Article

Leg length and temperature determine the use of unipedal roosting in birds

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The function of standing on one leg in birds has long been attributed to reducing heat loss from the unfeathered legs to the external environment. Whilst a handful of single-species studies correlate the use of the behaviour with ambient temperature, the degree to which it is used across taxa is unknown. Given that leg-length varies between species, the length of the leg (relative to body size) may mediate the use of this thermoregulatory behaviour, such that birds with longer legs should roost on one leg more than those with relatively shorter legs at any given ambient temperature. We tested this prediction through field observations and comparative analyses of nine shorebird species, with varying tarsi length relative to body size. Six of the nine species examined used unipedal standing more as temperatures decrease, indicating its role as a heat conservation behaviour. We also found that species with relatively longer legs roosted on one leg more frequently across a wide range of temperatures. Species with shorter leg lengths likely rely less on this posture to insulate the relatively smaller surface area of the legs. Our findings showed that the long accepted notion that birds stand on one leg more at colder temperatures holds, and that species with smaller relative leg length were less reliant on this behaviour to minimise heat loss from these bare appendages.

Keywords: climate adaptation, tarsi length, thermoregulation

Introduction

As is the case for all endotherms, the evolution of birds has been driven and constrained by the need to regulate body temperature through physiological, morphological and behavioural adaptations (Wolf and Walsberg 2000, Symonds and Tattersall 2010, Tattersall et al. 2012). With their body predominantly covered in insulative plumage, the unfeathered appendages often account for the majority of heat lost to the external environment (Steen and Steen 1965, Phillips and Sanborn 1994, Tattersall and Cadena 2010). This is especially true of the legs (Steen and Steen 1965, Baudinette et al. 1976, Martineau and Larochelle 1988, Dawson and Whittow 1999) and the bill (Hagan and Heath 1980, Phillips and Sanborn 1994, Scott et al. 2008, Tattersall et al. 2009).

It is not surprising therefore that bill and, to a lesser extent, leg morphology are under selective pressure to minimise unwanted heat loss or excess heat load (Cadena et al. 2012, Greenberg et al. 2012, 2013, Tattersall et al. 2017). In accordance with Allen's (1877) rule, there are strong positive relationships of bill and leg size with environmental temperatures with many species from warmer climates tending to have larger bills and longer legs, after controlling for phylogeny (Cartar and Morrison 2005, Nudds and Oswald 2007, Symonds and Tattersall 2010).

The anatomical evolution for larger or smaller surface areas of exposed body parts is likely to minimise the metabolic stress associated with maintaining core body temperature given the typical ambient temperatures experienced within species' home ranges (smaller bare areas result in less unwanted heat loss, larger appendages enable greater heat dissipation at high ambient temperatures) (Phillips and Sanborn 1994, Scott et al. 2008, Tattersall et al. 2009). However, coping with short-term fluctuations in ambient temperature, or opportunities for energy conservation, must be dealt with by behavioural adaptations, such as seeking shade (Lustick et al. 1978, Walsberg 1985, 1986), body orientation in relation to the sun (Lustick et al. 1978, Brodsky and Weatherhead 1984), heat dissapating or generating behaviours (e.g. panting, shivering and ptiloerection) (Hohtola et al. 1980, Walsberg 1985, Stevens et al. 1986, Tattersall et al. 2012) or the deliberate covering of exposed body regions with the insulating plumage (Carrascal et al. 2001, Carr and Lima 2011). The covering of bare appendages generally increases with decreasing ambient temperature (Amlaner and Ball 1983, Ryeland et al. 2017). For example, placing the bill back and within the plumage, and standing on one leg occurs more at low ambient temperatures, across all temperatures studied (Midtgård 1978, Anderson and Williams 2010, Bouchard and Anderson 2011, Javůrková et al. 2011, Ryeland et al. 2017, Yorzinski et al. 2018).

