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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.

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

affect behaviour in ectotherms (reviewed in Keogh & DeSerto 1994).

First, we tested whether diurnal temperature regulation influences a gecko's level of activity, level of mobility, maximal sprint speed, and ability to maintain maximal sprint speed over successive runs (hereafter referred to as 'perpetual speed'). We used these traits to indicate physiological capacity because they are relevant to the performance of adult male velvet geckos during territorial contests. Geckos engage in contests outside retreat sites (Kondo 2003). Levels of activity and mobility thus indicate the chances that a gecko will be exposed to and encounter a potential opponent (e.g. McPeek 1990; Formanowicz et al. 1991; Griffiths 1991; Skelly 1994). Sprint speed should relate to the ability of an animal rapidly to approach or flee opponents during fights, whereas perpetual speed should relate to the ability of an animal to sustain physical fights below their maximal aerobic capacity (Garland et al. 1990; Swoap et al. 1993; Stutt & Willmer 1998; Robson & Miles 2000). Second, we tested whether diurnal temperature regulation influences a velvet gecko's ability to win contests. Except for the sprint speed and perpetual speed trials, we used plastic tubs (500 × 1000 mm and 530 mm high), the inner sides of which were coated with Fluon to prevent geckos from climbing out. We recorded the behaviour of animals on videotape with surveillance cameras and a video recorder. Red lights were positioned above the cameras to illuminate the tops of the experimental tubs.

Activity and mobility

From each diurnal temperature treatment, we randomly selected a subset of 16 geckos for the activity and mobility trials (i.e. across treatments 48 geckos were used). At 1930 hours a lizard was placed inside one unheated retreat site (100 × 200 mm) located centrally in an experimental tub. We then simulated an artificial dusk, and left the animals undisturbed overnight. Their behaviour was recorded from 2000 to 0600 hours. From the videotapes, every 15 min we scored whether the gecko was hidden within the retreat site (not active) or not hidden within the retreat site (active). If the gecko was active, we scored whether it was moving or stationary for more than 20 s. We calculated 'activity' as the number of observation periods that the lizard was active divided by the total number of observation periods. We calculated 'mobility' as the number of observation periods that the lizard was mobile divided by the total number of observation periods spent active. To analyse variation in these data we used ANOVA with diurnal rock temperature as the factor. Before conducting the ANOVA we confirmed that the assumptions of this test were not violated. Upon detecting a significant main effect, we performed Tukey−Kramer honestly significant difference tests (HSD) to examine significant variation among pairs of treatments.

Locomotor performance

We estimated sprint speed by forcing rested animals to sprint maximally. We estimated perpetual speed by measuring the reduction in sprint speed over four successive maximal sprints. Each measure was estimated during three separate trials per animal at each diurnal temperature. Since sprint speed does not vary significantly between 2000 and 2430 hours (Kondo 2003), we measured performance between 2000 and 2130 hours when the geckos were most active (see below).

We used a 1-m racetrack that was 40 mm wide and lined with coarse sand. Photocells receiving an infrared beam were placed at 250-mm intervals along the track. The time at which the lizards passed the photocells was recorded as they ran down the track, breaking the light beams. In all trials the racetrack was used in a horizontal position. Individuals were placed at exactly the same position at the start of the track and gently prodded to within 1 cm of the tail with a soft paintbrush to encourage them to run the full length. We measured sprint speed by chasing the geckos along the track; the geckos were rested for 24 h between trials. We estimated perpetual speed by chasing geckos along the track four times with 3-min intervals between runs; the geckos were rested for 48 h between trials.

We used 60 geckos in this experiment, randomly assigned to two of the three temperature treatments. We rested the geckos for 3 weeks between trials at different diurnal temperatures and therefore considered data from the same animal to be independent (i.e. across treatments 120 individuals were used). For our analyses of locomotor performance, we excluded data from two geckos that, although healthy, were clearly performing at less than their maximal capacities (Losos et al. 2002). From the three sprint speed trials, we used the fastest speed (cm/s) over any 25-cm interval as the dependent variable in an ANOVA with temperature treatment as the factor. This measure over 25 cm provides an index of maximal speed. To calculate perpetual speed, we subtracted the speed of the fourth run from the speed of the first run. From the three perpetual speed trials, we used the smallest difference over any 25-cm interval as the dependent variable in an ANOVA with temperature treatment as the factor. Before conducting the ANOVA, we confirmed that the assumptions of this test were not violated. Upon detecting a significant main effect, we performed HSD tests to examine significant variation among pairs of treatments.

