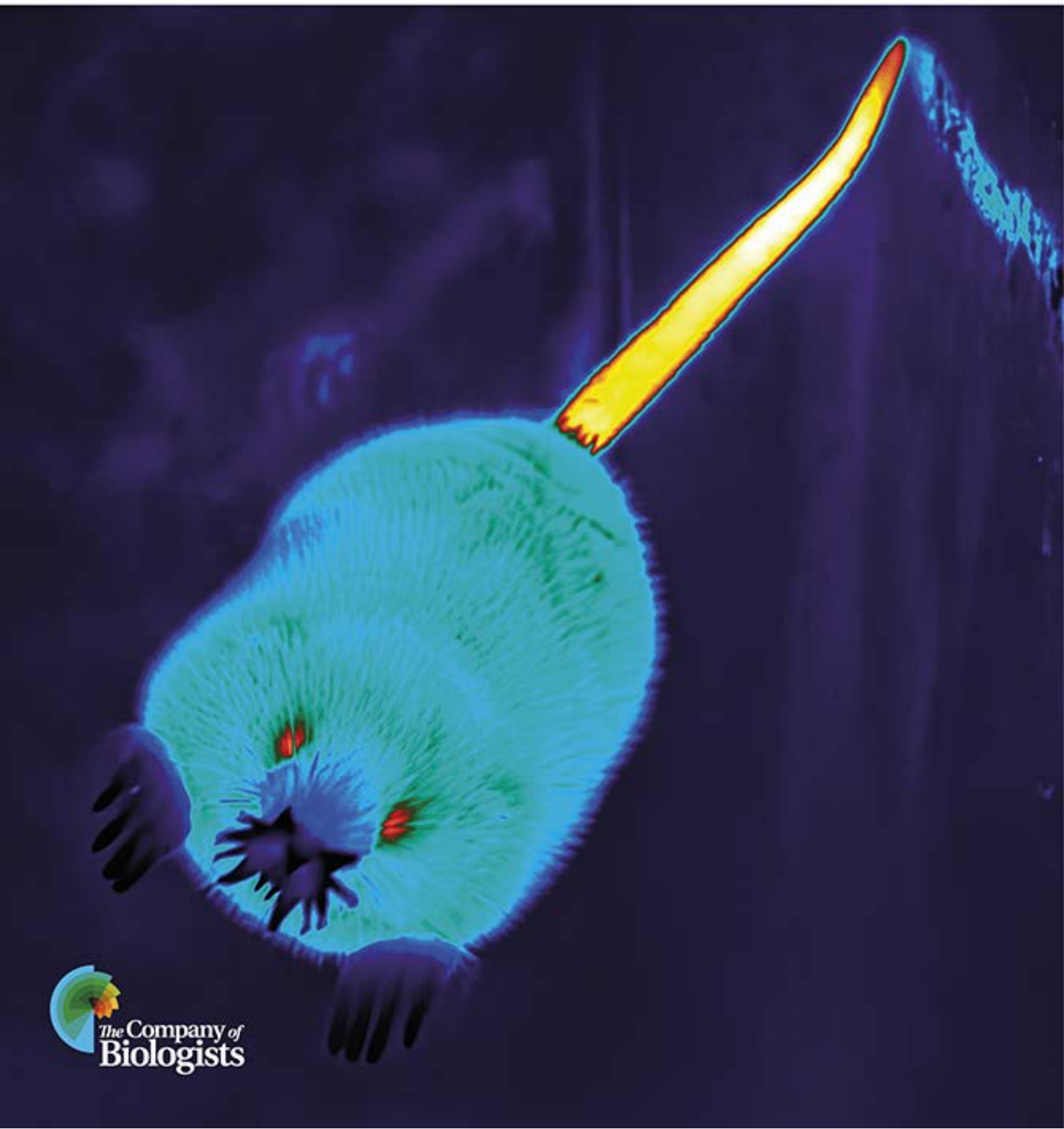


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## SHORT COMMUNICATION

## Thermoconforming rays of the star-nosed mole

Glenn J. Tattersall<sup>1,\*</sup> and Kevin L. Campbell<sup>2</sup>

## ABSTRACT

The star-nosed mole (*Condylura cristata*) is renowned for its densely innervated 22 appendage star-like rostrum ('star') specialized for tactile sensation. As a northerly distributed insectivorous mammal exploiting aquatic and terrestrial habitats, these vascularized nasal rays are regularly exposed to cold water and thermally conductive soil, leading us to ask whether the star surface temperature, a proxy for blood flow, conforms to the local ambient temperature to conserve body heat. Alternatively, given the exquisite sensory nature of the star, we posited that the uninsulated rays may be kept warm when foraging to maintain high mechanosensory function. To test these hypotheses, we remotely monitored surface temperatures in wild-caught star-nosed moles. Although the tail acted as a thermal window exhibiting clear vasoconstriction/vasodilation, the star varied passively in surface temperature, with little evidence for thermoregulatory vasomotion. This thermoconforming response may have evolved to minimize conductive heat loss to the water or wet soils when foraging.