Covering the feet, tarsi and metatarsi by roosting on one leg or sitting on the ground can reduce heat loss across the surface of these appendages by as much 50% in avian species (Dawson and Whittow 1999). However, these postures may also be costly in terms of compromising reaction time to predators and subsequent successful escape (Carr and Lima 2011, Javůrková et al. 2011), and they limit normal activities such as foraging. Birds are therefore expected to roost in these thermoregulatory postures only when thermoregulatory benefits outweigh any costs.

Whilst it has long been recognised that the legs are an important thermal window in birds (Chatfield et al. 1953, Kahl 1963, Steen and Steen 1965), no interspecific behavioural studies are available, and only a handful of intraspecific studies exist. Interspecific differences in leg length (and therefore the surface area where heat can be lost across) may obviate or mediate the use of standing on one leg. In a previous study we found that bill size explains variation in patterns of behavioural thermoregulation across bird species, with larger billed species spending more time in back rest postures than smaller-billed species across a wide range of ambient temperature (Ryeland et al. 2017). Here we investigate whether leg length influences the use of standing on one leg (unipedal posture) in shorebird species. Because of the potentially higher rates of heat loss in species with longer legs (as suggested by the latitudinal and altitudinal clines in leg length between species; Nudds and Oswald 2007, Symonds and Tattersall 2010), we therefore predicted similar requirement for species with longer legs to, on average, use unipedal standing relatively more to reduce heat loss, within the range of ambient temperatures commonly experienced by these species.

To test whether longer-legged species spent a greater proportion of time on average in thermoregulatory postures that cover the legs (i.e. standing on one leg), the percentage of time spent roosting on one leg was observed and compared across ambient temperatures for each species separately, and then compared between species in relation to their different leg lengths.

Methods

Observations of shorebird behaviour

Nine shorebird species from four families were studied along the coastlines of Port Phillip and Westernport Bays, southern Victoria, Australia (Supplementary material Appendix 1 Table A1–A2), during spring and summer (October, 2013–February, 2014). The species were: sharp-tailed sandpiper *Calidris acuminata* (n = 42 individuals), curlew sandpiper *Calidris ferruginea* (n = 38), red-necked stint *Calidris ruficollis* (n = 39), red-kneed dotterel *Erythrogonys cinctus* (n = 39), pied oystercatcher *Haematopus longirostris* (n = 43), black-winged stilt *Himantopus himantopus* (n = 53), red-necked avocet *Recurvirostra novaehollandiae* (n = 41), common greenshank *Tringa nebularia* (n = 38) and masked lapwing *Vanellus miles* (n = 42). These species are all sexually monomorphic; therefore, the sexes were combined in our analyses.

During the austral summer, these species forage and roost locally, although some short-distance movements occur between, in particular, near-coastal roost sites and tidal foraging localities (Nebel et al. 2013). Full details of the species and their foraging and roosting habitats is provided in Ryeland et al. (2017). The birds studied mostly roosted at high tide (Rogers et al. 2006). Given filming occurred across a five month study period, variations in tidal height are likely captured evenly for each species. Additionally, as most roosting was not captured in marine waters, there is less variation in tidal height, without the high tide extremes experienced in marine waters.

Undisturbed roosting birds that were in exposed areas (i.e. not undercover from vegetation) were videoed with a Canon 60D DSLR camera using a Canon 100–400 mm lens (Canon, Tokyo, Japan) or 'digiscope' (Swarovski ATM 80HD Spotting Scope, Swarovski Optik, Absam, Tyrol, Austria). Birds roosted on either bare earth, in shallow fresh, brackish

or saline waters or in low vegetation, which was noted during filming. However, due to the nature of the observations (taken from a distance), we were unable to record detailed quantifications of subtrate differences, and therefore this was not included in any modelling. An individual bird was classified as roosting (and qualified for video recording) once it was immobile in standing (on one or both legs) or sitting position for > 120 s. While in this position the placement of the legs was recorded (see Supplementary material Appendix 1 Table A3 for further description). When the legs were not visible (e.g. they were behind a rock or vegetation), the bird was excluded from the analyses.