Social interactions

We staged encounters between two geckos maintained at the following temperatures during the day: (1) hot versus hot ($N = 26$); (2) hot versus warm ($N = 23$); and (3) hot versus cold ($N = 30$). Groups of up to 60 male lizards were tested repeatedly during three separate trials. Each time one-third of pairs tested were from each of the three treatments. We housed geckos individually for 4 weeks between trials, and geckos were never paired with a previous contestant. There was no significant interaction between the outcome of a gecko's first contest and the probability that it won a subsequent contest (chi-square test: $\chi_4^2 = 2.77$, $P = 0.59$). All pairs of lizards were matched for body mass (± 0.3 g) and snout−vent length (± 2 mm).

At one end of the experimental tub (700 × 700 mm) one unheated retreat site (100 × 100 mm) was provided

as the limiting resource over which geckos competed. We used a sheet of transparent plastic covered with black mesh (4 × 4 mm) as the roof so that we could observe interactions within crevices. Experiments were conducted between 1930 and 2130 hours. To avoid physically handling the lizards before starting trials, we transported them within retreat sites from their home cage into the experimental tub. The retreat sites were placed side by side, and 100 mm apart, at the end of the experimental tub that was opposite the limiting resource. We then turned off the light, removed the roofs of the retreat sites, and shortly after the geckos moved onto the arena we removed the base (by lifting it with strings). We commenced the trial as soon as the geckos approached to within 50 mm of each other (hereafter termed an 'encounter') or clearly noted each other's presence by orienting towards each other. After 20 min, we simulated an artificial dawn by gradually increasing the brightness of a light over a 5-min period. The animals were left undisturbed for the following 5 min, during which time one or other gecko gained exclusive occupancy of the retreat site; we assumed that individual was dominant.

From real time videotapes, we scored all encounters as being one of the following behaviours, listed in rank order of least to most aggressive: (1) nonaggressive: one lizard walked directly towards the other and neither animal showed either overt aggressive or submissive displays; (2) threat: one or both lizards showed aggression towards each other by waving their tails or raising their bodies; (3) chase: one or both lizards threatened each other followed by one or other lizard fleeing from its opponent; (4) attempted bite: one lizard attempted to bite its opponent followed by one or other lizard fleeing from its opponent; and (5) attack fight: one lizard bit its opponent for at least 2 s, followed by one or other lizard fleeing from its opponent. We also recorded which individual in the pair solicited each encounter, displayed aggressively and fled at the end of the interaction. We recorded the number of tail waves of each individual, and the amount of time that each lizard was closer to the retreat site than its opponent. At the end of the trial we considered a clear dominance hierarchy to have been established if only one of the geckos exclusively occupied the retreat site.

None of the geckos sustained any injuries (i.e. broken skin, bleeding or obvious bruising) during the experiments. Male velvet geckos bite each other in combat in nature (S. J. Downes, personal observation). This behaviour was observed frequently throughout the study and involved both geckos in a pair biting each other's tails and circling in a wrestling fashion. These wrestles broke when one gecko fled from the other, and shortly thereafter contestants often chased each other. Our test arenas were large enough to allow a gecko to flee far enough away from its opponent to discourage further chasing. We planned to terminate trials if there had been biting that caused wounding or repeated attacks that may have led to injury. We did not need to implement these plans.

For contests that resulted in exclusive retreat site occupancy, we used goodness-of-fit tests to examine the interaction between pair type and whether the gecko from the suboptimal retreat site was dominant. For this analysis

we assumed that each animal in a hot versus hot pair had a 50% chance of winning an encounter.

We conducted further statistical analyses only on the 87% of contests that resulted in exclusive retreat site occupancy. We calculated an aggression score for each pair for the entire trial as the sum of the number of encounters in each category multiplied by the corresponding rank order. We used aggression score and number of encounters as dependent variables in a multivariate ANOVA (MANOVA) with pair type as the effect. We calculated aggression per encounter by dividing the aggression score by the number of encounters for a pair. This measure was used as a dependent variable in an ANOVA with pair type as the effect. Upon detecting a significant main effect using MANOVA or ANOVA, we performed HSD tests for each dependent variable to examine significant variation among pairs of treatments.

We calculated aggression scores for individuals using the method described for pairs but we included only interactions in which the gecko was aggressive (i.e. solicited the interaction or willingly engaged in a fight). We scored each pair as having either a hot contestant with the highest score or a suboptimal contestant (warm or cold) with the highest score. Similarly, we scored each pair as having either a hot contestant with a greater number of tail waves or a suboptimal contestant with a greater number of tail waves. We used goodness-of-fit tests to examine the interaction between pair type and the frequency of the suboptimal animals in a pair (1) to be most aggressive or (2) to display tail waves most often.

