0.303	0.376	9.7	MS	Winter	1.097	26	Wild-caught
Common redpoll	*Acanthis flammea*	14.6	0.020	0.026	30.8	MS	Winter	1.308	27	Captivity, 9–11 months
Brambling	*Fringilla montifringilla*	24.1	0.485	0.546	1.8	MS	Summer	0.982	28	Some acclimated
Migration										
Ruddy turnstone	*Arenaria interpres*				24.0	MS	Breeding		29	Sn. Sweden vs. Arctic
Ruddy turnstone	*Arenaria interpres*				30.0	MS	Migration		29	Sn. Sweden vs. Africa
Dunlin	*Calidris alpina*				10.0	MS	Breeding		29	Sn. Sweden vs. Arctic
Curlew sandpiper	*Calidris ferruginea*				30.0	MS	Breeding		29	Sn. Sweden vs. Arctic
Curlew sandpiper	*Calidris ferruginea*				22.0	MS	Winter		29	Sn. Sweden vs. Africa

Table 1 continued

		M_b (g)	BMR 1 (W)	BMR 2 (W)	Magnitude (%)		Increase direction	W/S	Reference	Comments
Red knot	*Calidris canutus*				11.0	MS	Winter		29	Sn. Sweden vs. Africa
Great knot	*Calidris tenuirostris*	160			33.0	MS	Migration		30	
Little stint	*Calidris minuta*				0.0	MS			29	Sn. Sweden vs. Arctic
Dunlin	*Calidris alpina*				15.0	MS	Migration		29	Sn. Sweden vs. Africa
Common redshank	*Tringa totanus*				20.0	MS	Migration		29	Sn. Sweden vs Africa
Ringed plover	*Charadrius hiaticula*				0.0	MS			29	Sn. Sweden vs Africa
Bar-tailed godwit	*Limosa lapponica*				9.0	MS	Winter		29	Sn. Sweden vs Africa
Yellow-rumped warbler	*Dendroica coronata*	12.3	0.214	0.281	31.3	T	Spring		31	Spring vs. autumn migration
Thrush nightingale	*Luscinia luscinia*		0.326	0.370	13.3	T	Early aut.		32	Early vs late autumn, n=1
Thrush nightingale	*Luscinia luscinia*				22.7	T			32	3-day refueling period, n=1
Garden warbler	*Sylvia borin*	23.3	0.240	0.377	20.2	MS			33	2−6 day starvation period

Body mass (M_b) and the lower (1) and higher (2) values of BMR are provided, as well as the magnitude of the difference (expressed as a percentage of the lower BMR value) and whether the magnitude was calculated from total (T) or mass-specific (MS) BMR. For most species in which BMR was examined in the context of seasonal acclimatization, the ratio of winter BMR/summer BMR is also given (W/S)

* Significant variation in body mass between upper and lower BMR values

References: 1. Riddle et al. (1934), 2. McKechnie et al. (2007), 3. Vezina et al. (2006), 4. Tieleman et al. (2003), 5. Williams and Tieleman (2000), 6. Klaassen et al. (2004), 7. Wallgren (1954), 8. Swanson and Weinacht (1997), 9. Liknes and Swanson (1996), 10. Merola-Zwartjes and Ligon (2000), 11. Weathers and Caccamise (1978), 12. Wijnandts 1984, 13. Piersma et al. (1995), 14. Maddocks and Geiser (2000), 15. Rising and Hudson (1974), 16. Sharbaugh (2001), 17. Cooper and Swanson (1994), 18. Swanson and Olmstead (1999), 19. Cooper (2000), 20. Swanson (1991), 21. Southwick (1980), 22.O'Conner (1995), 23. Dawson et al. (1985), 24. Arens and Cooper (2005), 25. Liknes et al. (2002), 26. Dawson and Carey (1976), 27. Pohl and West (1973), 28. Pohl (1971), 29. Kvist and Lindström (2001), 30. Battley et al. (2001), 31. Swanson and Dean (1999), 32. Lindström et al. (1999), 33. Klaassen and Biebach (1994)