Full details of the filming parameters of video sessions are described in Ryeland et al. (2017). Briefly, filming bouts were a maximum of 25 min in duration (17.28 ± 7.60 (mean $\pm$ SD) min) with a minimum of six individuals of each species observed for each of six ambient temperature brackets (11–15, 16–20, 21–25, 26–30, 31–35 and ≥ 36°C). Ambient temperature and wind speed were recorded at 5-min intervals (and averaged) during each video bout (taken as close to the birds as possible without causing disturbance) using a Kestrel 3000 pocket weather meter (Nielsen-Kellerman Company, Boothwyn, PA, USA). Ambient temperature has been shown in previous studies to effect the use of thermoregulatory behaviours (Midtgård 1978, Anderson and Williams 2010, Bouchard and Anderson 2011, Javůrková et al. 2011, Ryeland et al. 2017, Yorzinski et al. 2018) and is therefore appropriate to use here. Furthermore, gaining operative or microclimate temperature would cause disturbance to the birds, which would result in modification of behaviours.

From each video bout, focal individuals were chosen to record the duration and frequency with which they displayed each posture. The individuals on screen were assigned a number sequentially from left to right then top to bottom, and then focal individuals were selected using a random number generator, thereby limiting the chance of overrepresentation of any specific posture. The duration and frequency of postures were coded ('iObserver' app for iPad, Skware 2011). Roosting postures were timed separately and non-roosting behaviours were identified so they could be excluded from analysis of roosting behaviour. The total proportion of each video bout representing each posture was then calculated.

Intraspecific analysis

We constructed generalised linear mixed models, with proportion of roosting time per observation period spent roosting on one leg as the response variable, and mean ambient temperature as predictor, with mean wind speed over the video bout as a covariate. All birds were observed by a single observer within a stationary car (acting as a bird hide; Bennett et al. 2011) which, in combination with monitoring for any disturbance, ensured disturbed birds did not feature in the dataset. As such, distance from the observer should not be an influencing factor, as the car would be visible to the birds at all distances studied and there should not bias

the observations. The distance from the observer was also not found to be a significant variable on thermoregulatory postures in previous findings (Ryeland et al. 2017).

As multiple birds were observed from particular filming sessions (Ryeland et al. 2017), the possibility that individuals in close proximity during video bouts may have influenced each other's behaviour (Beauchamp 2007, 2008) was controlled for by including video bout identity as a random effect in all models. As the time standing on one leg is proportional to the length of the video bout (and restricted to values between 0 and 1), mixed effects logistic regression models with a binomial error and logit-link function (fitted by maximum likelihood with a Laplance approximation) were employed (Crawley 2005). This treats each minute of observation as a 'presence' (i.e. bird standing on one leg) or 'absence' (i.e. bird not standing on one leg, e.g. bird standing on two legs or sitting) behaviour within a fixed number of Bernoulli trials (total minutes of observation). In one case, the pied oystercatcher, using the raw data resulted in lack of convergence, consequently we z-transformed temperature and wind speed for that analysis.

For each species we sought to identify the best approximating model that described variation in time spent roosting on one leg. We employed a model selection approach using Akaike's information criterion (AIC) (Burnham and Anderson 2002). We identified the most parsimonious and best approximating models by comparing AIC scores (lower scores are 'better models'), with models with differences of < 2 AIC units (ΔAIC < 2) being deemed effectively equally worthy of consideration. Models that were less highly ranked, but were just more complex versions of better ranked simpler models were considered to be uninformative (Burnham and Anderson 2002, Richards 2005) and were removed from the analyses. With the remaining models we calculated Akaike weights, which can be considered equivalent to the probability that the model is truly the best model of those considered for the data. We used these weights to produce a '95% credibility set' of best models – the models whose summed Akaike weight is > 95% (Symonds and Moussalli 2011). Intraspecific statistical analyses were carried out using the 'lme4' (Bates et al. 2014, Pinheiro et al. 2014) and 'MuMIn' (Bartoń 2014) packages in the R framework.

