

Behavioural evidence for heat-load problems in Great Knots in tropical Australia fuelling for long-distance flight

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Abstract. Migratory shorebirds that live in the tropics prior to embarking on long (>5000 km) flights may face heat-load problems. The behaviour of a large sandpiper, the Great Knot (*Calidris tenuirostris*), was studied in Roebuck Bay, north-west Australia, from February to April 2000. We determined the incidence of heat-reduction behaviour in foraging and roosting birds in relation to breeding-plumage score (an index of migratory preparation) and microclimate variables. Heat-reduction behaviour (primarily raising the back feathers) was significantly related to breeding-plumage score and solar radiation. Raising back feathers may reduce the external heat load for a bird, or increase convective or cutaneous evaporative cooling. The results suggest that managing heat loads in tropical-wintering waders may become more difficult close to departure on migration.

Introduction

Many migratory shorebirds (Order Charadriiformes) prepare for long flights to their breeding grounds from fuelling areas in the tropics. The time spent fuelling in these areas often coincides with the hot, humid part of the year (the wet season). Basal metabolic rates are lower in shorebirds wintering in tropical Africa than in temperate areas (Klaassen *et al.* 1990; Kersten *et al.* 1998), and this has been interpreted as an adaptation to reduce endogenous heat production. However, few studies have examined the effect of thermal constraints on the behaviour or physiology of waders when they are actively fuelling (Klaassen 1990; Klaassen and Ens 1990; Klaassen *et al.* 1990). Migratory shorebirds may be susceptible to heat stress in the tropics for the following reasons:

- (1) They migrate between climatically contrasting regions, such as between Arctic tundra breeding sites (where heat conservation may be imperative) and tropical mudflats (where overheating may be the issue). Because of this, they may not have the option of evolving specific physiological heat-loss adaptations (cf. Withers and Williams 1990) as these could compromise their heat-conservation abilities on the breeding grounds.
- (2) They live in open habitats, where their routines are determined by tidal, rather than daylight, rhythms. They

cannot behaviourally seek refuge from radiation (cf. Lustick *et al.* 1979; Davies 1982; Williams *et al.* 1999).

- (3) Their basal metabolic rate and the mass of heat-producing internal organs increase during fuelling (Piersma *et al.* 1996, 1999), presumably increasing metabolic heat production.
- (4) A thick layer of fat is deposited just under the skin, enveloping the torso (Piersma *et al.* 1999). This may hinder heat loss, particularly via cutaneous evaporative water loss, if the lipids form an impediment to water transfer.
- (5) Fuelling birds moult into breeding plumage, which is generally darker than the non-breeding plumage and may increase absorption of solar radiation and increase the plumage temperature (Lustick *et al.* 1978; Wolf and Walsberg 2000).
- (6) Birds may increase their foraging activity during migratory fuelling.

If peak fuelling activity (which generates the most internal heat) coincides with climatic conditions unfavourable for heat loss, tropical-wintering shorebirds could suffer heat-stress problems. Roebuck Bay, north-west Australia (18°00'S, 122°22'E), is a fuelling site for migratory shorebirds where these conditions are likely. The fuelling period (February–April) overlaps with the end of the 'wet season' (Kenneally *et al.* 1996), and the climate is typically warm,

humid and often sunny (March long-term averages at Broome Airport from the West Australia Bureau of Meteorology: maximum temperature 33.9°C, minimum temperature 25.4°C, relative humidity 69%, 8.7 sunshine hours per day).

Earlier observations of fuelling waders in Mauritania suggested that heat stress was not a problem for roosting waders (Klaassen 1990), though it has become clear that the Banc d'Arguin in Mauritania is a fairly 'cool' site compared with true tropical sites. In Guinea-Bissau, for instance, waders were observed foraging with back feathers raised and roosting in shallow water, presumably to minimise heat gain and maximise heat loss (TP, unpublished). It is expected that heat-load problems will occur more frequently in places where heat gain is high (high temperatures and radiation), especially if the heat-loss potential is low (low winds, high humidity: Webster and King 1987). Furthermore, if migratory preparation results in increased heat generation and heat absorption, as well as impaired heat loss, there should be a relationship between heat avoidance and fuelling state.