**KEY WORDS:** Sensory organ, Thermoregulation, Insectivore, Thermal window, Thermography

## INTRODUCTION

The star-nosed mole (*Condylura cristata*) is a highly specialized insectivore uniquely adapted to foraging in terrestrial and aquatic habitats (Catania, 1999, 2000). Found throughout eastern North America, and extending to the southern limit of permafrost, this nearly blind predator relies on its incredibly touch-sensitive nasal appendages to rapidly identify and consume hundreds of tiny prey per day to fuel its high rate of metabolism relative to allometric predictions (Campbell et al., 1999; Catania and Remple, 2005). Owing to its distinctive morphology, the eponymous nose ('star') of the star-nosed mole has been extensively studied for its sensory functions (Catania, 2000; Gould et al., 1993; Sachdev and Catania, 2002; Sawyer et al., 2014). The rostrum houses 22 separate rays, 11 per side, that sample the tactile environment 10 to 15 times per second (Catania and Remple, 2005; Gerhold et al., 2013). The star is highly vascularized, with two large non-muscularized blood sinuses occupying approximately 40% of the ray volume. Capillaries are evident throughout the dermis, underlying the roughly 30,000 sensory papillae (Eimer's organs) forming the thin uninsulated epidermal surface (Catania, 1995; van Vleck, 1965).

The star acts as the primary mechanosensory organ, with >100,000 myelinated nerve fibres innervating the Eimer's organs

(Catania, 1995, 1999). Although all rays contribute to the remarkable tactile acuity of the star, the innermost 11th ray serves as a mechanosensory fovea (Catania, 2011; Sachdev and Catania, 2002), and moles will redirect their attention to allow this appendage to investigate stimuli immediately prior to consumption. Star-nosed moles can locate, identify and ingest prey items within 120 ms, crowning them as one of the fastest eaters of the animal kingdom (Catania and Remple, 2005). In principle, the sensory structures of endotherms are metabolically active, and highly temperature-sensitive tissues are expected to function more effectively when maintained at a stable, warm temperature (Glaser and Kroger, 2017). The elephant's (*Loxodonta africana*) trunk, for example, is the warmest part of the skin (Weissenboeck et al., 2010). During development, sensory nerves provide a map for arterial growth (Mukouyama et al., 2002), and thus sensory activity may be associated with changes in blood flow and, therefore, body heat. For example, the sensory vibrissae of seals maintain high temperatures owing to the high vascularity serving the metabolically active sensory tissue and do not demonstrate vasoconstriction in the cold (Dehnhardt et al., 1998). Similarly, the eye heater organ found in billfish (Carey, 1982) evolved as a means of enhancing sensory acuity in cold environments (Fritsches et al., 2005). Combined, there is reasonable precedence to expect that the nasal epidermal tissue of *C. cristata* would show elevated temperatures (relative to local ambient temperature) based on high rates of blood flow supporting the underlying metabolically active nervous tissues.

Endotherms typically have poorly insulated peripheral appendages that tend to exhibit strong vasomotor control, reflecting their involvement in redistributing body heat between the core and the periphery (Erdsack et al., 2012; Tattersall et al., 2012; Weissenboeck et al., 2010). These changes in blood flow can be assessed by examining how the surface temperatures of these uninsulated appendages change under different heat loads. This methodology has revealed classic examples of adjustable thermal radiators, including elephant ears (Phillips and Heath, 1992), the toucan bill (Tattersall et al., 2009) and rodent tails (Rand et al., 1965). These surfaces contribute to the body's capacity to dissipate heat, but are subject to emotional influences, such as fear-induced (e.g. sympathetic) vasoconstriction (Herborn et al., 2015; Vianna and Carrive, 2005). For subterranean species, conductive heat loss to the soil would be particularly high from structures in direct contact with the substrate (see Plestilova et al., 2020). Given that the shallow surface tunnels of star-nosed moles are typically excavated in water-saturated soils, heat transfer from the naked sensory appendages of the mole's star is thus potentially extensive (Campbell et al., 1999). This is also the case during winter months, when aquatic foraging is more prevalent (Hamilton, 1931). However, owing to the amphibious life history of the star-nosed mole and the highly specialized sensory nature of its nasal rays, sustaining high rates of warm arterial blood flow to the star would be energetically expensive to maintain.

We thus tested whether star-nosed moles keep their nasal sensory appendages warm through vasodilation when exposed to the cold

<sup>1</sup>Department of Biological Sciences, Brock University, 1812 Sir Isaac Brock Way, St Catharines, ON, Canada L2S 3A1. <sup>2</sup>Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada, R3T 2N2.

\*Author for correspondence (gtattersall@brocku.ca)

 G.J.T., 0000-0002-6591-6760; K.L.C., 0000-0001-7005-7086

(thereby incurring high energetic costs) versus an energy conservation hypothesis wherein despite its high vascularity, the uninsulated star will show passive warming and cooling responses (i.e. thermoconformation). We did this by exposing moles to different water temperatures and examining the patterns of surface temperatures from their potential thermal windows (eye, tail, limbs and nasal rays).