Interspecific analyses

To evaluate the relationship of morphology and ambient temperature to use of standing on one leg behaviour across species, we employed a Bayesian phylogenetic generalised linear mixed modelling approach, as implemented through the package 'MCMCglmm' (Hadfield 2010) in R. This controls for the statistical non-independence of species by including species ID as a random effect.

The phylogeny used as the basis for analysis was derived from the Global Phylogeny of Birds website – birdtree.org (Jetz et al. 2012). We downloaded 2000 putative phylogenies from the pseudo-posterior distribution of trees using

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the Hackett et al. (2008) 'backbone'. A majority rule consensus phylogeny was then calculated from the 2000 trees using Mesquite software (Maddison and Maddison 2010; Supplementary material Appendix 1 Fig. A1), with branch lengths assigned using the Grafen (1989) algorithm whereby the depth of each node in the tree is equal to the number of daughter species derived from it.

To evaluate the effects of the relative leg size on use of unipedal standing, we collated data on mean tarsus size (length from the inner bend of the tibiotarsal articulation to the base of the toes) and body mass from the literature for each species (Barter 1984, 1986, Rogers 1990, Marchant and Higgins 1993, Higgins and Davies 1996, Rogers et al. 1996, Nebel et. al. 2013) using weighted species averages for live birds (both sexes combined) with Victorian captured birds used in preference (where data were available). Tarsus is the only leg measurement routinely measured in shorebirds (Baker et al. 1997) and as such, tarsi lengths were used as a proxy for leg length and are referred to here more generally as 'leg length'.

We then constructed our mixed model using average temperature, tarsus length and body mass (the latter to control for body size) as fixed effects, with video bout and species as random effects. We also examined whether species with different tarsus lengths might show different behavioural responses across the range of temperatures by including a tarsus length:temperature interaction term. To improve distribution, both tarsus length and body mass were $\log_{10}$-transformed prior to analysis, and all three fixed predictors were z-transformed to standardise them.

As with our intraspecific analyses, the phylogenetic GLMM modelled the response variable (proportion of time standing on one leg) as a binomial response with logit-link function (family = 'multinomial2' in 'MCMCglmm'). We used uninformative priors, carrying out 401 000 iterations with a burn-in of 1000 and thinning interval of 400, generating an effective sample size for the Bayesian posterior distribution of 1000 (convergence was checked by visual inspection of plots of parameter estimates). The results therefore produce a Bayesian posterior mean estimate, with 95% credibility intervals for the distribution of estimates, and a probability estimate (pMCMC) which is two times the probability that the posterior mean is less than or greater than zero (whichever is the smaller). All R code used in analyses and the raw data are presented in Supplementary material Appendix 1.

Data deposition

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3vh00dm/1> (Ryeland et al. 2019).

Results

Intraspecific analysis

Ambient temperature alone featured as the predictor in the best models predicting the proportion of time spent standing on one leg in six shorebird species (Table 1 – red-necked stint, red-kneed dotterel, pied oystercatcher, black-winged stilt, common greenshank and masked lapwing). In all of these cases the parameter estimates were significantly different from zero (the confidence intervals on the estimate did not include zero), and the relationship with the proportion of time standing on one leg was negative: i.e. the behaviour was used less as ambient temperature increased.

Table 1. Individual species best-approximating models, predicting standing on one leg behaviour (temperature and wind speed as possible predictors). For each species, where appropriate the 95% credibility set of top models predicting the percentage of time spent standing on one leg are shown, with Akaike weight (w_i). More complex models that are less highly weighted than simpler models are not shown. Parameter estimates and 95% confidence intervals are in parentheses. The models have a binomial logistic response variable, hence, these estimates are non-exponentiated odds ratio parameters.