The direction and magnitude of seasonal BMR adjustments have been widely accepted as varying with M_b (e.g., Hayworth and Weathers 1984; Swanson 2007; Swanson and Weinacht 1997) on the basis of an analysis presented for "fasting metabolic rate" by Weathers and Caccamise (1978). In the latter study, data on seasonal metabolic adjustments in 20 species revealed a negative relationship between M_b and the ratio of winter to summer metabolic rate, with species smaller than 200 g generally increasing their metabolic rate during winter, but with the opposite pattern in larger species (Fig. 1a). Closer examination of the data used by these authors, however, reveals a number of potentially confounding factors. First, the Weathers and Caccamise (1978) analysis included metabolic data irrespective of whether or not they met the criteria for BMR (Table 2). Of the 22 data included, 7 met the criteria for BMR, whereas 9 did not (Table 2). The measurement conditions for a further three species were not specified in sufficient detail to determine whether BMR criteria were met (Table 2). Weathers and Caccamise's (1978) own data for monk parakeets (*Myiopsitta monachus*) reveal the problems that can arise if BMR and non-BMR data are analyzed together. In *M. monachus*, metabolic rates that met the criteria for BMR were 28% higher in summer compared to winter, but measurements during the active phase (i.e., daytime) and included in the analysis discussed above were almost identical across seasons (Weathers and Caccamise 1978). There are also several inconsistencies between Table 3 and Fig. 5 of Weathers and Caccamise (1978), with some of the winter/summer ratios calculated from the metabolic rates provided in Table 3 not matching any of the ratios plotted in Fig. 5. The slightly different regression equation in Fig. 1a of the present paper compared with Fig. 5 of Weathers and Caccamise (1978) reflects these differences.

Assessment of the M_b-dependence of the direction and magnitude of seasonal BMR adjustments is further complicated by variation among studies in terms of the origins of experimental populations and/or housing conditions prior to metabolic measurements. The available data comprise a combination of measurements from free-ranging birds, in which BMR was measured shortly (typically within 24 h) after capture (e.g., Arens and Cooper 2005; Cooper 2000; Liknes and Swanson 1996), birds that had spent periods of weeks to months in captivity (e.g., Maddocks and Geiser 2000; Rising and Hudson 1974; Sharbaugh 2001), and captive-raised birds that were acclimatized to natural patterns of temperature and photoperiod in outdoor enclosures (Swanson and Weinacht 1997). Moreover, the data set analyzed by Weathers and Caccamise (1978) included BMR measurements for individuals that were acclimatized to natural temperature and photoperiod conditions (e.g., Dawson and Carey 1976), as well as individuals that were

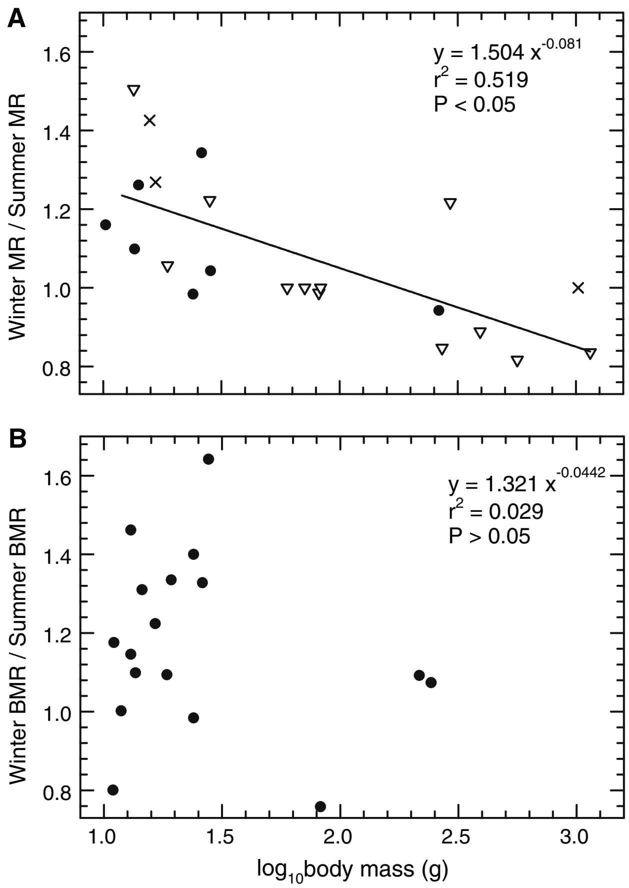

Fig. 1 Relationships between body mass and ratio of winter/summer metabolic rate (MR) in birds. The *upper* graph (**a**) shows the data analyzed by Weathers and Caccamise (1978), with data that meet the criteria for basal metabolic rate (BMR) shown as *solid circles*, and data that do not meet the criteria for BMR or for which conditions were not fully specified shown as *triangles*. Three data for which I was unable to obtain the original references are indicated with *crosses*. The lower graph (**b**) shows the corresponding relationship in species for which seasonal BMR data are currently available (Table 1)

acclimated to artificial conditions indoors (e.g., Riddle et al. 1934; Wallgren 1954). Avian BMR scales differently in captive-raised and wild-caught birds (McKechnie et al. 2006), and reductions in pectoral muscle oxidative capacity (Saarela and Hohtola 2003) and BMR (McKechnie et al. 2007) have been linked to reduced activity levels in small cages. Collectively, these observations call into question whether seasonal metabolic adjustments are directly comparable among populations that differ in acclimation/acclimatization history and/or housing conditions. Although seasonal metabolic adjustments have been measured shortly after capture in wild populations of a number of species (Table 1), the range of M_b is too small to rigorously examine the M_b-dependence of seasonal adjustments. A pooled data set combining seasonal BMR adjustments from wild populations, populations maintained in captivity for weeks to months prior to measurements, and captive-raised populations does not reveal any significant relationship with M_b (Table 1, Fig. 1b), although too few data for species with M_b> 30 g are currently available to draw any conclusions regarding the M_b-dependence of seasonal BMR adjustments.

