Metabolic correlates of leg length in breeding arctic shorebirds: the cost of getting high

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INTRODUCTION

The manner in which the local environment shapes adaptations in organisms is of fundamental interest in evolutionary biology. In the case of morphological traits, many ecogeographical ‘rules’ have been posited to account for latitudinal and elevational variation within and among closely related species (Brown & Lomolino, 1998). These include Bergmann’s rule, where surface area/volume decreases with increasing latitude/altitude, and Allen’s rule, where appendages shorten with increasing latitude/altitude. While controversial in application (Ashton et al., 2000; Freckleton et al., 2003), both Bergmann’s and Allen’s rules are theoretically sound as they are predicated on basic principles of ecophysiology: namely that in cold climates, heat loss of homeotherms can be reduced by decreasing surface area relative to volume of a body, and by reducing the length of body appendages.

Long body appendages are not just bigger radiators of heat. When these appendages are legs, they also position the body trunk farther from the ground. Wind speed is reduced dramatically near the ground surface owing to friction between the air and surface, producing a ‘boundary layer’, the size and shape of which depends on overall wind speed and texture and morphology of the substrate (Campbell, 1977). Hence longer legs will elevate the body into a zone with higher wind speeds, leading to an increase in convective cooling.

In this paper, we consider convective cooling as an influence on leg length in a group of shorebirds (family Charadriidae)
that differ enormously in leg length, in other morphological
traits (e.g. body mass, bill and wing length), and in geographical
range. As these shorebirds nest in the arctic, a region
known for its cold and unpredictable climate (e.g. Myers &
Pitelka, 1979) but relatively simple habitat structure
(i.e. tundra), they form a logical group in which to test for
climate-based constraints on morphology. All of these species
are migratory, but they winter in climatically more benign
temperate and tropical habitats, which suggests that climate on
the breeding grounds might more strongly influence their
morphology. Indeed, tundra-breeding shorebirds have some of
the highest measured rates of energy expenditure during
incubation that have been reported (Piersma et al., 2003).
Presumably, the energetic stresses of arctic breeding are
compensated for by food availability and long summer
photoperiod. We test the hypothesis that shorebird species
breeding in more metabolically stressful environments have
relatively shorter legs, which may reduce heat loss by moving
them farther into the ground’s boundary layer where they
experience lower wind speeds.

**METHODS**

To estimate the average daily maintenance metabolic costs
(thermostatic costs) incurred by a bird of a given species at a
given location and date, we used a model whose inputs
included three species-specific morphological variables (body
mass, diameter and height), and 3 day- and site-specific
weather variables known to affect the metabolism of homeo-
thersms (temperature, wind speed and global solar radiation).
The details of the model appear in Cartar & Morrison (1997),
along with an evaluation of the model’s sensitivity and validity.
Data for tarsus length, wing length and bill length are values
for adult females listed by Prater et al. (1977). Data for body
mass were obtained from Johnsgard (1981). Data for body
diameter and height of the ‘representative’ white-rumped
sandpiper (see below) came from photographs in Chandler

Weather data were available from 37 weather stations across
the Canadian arctic collected by the Atmospheric Environment
Service of the Canadian Government, spanning the period
1953 through 1990 (averaging 29.6 years from each station,
SD = 8.2). Many stations, however, were concentrated along
the distant early warning (DEW) line of military radar stations
(latitude c. 68°N), so to avoid sampling disproportionately
from this latitude when characterizing the thermal environ-
ment of breeding ranges across the arctic, we omitted 10 DEW
line weather stations from our analyses. We used range maps
from Godfrey (1986) to define the breeding range of each
species (Table 1) at each of the 27 weather stations (Fig. 1)
on a simple presence/absence basis. All species commonly
breeding in the Canadian arctic were included in the analysis
(n = 17 species, Table 1).

To characterize the thermal environment experienced at
each weather station at each time, we needed a measure of the
basic metabolic costs incurred by the birds at that location,
which is independent of a species’ morphology. Such a
measure would integrate the joint effects of temperature, wind
and global solar radiation into a single measure of metabolic
stress. This measure, sometimes known as ‘thermostatic cost’
(see below), can then be combined with range maps to
estimate the average stress of environments in which the
different species breed. Leg length and metabolic stress can
then be compared such that ‘metabolic stress’ has the same
meaning for all species in the comparison. We used the white-
rumped sandpiper’s morphology (mass = 46 g, height at
centres of gravity = 5.3 cm, diameter of torso = 4.7 cm) to calculate this Reference metabolic rate (Reference MR) using Cartar & Morrison’s (1997) equation. The predictive equation developed by Cartar & Morrison (1997) is a hybrid of a theoretical model of dry heat transfer and empirical allometric relationships, which predicts daily thermostatic costs (the sum of resting metabolic rate and weather-based metabolic rate, but not including the costs of activity) from three morphological variables (body mass, torso diameter, height of torso), three weather variables (temperature, wind speed, solar radiation), and one habitat variable (height of vegetation). Tundra vegetation was assumed to have an average height of 3 cm: shorebirds are essentially species of open habitats, and the value for this variable is intended to typify the open habitats in which all of these species of shorebirds exist in different parts of the arctic during the breeding season. Overall, using Reference MR allows an answer to the question ‘how metabolically stressful is this species’ environment?’ in a manner that is independent of a species’ morphology.