Species (+ common name)		Model order	ΔAIC	w_i
Calidris acuminata sharp-tailed sandpiper	1	(null)	0	0.57
Calidris ferruginea curlew sandpiper	1	(null)	0	0.42
Calidris ruficollis red-necked stint	1	Temperature (−0.228; CI = −0.509 to −0.0189)*	0	0.44
	2	Wind (−1.035; CI = −2.504 to 0.081)	1.14	0.25
	3	(null)	2.16	0.15
Erythrogonys cinctus red-kneed dotterel	1	Temperature (−0.303; CI = −0.717 to −0.020)*	0	0.50
	2	(null)	2.02	0.18
Haematopus longirostris pied oystercatcher	1	Temperature (−1.886; CI = −4.159 to −0.143)*	0	0.57
	2	(null)	2.13	0.20
Himantopus himantopus black-winged stilt	1	Temperature (−0.294; CI = −0.696 to −0.043)*	0	0.60
	2	(null)	2.99	0.14
Recurvirostra novaehollandiae red-necked avocet	1	(null)	0	0.45
Tringa nebularia common greenshank	1	Temperature (−0.483; CI = −1.072 to −0.076)*	0	0.64
	2	(null)	3.14	0.13
Vanellus miles masked lapwing	1	Temperature (−0.375; CI = −0.827 to −0.103)*	0	0.66
	2	(null)	3.56	0.11

*95% confidence intervals on parameter estimates do not cross zero.

Table 2. Phylogenetic generalised linear mixed model predicting proportion of time spent standing on one leg across the nine shorebird species. Presented are the predictor posterior mean estimates plus associated 95% credibility intervals associated probability values calculated from the posterior distributions.

Parameter	Estimate	95% CI	pMCMC
Temperature	−1.633	−2.405 to −0.826	< 0.001
Tarsus length	2.491	−0.033 to 4.793	0.046
Temperature: tarsus length	−0.040	−0.871 to 0.760	0.930
Body mass	−1.385	−3.497 to 0.496	0.128
Intercept	−2.208	−5.973 to 1.431	0.200

Wind speed did not feature in any of the top models for any species.

Interspecific analysis

After controlling for body mass, both ambient temperature and tarsus length strongly determined the proportion of time spent roosting on one leg across species (Table 2, Fig. 1). Across the range of temperatures recorded, species with relatively longer legs roosted on one leg a greater proportion of the time, while species with shorter legs tended not to stand on one leg to a great extent at any ambient temperature. The red-necked stint, with the smallest relative leg length used the behaviour least and the black-winged stilt and red-necked avocet, with the longest relative leg lengths, spent the most time standing on one leg, across all ambient temperatures. There was no evidence, however, of an interaction between tarsus length and temperature in predicting unipedal standing.

Discussion

The idiosyncratic behavior of birds roosting on one leg has long been proposed to be thermoregulatory in nature, but few papers have confirmed this hypothesis and those that have used within-species designs (Kahl 1963, Martineau and Larochelle 1988, Anderson and Williams 2010). No studies, to our knowledge, have compared the behavior across species. Here, we demonstrated that this hypothesis holds true for the majority, but not all, of the species we studied. The posture of tucking one leg into the belly plumage (unipedal roosting), for most species, was temperature dependent. For six out of nine species, the behavior was observed significantly more often as the ambient temperature decreased, and less often as it increased.