Migratory cycles

Long-distance avian migration involves cyclical physiological and morphological adjustments, primarily driven by changes in body composition (Battley et al. 2000; Dietz et al. 1999; Karasov and Pinshow 1998; Piersma and Lindström 1997). Relatively few studies have directly compared BMR across different stages of long-distance migration cycles, but those that have done so have revealed substantial phenotypic flexibility. In yellow-rumped warblers migrating northwards during spring, total BMR was 31% higher compared to during the southward autumn migration (Swanson and Dean 1999). Great knots migrating from northwestern Australia to southern China exhibited reductions of 42–46% in total BMR and 33–40% in mass-specific BMR during their migratory flight (Battley et al. 2001, 2000).

A more common approach to investigating metabolic adjustments in long-distance migrants is to compare metabolic rates among studies conducted in different regions (Kersten et al. 1998; Kvist and Lindström 2001; Lindström 1997; Lindström and Klaassen 2003). Although this approach suffers from the limitation of methodological variation across studies (Kvist and Lindström 2001), these studies have been instrumental in revealing metabolic adjustments in long-distance migrants. The pattern that has emerged for a number of species that migrate between Arctic breeding grounds and winter quarters in tropical Africa is that BMR is highest in the Arctic and lowest on the African winter range (Kvist and Lindström 2001; Lindström and Klaassen 2003). In a study of 19 wader species, Kvist and Lindström (2001) found an average reduction in BMR of 16% between the Arctic and southern Sweden, and a further but non-significant average reduction of 8% between southern Sweden and Africa.

The most rapid changes in avian BMR yet documented have been reported in migrants. In a single thrush nightingale (*Luscinia luscinia*) that underwent a simulated 6,300 km migration in a wind tunnel, total BMR increased on average by 22.7% during each 60 h refueling period between 12 h flights, concomitant with an average increase in M_b of 24.3% (Lindström et al. 1999). Garden warblers (*Sylvia borin*) that were starved in order to simulate a migratory flight exhibited a decrease in mass-specific BMR of approximately 20% over a 2–6 day period (Klaassen and Biebach 1994).

Table 2 Metabolic rates analyzed by Weathers and Caccamise (1978), the ratio of winter to summer metabolic rate (W/S), and whether or not the metabolic rates met the criteria for basal metabolic rate (BMR?)

Species	Body mass (g)		Metabolic rate (W kg^{-1})		W/S	Reference	BMR
	Winter	Summer	Winter	Summer			
Acanthis flammea	13.8	13.1	33.73	22.41	1.505	1	No
Acanthis flammea	15.6	12.8	26.33	20.91	1.259	2	Yes
Branta bernicla	1168	1130	3.96	4.74	0.835	3	No
Carduelis carduelis	16.6	16.7	25	19.71	1.268	4	
Columba livia	280	250	4.71	5.01	0.940	5	Yes
Columba livia	405	381	6.86	7.72	0.889	6	No
Corvus caurinus	306	282	15.63	12.84	1.217	3	No
Corvus corax	1069	975	8.51	8.51	1.000	7	
Emberiza citrinella	28.4	28.9	18.19	17.47	1.041	8	Yes
Fringilla montifringilla	25.8	22.5	21.16	21.55	0.982	9	Yes
Hesperiphona vespertina	62.1	58	26.61	26.61	1.000	6	No
Lagopus lagopus	590	539	5.79	7.09	0.817	10	No
Larus ridibundus	290	253	7.37	8.7	0.847	11	Conditions n.s.
Myiopsitta monachus	80.4	83	9.37	9.49	0.987	12	No
Parus atricapillus	10.3	10.3	28.44	24.56	1.158	13	Yes
Parus major	18.4	19	20.65	19.54	1.057	14	Conditions n.s.
Passer domesticus	29.4	27.1	30.38	24.85	1.223	6	No
Perisoreus canadensis	71.2	71.2	9.77	9.77	1.000	15	Conditions n.s.
Serinus canaria	15.8	15.6	28.13	19.73	1.426	4	
Spinus tristis	14.5	12.8	25.96	23.67	1.097	16	Yes
Sturnus vulgaris	86.8	79.6	21.18	21.18	1.000	6	No
Zonotrichia leucophrys	25.5	27	18.74	13.97	1.341	17	Yes

