

Competition during thermoregulation altered the body temperatures and hormone levels of lizards

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Summary

1. Every organism must thermoregulate to maximize its performance, but competing organisms limit access to preferred microclimates. Such competition often creates hierarchies in which dominant individuals have more access to limited resources than subordinate individuals.
2. To assess the costs of competition during thermoregulation, we measured thermoregulation, movement, and hormones of male lizards (*Sceloporus jarrovi*) when alone and when paired with a smaller or larger conspecific.
3. Large males were 31% closer to the heat source when paired than when alone, resulting in a higher mean body temperature (35.7 vs. 33.9 °C). Conversely, small males were 40% farther from the heat source when paired, resulting in lower mean body temperature (32.1 vs. 33.6 °C).
4. When paired, large and small males circulate 26 and 44% more corticosterone, respectively. Conversely, large males circulated 26% more testosterone when paired, whereas small males circulated 26% less testosterone.
5. Both dominant and subordinate males incurred costs when paired, including poorer thermoregulation, more movement and greater physiological stress. Thus, competition for thermal resources should feature more prominently in ecological and evolutionary models of thermoregulation.

Key-words: aggressive interaction, body temperature, corticosterone, dominance hierarchy, movement, testosterone

Introduction

In many species of animals, individuals compete aggressively to secure access to limited resources (Trivers 1976; Chase *et al.* 2002; Sapolsky 2005; Wilson *et al.* 2007). Winning competitive interactions enhances growth, survival or reproduction, but also costs energy and imposes risk (Maynard Smith & Harper 2003). Thus, when competition persists, individuals establish dominance hierarchies that minimize the need for costly aggression (Barnard & Burk 1979; Chase *et al.* 2002; Tattersall *et al.* 2012). Within a dominance hierarchy, an individual's position depends on phenotypes (e.g. size, speed or colour) that presumably signal its ability to compete (Garland, Hankins & Huey 1990; Maynard Smith & Harper 2003; Senar 2006). In turn, social rank alters behaviour and physiology, especially in subordinates (Leshner 1975; Greenberg & Wingfield 1987; Sapolsky

2002) because higher ranking individuals gain greater access to resources (Barnard & Burk 1979; Downes & Shine 1998; Sapolsky 2005). In this way, social dominance enhances growth, survival or reproduction (Emlen & Oring 1977; Petren & Case 1996; Ybarrondo & Heinrich 1996), ultimately conferring greater fitness to dominant individuals (Defries & McClearn 1970; Schuett 1997; Koenig 2002).

Although competition for food or mates has received the most attention (Schoener 1982; Andersson 1994; Wiley & Poston 1996; Wong & Candolin 2005), animals also compete for microclimates needed to regulate temperature and hydration (Magnuson, Crowder & Medvick 1979; Schoener 1983; Valeix *et al.* 2008). In cold environments, rare sources of heat enable individuals to elevate their temperature and improve performance (Donkoh 1989; Angilletta 2001; Rojas, Körtner & Geiser 2012). In hot environments, rare sources of shade enable individuals to stay cool and conserve water (Kearney, Shine & Porter 2009; Sears & Angilletta

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2015; Sears *et al.* 2016). As preferred microclimates occur heterogeneously in space, dominant individuals can exclude others from desirable microclimates (Magnuson, Crowder & Medvick 1979; Downes & Shine 1998; Žagar *et al.* 2015). Connell's (1961) classic study of barnacles illustrates the advantage of monopolizing certain microclimates; the dominant species occupied cooler and wetter sites, forcing the subordinate species to occupy sites that reduced growth, reproduction and survival. Alternatively, some species of ants leave their nests only during hot periods of the day to avoid aggression from dominant species during cooler periods of the day. Activity during hot periods may reduce locomotor performance but enhances foraging and survival (Cerdeña, Retana & Manzaneda 1998; Albrecht & Gotelli 2001). Within a species, competition for microclimates leads to territoriality, whereby dominants exclude subordinates from their territories. Consequently, subordinates thermoregulate less effectively and exhibit more stress when territoriality prevents them from accessing preferred microclimates (Beitinger & Magnuson 1975; Downes & Shine 1998; Summers 2002).