The legs are a significant site of heat loss in birds (Steen and Steen 1965, Martineau and Larochelle 1988, Cartar and Morrison 2005), and therefore it follows, at least for the red-necked stint, red-kneed dotterel, pied oystercatcher, black-winged stilt, common greenshank and masked lapwing, that they will reduce heat loss at colder ambient temperatures by placing the otherwise uninsulated leg into the body plumage when roosting. This apparently reduces heat loss and the consequent metabolic costs associated with thermoregulation (Steen and Steen 1965, Cartar and
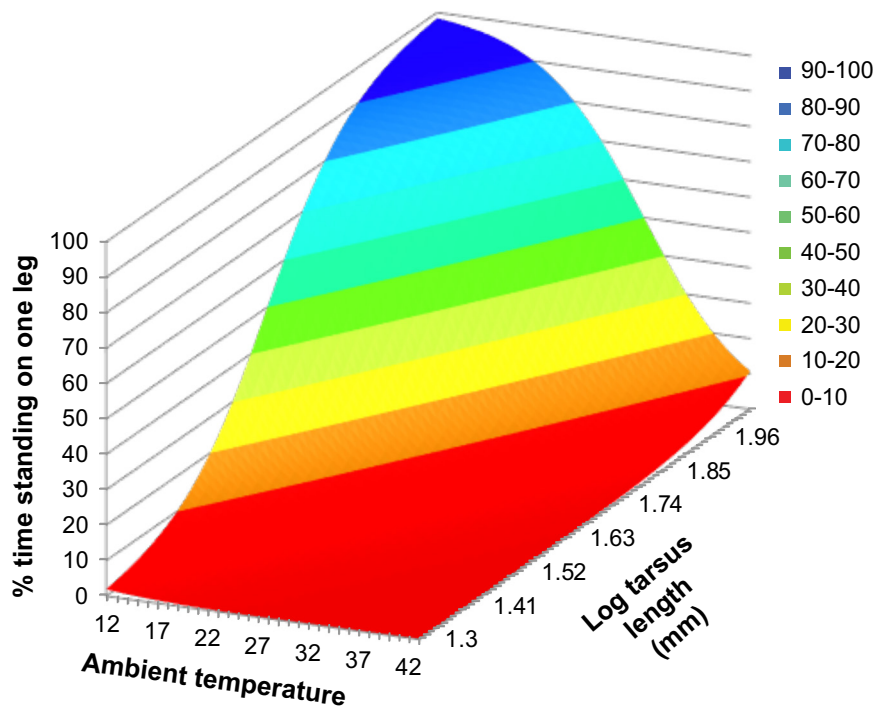

Figure 1. Phylogenetic GLMM predicted relationship across all species of percentage of time spent standing on one leg while roosting in relation to ambient temperature (°C) and tarsus length (log mm).

Morrison 2005), though further testing, using physiological techniques such as thermal imaging, would need to be undertaken to test this in an ex situ, manipulative study. When roosting on both legs, birds should have an increase in the exposed uninsulated surface area over which to dissipate heat at higher ambient temperatures (Steen and Steen 1965, Baudinette et al. 1976, Brodsky and Weatherhead 1984, Carr and Lima 2011).

Interestingly, temperature did not feature in the best predicting model for the red-necked avocet, sharp-tailed sandpiper or curlew sandpiper. It is not apparent that this is a consequence of relative leg length (these species have neither the largest nor smallest relative leg lengths), phylogenetic conservatism (all three species are not from the same genus), or a lack of sampling at low ambient temperatures. The two calidrine species not exhibiting the temperature effect are migratory, and experience polar and tropical climates annually (Supplementary material Appendix 1 Table A4), as do several other species showing a temperature effect (Marchant and Higgins 1993, Higgins and Davies 1996), and as such, the absence of an effect in these species is perplexing. The avocet is the only species studied which routinely swims while foraging, completely immersing its legs in water (rather than wading); perhaps particularly well developed physiological adaptations obviate the need to cover a leg while roosting. It is possible that other factors may be important in the use of unipedal roosting. Such variables may include differences in antipredator behaviours (Yorzinski et al. 2018). The relationship between unipedal roosting and ambient temperature may be complicated by the fact that heat loss is decreased by the use of the counter-current heat exchange mechanism in the legs of all birds studied (Ederstrom and Brumleve 1964, Steen and Steen 1965, Johansen and Millard 1973). It is conceiveable that these mechanisms vary in effectiveness between species, but we have no direct information in this regard for the study species. It may also be possible that the relationship between ambient temperature and operative temperature (which was not able to be recorded in this study) may differ between species, but again, we have no evidence to suggest this is the case. Wind speed also did not feature in any of the top models for any species.