I was unable to obtain the original sources for the *Corvus corax*, *Carduelis carduelis* and *Serinus canaria* data

References: 1. West (1972a), 2. Pohl and West (1973), 3. Irving et al. (1955), 4. Gelineo (1969), 5. Riddle et al. (1934), 6. Hart (1962), 7. Veghte (1975), 8. Wallgren (1954), 9. Pohl (1971), 10. West (1972b), 11. Davydov (1972), 12. Weathers and Caccamise (1978), 13. Rising and Hudson (1974), 14. Hissa and Palonkangas (1970), 15. Veghte (1964), 16. Dawson and Carey (1976), 17. Southwick (1980)

Short-term thermal acclimation

In a number of species, BMR has been found to vary over time scales of days to weeks within captive individuals in response to changes in thermal environments (Table 1). Gelineo's (1964) observation that birds typically up-regulate BMR when acclimated to cold conditions has been supported by several more recent studies (Klaassen et al. 2004; McKechnie et al. 2007; Tieleman et al. 2003; Vezina et al. 2006; Williams and Tieleman 2000). The magnitude of BMR adjustments associated with short-term thermal acclimation varies among species and may involve increases in BMR of up to 42% (Table 1). Even among closely related species, metabolic responses to acclimation differ. In four species of larks, the BMR of individuals acclimated to $T_a = 15°C$ ranged from 5 to 29% higher than that of individuals acclimated to $T_a = 35°C$ (Tieleman et al. 2003). When variation in acclimation T_a among recent studies is taken into account, the magnitude of BMR adjustments ranges from 0.2 to 1.5% per 1°C change in acclimation T_a (McKechnie et al. 2007). The latter values were calculated using the full range of acclimation T_as used in each study, although metabolic upregulation may a priori be expected only at acclimation T_as below the thermoneutral zone (TNZ). However, in laughing doves with a lower critical limit of thermoneutrality (T_{lc}) of ca. 30°C, BMR upregulation between acclimation $T_a = 35°C$ and 22°C was quantitatively similar to upregulation between $T_a = 22°C$ and 10°C, with the result that BMR was linearly related to acclimation T_a (McKechnie et al. 2007). If BMR upregulation had occurred only in response to acclimation $T_a < T_{lc}$, then the relationship between BMR and acclimation T_a would presumably have been non-linear over the three acclimation T_as used (10, 22 and 35°C).

The majority of studies of BMR adjustments during short-term thermal acclimation have involved comparisons of BMR among groups of experimental birds, each acclimated to a single T_a. In a study that examined variation within individuals, rather than among experimental groups, laughing doves (*Streptopelia senegalensis*) exhibited BMR adjustments that were reversible in direction, with individuals that initially upregulated BMR during acclimation to cold temperatures subsequently downregulating BMR when moved into a warm room and vice versa (McKechnie et al. 2007).

Mechanisms of within-individual BMR adjustments

In a review of the mechanisms driving seasonal metabolic adjustments in birds, Swanson (2007) has identified three major physiological and morphological pathways whereby metabolic rates are up- or downregulated, namely adjustments in transport capacities for oxygen and metabolic substrates, adjustments in the mass-independent metabolic intensities of specific organs, and/or adjustments in organ masses. Whereas adjustments in transport capacities are important for changes in summit metabolism (M_{sum}) and maximal metabolic rate (MMR), BMR represents minimum maintenance energy turnover and predominantly reflects the mass and metabolic intensities of the major organs (Swanson 2007). Intra-specific variation in BMR has been correlated with the mass of organs such as the heart, intestine, liver, spleen and kidneys (Chappell et al. 1999; Daan et al. 1990; Hammond et al. 2000; for review see Table 1 of Piersma 2002). However, Vézina and Williams (2005) have pointed out that relationships between organ masses and BMR are often inconsistent among studies, probably reflecting changes in mass-specific metabolic intensity within and among organs. In European starlings (*Sturnus vulgaris*), the mass-specific metabolic intensity of organs (measured as citrate synthase activity) varied through time, but not in a consistent fashion among organs (Vézina and Williams 2005). Further evidence for the importance of adjustments in mass-specific metabolic intensity comes from the observation that captive red knots exhibited increases in lean mass, yet a decrease in BMR when switched to a less digestible diet (Piersma et al. 2004).