## MATERIALS AND METHODS

### Animal handling

Three juvenile star-nosed moles [*Condylura cristata* (Linnaeus 1758)] of unknown sex were captured using Sherman and pitfall traps in the Willard Lake region, Ontario, Canada (49°49'41.9088" N, 93°58'5.2896" W), in June 2022 under the authorization of an Ontario Ministry of Natural Resources Wildlife Scientific Collector's permit (no. 1101339). During their 21 days in captivity, each mole was housed within a two-chambered Rubbermaid™ system; one 76-liter chamber, filled with moist soil to a depth of ~15 cm, housed a small wooden nesting enclosure that was connected via plastic (ABS) piping to a second 76-liter feeding chamber containing water to ~0.5 cm depth. Moles were allowed access to soil via an ABS tee wye connector attached to the nesting enclosure. Moles were fed commercially sourced earthworms (*Lumbricus* spp.; 14–16 per day per animal) supplemented by wild-caught invertebrates from the site of collection. The nesting chambers were cleaned or replaced daily, while the feeding containers were thoroughly washed 2–3 times daily. All procedures were approved by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry Wildlife Animal Care Committee (protocol no. 22-493).

### Thermal manipulations

Pilot observations conducted in air suggested that the nasal rays of the star-nosed mole closely corresponded to surface/air temperatures. We thus experimentally exposed moles to warm (~30–32°C) or cold (2–4°C) water to elicit maximal thermal responses. Briefly, individual moles were transferred to a clean 19-liter Rubbermaid™ container held at room temperature (17–20°C) for 10 min (post-handling period), exposed to warm or cold water (water foraging period) at a depth of 1.5 cm for 10 min (in which they frequently submerged the star), and subsequently transferred to a dry container for a further 10-min recovery period at room temperature. Each mole underwent this 30-min procedure twice, once for each of the warm- or cold-water challenges. During the 10-min water exposure, moles were periodically provided with small earthworms (which were rapidly located and consumed regardless of water temperature) to encourage natural underwater exploratory and foraging behaviours.

### Thermal imaging

Time-lapse infrared thermal imaging videos were captured every second with FLIR Research Studio software using a calibrated FLIR A8581 Mid-Wave Infrared Camera (resolution 1280×1024 pixels, 25 mm lens, thermal sensitivity <25 mK, accuracy ±1°C). The camera was mounted ~0.5 m above the animal, providing a full view throughout the measurement period. We assumed emissivity of 0.95 and set object parameter settings in the software to the local air temperature (~17–20°C). From the captured videos, we extracted still frames at various time points throughout the post-handling, water foraging and recovery periods. These still frames were extracted as 32-bit TIF files and exported for analysis in FIJI/ImageJ (Schindelin et al., 2012). Regions of interest were drawn

over the front limbs, nose, nasal rays, eye and tail using the free-hand tool, and the average temperature for each region was extracted from each still frame. Sample thermal images are depicted in Fig. 1.

