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SHORT COMMUNICATION

Huffin' and puffin: seabirds use large bills to dissipate heat from energetically demanding flight

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ABSTRACT

Endothermic animals regulate body temperature by balancing metabolic heat production and heat exchange with the environment. Heat dissipation is especially important during and immediately after demanding activities such as flapping flight, the most energetically expensive mode of locomotion. As uninsulated appendages, bird bills present a potential avenue for efficient heat dissipation. Puffins possess large bills and are members of the bird family with the highest known flight cost. Here, we used infrared thermography to test whether wild tufted puffins (*Fratercula cirrhata*) use their bills to dissipate excess heat after energetically expensive flight. Both bill surface temperature and the proportion of total heat exchange occurring at the bill decreased with time since landing, suggesting that bills are used to dissipate excess metabolic heat. We propose that bill size in puffins may be shaped by opposing selective pressures that include dissipating heat after flight and conserving heat in cold air and water temperatures.

KEY WORDS: Alcidae, Allen's rule, Energetics, Thermal imaging

INTRODUCTION

Endothermic animals regulate body temperature closely to maintain thermal equilibrium even in the face of highly demanding activities. Limits to heat dissipation may constrain biological processes generally. For example, in mice, elevated ambient temperature can limit milk energy output during lactation (Król and Speakman, 2003). Like lactation, muscle-powered flight requires extremely high rates of metabolic energy expenditure (Elliott et al., 2013a; Norberg, 1990), and metabolic heat production during flight can be 10–30 times higher than at rest (Elliott et al., 2013b; Tucker, 1968), the highest known rate of energy expenditure of any mode of locomotion (Norberg, 1990). As a consequence, birds can show signs of hyperthermia after landing (Guillemette et al., 2016; Martineau and Larochelle, 1991).

Recent studies have demonstrated that the avian bill can play an important role in thermoregulation (Tattersall et al., 2009, 2018; van de Ven et al., 2016). Akin to elephant ears (Phillips and Heath, 1992; Scholander, 1955), bills are highly vascularized yet poorly insulated, so they are able to efficiently radiate excess heat (Hagan and Heath, 1980; Tattersall et al., 2009). Evidence for bird bills serving as heat exchange exaptations is especially striking in large-billed species: heat exchange between the bill and the environment

can range from 2% to 400% of basal heat production in the toco toucan (*Ramphastos toco*; Tattersall et al., 2009). Equally, many birds minimize heat loss through the bill by tucking it under the body's plumage at low ambient temperature or by regulating blood flow (Ryeland et al., 2017; Tattersall et al., 2009).

Puffins (Alcidae; 'Auks') are diving seabirds with extreme flight costs. During flight, closely related thick-billed murres have an energy expenditure 31× greater than basal metabolic rate, the highest known for any vertebrate (Elliott et al., 2013b). In addition to high flight costs, puffins have large bills (∼6% of total surface area; Harris, 2014). Thus, for puffins, the bill may represent an important avenue for heat dissipation during and after flight.

We used temperature measurements obtained through infrared thermography to test whether and to what extent tufted puffins (*Fratercula cirrhata*) use their bills to dissipate heat generated during flight. Tufted puffins are the largest puffin species, so we might expect that they experience especially large challenges in dissipating excess metabolic heat as a result of their comparatively small surface area:volume ratio. We predicted that bill surface temperatures would decrease gradually with time since landing as metabolic heat production decreased but that insulated body parts like the feathered back would not show this pattern. Consequently, the proportion of total heat loss due to heat loss through the bill would also decrease with time.

MATERIALS AND METHODS

We recorded surface temperatures of free-ranging adult tufted puffins [*Fratercula cirrhata* (Pallas 1769)] observed on Middleton Island, Alaska, USA (59.42°N, 146.34°W) between 19 July and 13 August 2018. Puffins spend most of the year at sea (Gaston and Jones, 1998), but breed in underground burrows in summer, when they frequently rest on cliffs near their burrows between bouts of flight.

We used a thermal imaging camera (FLIR T-420; FLIR Systems, Wilsonville, OR, USA; image resolution 240×320 pixels) to record bill and body surface temperatures of resting puffins at locations where tufted puffins consistently aggregated. Vegetation and a high vantage point provided a natural blind. We approached discretely and only recorded images when certain that the birds did not detect our presence. For each bird that landed within the camera's field of view, we noted the time of landing and estimated the distance from camera to bird (usually 5–10 m). We then took IR images approximately every 2 min until the bird flew away or entered a burrow, aiming to take a picture only when the bill was held perpendicular to the camera. Birds were not colour-banded, making it possible that we recorded an image sequence from the same bird more than once. However, each recording was made after an independent bout of flight. We recorded image sequences after 50 independent landing events. All work was conducted under animal use protocol 2017-7962 from McGill University's animal care committee, as well as state and federal permits.