Short-term adjustments of BMR during thermal acclimation appear to be driven primarily by changes in organ mass. The energy demand hypothesis proposes that the masses of organs involved in supplying energy for thermogenesis are matched to changing food requirements (Williams and Tieleman 2000). According to this idea, increased food intake at low T_a leads to increases in the masses of organs, which in turn results in an elevation in BMR (Tieleman et al. 2003; Williams and Tieleman 2000). Several studies have reported increases in food intake and the masses of organs such as the liver, kidney and intestines in birds acclimated to cold conditions (Tieleman et al. 2003; Williams and Tieleman 2000). However, increased BMR in birds acclimated/acclimatized to cold conditions may also reflect the upregulation of tissues responsible for heat generation, such as the pectoral muscles, with a concomitant increase in maintenance costs (Piersma 2002). Recently, Vezina et al. (2006) used ultrasonography to examine body composition correlates of metabolic adjustments during short-term thermal acclimation in red knots (*Calidris canutus islandica*), and found that, in general, within-individual changes in BMR were related to neither gizzard size nor pectoral muscle thickness. Instead, these authors argued that the elevated BMR of cold-acclimated birds reflected increases in the masses of organs such as the liver, as has been observed during acclimation in a number of species of larks (Tieleman et al. 2003; Williams and Tieleman 2000).

Implications of phenotypic flexibility in avian BMR for comparative analyses

Metabolic scaling

Plastic allometry has been documented in morphological traits (Schlichting and Pigliucci 1998), and recent work has revealed similar plasticity in avian metabolic scaling. The allometric exponent for avian BMR depends on the origin of populations used for metabolic measurements, with captive-raised birds exhibiting a significantly shallower slope (0.670) than wild-caught birds (0.744; McKechnie et al. 2006). Whereas the environmental factors and physiological mechanisms that contribute to these differences remain unclear, it is likely that both phenotypic flexibility and developmental plasticity (sensu Piersma and Drent 2003) are involved (McKechnie et al. 2006). Plasticity in metabolic scaling is not limited to birds; there is increasing evidence that scaling coefficients among arthropods are significantly affected by metabolic responses to acclimation (Chown and Terblanche 2007; Terblanche et al. 2007). Collectively, these findings significantly complicate the process of controlling for the effects of M_b in comparative analyses. In the case of avian BMR, the origins of study populations need to be taken into account, and pooling data for wild-caught and captive-raised individuals will potentially confound analyses of metabolic variation correlated with environmental factors and/or organismal traits.

Identifying metabolic adaptation

The realization that avian BMR exhibits considerable phenotypic flexibility greatly complicates the process of identifying metabolic adaptation. Traditional approaches to comparing BMR among groups of species, or comparing the BMR of a species of interest to allometrically expected values, implicitly assume that BMR is a fixed, taxon-specific trait. The latter limitation also applies to analyses that involve methods for detecting phylogenetic signals and controlling for phylogenetic non-independence of data (Blomberg et al. 2003; Freckleton et al. 2002; Garland et al. 1993, 1992; Garland and Ives 2000; Martins and Hansen 1997; Pagel 1994, 1999), although potential bias associated with within-species variation and/or traits that exhibit low repeatabilities is increasingly being recognized (Adolph and Hardin 2007; Ives et al. 2007). In the case of avian BMR, the trait values observed in experimental populations are dependent on the acclimation/acclimatization states of the individuals involved, and the conclusions reached in comparisons of observed vs. predicted BMR values similarly depend on acclimation/acclimatization history (Fig. 2).

There is considerable overlap in magnitude between adjustments of BMR within species/individuals (Table 1) and variation reported among groups of species that differ in habitat or other traits. For instance, the BMR of desert birds is on average 17% lower than that of non-desert birds (Tieleman and Williams 2000), and BMR in tropical species is 10–18% lower than in temperate species (Wiersma et al. 2007). However, BMR may vary within individuals by >30% in response to acclimation or acclimatization (Table 1). The latter observation reiterates the importance of taking phenotypic flexibility into account as a source of variation in comparative analyses of BMR among groups of taxa that differ in habitat, diet or other traits. Currently, metabolic adjustments in response to acclimation or acclimatization have been examined in too few species to directly assess the relative contributions of phenotypic flexibility and genotypic adaptation to observed relationships between avian BMR and variables such as aridity (Tieleman and Williams 2000), diet (McNab 1988) and temperature (White et al. 2007).

