


Belly-soaking: a behavioural solution to reduce excess body heat in the Kentish plover *Charadrius alexandrinus*

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Abstract During nesting, many temperate and tropical shorebirds are exposed to direct solar radiation and face heat stress. The aim of our study was to determine whether belly-soaking (wetting of ventral plumage) contributes to reducing excess body heat in Kentish plovers *Charadrius alexandrinus*. We captured incubating plovers on sunny days at their exposed nests, and placed them inside cloth bags at ground level in exposed sites for 5 min. This produced an increase in the ambient temperature experienced by the plovers, as well as an increase in the body temperature of the plovers. We simulated belly-soaking by submerging the ventral parts in water for about 10 s immediately after removing the birds from the bag. The body temperature of the plovers was lowered after simulated belly-soaking. Our results indicate that belly-soaking is a behavioural strategy to quickly reduce body temperature in heat-stressed plovers.

Keywords Behavioural thermoregulation · Body temperature · Cooling behaviour · Heat loss · Plumage wetting · Shorebirds · Thermal stress

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Introduction

Many shorebird species (*Charadrii*) nest in sites exposed to direct solar radiation (hereafter exposed sites) as a way to reduce predation risk on incubating adults (Grant 1982; Maclean 1984; Amat and Masero 2004a). This may represent a serious challenge for species nesting in hot environments, as they have to face stressful thermal conditions (Grant 1982; Brown and Downs 2003; Amat and Masero 2004b). Because of high radiant heat loads, ground-nesting shorebirds usually become heat-stressed as ambient temperatures (T_a) rise (Grant 1982; Brown and Downs 2003; Amat and Masero 2004b). Thus, in the Kentish plover *Charadrius alexandrinus*, the body temperature (T_b) increases with T_a (Amat and Masero 2007).

Shorebirds incubating in exposed nests show remarkable plasticity in their behavioural and physiological strategies to alleviate heavy heat loads (Grant 1982; Downs and Ward 1997; Brown and Downs 2003; Amat and Masero 2004b). Incubating Kentish plovers resorted to belly-soaking (i.e., wetting of the ventral plumage; Maclean 1974) at $T_a \leq 36^\circ\text{C}$ (Amat and Masero 2007). Above this T_a , the T_b of plovers may increase up to 3°C above the average T_b (Amat and Masero 2007), which for shorebirds is 41°C (McNab 1966; Prinzinger et al. 1991).

The increase in T_b with increasing T_a may be either regulated by the individual itself or forced if total heat storage exceeds the capacity for heat loss (IUPS Thermal Commission 2003). Kentish plovers deserted their nests in southern Spain when $T_a \leq 45^\circ\text{C}$ and they had no possibility of belly-soaking (Amat and Masero 2004b), which suggests that the increase in T_b with increasing T_a in this species is unregulated. In addition, when the plovers leave their nests to belly-soak, egg temperatures increase to levels that may compromise embryo survival (Amat and Masero 2007).

Therefore, any mechanism that allows the plovers to maintain T_b within tolerable limits would facilitate nest attentiveness, and consequently nesting success.

The operative temperature (T_e) is the temperature experienced by an animal as a result of the sum of T_a and any temperature increment or decrement that results from radiative and convective factors (Bakken 1976). At the temperatures at which Kentish plovers were observed to belly-soak in southern Spain (36.8–43.6°C, Amat and Masero 2007), the operative temperatures experienced by plovers attending nests in standing postures would range from 45 to 54°C (Amat and Masero 2004b). Because in these situations $T_e \ll T_b$, the heat flux would be driven into the animals' bodies, and the plovers would be in thermal stress. Given that the increase in T_b with T_a in Kentish plovers seems unregulated, a possibility for plovers attending nests in exposed sites to reduce T_b without losing body water through evaporative cooling would be via behavioural mechanisms such as belly-soaking, which may increase heat loss through convection. Although it has been suggested that belly-soaking is a behavioural solution to quickly reduce excess body heat (see Amat and Masero 2007), an empirical demonstration of this is lacking. Therefore, in this paper we tested whether belly-soaking would cause a reduction in T_b in heat-stressed Kentish plovers nesting in a hot environment.