We then used FLIR Tools+ v5.4.1 software (FLIR Systems, Wilsonville, OR, USA) to measure surface temperature of the bill

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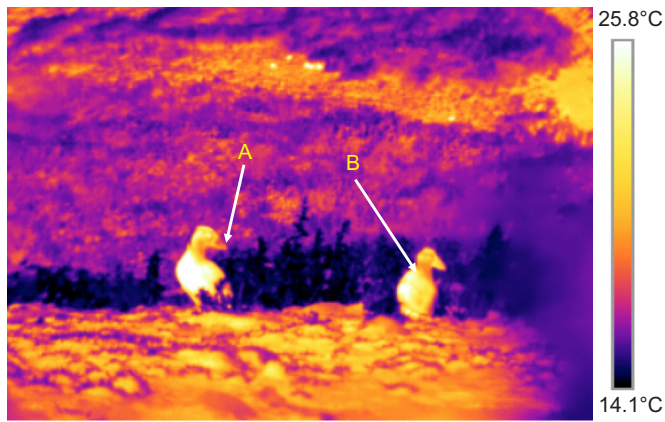
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Fig. 1. Thermal image of tufted puffins (*Fratercula cirrhata*). Arrows indicate measurement location of (A) bill surface temperature and (B) back surface temperature. Image taken with a FLIR T-420 thermal imaging camera (emissivity=0.96, reflected temperature=20°C, distance to target as estimated in the field, air temperature as measured at weather station 800 m south of study area).

and feathered back in each image (Fig. 1). Image resolution was often not high enough to reliably obtain average temperatures of outlined shapes, so we used spot measurements in the centre of the bill or back instead. We discarded images that did not allow for unambiguous temperature measurements (typically due to suboptimal positioning of the bird relative to the camera or large distance from the camera). Using the approach described by Tattersall and colleagues (Tattersall et al., 2009, 2017), we calculated radiative and convective heat exchange at the bill and the body (assuming that the spot measurement was representative of the entire area). We estimated bird body surface area from the scaling equation derived in Walsberg and King (1978), and bill surface area from published bill length and depth values (Piatt and Kitaysky, 2002). Heat exchange was calculated using the R package 'Thermimage' (https://cran.r-project.org/package=Thermimage).

We used linear mixed models to determine whether bill and back surface temperature changed as a function of time since landing, and whether the proportion of total heat loss due to heat loss through the bill [bill/(bill+body)] changed as a function of time since landing. Models included time since landing (in min) as a fixed effect and a random intercept for each image sequence to account for the non-independence of repeated measurements from the same sequence. In addition, we included a simple first-order autoregressive correlation structure (corAR1) in the residuals to account for temporal autocorrelation between sequential temperature measurements (Reynolds, 1994; Zuur et al., 2009). We did not include second- or third-order polynomial effects of time since landing (i.e. presence of an asymptote) because of the temporal resolution of our measurements and to avoid the risk of overfitting. All models were fitted in R v.3.3.0 (https://www.r-project.org/) using the package 'nlme' (https://cran.r-project.org/package=nlme). Estimates and confidence bands for plotting were calculated using the 'effects' package (https://cran.r-project.org/package=effects). See Table S1 for complete heat exchange calculations and script for statistical analysis.

RESULTS AND DISCUSSION

We measured bill surface temperatures in 172 images following 50 independent landing events. Image sequences contained 1–19 images (up to 33 min), with many sequences containing fewer than 10 images. Bill surface temperature decreased with time since landing ($\beta=-0.144$, $t=-4.113$, $P<0.001$; Fig. 2A), while back surface temperature did not decrease significantly ($\beta=-0.055$, $t=-1.511$, $P=0.136$). Upon landing birds lost 1.14 W through radiative and convective heat exchange, this decreased to 0.76 W after 30 min. The proportion of total heat exchange due to heat exchange at the bill also decreased significantly with time since landing ($\beta=-0.266$, $t=-2.123$, $P=0.038$), from 18.1% at landing to 10.1% after 30 min (Fig. 2B).