The behaviours of the aggressive and submissive lizards were correlated because they both tended to spend a lot of time either away from or near the retreat. We therefore calculated the difference in the amount of time that each gecko in a pair spent closer to the retreat site than its opponent by subtracting the values for optimal geckos from those of suboptimal geckos (warm or cold). For trials with hot versus hot pairs, we randomly assigned individuals as being 'hot' or 'suboptimal', and assumed that each animal would have a 50% chance of being more aggressive. We used this measure as the dependent variable in an ANOVA with pair type as the effect.

RESULTS

Activity and Mobility

Geckos were most active between 2000 and 2130 hours. Geckos from the different diurnal temperature treatments spent similar amounts of time outside their retreat site during the trial (hot: $\overline{X} \pm SE$ minutes active $= 326.3 \pm 24.9$; warm: 297.2 ± 34.2; cold: 348.5 ± 31.9; ANOVA: $F_{2,45} = 0.7$, $P = 0.50$). However, diurnal temperature exposure significantly affected levels of mobility by geckos that were active (ANOVA: $F_{2,45} = 4.0$, $P = 0.02$). Geckos that were colder during the day were significantly less mobile than geckos that were hot during the day but there was no significant variation in mobility of geckos from warm versus hot treatments or warm versus cold treatments (hot: $\overline{X} \pm SE$ minutes mobile $= 198.2 \pm 11.0$;

warm: 165.0 ± 14.4; cold: 153.5 ± 11.9; HSD: critical difference $= 42.8$; hot versus warm: 11.9; hot versus cold: 44.7; warm versus cold: 32.8).

Locomotor Performance

Diurnal rock temperature significantly influenced maximal sprint speed over 25 cm (ANOVA: $F_{2,115} = 3.2, P = 0.04$) and perpetual speed over 25 cm ($F_{2,115} = 6.4, P = 0.002$). Geckos from cold diurnal retreat sites were significantly slower sprinters than geckos from hot diurnal retreat sites but there was no significant variation in sprint speed among geckos from hot versus warm treatments or warm versus cold treatments (hot: $\overline{X} \pm SE = 89.1 \pm 3.1$ cm/s; warm: 83.7 ± 2.2 cm/s; cold: 80.2 ± 2.2 cm/s; HSD: critical difference $= 8.4$; hot versus warm: 3.5; hot versus cold: 8.9; warm versus cold: 5.5). Perpetual speed was lower for geckos from cold diurnal retreat sites than for geckos from warm and hot diurnal retreat sites (hot: $\overline{X} \pm SE = 24.5 \pm 1.4$; warm: 26.1 ± 1.6; cold: 31.9 ± 1.6; HSD: critical difference $= 5.2$; hot versus warm: 1.6; hot versus cold: 7.4; warm versus cold: 5.7).

Social Interactions

A clear dominance hierarchy was established in 69 of the 79 trials we conducted. There was no significant interaction between pair type and the frequency of trials with a dominant individual (chi-square test: $\chi^2_2 = 2.4, P = 0.31$; Table 1). During these 69 trials there was no significant interaction between the diurnal rock temperatures available to individuals comprising pairs and the tendency of colder animals to win contests ($\chi^2_2 = 1.6, P = 0.44$; Fig. 1).

The aggression per encounter for a pair was not significantly different between the three types of pairs of geckos (ANOVA: $F_{2,76} = 0.1, P = 0.89$; Table 1). However, there was significant variation among paired treatments in aggression over the trial and the number of interactions among contestants (MANOVA: $F_{3,67} = 5.3, P < 0.01$; Table 1). Thus, differences in aggression score over the trial were primarily induced by variation in the number of encounters, not by aggression score per encounter.

Contests between hot versus cold pairs were more aggressive and interactive than were those between hot versus hot pairs (HSD: aggression: critical difference $= 5.4$, difference $= 5.8$; encounters: critical difference $= 2.2$, difference $= 2.9$), whereas there was little difference in aggression or interaction during contests between hot versus hot pairs compared with hot versus warm pairs (aggression: critical difference $= 5.4$, difference $= 1.8$; encounters: critical difference $= 2.2$, difference $= 0.4$). Contests between hot versus cold pairs were more interactive than those between hot versus warm pairs (encounters: critical difference $= 2.2$, difference $= 2.5$), but there was no significant difference in aggression between these two types of contests (aggression: critical difference $= 5.4$, difference $= 4.0$).