Furthermore, the temperature range tested within this study (11°C–42.5°C) represents relatively warm temperatures compared with the global range of temperatures that shorebirds experience. It is likely that at very low temperatures, other thermoregulatory behaviours such as body orientation in relation to the sun (Lustick et al. 1978, Brodsky and Weatherhead 1984) or heat generating behaviours (e.g. shivering and ptiloerection) (Hohtola et al. 1980, Walsberg 1985, Stevens et al. 1986, Tattersall et al. 2012) may become important. Similarly, other behavioural mechanisms may be used at very high ambient temperatures such as seeking shade (Lustick et al. 1978, Walsberg 1985, 1986), body orientation away from the sun (Lustick et al. 1978, Brodsky and Weatherhead 1984) and heat dissipating behaviours (e.g. panting or gaping) (Hohtola et al. 1980, Walsberg 1985,

Stevens et al. 1986, Tattersall et al. 2012). These behaviours were not tested in this study, but may also interact with the postural changes shown to be important here. It may be possible that at very high temperatures, namely those above the body temperature of the animal, thermoregulatory postures (unipedal roosting and back rest) may be used to prevent heat gain from the surrounding environment. By either tucking the bill and leg within the plumage or simply shading the appendages by drawing them close to the body, heat conduction from the ground (through the legs) and radiation from the surrounding air may be minimized, reducing the heat gained at high temperatures. There is some evidence for the use of back rest in the upper temperature limits examined in this study (Ryeland et al. 2017), however we see no evidence within the temperatures observed here for the use of unipedal roosting to insulate from heat gain at high ambient temperatures. We cannot, however, rule out its use at extreme high ambient temperatures, above those examined here.

Leg length was a key determinant of the extent to which birds roosted in a unipedal posture, with relatively longer-legged (e.g. the red-necked avocet and black-winged stilt) birds tending to employ the behaviour more frequently compared to shorter-legged birds (e.g. the red-necked stint). The model indicates that this pattern holds across all temperatures considered, but most species roost on one leg relatively rarely in very hot temperatures (i.e. > 35°C), and therefore all species spend a similar percentage of time in unipedal roosting at these temperatures. Conversely, when the ambient temperature was cold, species with the shortest legs roost on two legs most of the time, whereas birds with relatively long legs often roost on one leg for over half of the time observed.

Limitations of unipedal roosting may also be interacting with these relationships for some species. Unipedal roosting may be less efficient for shorter-legged shorebirds, perhaps due to biomechanical constraints associated with balance. For example, the red-necked stint, with the shortest leg length (relative and total), roosted less on one leg as wind speeds increased in the second best predicting model. This might conceivably be due to its relatively light body mass and short leg length, making it difficult to balance on one leg in windy conditions. The absolute mass of heavier species may make maintaining balance during unipedal roosting easier, particularly at higher wind speeds. Indeed there is some evidence from that standing on one-leg requires less muscle activity and increases stability (Chang and Ting 2017). It may however, also be that heavier birds may be unable to use unipedal roosting for extensive roosting bouts, as it may be less comfortable to stand on one leg (potentially causing leg cramping, known to occur in roosting shorebirds; Clark and Clark 2002). Alternatively, higher relative metabolic rates may occur in relatively smaller birds that will therefore have higher heat production (Lasiewski and Dawson 1967, Bennett and Harvey 1987), requiring smaller birds to make postural adjustments more frequently to reduce their heat load.