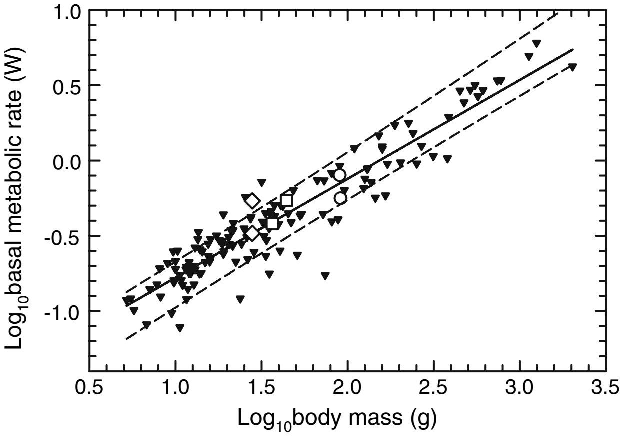

Fig. 2 The maximum and minimum BMR observed during acclimation in laughing doves (*Streptopelia senegalensis*; *pair of circles*; data from McKechnie et al. 2007) and hoopoe larks (*Alaemon alaudipes*; *pair of squares*; data from Williams and Tieleman 2000), and during seasonal acclimatization in house sparrows (*Passer domesticus*; *pair of diamonds*; data from Arens and Cooper 2005). These species were chosen as they provide instructive examples over a threefold range of body mass. Data for wild-caught populations of 137 species (McKechnie et al. 2006) are shown as *triangles*. The *solid line* is a conventional least-squares linear regression fitted to the latter data, and the *dashed lines* are phylogenetically independent 95% prediction intervals for the BMR of *P. domesticus*, calculated following Garland and Ives (2000). Note that the lower (summer) value for P. *domesticus* falls within the prediction intervals, whereas the upper (winter) value lies above the upper prediction interval

The changing view of avian metabolic diversity

Birds, like other organisms, show considerable variation in physiological traits, and analyses of BMR have been instrumental in elucidating patterns of avian metabolic diversity. Traditionally, comparative analyses of avian BMR have focused on several key sources of variation, namely allometric scaling (Brody and Proctor 1932; Lasiewski and Dawson 1967; McKechnie et al. 2006), metabolic variation among higher-order taxa (Bennett and Harvey 1987; Lasiewski and Dawson 1967; Reynolds and Lee 1996), and/or M_b-independent variation correlated with climate (Ellis 1984; Tieleman and Williams 2000; Weathers 1979; White et al. 2007) and factors such as foraging mode and diet (Bennett and Harvey 1987; McNab 1988, 2001, 2003). In the vast majority of cases, these analyses have involved a single BMR value per species, which has usually been implicitly assumed to represent a fixed, species-specific value. In contrast, the emerging view of avian BMR is of a trait continually adjusted in response to fluctuating environments (Broggi et al. 2007; Swanson and Olmstead 1999). The realization that avian BMR exhibits considerable phenotypic flexibility and varies within individual birds through time calls for new approaches to comparing metabolic rates among taxa. Below, I outline several key questions that need to be addressed.

What are the shapes of avian BMR reaction norms?

Several properties of a reaction norm [i.e., the range of phenotypic trait values that a single genotype can produce (Schlichting and Pigliucci 1998)] apply to patterns of phenotypic flexibility in avian BMR, including the magnitude, shape and rapidity of responses. Whereas numerous studies have reported the magnitude of BMR adjustments, information on the shape of BMR reaction norms is virtually nonexistent, because most studies involved acclimation to one of only two T_as (Gelineo 1969; Klaassen et al. 2004; Tieleman et al. 2003; Williams and Tieleman 2000). In a study where laughing doves (*Streptopelia senegalensis*) were acclimated to one of three T_as (10, 22, or 35°C), BMR was linearly related to acclimation T_a (McKechnie et al. 2007), despite the fact that one of the acclimation T_as used was ca. 5°C above the T_{lc} for this species (see discussion above). These data for *S. senegalensis* suggest that avian BMR reaction norms may be approximately linear in shape. However, up- or downregulation of BMR is presumably limited by physiological and morphological constraints, and we might thus expect that avian BMR reaction norms represent linear relationships between upper and lower bounds (Fig. 3a).

The rapidity of avian BMR adjustments (i.e., the rate at which BMR is up- or downregulated) also remains largely unknown. In the majority of studies involving short-term thermal acclimation, birds were acclimated for approximately 3 weeks. In two species of larks, BMR measured 2 weeks after the start of thermal acclimation did not differ from BMR measured after 3 weeks, revealing that BMR adjustments took place in less than 2 weeks (Tieleman et al. 2003). In laughing doves in which BMR was measured every few days following a change in thermal environment, BMR was adjusted by 0.5–0.7% per day (Chetty 2006).

How do the properties of BMR reaction norms differ among avian taxa?

