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Does social behaviour reliably reflect temperature-dependent physiological capacity in geckos?

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Animals with low energy budgets may attempt to deceive their opponents during contests by producing social displays that falsely indicate their physiological state. We used overnight laboratory experiments to examine the relation between physiological capacity and social behaviour in a nocturnal gecko. Velvet geckos, *Oedura lesueurii*, use loose surface rocks that vary considerably in temperature as diurnal retreat sites. At night males defend retreat sites and the outcomes of contests are resolved via physical duels. We manipulated a gecko's physiological state at night by allocating geckos to diurnal retreat sites with different thermal regimes. At night geckos from colder diurnal retreat sites were less mobile, and had poorer locomotor performance, than conspecifics from warmer diurnal retreat sites. We hypothesized that such differences in physiological capacity would be reflected in outcomes of territorial contests between pairs of adult males. However, geckos from colder diurnal retreat sites were just as likely to win nocturnal contests for a limited resource as were geckos from warmer diurnal retreat sites. This result may reflect differences in the behaviour of geckos with different thermal exposure. Geckos from colder diurnal retreat sites were significantly more aggressive during contests than conspecifics from warmer diurnal retreat sites. Thus, animals may attempt to deceive opponents by producing a social display that vastly overstates their current physiological state.

Keywords: locomotor performance; nocturnal lizard; *Oedura lesueurii*; physiological capacity; temperature regulation; territorial contest; velvet gecko

Ectothermic animals generate negligible heat from their own metabolic processes, and hence rely on external heat sources to attain body temperatures that maximize performance capacities (reviewed in Huey 1982; Huey et al. 1989). Failing to use microhabitats that enable optimal temperature regulation can have serious consequences for the fitness of ectotherms (Autumn & De Nardo 1995; Martin & Lopez 2001). For instance, body temperature can affect digestive efficiency (Lichtenbelt et al. 1993; Angilletta et al. 2002a) and metabolic rate (Beyer & Spotila 1994). Changes in physiology may influence several aspects of ecology, such as activity level (Bennett 1983), locomotor performance (Zani 2001; Angilletta et al. 2002b), foraging efficiency (Ayers & Shine 1997), and antipredator behaviour (Keogh & DeSerto 1994; Mori & Burghardt 2001). During acute exposure to a broad range of temperatures, the relation between body temperature and a specific type of performance is described by an asymmetric function, in which performance is maximized at an intermediate temperature (Huey 1982; Angilletta et al. 2002a).

Many studies have found strong positive correlations between different types of traits in the effects of temperature regulation on performance (e.g. Beuchat & Ellner 1987; Angilletta et al. 2002b). However, the efficacy of some measures of performance may not depend on temperature, and therefore these behaviours may be used more often at lower body temperatures. For instance, many ectotherms shift antipredator behaviour from fleeing when they are warm to threat displays when they

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are cold (Hertz et al. 1982; Chai & Srygley 1990; Mautz et al. 1992). In this scenario, animals that are incapable of evading an attack attempt to 'bluff' opponents by producing a display that overexaggerates their current physiological state (Whitaker & Shine 1999).

One way to test the relation between variation in performance and the expression of a particular behaviour is to compare the expression of the potentially labile trait with that of a trait that is reliably linked to physiology, across the same range in temperatures. The energetic capacity and power of leg muscles depend on temperature, and measuring locomotor performance is thought to provide an accurate representation of physiology in an ecological context (e.g. Irschick & Losos 1998; Jayne & Irschick 2000; Chick & Garland 2001; Losos et al. 2002; Van Hooydonck & Van Damme 2003). Usually, colder animals are substantially slower than warmer animals (e.g. Mautz et al. 1992; Angilletta et al. 2002b). In ectotherms the outcomes of physical duels may also depend on temperature but the expression of social behaviour may not accurately reflect physiological capacity (Crowley & Pietruszka 1983; Mautz et al. 1992). For example, island night lizards, *Xantusia riversiana*, chased down a racetrack were most aggressive at low body temperatures that were suboptimal for sprinting (Mautz et al. 1992). Locomotor performance and social aggression are therefore ideal for comparing the expression of a labile trait with that of one that is linked to physiology (see also Lailvaux et al. 2004; Perry et al. 2004).