Leg length, which was historically considered to be a relative measurement to body size (i.e. allometric scaling), has been long known to evolve independently of body size, with differing selective pressures (Grant 1971). Differences in leg length are often considered as a function of non-flying movement and support (i.e. perching behaviour, ground foraging and predation strategies in carnivorous and omnivorous birds) (Baker 1979, Moreno and Carrascal 1993, Barbosa and Moreno 1999, Zeffer et al. 2003). Our findings also suggest that interspecific differences in leg length affect thermoregulation in birds, and further research should be directed to determine whether this may be an evolutionary constraint. Across species, leg length is generally positively correlated with the minimum ambient temperature of the species' range (Cartar and Morrison 2005, Nudds and Oswald 2007, Symonds and Tattersall 2010); though this does not hold across all taxonomic groups (Symonds and Tattersall 2010). The groups in which this gradient have been found follow Allen's rule (Allen 1877), i.e. colder climates are associated with shorter legs and vice versa. The findings in our paper further elucidate this link, demonstrating that birds with differing leg lengths and inhabiting a similar climate, may cope with local climatic variation thorough behavioural means. This behaviour likely expands the thermal niche which is inhabitable by these species. Shorebirds inhabit a vast array of thermal environments, and migratory species (such as some of the study species), live in or transit through polar, tropical, subtropical and temperate environments annually. The capacity to have plastic thermal tolerances mediated by behaviour would likely be highly adaptive, and perhaps critical, to the ability to migrate transglobally.

Insulating the legs through unipedal roosting is one of several ways birds may reduce heat loss, but it appears to be an important aspect of behavioural thermoregulation. Birds may also tuck the uninsulated bill between the plumage (Reebs 1986, Ryeland et al. 2017) or move to thermally favourable microhabitats (e.g. sheltering) (Walsberg 1993). These postures may be used simultaneously or alone, as they both act to insulate otherwise uninsulated appendages. A recent comparative analysis also found that the two behaviours tend to be coupled, with species that use back rest also tending to use unipedal roosting (Pavlovic et al. 2019). For the species that use these postures, it is likely that when temperatures are very low, birds both tuck their bill and one leg into the plumage. This would minimize heat loss further, but may make the bird more susceptible to predation, as discussed below. Similarly at very hot temperatures, birds are likely to both remove the bill and the legs from the insulating plumage. We have no evidence that, for species which showed no effect of temperature on unipedal roosting, back rest was used as an alternative posture. In fact, one of these three species, the red-necked avocet, also showed no effect of temperture on the use of back rest (Ryeland et al. 2017) and therefore it does not appear to be using the back rest posture preferentially to unipedal roosting to minimize heat loss. Many ground foraging and wading species of bird may also squat or sit on either dry or wet substrate ('wet sitting') (Battley et al. 2003, Delord et al. 2016). This may be another method of reducing heat loss at cold ambient temperatures (sitting on dry substrate) or potentially increasing heat dissipation at high ambient temperatures (through wet sitting) (Scholander et al. 1950, Steen and Steen 1965). Whilst this study did not include sitting, it has been shown to be more commonly used by larger birds, and that species that use unipedal standing also tend to use sitting, potentially as a alternative thermoregulatory posture (Pavlovic et al. 2019).

Insulating the legs within the plumage of the body may be an important aspect of the ability of birds to deal with daily fluctuations in ambient temperature, but is also likely to have trade-offs with anti-predator behaviours and foraging behaviour. Such thermoregulatory behaviours must be balanced with other important behavioural functions, such as anti-predator defences (Baudinette et al. 1976, Cartar and Morrison 2005, Carr and Lima 2011). In particular, postures such as unipedal roosting may reduce the ability and speed of a bird to escape from a detected predator (Carr and Lima 2011). This is perhaps why no birds (even those with the longest relative leg length) always roosted on one leg, even at the mimimum temperatures studied.

Although there is conflicting evidence as to whether bird leg morphology across taxa conforms to Allen's rule (Cartar and Morrison 2005, Symonds and Tattersall 2010), here we demonstrated that interspecific variation in leg length is particularly important in mediating the thermoregulatory costs associated with daily fluctuations in ambient temperature. Whilst other behavioural and physiological differences clearly influence unipedal roosting, with the behaviour evidently not temperature dependant within several species, relative leg length is likely to be an important aspect of a species ability to deal with seasonal and long-term change in climate.

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Supplementary material (available online as Appendix jav-02008 at <www.avianbiology.org/appendix/jav-02008>). Appendix 1.