The first attempt to frame a hypothesis of avian metabolic adaptation in terms of the properties of BMR reaction norms was recently made by Tieleman et al. (2003), who used four species of larks to test the idea that species inhabiting environments of high temporal heterogeneity (deserts) have evolved greater phenotypic flexibility than species in more predictable (non-desert) habitats. In this study, larks were acclimated to one of two acclimation T_as (15 or 35°C) and the magnitude of BMR adjustments compared across species, but no correlation was found with habitat aridity. The “greater flexibility in desert species” hypothesis put forward by Tieleman et al. (2003) provides a useful example with which to explore the approach of generating metabolic adaptation hypotheses in a reaction norm framework. The shapes of reaction norms for avian BMR could potentially differ between desert and non-desert species in a number of ways (Fig. 3b–e) similar to the various patterns of physiological acclimation documented in ectotherms (Cossins and Bowler 1987; Precht 1973; Prosser 1973). Alternately, the shapes of BMR reaction norms might be similar, but the rapidity of responses may differ (Fig. 3f). Tieleman et al. (2003) implicitly tested the prediction that, for a given change in acclimation T_a, desert species exhibit a larger fractional adjustment in BMR, i.e., the slope of the BMR vs.. T_a reaction norm is steeper in desert birds (Fig. 3c). However, patterns of phenotypic flexibility could potentially differ in a number of other ways that were not considered in the latter study (Fig. 3).

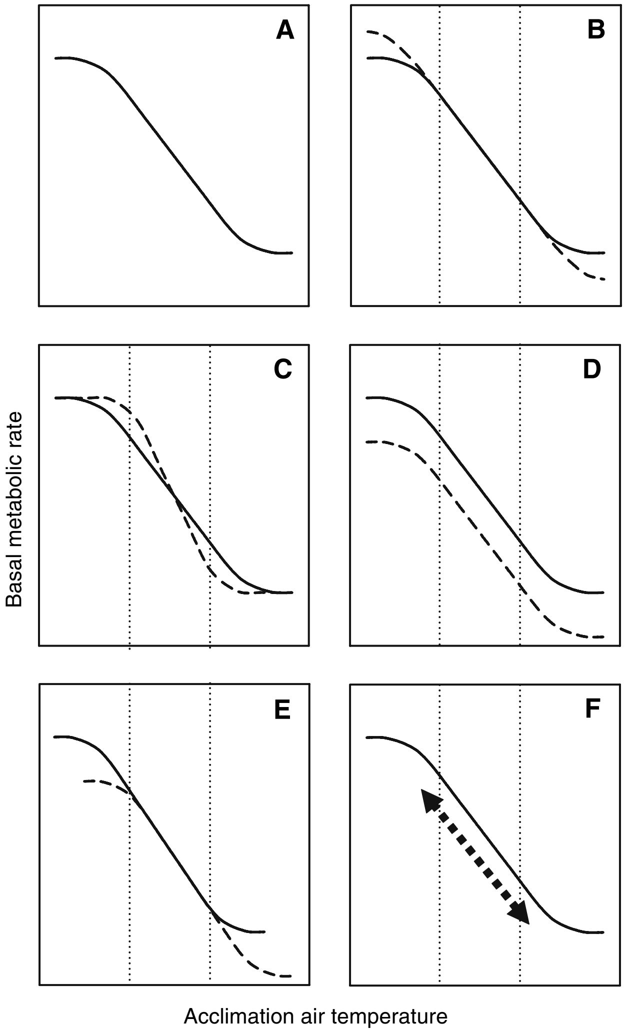

Fig. 3 A hypothetical reaction norm (**a**) for avian BMR relative to air temperature (T_a), where BMR is linearly related to the T_a between upper and lower bounds. **b**–**f** are graphical representations of five non-mutually exclusive hypotheses concerning differences that might exist between desert (*dashed line*) and non-desert (*solid line*) species. The *dashed lines* in (**b**)–(**f**) represent two arbitrary acclimation T_as, and illustrate how the predicted differences in BMR between desert and non-desert species vary between scenarios. In scenario (**b**), BMR is more flexible in desert species in the sense that it can be adjusted over a wider range of T_a. In scenario (**c**), the slope of the reaction norm is steeper in desert species, and a larger difference in BMR is predicted for a given combination of acclimation T_a values. In (**d**)–(**f**), the slopes of the reaction norms are the same, but the reaction norm of desert species is shifted downwards compared to non-desert species (**d**), and shifted downwards as well as towards higher T_a values (**e**). In (**f**), the shape of the reaction norm is identical for desert and non-desert species, but desert species adjust BMR more rapidly

Does the magnitude of BMR adjustments scale with body mass?