We tested for this relationship in Great Knots (*Calidris tenuirostris*) in Roebuck Bay. The behaviour of foraging and roosting birds was studied, specifically focussing on what we considered heat-avoidance behaviours. We concurrently collected climate data with a portable climate station. This allowed us to test which environmental factors influenced the occurrence of heat-reduction behaviours during fuelling. We predicted that heat reduction would increase with migratory preparation (using breeding plumage scores to represent migratory state: see Battley *et al.* 2004).

The Great Knot is a long-haul migrant that leaves north-west Australia in late March and early April and flies 5400–6000 km non-stop to staging sites in eastern China and Korea (see Battley *et al.* 2000). Great Knots possess the characters likely to predispose birds to heat stress. They have large fat deposits, primarily in a thick subcutaneous layer (predeparture birds collected in 1998 weighing 231–256 g contained 96–97 g of fat: Battley *et al.* 2001b). Before migration they also have high basal metabolic rates (BMR): BMR of five Roebuck Bay birds weighing, on average, 198.2 g was 1.85 W (Battley *et al.* 2001a), 48% above the predicted BMR (1.25 W) from an interspecific equation for tropical-wintering waders (Kersten *et al.* 1998). Their breeding plumage, into which they moult from January to March, is predominantly black and dark grey-brown.

Materials and Methods

Fuelling Great Knots were studied in Roebuck Bay, from February to April 2000. Fifty-five behavioural scans were made of feeding and roosting flocks of Great Knots. During these scans, time, place, substrate, activity, breeding-plumage score and any apparent heat-reduction behaviour (raising of mantle and scapular feathers, gaping, panting, and standing with one leg raised off the substrate but hanging below the body) were noted for individual birds. Feather-raising was recorded only on birds for which it was clear that the feathers were actually raised rather than blown by the wind. Observations were made

only on settled birds. A portable climate station was used to measure climatic conditions during most scans, or immediately afterwards if setting the station up would have disturbed the birds. The unit (Automatic Weather Station, Monitor Sensors, Caboolture, Queensland, Australia: www.ats.com.au/monitor) measured air temperature (°C), wind speed at ~1.5 m height (m s^{-1}), relative humidity (%) and incoming solar radiation (W m^{-2}). Additionally, during most scans one or two temperature sensors recorded the temperature just under the surface of the substrate (if mud or sand) or out of direct radiation under a small overhang or under a pebble (if rocky). If more than one substrate sensor was used, values were averaged. The main climate station was used in 47 scans, but substrate temperature was measured in only 42 scans. For general comparisons, climate summaries were obtained from the Bureau of Meteorology, West Australia, for Broome Airport and Broome Post Office.

One-way Mann–Whitney U-tests were used to determine whether birds that showed heat avoidance had higher breeding plumage scores than those that did not (within each scan, and also for pooled individuals from low tide, high tide, and both tides together). Histograms of the frequency of plumage scores within each tide type category showed that the distributions were similar. When testing for the influence of plumage and climate on the incidence of heat-reduction behaviour, the proportion of birds that showed heat reduction in each scan was calculated, then arcsine-transformed. This became the dependent variable in a multiple regression against mean plumage score for the scan, and five climate variables (mean air temperature, substrate temperature, wind speed, humidity and radiation during the scan). Partial residuals were saved for plotting the direct effect of significant variables on heat reduction. We had prior expectation of the direction of the effects of plumage and climate on heat reduction (a positive relationship between heat reduction and the variable score for plumage, air temperature, humidity, substrate temperature and radiation; a negative relationship for wind speed), so the two-tailed significance values of the multiple regressions were halved.

Results

Heat-reduction behaviours in roosting and feeding flocks

Overall, of 2464 birds scanned, 704 (29%) showed heat-reduction behaviours. At low tide, most birds scanned showed heat avoidance (58.1% of individuals; average proportion in 21 scans = 57.7%). At high tide, early scans (6–21 March) recorded very few birds behaviourally avoiding heat (28 birds of 989 scanned; 2.8% of individuals; average proportion in 22 scans = 1.9%), whereas later scans (22 March–10 April) showed a much higher incidence of heat avoidance (169 of 602 birds scanned; 29.5% of individuals; average proportion in 14 scans = 28.1%). The difference is probably partially climate-related – later scans were warmer on average (air temperature 1.4°C hotter, substrate temperature 2°C), with lower wind speeds (11%) and higher radiation (20%) (climate data are from only 15 and 12 scans respectively).