We restrict our analyses to the period of time at which shorebirds are present on the breeding grounds; from Julian date 150 (30 May) to Julian date 240 (28 August). To describe average Reference MR, we calculated costs at 10-day intervals throughout the breeding season. To increase the accuracy of estimates of metabolic costs at each date, measurements for the previous and subsequent 2 days, in addition to those of the stated day, were used. For example, metabolic estimates reported for Julian date 200 are based on days 198 through 202, inclusive. Metabolic estimates for the entire breeding season are therefore an average of the ten 10-day values.

The independent effect of Reference MR on tarsus length as determined in a multiple regression is presented as a leverage plot that statistically accounts for the variance due to all other effects specified in the model (JMP, 2002). An initial multiple regression predicting tarsus length from body mass, wing length, bill length (all ln-transformed) and Reference MR was ill-conditioned by two strongly correlated variables: the variance inflation factors (VIFs) for body mass (26.2) and wing length (23.1) were much greater than 10, producing unreliable estimates of their individual effects. To provide interpretable results, we omitted the variable with the greater VIF (body mass) from further analysis. It is therefore reasonable to consider the use of wing length in this paper as a measure of body mass, too.

Comparative analysis was performed on standardized contrasts (Felsenstein, 1985) with the parsimony-derived phylogeny (Fig. 3b) based on molecular data from Borowik & McLennan (1999); their Fig. 3), supplemented for missing taxa by the phylogeny in Reynolds & Székely (1997). The phylogenetic position of Charadrius semipalmatus was estimated. Branch lengths were set to unity based on the order of branching, and nodes were calculated using only the 17 taxa included in the analysis. Contrasts of tarsus length were based on residuals of a multiple regression predicting tarsus length from bill length and wing length, with all three variables ln-transformed to normalize the distribution of residuals of the whole-model fit. Statistical analysis was performed using JMP 5. 0 (JMP, 2002). Residuals from all model fits were checked for normality and homogeneity.

**RESULTS**

The nonlinear and dramatic effect on metabolism of elevating the position of the body by increasing leg length, while keeping all else equal, is demonstrated using predictions of thermostatic costs for the smallest- and largest-bodied shorebirds in our analysis (Fig. 2). Note that the strongest effects on metabolism occur nearest to the ground surface. Weather
data for the centre-most weather station (Makar Inlet) are used to illustrate the effect of body height (Fig. 2); note that neither of the shorebird species shown breeds near this station.

After controlling for wing length ($t_{13} = 6.02, P < 0.0001$), and bill length ($t_{13} = 1.23, P = 0.24$) in a multiple regression (overall model $F_{3,13} = 41.36, P < 0.0001$, $R^2_{adj} = 0.88$), there was a significant negative relationship between tarsus length and Reference MR (Fig. 3a). This supports the hypothesis that leg length and metabolic harshness (thermostatic costs) are negatively related. This result was confirmed in the comparative analysis: tarsus residuals (from which the effects of body mass, wing length and bill length were statistically removed by a multiple regression) were significantly and negatively correlated with Reference MR contrasts (Fig. 3c).

**DISCUSSION**

We have demonstrated that tarsus length of shorebirds breeding in ‘colder’ places is shorter, supporting the hypothesis that wind-related metabolic stress on the breeding grounds may shape shorebird morphology. This result is not simply an outcome of Bergmann’s or Allen’s rules, because we statistically controlled for body mass (via wing length) (Bergmann’s rule) and for the lengths of other appendages (wing and bill – Allen’s rule).

In this paper, we have focused on metabolic costs in the breeding season as the determinant of leg length. However, many factors can potentially affect the ability of shorebirds to occupy different parts of the arctic, including climate (and hence metabolic/thermostatic costs), migration distance, length of breeding season in relation to size of species (longer incubation time required by larger species), competition, and food availability (timing and duration of peaks). In addition, all of the shorebird species used in our analyses undertake long-distance migrations to temperate, subtropical and tropical wintering areas, through a range of temperate habitats. While other habitats and times of year may potentially play a role in influencing leg length, the present results support Hale’s (1973) argument that selection on body size of redshank ($\textit{Tringa totanus}$), and on tarsus length of all shorebirds (Hale, 1980) is based on temperatures experienced in the breeding season, not the non-breeding season. Further support for this idea comes from Battley (2002), who noted that long-distance migrant shorebirds refuelling in tropical conditions appear to be more susceptible to heat stress than local breeders or short-distance migrants, and commented that this may be because the arctic-breeding species do not have the option of evolving specific physiological heat loss adaptations because these could compromise heat conservation abilities on the breeding grounds where heat conservation may be imperative. This suggests that metabolic considerations in the arctic may override those pertaining elsewhere.