Trials between hot versus cold lizards were more likely to result in suboptimal individuals showing greater aggression than were trials between hot versus warm and hot versus hot lizards (chi-square test: $\chi^2_2 = 5.7, P = 0.05$; Table 1). Moreover, trials between hot versus cold lizards were more likely to result in suboptimal individuals tail waving at higher rates than were trials between hot versus warm and hot versus hot lizards ($\chi^2_2 = 6.5, P = 0.04$; Table 1). There were no significant differences between the different types of pairs in the difference in time that optimal and suboptimal contestants spent closer to the retreat site than their opponent (ANOVA: $F_{2,66} = 0.1, P = 0.93$; Table 1).

DISCUSSION

Our study shows that available diurnal rock temperature significantly influences several aspects of the nocturnal ecophysiology of velvet geckos. At night, geckos from colder diurnal retreat sites were less mobile, slower at sprinting and with poorer perpetual speeds than conspecifics from warmer diurnal retreat sites. However, the diurnal temperature available to geckos did not affect their chances of winning nocturnal contests for a limited resource. This result may reflect differences in the behaviour of geckos from retreat sites of different diurnal temperature. For instance, our results suggest that geckos from colder diurnal retreat sites that have low physiological capacity are significantly more aggressive during territorial contests than conspecific geckos from warmer diurnal retreat sites that have high physiological capacity.

Our main motivation for manipulating the temperatures available to geckos in retreat sites was significantly to alter physiological capacities. However, our finding that diurnal temperature significantly alters nocturnal performance is important in its own right. Most work on temperature-dependent performance in ectotherms has focused on diurnal species that thermoregulate during their active period (reviewed in Huey 1982; Kearney & Predavec 2000). Our results show that patterns of temperature regulation

Table 1. The expression of behaviour during nocturnal contests between pairs of male geckos maintained during the day at hot versus hot, hot versus warm, and hot versus cold temperatures

Behavioural measure	Hot versus hot	Hot versus warm	Hot versus cold
% Contests with dominance	92	91	80
Aggression score	11.27 ± 1.31	13.04 ± 1.69	17.07 ± 2.35
Number of encounters	4.12 ± 0.42	4.48 ± 0.48	7.00 ± 1.09
Aggression per encounter	2.81 ± 0.22	2.97 ± 0.24	3.01 ± 0.37
Difference in time closer to retreat (min)	8.50 ± 1.30	8.26 ± 1.52	7.81 ± 1.28
% Trials with more aggressive suboptimal	46	39	70
% Trials with more tail waves by suboptimal	40	26	63

Values are means $\pm$ SE. Suboptimal refers to the contestants in a pair maintained at cold or warm temperatures. For trials with hot versus hot pairs we randomly assigned individuals as being hot or suboptimal.
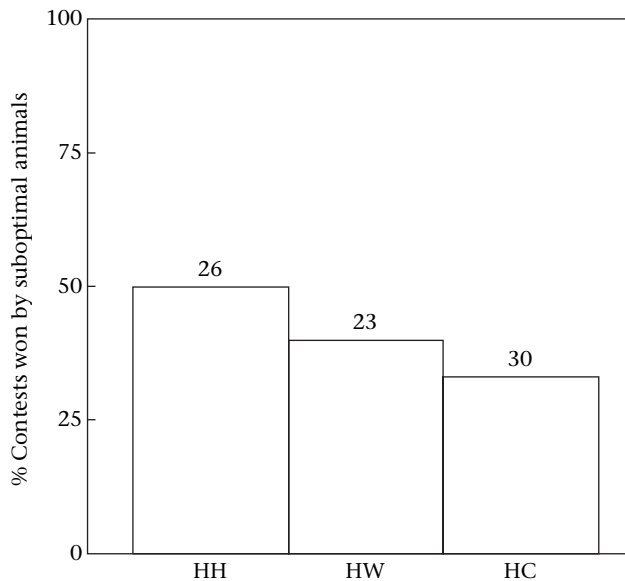
Figure 1. The percentage of nocturnal contests that resulted in the suboptimal animal in a pair winning the retreat site, assuming that each lizard in a hot versus hot pair had a 50% chance of gaining exclusive occupancy of the retreat site. Data are presented for animals in three pair types reflecting the diurnal temperatures available to the contestants: hot versus hot (HH), hot versus warm (HW) and hot versus cold (HC). Numbers above each column indicate sample sizes.

during diurnal inactivity have important consequences for the physiology and behaviour of geckos at night. Presumably, rates of energy assimilation in nocturnal species depend on diurnal temperatures (Huey 1991). Thus, nocturnal animals that are exposed to optimal temperatures during the day may have larger energy budgets for activity at night than do animals that are exposed to suboptimal diurnal temperatures (Autumn & De Nardo 1995).