Three main heat-avoidance behaviours were observed in the field: raising of the 'back' feathers (ptilorection – scapulars and mantle; Fig. 1), gaping and panting (Table 1). Whether ptilorection serves to avoid a heat load or dissipate heat is not critical to this analysis – the behaviour nevertheless represents heat management. We also recorded 49 birds roosting with one foot lifted off the substrate, and 36 birds with one foot hanging below the body. While these may func-



Fig. 1. Foraging Great Knot with 95% complete breeding plumage showing the characteristic heat avoidance behaviour of raising its back feathers (ptilorection). Photograph by Jan van de Kam.

tion as heat-reduction behaviours, the same behaviours were also seen in waders roosting on a damp beach at night (when minimising heat transfer from the substrate is presumably irrelevant). Because these behaviours are ambiguous, we have not included them in analyses as heat avoidance.

Of the 57 scans of Great Knot flocks, the relationship between plumage and heat-reduction behaviour could be tested in only 26. In the remaining flocks, only one category of heat-avoidance behaviour was found (in 19 scans no birds showed heat avoidance; in four scans all birds showed heat

Table 1. Occurrence of different heat-avoidance behaviours by Great Knots at high tide and low tide

Behaviour	High tide	Low tide	Total
Raised 'back' feathers	164	506	697
Raised feathers + gaping	19		19
Raised feathers + gaping + panting	2		2
Gaping	7	1	8
Panting	2		2
Gaping + panting	3		3
Total	197	507	704

Table 2. Summary of climatic conditions measured with a portable climate station during observations in Roebuck Bay, March–April 2000

Substrate temperatures refer to mud at low tide as well as sand or rock substrates over high tide

	Air temperature °C	Substrate temperature °C	Wind speed m sec ⁻¹	Radiation W m ⁻²	Relative humidity %
Mean	30.5	34.9	2.8	703.1	78.2
Minimum	27.9	30.5	0.9	185.4	54.2
Maximum	34.8	39.7	5.7	1028.0	86.2
<i>N</i>	46	41	46	46	46

avoidance) or a category had only one or two individuals (eight scans). Eleven flocks showed significant differences in plumage between birds showing and not showing heat avoidance – in all cases birds showing heat avoidance had higher breeding-plumage scores (Mann–Whitney U-tests, $P < 0.05$). When data for all individuals were pooled, the same effect was found at low tide ($P < 0.001$), high tide ($P < 0.001$) and for both tides combined ($P < 0.001$) (Fig. 2).

Climatic conditions

Climatic conditions during the study were unusually damp and cool for much of the premigratory period. Rainfall was 1.4 times the long-term average in January, 2.4 times higher in February, 4 times higher in March and 8.6 times higher in April. Compared with the long-term average, temperatures were similar in February, but lower in March. March 2000 had seven days with the maximum temperature less than 30°C, compared with the average of one day, and no days above 35°C, compared with the average of 8.9 days. In comparison with recent years (1996–1999, 2001–2002), the 2000 season was also similar in February but cooler in March (mean 31.5°C, maximum 34.4°C, cf. mean 33.8°C, and maximum 37.8°C for other years).

The climate conditions experienced during the scans are briefly summarised in Table 2. There were no differences in

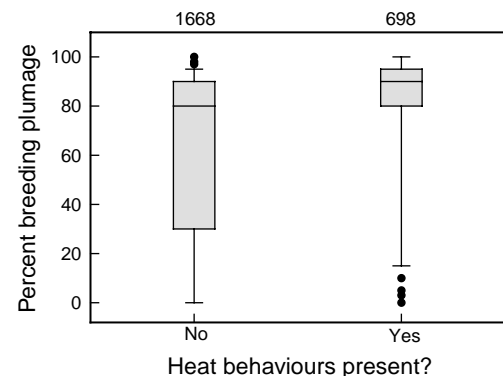


Fig. 2. Breeding plumage scores in relation to heat avoidance behaviour for Great Knots in Roebuck Bay, March–April 2000. Samples are pooled from low tide feeding and high tide roosting scans. Samples sizes are shown above the boxes. Boxes enclose the 25%, 50% and 75% quartiles, the whiskers denote the 10th and 90th percentiles, and outliers are shown as small dots.

climate conditions between high-tide and low-tide scans in air temperature, wind speed, radiation and relative humidity. Substrate temperatures did differ slightly (which is to be expected, low tide measurements being on wet mud, high tide on damp or drying sand and rock; mean \pm s.e., low tide = $33.5 \pm 0.5^\circ\text{C}$, high tide $35.6 \pm 0.6^\circ\text{C}$, $t_{40} = 2.732$, $P = 0.009$).