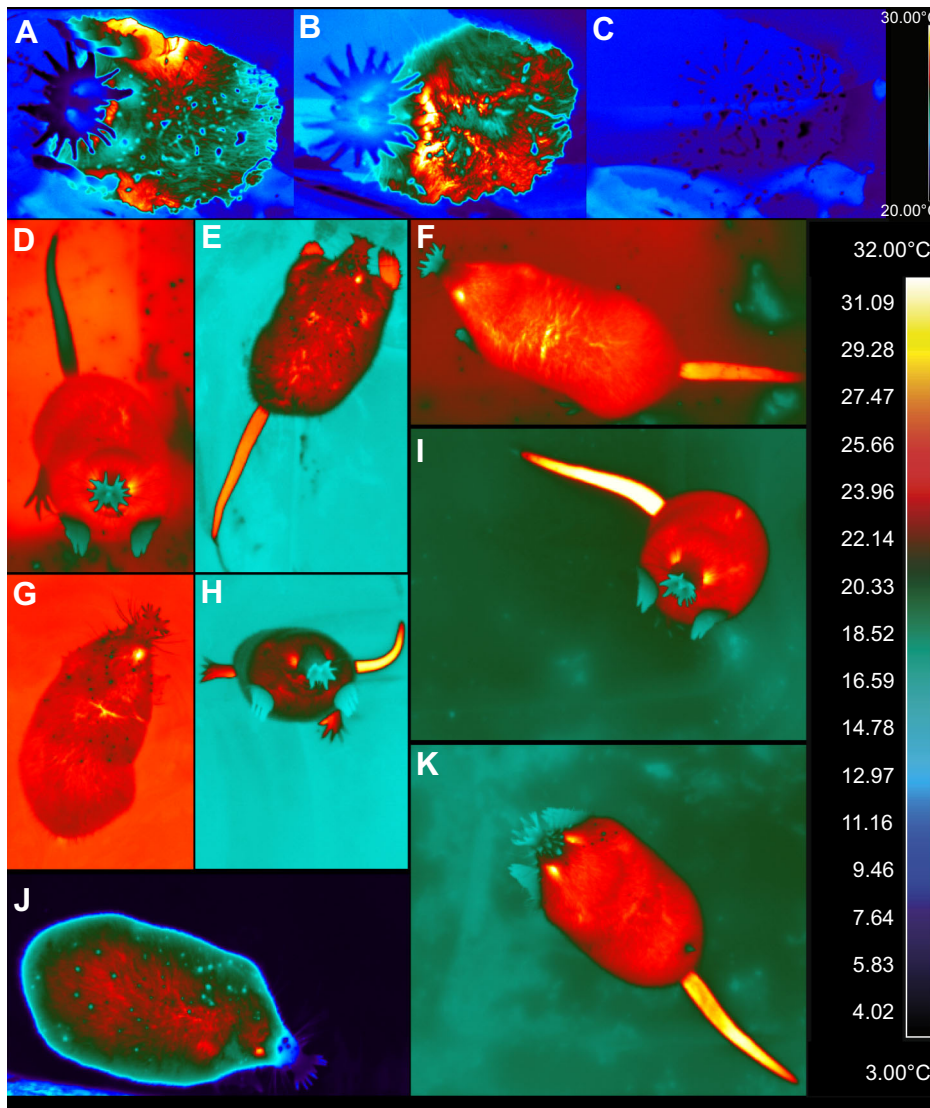
### Data analysis

Acknowledging that the small sample size limits broad conjectures based on biologically distinct replicates, we endeavoured to draw inferences of how various body part surface temperatures differed from prevailing ground or water temperatures based on biophysical principles outlined previously (Klir et al., 1990; Tattersall, 2016). Surfaces that receive little blood flow or are insulated from warm blood (i.e. fur) are expected to be similar to local ground or water temperatures, and owing to principles of thermoconformity, should have slopes close to 1. This hypothesis was tested using simple pairwise *t*-tests (*P*-values corrected using Bonferroni procedures for multiple hypotheses). Surfaces that have high and non-varying blood flow are expected to deviate from local temperature and to have a low slope (<<1) with respect to local temperature (tested by model comparison with a model where the slope is set to 1 using the offset function in R). Vasoactive body surfaces (i.e. adjustable thermal windows) would differ from local temperature when warm and exhibit a non-linear relationship with respect to local temperature, especially if vasoconstricted in the cold and vasodilated under warm conditions. Although the slope between surface and local temperature may be less than 1, the obvious departure from linearity (tested by analysing whether the more complex model significantly reduces the residual sums of squares via a likelihood ratio test) reflects the vasoactive nature of the body surface. Statistical analyses were conducted in R (version 4.2.0).

## RESULTS AND DISCUSSION

Body surface temperatures of star-nosed moles were dependent on the ground and water temperature but in varying manners (Fig. 1). The nasal rays and front limbs were primarily thermoconforming body surfaces (Figs 2 and 3) whereas the surface temperatures of the tail and eyes tended to be elevated. Eye surface temperatures differed significantly from local temperature ( $t_{47}=9.4$ ,  $P=9.03\times 10^{-12}$ ) and exhibited a slope significantly lower than 1 ( $\chi^2_1=148$ ,  $P<2\times 10^{-16}$ ). The star and front limb temperatures were not significantly different from local ambient temperatures ( $t_{47}=-1.76$ ,  $P=0.39$  and  $t_{47}=-8.55\times 10^{-5}$ ,  $P=1$ , respectively), showing a mostly linear, thermoconforming relationship. The tail was the most variable surface, being significantly warmer than local temperature ( $t_{47}=4.25$ ,  $P=0.00058$ ) but also exhibiting a non-linear relationship with local ground and water temperatures ( $\chi^2_1=8.9$ ,  $P=0.0029$ ). Indeed, this surface was warmest at mid-range (~20°C) temperatures and thermoconforming at higher and lower temperatures (Fig. 3). While searching for food at room temperature, the nasal rays remained close to the temperature of the ground surface (Movies 1 and 2). We only once observed what might be evidence of vasodilation in the star, and this occurred during a prolonged, relaxed grooming session (Movie 3).

We demonstrated using surface temperature measurements that the nasal rays and forelimbs of the star-nosed mole passively track (i.e. thermoconform) local water and ground temperatures, providing support for an energy conservation role for the star, whereas the tail acts as an adjustable thermal window, typical of many small mammals (Meyer et al., 2017). For the most part, the star acts passively in terms of vasomotor responsiveness, with little evidence of vasodilation under heating scenarios; likely owing to evaporative cooling, the nasal rays were slightly cooler than ambient at temperatures >20°C, a response seen in vampire bats (Kürten and