Materials and methods

Study site and field procedures

The study was conducted at Fuente de Piedra lake in southern Spain (37°06' N, 4°45' W), described in Amat et al. (1999). At this lake, Kentish plovers mainly nest in exposed sites, and face stressful thermal conditions (Amat and Masero 2004a, b).

To record T_b of plovers and simulate the effects of belly-soaking, we captured incubating birds ($n = 31$) at their nests using walk-in traps between 1200 and 1500 h (GMT) on sunny days. This period corresponds to the hottest part of the day (Amat and Masero 2004b). Upon capture, we noted the sex of the birds and whether they were panting (see description in Grant 1982), which would indicate that they were heat stressed. A 36-gauge copper-constantan thermocouple probe (Omega Engineering, Stamford, CT, USA) was inserted about 1 cm into the cloaca, and T_b was measured to the nearest 0.1°C with an Omega HH21 microprocessor thermometer, which was calibrated to the nearest 0.1°C against a standard thermometer. Air temperature was measured 5 cm above ground level (T_{a5}) immediately after we took T_b .

To induce an increase in T_b , we then placed the plovers inside cloth (cotton) bags on the ground in exposed sites for 5 min. After 5 min we again measured T_b and temperature inside the bag. We used cloth bags because they allowed circulation of air inside them. We noted whether or not the birds were panting when they were removed from the bag. Immediately after this second measurement of body temperature, we wetted the ventral parts of plovers by submerging these parts in fresh water (2 cm deep, 20–25°C) for about 10 s. In less than 5 s after this, we measured T_b for a third time. The time elapsing from the moment at which the bird was removed from the bag until ventral wetting was ≈ 90 s.

An elevation in T_b inside the bag may be a consequence not only of exposure to high temperature, but also to the stress of capture. Note, however, that with our experimental procedure we did not aim at simulating the thermal conditions experienced by the plovers at their nests, but only to test whether after elevating body temperature, the plovers may alleviate excessive body heat by belly-soaking.

Statistical analyses

We found no significant difference between T_b of males (41.4 ± 0.63 , $n = 11$) and females (41.2 ± 0.84 , $n = 20$) (Student's *t*-test for independent data: $t = 0.87$, $df = 29$, $P = 0.389$), and therefore analysed the data of the two sexes together. A general linear mixed model (GLMM) was used to test the effect of treatment (three fixed levels: plover incubating, plover inside the bag, and plover wetted) on T_b . Plover identity was included as a random effect in the model, since GLMMs can be viewed as an extension of general linear models accounting for repeated measures of the same individual by including subject as a random factor in the model. For post-hoc analyses, we used pair-wise comparisons (Tukey HSD test). Statistical analyses were conducted using STATISTICA (StatSoft 2001). Mean values are presented with ± 1 SD.

Ethical note

For the experiment we only captured birds nesting in exposed sites, which are in better body condition than those nesting in covered sites (Amat and Masero 2004a). The maximum temperature inside the cloth bag during our experiment was slightly lower (range 36.2–49.3°C, Fig. 1) than the maximum T_{a5} faced by incubating Kentish plovers at Fuente de Piedra (51°C, J.A. Amat, unpublished data). Our experimental protocol had no negative effects on nesting success, as the plovers resumed incubation shortly after being released. To prevent the eggs from overheating while the nest was unattended because the adults had been