To assess the independence of the climatic variables, multiple regression was used to test for autocorrelation between variables. Four of the 10 comparisons were significant: a negative relationship between air temperature and humidity (hotter days were also less humid), and positive relationships between air and substrate temperatures, radiation and substrate temperatures, and wind and relative humidity (Table 3). The decrease in relative humidity with temperature was largely due to changes in temperature – absolute water vapour pressure did not vary systematically with temperature.

Influence of climate and plumage

Individual regressions between the proportion of birds in a scan showing heat avoidance and plumage and climate variables gave significant relationships with mean plumage score for the flock ($F_{1,44} = 6.463$, $P = 0.015$) and solar radiation ($F_{1,44} = 5.129$, $P = 0.029$). Because the climate variables are not independent, multiple regression was used to test all of the climate variables together (plumage was also included). Initial regression of the whole data set gave a non-significant overall relationship ($F_{6,35} = 2.250$, $P = 0.061$), but with a warning that one scan had high leverage on the analysis. This scan was at an unusually cool, dull and humid time. When this flock was omitted from the analysis (reducing the overall variance), the overall regression was significant ($F_{6,34} = 2.480$, $P = 0.042$, multiple $r^2 = 0.304$), and both plumage and radiation remained as the significant variables (Table 4; Fig. 3).

Discussion

Roebuck Bay has a tropical climate, characterised by hot, humid and rainy summers (the 'wet' season) and cooler, drier winters. Shorebird migration occurs towards the end of the wet season, but because of variation in the timing of the end

of the wet season, environmental conditions for fuelling shorebirds differ from year to year. The 2000 field season was unusually wet, and air temperatures were depressed for much of the fuelling period. Another consequence of the frequent rains was that, until early March, shorebirds seldom had to contend with dry sand conditions on beaches during high tide. This was in strong contrast to previous seasons when we have worked at Roebuck Bay, when conditions were hotter, drier and with little cloud (for example, mean temperature and rainfall in March 1998 were 34.8°C and 46.8 mm respectively; equivalent values in March 2000 were 31.5°C and 498 mm). This current study encountered relatively mild and amenable conditions, but even so, heat-reduction behaviours were common in Great Knots. We expect that in hotter years the incidence of heat reduction will be higher, and the relationships between heat reduction and plumage and climate will become stronger.

Internal and external influences on heat management by shorebirds

The two factors that had a significant effect on the incidence of heat avoidance in Great Knots were plumage score and solar radiation. Among individuals, birds with a higher breeding plumage score were more likely to show heat avoidance (Fig. 2). Among flocks, mean breeding plumage score in scans was positively related to the proportion of birds in the scan that showed heat avoidance (Fig. 3A). The proportion of birds in a flock that showed heat avoidance also increased with solar radiation (Fig. 3B).

Because changes in the plumage of Great Knots are associated with changes in body mass (and presumably body composition and metabolic rate), a correlation between heat avoidance and breeding-plumage score in a migrant bird does not demonstrate that the plumage itself is the cause of the relationship. In addition to increased heat absorption by the darker plumage, birds with a higher breeding-plumage score could be more prone to heat problems from increased internal heat production during fuelling (organ hypertrophy: Piersma *et al.* 1999) and increased insulation (and hence

Table 3. Interrelationships between climatic variables

Values are significance levels from multiple regression analyses relating one climatic variable to the remaining four. This shows which variables are significantly related when all variables are considered simultaneously. Significant relationships are shown in bold. The overall multiple regressions are significant for air temperature, radiation, humidity and substrate temperature (all $P < 0.001$), but not for wind speed ($P = 0.085$)

Independent variables	Dependent variable			
	Air temp.	Wind	Radiation	Humidity
Air temperature				
Wind speed	0.167			
Radiation	-0.053	0.525		
Relative humidity	-0.000	0.035	-0.097	
Substrate temperature	0.012	0.566	0.000	0.061

decreased heat-loss ability) due to a thick subcutaneous fat layer.