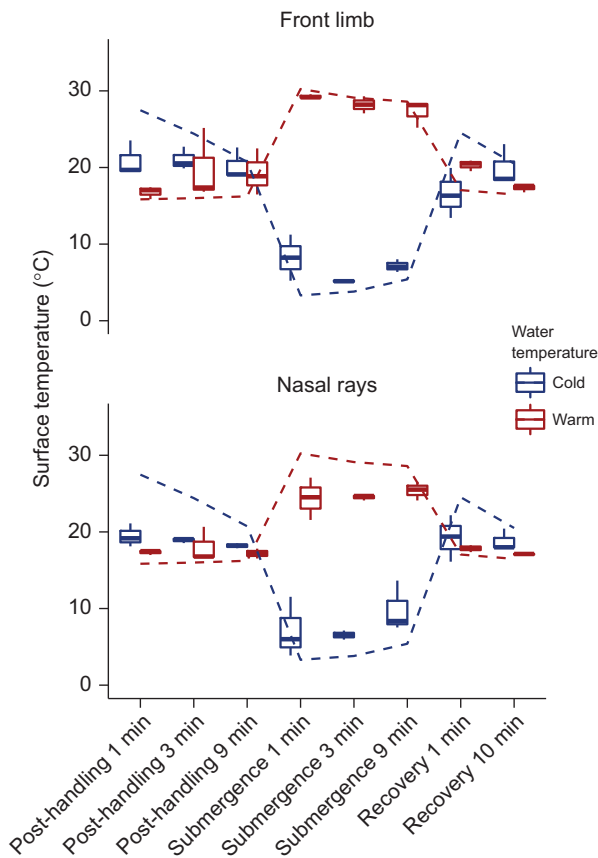


**Fig. 1. Representative thermal images of the star-nosed mole.** Close-up image through a thin polyethylene sheet showing (A,B) the warmer nostrils and distinctly cooler nasal rays when played out in surface contact and (C) the cool impressions left behind at room temperature. Unless noted, the remaining images were captured at  $\sim 18^{\circ}\text{C}$  during/ following exposures to warm ( $\sim 28\text{--}30^{\circ}\text{C}$ ) and cold ( $\sim 2\text{--}4^{\circ}\text{C}$ ) environments: (D) immediately following handling after being placed into warm environment, (E) immediate recovery after exposure to warm water showing warm limbs, (F) prior to being exposed to cold water while at  $18^{\circ}\text{C}$ , (G) while foraging in warm water, (H) recovery from exposure to warm water, (I,K) exposure to  $18^{\circ}\text{C}$  ground conditions and (J) during foraging in cold water. Temperature scale in upper right pertains to A–C; larger temperature scale on the right pertains to D–K.

Schmidt, 1982), canids (Balint et al., 2020) and numerous carnivores (Glaser and Kroger, 2017).

Owing to linkages between skin temperature and tactile sensitivity, it has been argued that cold rhinaria are incompatible with a mechanosensory role (Glaser and Kroger, 2017). It is not unusual to expect warmer sensory structures to function more effectively given what has been described in facultatively endothermic animals (Carey, 1982; Fritsches et al., 2005). However, canine olfactory-based tracking behaviours are enhanced at lower temperatures and higher humidity (Jinn et al., 2020), although this response has not been linked to their typically cool nose. Thus, the strikingly lower temperature of the star relative to core body temperature ( $37.7^{\circ}\text{C}$ ; Campbell et al., 1999) begs the question of whether this trait aids or hinders the sensory function of the nasal rays. Although not systematically studied, observed reductions in star surface temperatures did not appear to be associated with reductions in prey detection ability, as moles rapidly located and consumed added prey items in both warm and cold water. The bigger question is how does the star maintain high sensitivity/acuity in the cold without elevated blood flow and/or temperatures? The epithelial cells are the dominant tissue of the rays, with much of the remaining volume composed of large sinuses

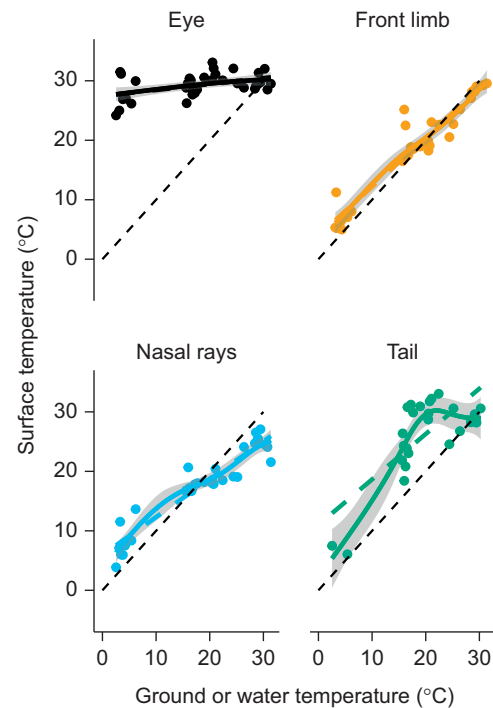
(van Vleck, 1965). Although thousands of nerve fibres are interspersed within each ray, the cell bodies are located centrally within dorsal root ganglia. Accordingly, an argument for high metabolic requirements demanding high blood flow (e.g. Dehnhardt et al., 1998) seems inadequate in the case of the star-nosed mole. Hints regarding the thermoconforming nature of the nasal star may be found in the specialized evolution of the sensory nerves innervating the nose. The mole's nasal sensory nerves are of trigeminal ganglion origin and enriched in the expression of ion channels involved in innocuous mechanosensation compared with the expression pattern in dorsal root ganglia innervating other body regions (Gerhold et al., 2013). By contrast, the trigeminal ganglia of this species are deficient in the expression of ion channels associated with thermosensation. Intriguingly, this same pattern was found in the trigeminal neurons of the highly mechanosensitive bill of tactile-feeding waterfowl (ducks) relative to visually foraging birds (Schneider et al., 2014). It was argued that the highly specialized rostra of these species evolved to provide extremely high tactile sensitivity at the cost of reduced thermosensation. However, because temperature-sensing ion channels have been implicated in the control of peripheral blood flow in mammals (Fromy et al., 2018), the reduction of temperature-sensing ion channels



**Fig. 2. Surface temperatures of the front limbs and nasal rays prior, during and following foraging in either cold (2–4°C) or warm (28–30°C) water.** Symbols represent box and whisker plots ( $N=3$ ), and the dashed lines represent the mean ground or water temperature for the respective cold or warm water exposures.

in the trigeminal ganglia, combined with the functional thermoconforming evidence of the star provided herein, suggests an additional explanation. Specifically, the low number of temperature-sensing ion channels within the nasal epithelia, previously linked to their intense anatomical specialization for mechanosensation (see Schneider et al., 2016), may be related to the thermally non-responsive blood supply to the star. In other words, the evolutionary diminution of temperature responding pathways may prevent the reactive thermoregulatory vasomotion of this structure. It should be stressed that, like star-nosed moles, tactile feeding waterfowl that similarly possess low numbers of temperature-sensing neurons in their bill do not exhibit reductions in feeding efficiency in the cold (Schneider et al., 2014). These observations suggest that evolutionary reductions in thermosensing ion channels may be a specialization for somatosensory organs that must operate well below core body temperatures.