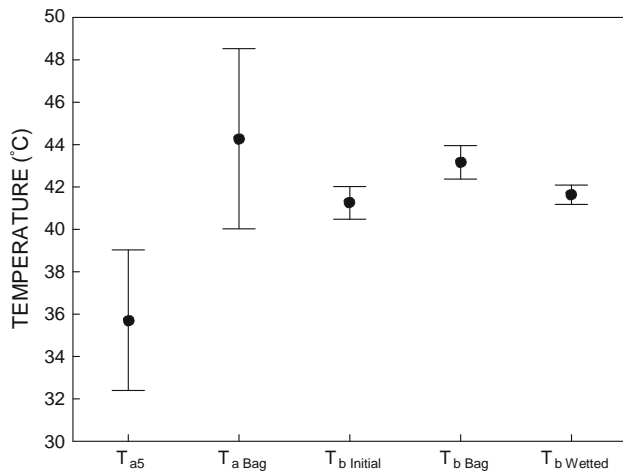


Fig. 1 Ambient temperature beside exposed nests (T_{a5}), temperature inside a cloth bag at ground level beside nests ($T_{a\text{ Bag}}$), and body (cloacal) temperatures of incubating Kentish plovers (mean \pm 1 SD) ($n = 31$). Temperatures of plovers were recorded immediately after being captured ($T_{b\text{ Initial}}$), then the plovers were placed inside a cloth bag for 5 min at ground level in exposed sites beside nests, after which body temperature was recorded again ($T_{b\text{ Bag}}$). Immediately after the plovers were removed from the bag, their ventral parts were wetted to simulate belly soaking, and body temperature recorded once more ($T_{b\text{ Wetted}}$).

captured, we shaded the nest with twigs of *Arthrocnemum glaucum* until adults returned to the nests.

Results

When we captured the plovers ($n = 31$), their T_b values were similar to the average T_b for shorebirds ($41.2 \pm 0.77^\circ\text{C}$, Fig. 1; see McNab 1966; Prininger et al. 1991), and only 6.5% of them were panting.

T_b differed significantly across the experiment (GLMM; treatment: $F_{2,60} = 80.3$, $P \setminus 0.0001$). After having been enclosed for 5 min in a cloth bag at ground level in exposed sites, inside which the temperature was on average 8.6°C higher than outside (Fig. 1), the Kentish plovers raised their body temperature on average 1.9°C , a highly significant difference when compared to their body temperature before being introduced into the bag (post-hoc Tukey's test: $P \setminus 0.001$). The plovers were likely heat stressed inside the bag, as 87.1% of them ($n = 31$) were panting when removed from it.

When we simulated belly-soaking by wetting the ventral parts immediately after removing the birds from the bag, the Kentish plovers lowered their T_b (Fig. 1) by 1.5°C , which was a significant difference when compared with T_b inside the bag (post-hoc Tukey's test: $P \setminus 0.001$). T_b after belly-soaking was only 0.4°C higher than T_b before the birds were introduced into the bag (Fig. 1); this difference was not significant (post-hoc Tukey's test: $P = 0.05$).

These results indicate that belly-soaking contributed to quickly reducing T_b in heat-stressed birds.

Discussion

An elevated T_b can not be maintained for long periods because the body proteins may suffer serious alterations that can lead to the death of individuals (Schmidt-Nielsen 1990). We have shown that belly-soaking served to reduce T_b of heat-stressed birds immediately after plumage wetting, suggesting that for Kentish plovers incubating in exposed nests in hot environments, belly-soaking is a thermoregulatory behavioural solution to quickly reduce excess body heat.

The body temperature of plovers was 0.4°C higher after experimental belly-soaking than before they were introduced inside the bag. We measured T_b immediately after plumage wetting, so it is possible that T_b continues to diminish over a longer period until it reaches values similar to those prior to belly-soaking, as happens with egg temperatures when moisture is applied to overheated eggs (Amat and Masero 2007).

The reduction in T_b after plumage wetting may be achieved by convection or by evaporative cooling from water on the body's surface. The first mechanism would be very important just immediately after belly-soaking, and would be more effective with an increasing difference in temperatures between the water and the body of individuals. The cooler the water the quicker the transmission of temperature between the individual and water. Evaporative cooling after belly-soaking may also be very important, especially once the birds return to their nests. When shorebirds belly-soak, their feathers are saturated with water (Howell 1979; Schardien and Jackson 1979; Grant 1982). Because of this, the total resistance, that is the total heat transfer from the environment to body tissues (IUPS Thermal Commission 2003), is probably reduced by reducing coat resistance, and in hot and arid environments the saturation of plumage with water may also determine the amount of water available for evaporation (McCafferty et al. 1997a, b). The saturation of the ventral plumage with water may be important because this would allow the plovers to stay for longer periods at their nest. This may be adaptive during hot conditions because when the plovers leave their nests, the eggs overheat to levels that may be critical for embryos (Amat and Masero 2007).

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