Of these reasons, the effect of a fat layer on heat loss is the least straightforward. Heat loss in birds is achieved primarily through evaporative cooling, and cutaneous evaporation often equals or exceeds respiratory evaporation (Dawson 1982). The main barrier to water loss across the body wall is the skin rather than the boundary layer or plumage, and lipids may impede water transport across the skin (Webster *et al.* 1985). However, the permeability of the skin has been shown to vary in relation to hydration state and heat acclimation (Menon *et al.* 1989; Peltonen *et al.* 1998), and there is also some suggestion that skin resistance is reduced at higher temperatures (Webster *et al.* 1985). Whether similar changes occur in the thick layer of fat that envelopes the torso of migratory waders such as Great Knots (see Piersma *et al.* 1999, fig. 2) is a different issue. This hydrophobic barrier may restrict general heat and water movement to the cooling surface, the skin, although it remains to be demonstrated that a fat layer actually does impair heat loss in birds.

Behavioural thermoregulation: losing or avoiding heat?

Gaping and panting are well known behaviours that increase evaporative heat loss. Erecting the back feathers may either maintain or avoid heat under different conditions. Usually, ptiloerection increases the thickness of the layer of air trapped within the feathers, lowering the thermal conductance across the plumage. This conserves heat in low temperatures, but such feather raising is also known in hot conditions, apparently also to decrease thermal conductance (Marder *et al.* 1989). In such conditions, the external heat load to the body is reduced. In sandgrouse (*Pterocles spp.*), feathers are erected at low temperatures, and also at high temperatures once air temperature exceeds body temperature, to maximise insulation (heat-load avoidance: Thomas 1984). Ptiloerection is also known from birds that increase

cutaneous evaporative cooling at high temperatures (e.g. Spinifex Pigeons, *Geophaps plumifera*: Withers and Williams 1990), suggesting that increased insulation is not involved (unless increased insulation and increased evaporation can be simultaneous). Instead, feather erecting may increase convective or evaporative cooling, or when radiation is involved, raise the 'heating surface' of the feathers as far away from the body as possible while increasing airflow through the feather layer (Bartholomew 1966; Louw 1993). Wolf and Walsberg (2000) show that ptiloerection can greatly reduce solar heat loads reaching the skin, at least in dark-plumaged birds. The difference between insulating and cooling effects is probably partly due to whether feathers are partially erected (trapping air) or fully erect (increasing airflow) (Willmer *et al.* 2000). In Great Knots it is not clear whether heat loss or heat-load avoidance was the reason for ptiloerection. The erect feathers often stood at an obvious angle from the body (Fig. 1), which would raise the heating surface away from the body but also increase airflow across the mantle (aiding convective and evaporative cooling).

We have not assessed the role of the bare parts in dissipating heat, but it is known that bare parts can be important in heat loss in high temperatures (e.g. Lustick *et al.* 1978, 1979; Bryant 1983; Udvardy 1983). Captive Red Knots could lose 16% of their metabolic heat production through

Table 4. Parameter values for a multiple regression analysis of the proportion of birds in scanned flocks that showed heat-avoidance behaviours, as a function of plumage and five climate variables

The proportion of the flock that showed heat-avoidance behaviours was arcsin-transformed before analysis. Because we had *a priori* expectation of the directions of the influences of the effects of the variables, the 2-tailed probability values given by Systat were halved. Significant variables are shown in bold

	Std coeff.	<i>T</i>	<i>P</i>
Constant	0.000	-1.478	0.075
Plumage	0.264	1.725	0.047
Air temperature	0.504	1.553	0.065
Substrate temperature	-0.119	-0.597	0.278
Wind speed	-0.204	-1.269	0.107
Relative humidity	0.257	0.792	0.217
Solar radiation	0.392	2.050	0.024