A further explanation for why the star-nose mole shows low vasomotor responses in the star and front limbs, at least up to  $\sim 32^{\circ}\text{C}$ , might be related to the already substantial thermal window afforded by the sparsely haired tail (Fig. 1). The star-nosed mole tail surface-temperature response to handling (see Fig. 1D) and changing environmental conditions correspond closely to that seen in rodent tails (Johansen, 1962; Romanovsky et al., 2002), whereby handling and cold exposure induces vasoconstriction (Rand et al., 1965; Vianna and Carrive, 2005). However, the tail of star-nosed moles is unusual among talpids in that it is relatively long and accumulates



**Fig. 3. Surface temperature relationships of exposed star-nosed mole surfaces relative to ground or water temperatures across all measurement intervals.** The front limbs and nasal rays are mainly thermoconforming surfaces. Eye surface temperature remained warm across all temperatures, whereas the tail showed a complex non-linear relationship reflective of vasoconstriction in the cold and vasodilation at higher temperatures. Bold dashed lines depict the linear regressions through the data, the black dashed lines depict the line of equality, and curves reflect a Loess smooth curve.

extensive fat stores during the fall and winter (Hamilton, 1931; Petersen and Yates, 1980). Accordingly, this high-surface-area appendage with low external insulation is well suited to serve as the primary adjustable peripheral heat exchange thermal window. The eye temperature response, in contrast, provides a unique perspective into the species functional morphology. The eyes of star-nosed moles are minute, have tiny optic nerves, and are likely only used for light/dark discrimination (Catania, 1999; Petersen and Yates, 1980). However, eye surface temperatures were elevated and remained nearly constant across all temperatures, demonstrating a continuous and high level of blood flow to an uninsulated organ that has been argued to serve only a minor contribution to overall sensory input.

A final unresolved question pertains to the mechanism underlying the thermoconforming nature of the star. Although the reduction of thermosensitive neurons innervating the star may in part underlie the lack of temperature-dependent vasomotion observed in this study, it does not provide insights into how the star is able to achieve relative thermoconformity with environmental temperatures. Although it is possible this ability arises via the operation of countercurrent heat exchangers in the rostral region, these structures have not been identified in this species. Alternatively, this trait may result from intermittent blood flow to the star arising from nasal ray movements. For instance, the nasal rays are oriented perpendicular to the nose while foraging (Fig. 1A,B), though these structures are shifted parallel to the nose when the head is raised (Fig. 1K) and while the mole is inactive. When not foraging, star-nosed moles routinely exhibit repetitive flexing and extension of the nasal rays and ‘groom’ the star with the forepaws.

The latter behaviour coincided with a sudden increase in blood flow during one of our experiments (Movie 3) and may be important for promoting blood flow to the large nasal sinuses in the nasal appendages. These competing mechanisms provide fruitful avenues of research on the thermal biology of this unusual insectivore.

## Conclusions

Unconventionally for a peripheral appendage, the nasal rays of the star-nosed mole show little evidence of reactive vasodilation that other mammalian appendages demonstrate. This thermoconforming response may be related to the high energetic consequences of heat dissipation from a typical peripheral tissue that would accompany the active foraging lifestyle of the star-nosed mole. Because they spend much of their life foraging in environments of high thermal conductance, any body heat reaching the uninsulated star would be rapidly dissipated to the environment. Extending these results to other 'sensory specialists' could be of great interest. For example, numerous ducks have highly sensitive mechanosensation in the bill yet still forage at variable water temperatures (Schneider et al., 2014), the duck-billed platypus (*Ornithorhynchus anatinus*) relies on an extensively innervated and well-vascularized bill for electroreception to forage underwater (Scheich et al., 1986), and the echidna (*Tachyglossus aculeatus*) bill is a specialized mechanosensory appendage (Proske et al., 1998). Whether these appendages also demonstrate heat conservation through promiscuous vasoconstriction while foraging is unknown, but the discovery of similar or divergent responses would shed light on the physiological conservatism between how thermoregulatory vascular control has evolved to minimize influences on the sensory systems.

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## Competing interests

The authors declare no competing or financial interests.

## Author contributions

Conceptualization: G.J.T., K.L.C.; Methodology: G.J.T., K.L.C.; Software: G.J.T.; Validation: G.J.T., K.L.C.; Formal analysis: G.J.T.; Investigation: G.J.T., K.L.C.; Resources: G.J.T., K.L.C.; Data curation: G.J.T.; Writing - original draft: G.J.T., K.L.C.; Writing - review & editing: G.J.T., K.L.C.; Visualization: G.J.T.; Supervision: G.J.T., K.L.C.; Project administration: G.J.T., K.L.C.; Funding acquisition: G.J.T., K.L.C.