To quantify costs of competition for thermal resources, we studied male spiny lizards (*Sceloporus jarrovi*) when paired with a larger or smaller conspecific. These lizards shuttle between sun and shade to regulate body temperature in artificial and natural settings (Mathies & Andrews 1997; Schuler, Sears & Angilletta 2011; Sears *et al.* 2016). During the breeding season, large males exclude small males from their territories, ensuring exclusive access to more space and thus more resources (Simon 1975; Ruby 1978; Moore 1987). As territorial behaviour of males increases throughout the season, so do circulating levels of corticosterone and testosterone (Moore 1986). These hormones influence a variety of behaviours, but typically have opposing effects. For example, testosterone often increases aggression and activity, whereas corticosterone reduces these behaviours (Moore 1988; DeNardo & Sinervo 1994; Schuett *et al.* 1996; Haanel *et al.* 2003). In some experiments, artificially elevated levels of corticosterone caused lizards to bask more frequently and prefer higher temperatures compared to controls (Belliere & Clobert 2004; Prest & Cree 2008). By measuring the movements, temperatures and hormones of males in artificial thermal arenas, we tested hypotheses about the costs and benefits of dominance when thermal resources were rare. When lizards were paired, we expected the larger individual to access thermal resources more frequently and thermoregulate more accurately and more precisely compared to small lizards. We also expected the smaller individual to experience greater physiological stress during competition compared to large lizards, reflected by lowered testosterone and elevated corticosterone circulating in plasma (Greenberg & Crews 1990; Schuett *et al.* 1996).

Materials and methods

COLLECTION AND HUSBANDRY OF ANIMALS

In August of 2012, we collected 24 adult males of *Sceloporus jarrovi* in the Chiricahua Mountains of Arizona (1500–2500 m). After capture, lizards were transported to the Sevilleta Field Station in New Mexico. Upon arrival, lizards were weighed (mean \pm SD = 26.2 \pm 4.0 g) and toe clipped for identification (Perry *et al.* 2011).

Lizards were housed individually in plastic terraria (30 \times 26 \times 13 cm) lined with paper towels. Terraria were heated from below at one end to create a thermal gradient, thus allowing lizards to freely thermoregulate. The operative environmental temperatures along this gradient ranged from 23 to 42 °C, as determined by hollow copper models of a lizard (Bakken & Gates 1975). Cardboard was placed between each terrarium to prevent lizards from viewing each other. Every other day, lizards were provided water and fed adult crickets (*Acheta domestica*) and larval beetles (*Tenebrio morio*) coated with a powder of vitamins and calcium (Rep-Cal, Los Gatos, CA, USA). Animals were maintained this way for 2 weeks before our experiment. Four lizards that refused to eat regularly were excluded from the study.

PREFERRED BODY TEMPERATURES

We measured the preferred body temperatures of lizards in artificial thermal gradients following the methods of Schuler, Sears & Angilletta (2011). These measurements enabled us to establish that lizards would thermoregulate in our arenas and determine the temperatures that they prefer. Thermal gradients were created in plastic containers (112 \times 35 \times 30 cm) with a substrate of sand (~1 cm deep). These containers were kept in a room at 20 °C and uniformly illuminated from above by fluorescent lights. A 150-W infrared lamp (Exo-Terra, Mansfield, MA, USA), suspended above one end of each container, created a range of operative temperatures from 22 to 44 °C. This type of gradient works well for lizards that thermoregulate by basking under natural conditions and forces the lizard to periodically retreat from the infrared lamp to avoid overheating (Angilletta 2009; Schuler, Sears & Angilletta 2011).

Each lizard was placed in a thermal gradient at 20.00 h, when infrared and fluorescent lights were off. The following morning, fluorescent and the infrared lights were turned on at 06.00 and 07.00 h, respectively, and were turned off at 20.00 and 17.00 h, respectively. On this day, lizards explored the thermal gradient undisturbed. On the next day, the bulbs were activated for the same periods, and body temperatures were recorded every 2 h between 08.00 and 16.00 h. To measure body temperature, each lizard was captured by hand and a quick-reading thermometer (T-4000; Miller & Weber, Inc., Queens, NY, USA) was inserted in its cloaca. During the 44 h that each lizard spent in a thermal gradient (36 h of habituation and 8 h of measurements) no food or water was provided. Based on a previous study, we do not expect that preferred body temperatures of *S. jarrovi* would have differed if food and water were provided (Schuler, Sears & Angilletta 2011). After these measurements, each lizard was returned to its terrarium, during which food and water were offered every other day.