Velvet geckos engage in contests outside retreat sites. The geckos in our study left their retreat sites at night regardless of their diurnal thermal environment. This result corroborates the findings of a recent field study during summer which showed that geckos virtually always leave their retreat sites at night (Kondo 2003). From this information we infer that geckos from rocks of different diurnal thermal quality will have similar opportunities to be exposed to potential opponents for territorial contests (McPeek 1990). Our results suggest that once outside their retreat sites, animals experiencing cooler diurnal temperatures will be significantly less mobile than animals experiencing warmer diurnal temperatures. Therefore, geckos from warmer diurnal retreat sites may range more widely and encounter conspecifics more often than those from cooler diurnal retreat sites (Formanowicz et al. 1991; Griffiths 1991). This situation is analogous to that in which highly mobile prey individuals are most likely to encounter predators (Skelly 1994; Downes 2001).

We hypothesized that differences in physiological capacity would be reflected by outcomes of territorial contests among adult males at night. Ecological theory predicts that dominance status and physiological

performance should be tightly correlated in ectotherms (see Introduction). In many cases, this relation is a positive one (Garland et al. 1990; Robson & Miles 2000). Our results predict that geckos from cooler diurnal rocks should be at a physiological disadvantage during nocturnal territorial contests with conspecifics from warmer diurnal rocks. However, there was no significant effect of diurnal retreat site temperature on the probability of geckos winning nocturnal contests. Moreover, contestants from thermally inferior diurnal retreat sites were more aggressive during trials than were contestants from thermally superior diurnal retreat sites (Table 1). Thus, in velvet geckos a correlation exists between aspects of social behaviour and physiology but the nature of this relation is negative rather than positive. One explanation for this result is that geckos in a poor physiological state compensate for this disadvantage by increasing their aggression during territorial contests. This situation is analogous to one in which ectotherms shift antipredator behaviour from fleeing when they are warm to threat displays when they are cold (e.g. Hertz et al. 1982; Chai & Srygley 1990; Braña 1993; Whitaker & Shine 1999).

Locomotor performance indicates physiological state because it is related to aerobic capacity (Swoap et al. 1993; Stutt & Willmer 1998) but it may also directly affect an animal's performance during territorial contests (Garland et al. 1990; Robson & Miles 2000). Encounters between pairs of male geckos usually begin with lizards displaying to each other by tail waving and raising their body. Generally, these threats escalate into both geckos in a pair biting each other's tails and circling in a wrestling fashion. These wrestles break when one gecko flees from the other, and shortly thereafter the contestants chase each other. Therefore, the suites of displays that serve to identify a dominant individual (e.g. threats, wrestles, chases) may be activities in which the duration and intensity of display are affected by variation in sprinting speed or perpetual speed. Previous studies have shown that contrasts in locomotor performance between pairs of animals are unrelated to contrasts in behavioural scores during social encounters (Garland et al. 1990; Robson & Miles 2000). Therefore, speed or perpetual speed may not correlate directly with the behavioural components of dominance, but rather reflect an overall index of vigour. Unfortunately, we cannot examine contrasts with the data from our experiment because in two-thirds of the contests individuals comprising pairs were exposed to different categories of diurnal temperatures. Moreover, in our study variation in locomotion among individuals reflects different temperature regulation opportunities rather than natural variation in performance.

A strategy of 'bluffing' opponents when physiological state is limiting may be driven by natural selection. The probability of this scenario depends on the frequency at which contestants with a high physiological capacity call the deceit of opponents with low physiological capacity, as well as the cost incurred upon being discovered as signalling dishonestly (Leal & Rodrîguez-Robles 1997). If the frequency and cost of discovery are both relatively low, on average the gamble may payoff. If this is true then the circumstances that govern the decision-making

process may be produced by natural selection (Andersson 1982; Pellis 1997). Our finding that intrinsic sprinting capacity does not significantly affect the outcomes of territorial contests suggests that physiologically inferior animals successfully deceive physiologically superior contestants at least as often as they do not. Our observations of contests between pairs suggest that dominant geckos closely defend the limiting resource rather than continually harass subordinate opponents. Therefore, the immediate physical cost of being discovered as signalling dishonestly may be relatively low.

We observed social interactions between geckos early in the evening and note that the effects of diurnal thermal availability on the outcomes of these trials may be transient. Future studies should examine the longevity of temperature-dependent changes to physiology and concurrent shifts in the expression of ecologically relevant behaviours. These studies should not be restricted to species that thermoregulate during their active period.

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