



# Immune activation influences the trade-off between thermoregulation and shelter use



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Animal behaviour is influenced by many environmental factors, including temperature and predation risk. Although many species utilize shelters to buffer ambient temperature and avoid predators, a trade-off can exist between thermoregulation and predator avoidance (e.g. an animal avoids a shelter that is too hot or cold at the expense of increased vulnerability to predators). Immune activation influences both thermoregulation and shelter use, yet its role in mediating a trade-off between these two important processes is unclear. Thus, we examined the dynamics of this thermoregulation–shelter use trade-off using the cornsnake, *Pantherophis guttatus*, and a repeated measures  $2 \times 2$  factorial design in a thermal gradient where shelter availability and immune activation status were manipulated. Immune activation (injection of lipopolysaccharide, LPS, an endotoxin found in the cell walls of Gram-negative bacteria) did not elicit behavioural fever or change shelter use when shelter was available across the entire thermal gradient. Although snakes strongly prioritized shelter use (e.g. snakes injected with saline were observed under shelter 98% of the time), their prioritization shifted during immune challenge. Snakes injected with LPS that were forced to choose between preferred temperature and shelter use maintained thermoregulation, but they spent up to nine-fold more time exposed relative to when they were injected with saline. These results demonstrate the plasticity of the widespread trade-off between thermoregulation and shelter use. Our results also indicate that immune-challenged animals not exhibiting fever may still exhibit important shifts in the prioritization of thermoregulation; thus, we recommend a more nuanced assessment of the effects of immune activation on thermoregulatory behaviour.

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The vast majority of animal species (99.9%) are ectothermic (Atkinson & Sibly, 1997) and, thus, are particularly sensitive to changes in ambient temperature. Temperature affects many life processes, including locomotion (Kubisch, Fernández, & Ibarquengoytia, 2011), digestion (Wang, Zaar, Arvedsen, Vedel-Smith, & Overgaard, 2003), growth (Yagi & Litzgus, 2013) and reproduction (El-Hafez, El-Sharkawy, & Hassan, 2014). Because ambient temperature varies spatially and temporally, thermoregulation (i.e. regulation of body temperature,  $T_b$ ) is a crucial behavioural process for most animal taxa (Blouin-Demers & Weatherhead, 2001; Caillon, Suppo, Casas, Woods, & Pincebourde, 2014; Deban & Lappin, 2011; Hoecherl & Tautz, 2015; Reinert, 1993; Sauter, Crawshaw, & Maule, 2001).

Several features of the environment promote thermoregulation, including shelters (refuge structures), which can exhibit different absolute temperatures and temperature variability than ambient conditions (van den Berg, Thompson, & Hochuli, 2015; Stahlschmidt, Shine, & DeNardo, 2012). In addition to promoting thermoregulation and other behaviours (e.g. ambush hunting: Bevelander, Smith, & Kennth, 2006; Clark, 2007), shelters can promote predator avoidance for many animals, from worms (Dill & Fraser, 1996) to primates (Cowlshaw, 1997). Both facilitation of thermoregulation and predator avoidance can coincide (Roper, Bennett, Conradt, & Molteno, 2001; Schwarzkopf & Alford, 1996), but shelters are not always thermally optimal (e.g. a log exposed to constant sunlight may be too hot to promote optimal growth for an animal: Downes, 2001). Thus, a trade-off can occur where an animal is forced to choose between thermoregulation and using a shelter for protection from predators (Amo, Pilar, & Martín, 2004; Stahlschmidt & Adamo, 2013a). Although behavioural thermoregulation improves locomotive performance (Angilletta, Hill, & Robson, 2002), predator avoidance is linked to immediate

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survival and, thus, has been shown to be prioritized in thermoregulation–predator avoidance trade-offs (Mabille & Berteaux, 2014).

Like other important trade-offs, the thermoregulation–predator avoidance trade-off may be plastic in response to environmental conditions (Dosmann, Brooks, & Mateo, 2015; Stahlschmidt & Adamo, 2013a; Stahlschmidt, O'Leary, & Adamo, 2014). For example, pathogen exposure varies temporally and spatially (Raucher, 2002; Suwanpakdee et al., 2015), and it can influence thermoregulation and predator avoidance independently. During immune activation, many animals putatively shift their  $T_b$  to create an undesirable thermal environment for pathogens (Bicego, Barros, & Branco, 2007; Kluger, 1986). This shift in  $T_b$  often presents as fever (increase in  $T_b$ ), such as in crayfish (Payette & McGaw, 2003), insects (reviewed in Stahlschmidt & Adamo, 2013b; but see Ballabeni, Benway, & Jaenike, 1995), mice (MacDonald, Begg, Weisinger, & Kent, 2012) and reptiles (Merchant, Fleury, Rutherford, & Paulissen, 2008; but see ; Zurovsky, Brain, Laburn, & Mitchell, 1987), but immune activation can have hypothermic effects on animals (Almeida, Steiner, Branco, & Romanovsky, 2006; Deen & Hutchison, 2001). Immune activation can also influence predator avoidance behaviour (e.g. cause an infected individual to react slower to predator attacks even at preferred temperature; Joop & Rolff, 2004; Lefcort & Eiger, 1993; Otti, Gantenbein-Ritter, Jacot, & Brinkhof, 2011; Rantala, Honkavaara, & Suhonen, 2010). The role of immune activation in the trade-off between thermoregulation and predator avoidance has been proposed (e.g. Nord, Sköld-Chiriac, Hasselquist, & Nilsson, 2014; Otti et al., 2011) but never explicitly tested.