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## Data availability

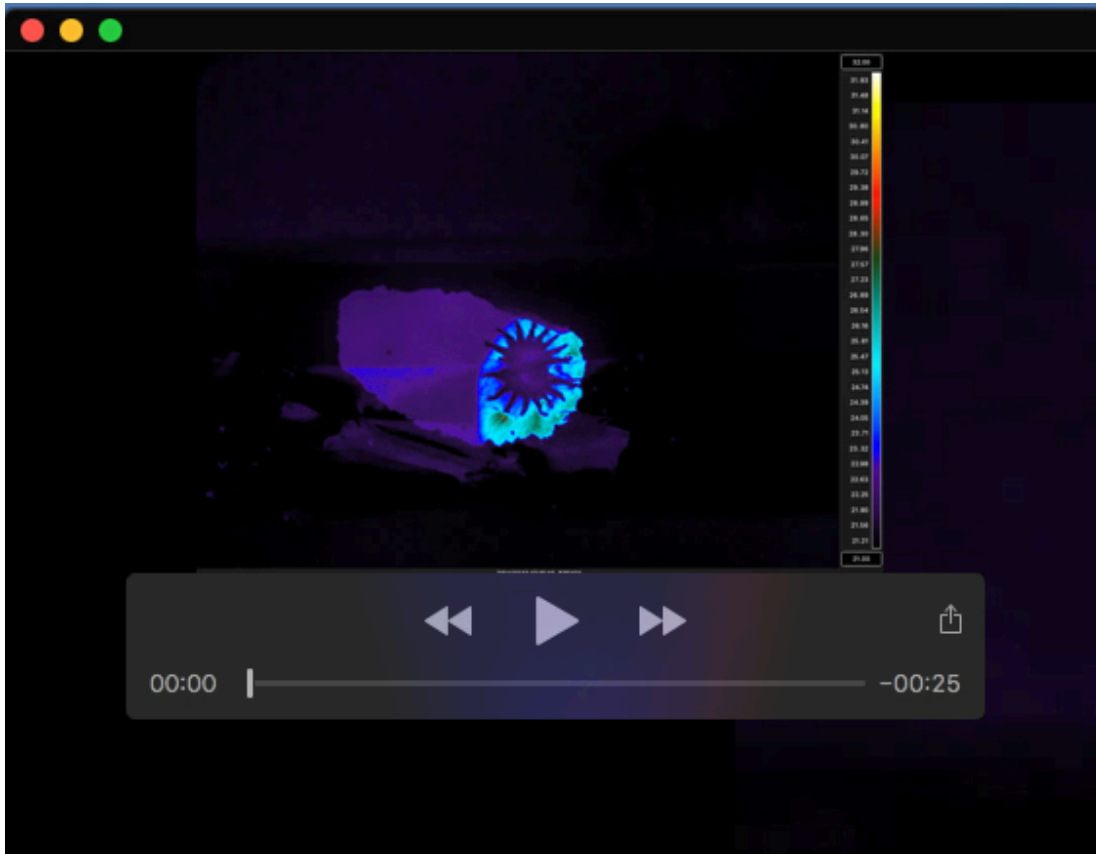
Raw data are available from the Brock University data repository: <http://hdl.handle.net/10464/16980>