Studies of BMR adjustments during acclimatization and/or acclimation have been conducted under a wide range of conditions, often precluding direct comparisons of the

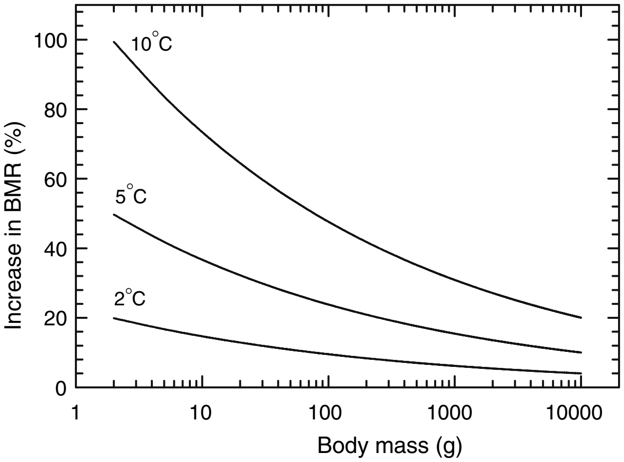

Fig. 4 Downward shifts in the lower critical limit of thermoneutrality (T_{lc}) require larger fractional increments in basal metabolic rate (BMR) in smaller species. The increments in BMR (%) required to decrease the T_{lc} by 2, 5 or 10°C were calculated using the equation: BMR = C_{min} (T_b−T_{lc}), where BMR is in J g^{-1} h^{-1}, C_{min} is minimum wet thermal conductance [J (g h°C)$^{-1}$] and T_b is body temperature (°C). Initial T_{lc} was calculated using BMR values predicted by McKechnie and Wolf (2004a); values of C_{min} were predicted by Schleucher and Withers (2001), and T_b = 38.5°C

magnitude of BMR adjustments among taxa. Before hypotheses concerning the adaptive value of inter- and/or intraspecific variation in the properties of BMR reaction norms can be tested, particularly in the context of mechanistic links between BMR and more ecologically relevant measures of energy expenditure, other sources of variation need to be accounted for. A simple model for the effect of BMR upregulation on the lower critical limit of thermoneutrality (T_{lc}) reveals that the fractional BMR increment required for a given shift in T_{lc} decreases with increasing M_b (Fig. 4). Thus, I predict that for a given set of T_as in experiments involving short-term thermal acclimation, fractional increments in BMR will be larger in smaller species. A quantitatively similar prediction can be made for shifts in the temperature at cold limit [T_{CL}, i.e., the lowest T_a at which a normothermic T_b can be defended (Saarela et al. 1988)] through adjustments in M_{sum}.

Does the rapidity of BMR adjustments scale with body mass?

Processes related to rates of change in organ mass and/or the properties of tissues that determine metabolic intensity may a priori be expected to be M_b-dependent. Carleton and Martinez del Rio (2005) tested the hypothesis that isotopic incorporation rates are related to metabolic rate, and found that the fractional rates of ^{13}C incorporation into avian blood scale to approximately $M_b^{-0.25}$. Since the rate at which carbon turns over in an organism's blood is proportional to mass-specific metabolic rate, it is reasonable to expect that rates of change in organ mass and/or cellular properties also vary with M_b. Hence, I predict that the rate of change in BMR during acclimation scales allometrically with a similar exponent to mass-specific metabolic rate.

Conclusions

Comparative analyses of the metabolic rates of birds date back to at least the 1920s (Benedict and Fox 1927; Giaja and Males 1928; Terroine and Trautmann 1927), and nearly a century later comparisons of BMR across taxa remain a fundamental aspect of avian ecological and evolutionary physiology (McKechnie et al. 2006; White et al. 2007; Wiersma et al. 2007; Wikelski et al. 2003). There is increasing evidence, however, that phenotypic flexibility in BMR is a general feature of avian physiological phenotypes. The realization that avian BMR is a flexible trait necessitates a critical re-examination of comparative methods. Most importantly, the hypotheses tested using comparative data need to explicitly take phenotypic flexibility into account (e.g., Tieleman et al. 2003).

Finally, ecological and evolutionary physiologists need to move away from the approach of measuring BMR just once per species (e.g., McKechnie and Lovegrove 2001, 2003; McNab 2001, 2005), since the BMR observed during once-off measurements depends on a number of factors related to acclimation/acclimatization and is thus usually not directly comparable across taxa. However, multiple measurements across seasons or in response to different acclimation T_as will often be difficult or even impossible in the case of species that are rare and/or occur in inaccessible areas, and there are a number of ways in which workers can improve the comparability of once-off BMR measurements. In addition to restricting analyses to data from either wild-caught or captive-raised populations (McKechnie et al. 2006; White et al. 2007), one approach is to standardize the time of year during which measurements are made. The latter approach was recently used by Wiersma et al. (2007) who included only BMR data measured in summer for their comparisons of tropical and temperate species.

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