The velvet gecko, *Oedura lesueurii*, provides a good model system for examining the relation between temperature and the expression of physiological capacity and social behaviour. These nocturnal ectotherms use loose surface rocks as diurnal retreat sites (Schlesinger & Shine 1994). In the laboratory, geckos select retreat sites that attain their preferred body temperatures of 29–32°C (Schlesinger & Shine 1994; Downes & Shine 1998; Kondo 2003). However, during spring, geckos within the same natural outcrop use retreat sites with maximum diurnal temperatures of 16–41°C ($\overline{X} \pm SE = 25 \pm 0.52$°C, $N = 54$; Kondo 2003). Therefore, at any one time conspecific individuals may be exposed to considerably different thermoregulatory opportunities. In nature, the availability of retreat sites of high thermal quality is relatively low (Webb & Shine 2000; J. Kondo & S. J. Downes, unpublished data). Adult male geckos are highly territorial and engage in physical battles with conspecific males over preferred retreat sites (Downes & Shine 1998). Geckos are active at night regardless of the temperature of their diurnal retreat sites (Kondo 2003), so the opportunity exists for animals with different diurnal thermoregulatory exposure to interact during this period.

We conducted a series of manipulative laboratory experiments that examined the relation between physiological capacity and social aggression in adult male geckos. We first tested the hypothesis that the temperatures available within diurnal retreat sites affect physiological state at night, as measured by levels of activity and locomotor performance. We then staged encounters to examine the hypothesis that differences in physiological state would be reflected in the outcomes of territorial contests between pairs of adult male geckos.

METHODS

Study Animals and Maintenance

This project was approved by the Australian National University Ethics and Experimentation Committee. In October 2002 we captured 60 adult male geckos by hand from Nattai National Park in New South Wales, Australia (under National Parks and Wildlife Service permit). The geckos were transported to our laboratory at the Australian National University.

Upon arriving they were uniquely marked with a small drop of Visible Implant Elastomer injected under the skin on the ventral side in specific combinations of locations (Kondo & Downes 2004). In all cases the drops were less than 1 mm wide and 2 mm long and the maximum number of tags used per individual was four. This technique served our need to mark animals both temporarily for this study and permanently for a separate capture–mark–recapture study. There are no adverse side-effects of this marking method for animals maintained in the laboratory (Kondo & Downes 2004).

Geckos were housed individually in plastic cages (120 × 200 mm and 100 mm high) maintained in a room at 18°C. Each cage contained a shelter in the form of two tiles (100 × 100 mm) separated vertically with squares of cardboard (10 × 10 mm and 5 mm high) to form a crevice. During the day 1 end of the shelter was heated from underneath to 35°C. The photoperiod was kept constant at 11:13 h light:dark, which approximates the corresponding cycle in nature. Water and house crickets supplemented with vitamins and calcium were provided ad libitum.

After the 4-month study each animal was returned to the rock under which it was captured. All of the geckos maintained their weight and health before release.

Experimental Procedure

We manipulated physiological capacity by altering the thermal regimes available to lizards during the day. Lizards were randomly assigned to the treatments. We chose treatments based on variation in the temperatures of diurnal retreat sites in nature (Webb & Shine 1998, 2000): (1) 'hot' rocks were maintained at 30°C; (2) 'warm' rocks were maintained at 24°C; and (3) 'cold' rocks were maintained at 18°C. These rock temperatures were manipulated with heat tapes placed under the individual home cages of geckos during the day. To control for the effect of current body temperature on performance, we lowered the body temperature of geckos, 30 min before commencing experiments, to the room temperature of 18°C. This regime represents the average ambient temperature recorded in the field overnight during the summer (Kondo 2003; also see Webb & Shine 1998, 2000). A pilot study confirmed that the internal body temperature of lizards always fell to 18°C within 30 min (Kondo 2003). Therefore, the history of diurnal temperature varied between treatments, but the body temperatures of geckos at the time of experiments were identical. This method is crucial because current body temperature can significantly