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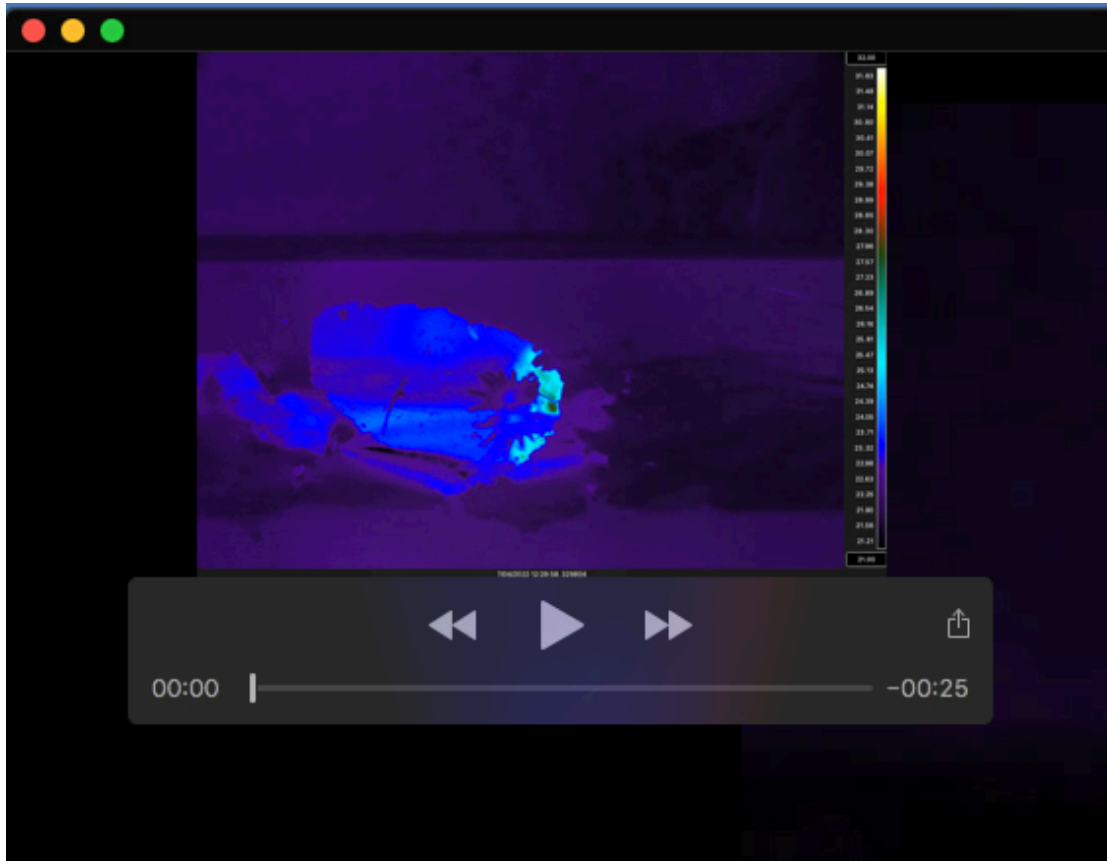
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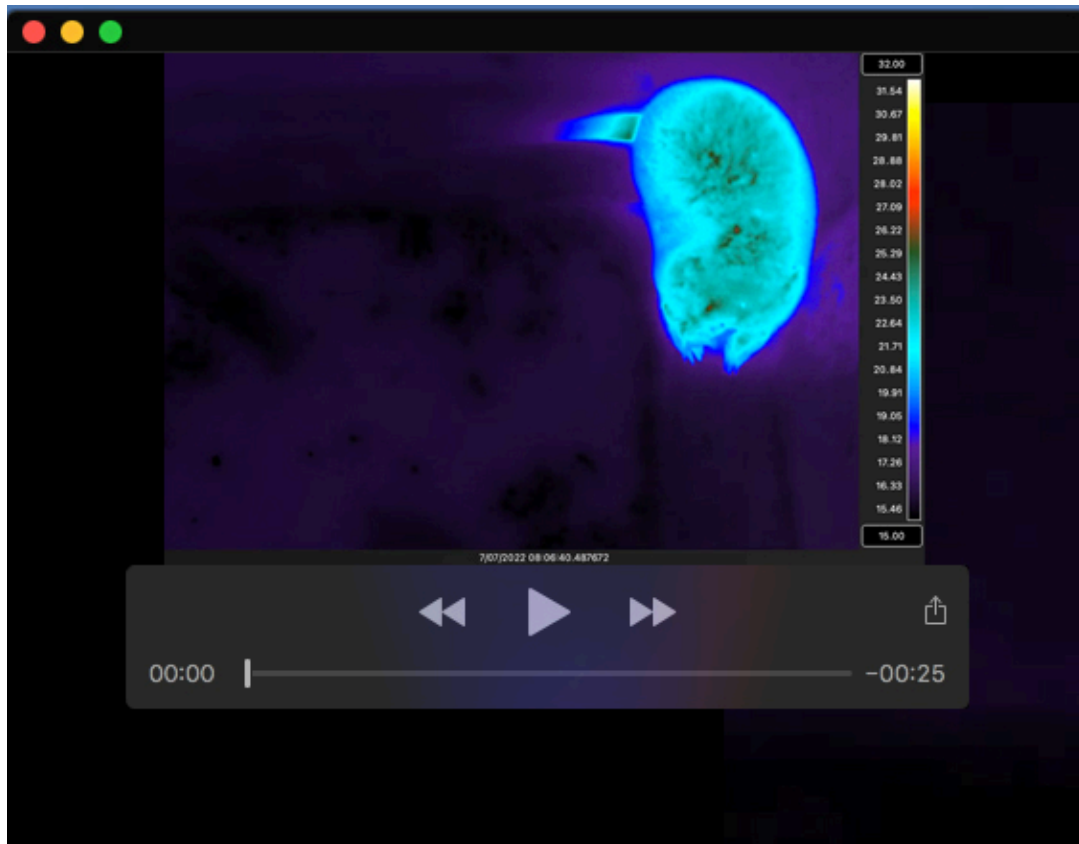


**Movie 1.** Thermal video (48 frames/sec) of a star-nosed mole scanning an open surface, passing over this surface in 0.48 seconds. The ‘window’ surface was a piece of plastic (Saran™ wrap) stretched over a hole within an artificial tunnel environment.





**Movie 2.** Thermal video (48 frames/sec) of a star-nosed mole scanning an open surface containing a small earthworm, which was detected and consumed in under 3 seconds. The ‘window’ surface was a piece of plastic (Saran™ wrap) stretched over a hole within an artificial tunnel environment.



**Movie 3.** Time-lapse thermal video (frame rate 1 Hz, playback rate 10 Hz) of a star-nosed mole grooming its nose. The star is not splayed open during grooming, and part-way through the video (Timestamp 08:11:48.5, UTC +0), a sudden rise in nasal ray temperature is evident. Since the front limbs are also warm during this video, it is not clear if heat is being transferred from the limbs or if this arises from vasodilation of the nasal rays.