Thus, we examined the dynamics of a thermoregulation–shelter use trade-off to test two hypotheses. We used the cornsnake, *Pantherophis guttatus*, to test our hypotheses because snakes utilize existing shelter (Hyslop, Cooper, & Meyers, 2009) and adjust their habitat selection to carefully regulate  $T_b$  (Aïdam, Michel, & Bonnet, 2013; Blouin-Demers & Weatherhead, 2001; Lorient, DeNardo, Gorelick, & Lourdaï, 2012; Lourdaï, Guillon, DeNardo, & Blouin-Demers, 2013; McConnachie, Greene, & Perrin, 2011; Stahlschmidt et al., 2012). Like other animals (Johnson, 2002; Lefcort & Eiger, 1993), snakes may exhibit a shift in  $T_b$  and increase shelter use due to immune activation; thus, we first hypothesized that immune activation influences thermoregulation and shelter use independently (sensu Kluger, 1986; Otti et al., 2011). Under this hypothesis, we predicted that snakes would undergo fever and increase their shelter use during an immune activation. Our second hypothesis was that immune activation affects the thermoregulation–shelter use trade-off. We predicted that animals normally prioritize shelter use over thermoregulation (sensu Mabille & Berteaux, 2014) but that this prioritization is reduced during an immune challenge due to the strong effects of immune activation on thermoregulation (Almeida et al., 2006; Deen & Hutchison, 2001; MacDonald et al., 2012; Merchant et al., 2008; Payette & McGaw, 2003; reviewed in ; Stahlschmidt & Adamo, 2013b; but see ; Zurovsky et al., 1987). The results of our study will give insight into how an important environmental factor (immune activation by pathogens) influences the trade-off between two widespread behaviours (thermoregulation and shelter use).

## METHODS

### Animals and Maintenance

*Pantherophis guttatus* is a member of the family Colubridae and is commonly found throughout the southeastern United States (Dorcas & Gibbons, 2005). The experiment used 23 captive-born *P. guttatus* (1.5–2 years of age; 14 males and 9 females; body

mass range 119–486 g) that were first- to fourth-generation progeny of snakes caught in Beaufort County, SC, U.S.A. Prior to trials, snakes were housed individually in translucent plastic enclosures (17 × 38 × 14 cm). To facilitate behavioural thermoregulation, subsurface heat tape at one end of the enclosures created a temperature range of 24.5–33 °C, which accommodates the preferred  $T_b$  of *P. guttatus* (Raske et al., 2012; Roark & Dorcas, 2000; Stahlschmidt, Jodrey, & Luoma, 2015). Snakes were fed frozen/thawed mice (10–20% of each snake's body mass) every 1–2 weeks and provided water ad libitum. Digestion can invoke  $T_b$  shifts in *P. guttatus* (Sievert et al., 2013) so snakes were nonabsorptive (>5 days postfeeding; Crocker-Buta & Secor, 2014) during trials. Throughout the study, snakes exhibited no inflammation or evidence of trauma at the sites of injection and, as further evidence that treatments were not overly stressful, they readily accepted food shortly after trials (see details below). All procedures were approved by the Institutional Animal Care and Use Committee of Georgia Southern University (protocol number I14004).

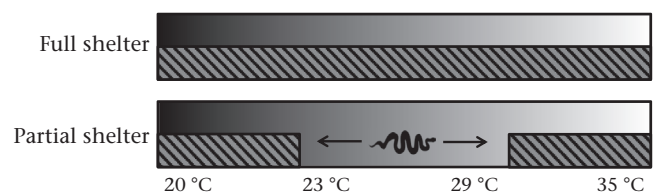
### Thermal Gradient

Experiments were performed in thermal gradient lanes (length: 2.4 m; width: 0.3 m; height: 0.4 m) within an arena (Fig. 1). The temperature gradient was achieved with modified Flex-Watt heat tape (Calorique, West Wareham, MA, U.S.A.) placed below 2–3 cm of sand (a temperature stable substrate). Substrate temperature ranged from 20 °C to 35 °C because *P. guttatus* exhibit a preferred  $T_b$  of 26–27 °C (Raske et al., 2012; Roark & Dorcas, 2000; Stahlschmidt et al., 2015). When trials were in session, the top of the arena was covered with acrylic glass to keep snakes inside and to help stabilize the temperature of the substrate.

### Experimental Procedures

To determine the role of immune activation on a thermoregulation–shelter use trade-off in *P. guttatus* ( $N = 23$ ), we used a repeated measures  $2 \times 2$  factorial experimental design in the thermal gradient arena. Two treatments were used, each with two levels: shelter availability (full and partial) and presence of immune status (challenge or control), as described below.

For the shelter availability treatment, we provided either shelter across the entire gradient ('full' shelter) or only at temperature extremes ('partial' shelter) (Fig. 1). In both cases, shelter consisted of a corrugated steel sheet (0.15 m wide) placed 3–4 cm above the substrate (Fig. 1). The temperature extremes in the partial shelter level were at least 2–3 °C below and above preferred  $T_b$  (20–23 °C and 29–35 °C, respectively); that is, the partial shelter level of treatment forced the snakes to choose between a shelter and their preferred temperature.



**Figure 1.** Diagram of shelter treatments in thermal gradient. Open area represents exposed space and diagonally patterned area represents sheltered space. Each snake underwent trials with both shelter types (full and partial) at two immune states (challenged and control). See text for details. A sample snake is shown to demonstrate how each snake had the option to move freely in any direction based on its temperature or shelter preference.

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