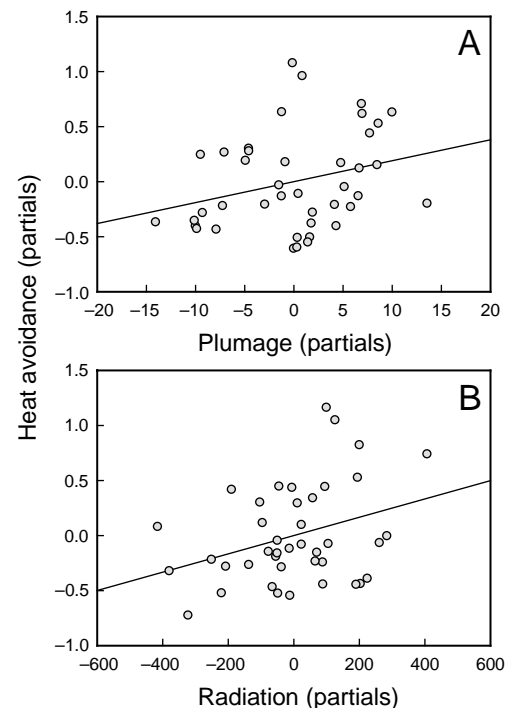


Fig. 3. Partial plots of the proportion of a scan showing heat avoidance in relation to (A) mean breeding plumage score, and (B) solar radiation. Partials were generated from a multiple regression of heat avoidance against plumage and five climate variables. The proportion of birds showing heat avoidance was arcsine-transformed before analysis.

their legs at 34.2°C air temperature (L.W. Bruinzeel, unpublished), but they could potentially lose all of their heat production if standing in water of 35°C (as the thermal conductivity of water is 25 times that of air). Roosting birds of most shorebird species in Roebuck Bay certainly hug the wet tide-line if possible, and larger long-legged birds such as Bar-tailed and Black-tailed Godwits (*Limosa lapponica* and *L. limosa*) stand in the wave-wash zone (authors' observations), suggesting that conductive heat loss is important during roosting. In active birds under direct solar radiation, heat avoidance was still common, indicating that managing heat loads is an ongoing issue, even in wet substrates.

Data from additional seasons are required to determine whether the incidence of heat avoidance that we recorded is unusually low. It also needs to be determined whether species with different fuel loads (reflecting different flight lengths) and plumage appearances show the same level of heat avoidance. We incidentally noted ptiloerection in substantial proportions of groups of Black-tailed Godwit, Bar-tailed Godwit, Red Knot (*C. canutus*), Grey-tailed Tattler (*Heteroscelus brevipes*), Curlew Sandpiper (*C. ferruginea*), and some Ruddy Turnstone (*Arenaria interpres*). Only one Greenshank (*Tringa nebularia*) and one Terek Sandpiper (*T. terek*) were seen erecting feathers, while Greater Sand Plovers (*Charadrius leschenaultii*) were never seen raising their feathers, even when standing on the drier parts of the beach at high tide. There are probably underlying physiological differences between species that affect their heat susceptibility.

Our finding that heat avoidance increases with migratory preparation (breeding plumage) indicates that we should not treat individual birds as being constant in regard to heat management. Intra- or interindividual changes in metabolic parameters are typically much greater than those found between species (Battley *et al.* 2001a), so the differences in heat production and management within and between individuals may be marked during fuelling.

Acknowledgments

Funding essential for our research was provided by the National Geographic Society (Washington, DC), the George Alexander Fund (Melbourne), the Ian Potter Foundation (Melbourne), the Stuart Leslie Bird Research Award (Birds Australia), the Australian Bird Environment Foundation, a PIONIER grant to TP from the Netherlands Organisation for Scientific Research (NWO), Griffith University and Charles Sturt University. We thank: Broome Bird Observatory staff (Bill Rutherford, Adrian Boyle and, initially, André and Rosalind Joubert); Humphrey Sitters, Joe Crisafio Proton, Autotrans, Pacific Transport, Ardrossan Customs Service, and the Western Australian Department of Conservation and Land Management (CALM), especially Alan Grosse (Broome), for assistance with vehicles; Reg Casey (Monitor Sensors) for climate station help; Grant Pearson (CALM,

Perth) for essential logistic support without which our research could not have been performed. Thanks to Sue Moore and two anonymous reviewers for comments on the manuscript. This is NIOZ publication No. 3546.

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Manuscript received 7 May 2002; accepted 25 February 2003