We found clear evidence that puffins use their bills to dissipate excess heat after flying. These findings echo those of earlier studies. A previous investigation showed that Brazilian free-tailed bats have 'hot spots' along their flanks that they presumably use as thermal windows during long distance migration and while flying at warm ambient temperatures (Reichard et al., 2010). Just like bird bills, these hot flank spots act as thermal windows and are highly vascularized and uninsulated. The bills of toco toucans warm up by about 6°C during flight over the course of minutes (Tattersall et al., 2009), a very similar magnitude to the temperature change we observed in the present study after flight stopped (ca. −5°C). Tattersall et al. (2009) reasoned that higher airspeed would equate to greater heat loss during flight; however, any facilitation that airspeed might provide to forced convective heat dissipation while flying would be lost once a bird lands, perhaps leading to the long cool down times observed here.

We found that the bill accounted for 10–18% of total heat exchange despite making up only 6% of surface area. This estimate may be biased upwards because we were unable to account for heat
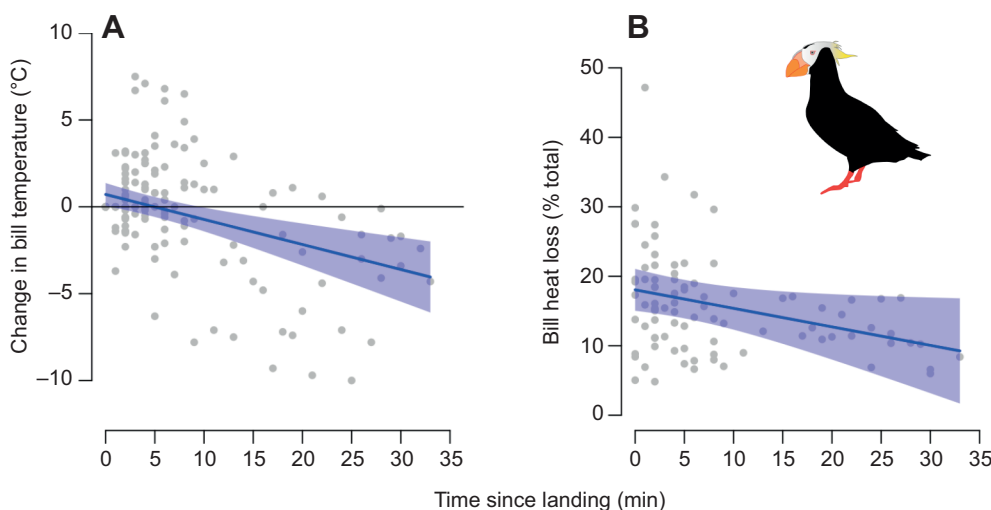

Fig. 2. Change in puffin bill temperature and proportion of total heat exchange due to bill after landing. (A) Change in bill relative to bill surface temperature recorded at landing, as a function of minutes since landing. (B) Proportion of total heat exchange due to bill. Shaded area shows 95% confidence intervals around predicted values of the response variable. *N*=50 independent landing events.

exchange occurring through the uninsulated legs and feet, which can be substantial (Baudinette et al., 1976). This value was lower than that observed in toucans, where heat exchange through the bill accounted for 35–60% of total heat exchange as ambient temperature increased from 10°C to 30°C (Tattersall et al., 2009). This is likely due to the toucan's proportionally larger bill. We were unable to test for a similar effect of ambient temperature since ambient temperature was almost constant (11.1–13.9°C). Nevertheless, our findings further underline the magnitude of heat exchange realised by the bill in large-billed birds.

A potential implication of our findings may concern Allen's rule (smaller appendages in cooler climates; Allen, 1877). Birds bills tend to follow Allen's rule: on average, smaller-billed birds are found in cooler climates (Symonds and Tattersall, 2010). Large-billed yet cold climate-inhabiting puffins (genus *Fratercula*) buck this trend. High flight costs and the subsequent need for efficient heat dissipation could help explain the large puffin bill. This may have ecological consequences. Among auks, large-billed puffins and razorbills have larger foraging ranges than smaller-billed murres (Thaxter et al., 2012). A larger bill may thus have released puffins and razorbills from the constraint of not being able to fly far because of overheating (Gaston et al., 2002).

The avian bill is a classic example of how evolution shapes morphology. Taking advantage of current IR imaging technology, we provide further evidence that thermoregulation is likely a factor contributing to the morphology of some bird bills (Symonds and Tattersall, 2010). Bills appear to be thermoregulatory exaptations, analogous to a desert hare's ears: an external structure that has been amplified to serve a new, thermoregulatory function. In birds, heat dissipation through the bill could facilitate sustained activity, even at warm ambient temperatures. We encourage further studies to consider the role of the avian bill as a thermoregulatory organ in studies of the distribution, ecology and behaviour of puffins and other birds.

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