As with all biogeographical rules, our test emphasizes a pattern that is selected in a particular environment, while being silent on the same pattern in other environments, other than to note that selection on the trait is more relaxed in
other environments. For example, Allen’s rule predicts that appendages are shorter in colder environments, and provides a mechanism for this prediction (minimizing heat loss). It does not predict why appendages are longer in warmer environments, where relaxed selection on the trait should result in a wider variety of lengths, whose mean is greater. Similarly, we predict that leg length is selected to be shorter in colder environments (minimizing convective thermal stress). We do not predict why leg length is longer in warmer environments, where relaxed selection based on convective heat loss should allow the trait to vary in response to other, unmeasured selective pressures. Note, however, that the variance in leg length associated with species breeding in more benign habitats is no greater than that in harsher habitats (Fig. 3a).

Our conclusion about the cost of a high centre of gravity in cold climates is conservative in that the biophysical model used to estimate thermostatic costs assumes that all heat loss is through the body. However, if heat loss through the legs is also important, the hypothesis advanced in this paper is only strengthened: the proximal portions of longer legs would experience more convective heat loss, and the extent of this loss depends on weather. Indeed, the observation that birds often rest with their bill and one leg tucked onto the body, anecdotally suggests that heat loss through appendages (the logical basis of Allen’s rule) is important. This is supported by a report that red knots can lose up to 16% of their metabolic heat production although their legs at 34.2°C and potentially all of their heat production if standing in water at 35°C (L.W. Bruinzeel, quoted in Battley, 2002), temperatures well above those experienced on the tundra. The postural sensitivity of roosting shorebirds to prevailing winds (Wiersma & Piersma, 1994) further supports this argument.

It is clear that shorebirds breeding on arctic tundra habitats incur considerable metabolic costs owing to the cold and exposed environments in which they live. In fact, Piersma et al. (2003) showed that tundra-nesting shorebirds have amongst the highest rates of energy expenditure reported to date. While shorebirds may be able to reduce energy expenditure by using tundra microhabitats (e.g. hummocks, depressions) that provide some shelter during activities such as roosting (Wiersma & Piersma, 1994) or incubating (Piersma et al., 2003), other important activities (e.g. foraging, display) will require them to make use of open and exposed habitats. Piersma et al. (2003) showed that foraging away from the nest in open habitats is almost twice as energetically demanding for red knots as incubating a four-egg clutch. We suggest that the ability to use open habitats is a requirement for shorebirds to be able to occupy any given part of the arctic, and that the energetic demands imposed by this requirement are likely to be a key selective force operating on the birds. We use this argument to justify the use of an average vegetation height of 3 cm to calculate the thermostatic costs experienced by shorebirds in open habitats in different parts of the arctic. While it could be argued that taller vegetation in warmer, metabolically less stressful places could reduce thermostatic costs, and that leg length might then reflect a response to place the bird’s body at an appropriate level relative to vegetation height, we suggest that conditions in open habitats will be more important in driving adaptive responses, a conclusion supported by the present results.

Although we do not test the hypothesis using intra-specific variation, it should hold equally well. For example, the semipalmated sandpiper (C. pusilla) shows strong geographical variation in morphology on the breeding grounds (Ouellet et al., 1973). We predict that the variation in leg length, after controlling for body size and the size of other appendages (bill and wing), would be shorter in more metabolically stressful habitats. Hale (1980) describes within-species patterns of bill length in two shorebird species that also follow Allen’s rule, but these analyses do not control for body size, a potentially confounding factor.

The effect of height on boundary layer-based stress advanced in this paper has parallels in other systems. For example, the morphology of sessile or almost sessile intertidal organisms is strongly affected by boundary layer-influenced flow of water over them (Dudley, 1985; Akester & Martel, 2000), and the morphology of plants is shaped by their location within the boundary layer (Henry & Thomas, 2002). Yet, while protruding out from a boundary layer brings physical costs, the converse is true when increased dispersal is desired (e.g. Washburn & Washburn, 1984; Cartar & Abrahams, 2000). Even the length of different sensory hairs in the cricket Gryllus bimaculatus is related to the position within the boundary layer (Shimozawa & Kanou, 1984). Overall, attention to flow may give us insights into the diversity of biotic morphology and behaviour of non-sessile organisms.

REFERENCES


**BIOSKETCHES**

**Ralph Cartar** is an evolutionary ecologist whose primary research involves applying theories of density-dependent habitat selection, and of work effort and lifespan, to natural systems, particularly the case of foraging bumble bees. He has a lifelong interest in shorebird ecology.

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