IMPLANTATION OF TEMPERATURE LOGGERS

Five days after measuring preferred body temperatures, we surgically implanted a miniature temperature logger (1.43 \pm 0.05 g;

Weedot, Alpha Mach, Inc., QC, Canada) into the abdominal cavity of each lizard. Each logger was programmed to record temperature at a 10-min interval for the duration of the experiment. To exclude fluids, loggers were coated first with a plastic sealant (Plasti Dip, Plasti Dip International, Blaine, MN, USA) and then with paraffin wax (Gulf Wax, Kalton, Ohio, USA). Surgical procedures followed those of Sears *et al.* (2016). Two weeks after surgery, we remeasured preferred body temperatures, as described above, to see whether the surgery affected thermoregulation. The mean and standard deviations of preferred body temperature estimated from statistical modelling (see Statistical analyses) were virtually identical: 34.0 ± 1.4 °C before surgery and 34.0 ± 1.4 °C after surgery. Furthermore, no individual showed a large change in preferred body temperature (see Fig. S1, Supporting Information).

EXPERIMENTAL DESIGN AND TREATMENTS

We recorded the body temperatures of male lizards when isolated and when paired with a larger or smaller conspecific. Observations were made in the same thermal gradients with the same diel cycles of fluorescent light and infrared light used to measure preferred body temperatures. Time-lapse cameras (Plant Cam; EBSCO Industries, Inc., Birmingham, AL, USA) were positioned 2 m above the gradients to capture the spatial positions of lizards every 5 min. A small plastic shelter, measuring $14 \times 14 \times 4$ cm, was placed on the cooler side of the gradient to provide refuge from aggression.

We paired lizards according to mass, predicting that a large lizard would dominate thermal resources (i.e. heat lamp) when paired with a small lizard (Regal 1971; Ruby 1978; Downes & Shine 1998). Three weeks after surgeries, we weighed the lizards and divided them into two groups: the 10 heaviest lizards (large) and the 10 lightest lizards (small). Mean masses of large and small lizards were 29.5 ± 2.1 g and 23.1 ± 2.6 g, respectively. Then, lizards were paired according to their relative mass in each group; the heaviest lizard in the large group was paired with the heaviest lizard in the small group, and so on. The mean difference in mass between paired lizards was 6.4 ± 1.5 g.

Each pair was randomly assigned to one of two treatment orders: (i) isolation followed by competition, or (ii) competition followed by isolation. Prior to experiments, lizards were given 48 h to habituate to a thermal gradient in isolation. After this period, half of the lizards were paired in a single gradient (competition treatment) and half were left alone (isolation treatment). Body temperatures and spatial positions were recorded from 08.00 to 17.00 h for the next 2 days. Because one lizard escaped from its arena, its pair was excluded from analyses.

Following the first treatment, we sampled blood from each lizard to measure circulating levels of corticosterone and testosterone. This sample was taken on the morning after the first treatment (09.00–09.30 h). Each lizard was captured by hand and ~50 µL of blood was collected in a capillary tube by rupturing the orbital sinus. Once filled, each tube was sealed with Critoseal (Fisher Scientific, Pittsburgh, PA, USA) and stored on ice. Blood samples were centrifuged within 1 h to separate red blood cells from plasma. Once separated, plasma was stored at -80 °C until assayed (see below). Blood samples were collected within 2 min of capture to minimize effects of handling stress on circulating corticosterone (Moore 1986; Langkilde & Shine 2006). After bleeding, lizards were returned to terraria with food and water for 7 days. Following this period, the entire procedure was repeated, except that lizards in the competition treatment were switched to the isolation treatment, and vice versa (see Table S6 for a diagram of events). At the end of the experiment, we had body temperatures, spatial positions, and blood samples for each lizard in isolation and in competition.

VIDEO ANALYSIS

We analysed the time-lapse photos to estimate the mean distance from the heat lamp and the total movement by each lizard throughout the experiment. For each photo, a Cartesian coordinate system was applied with computer software (Tracker, version 4.90, Douglas Brown, <http://physlets.org/tracker/>). Then, we used triangulation to measure the distance between the lizard's body, at the base of neck between the shoulder blades and the centre of the heat lamp. Similarly, the distances between successive positions were summed to estimate the total distance moved. Positions were analysed between 08.00 and 17.00 h, as were recorded body temperatures (see Statistical analyses).

HORMONE ASSAYS

For each blood sample, we quantified total plasma concentrations (both free and bound fractions) of corticosterone and testosterone. Hormones were measured with a commercial kit for enzyme-linked immunoassay (Enzo Life Sciences, Farmingdale, NY, USA). Samples were analysed in duplicate on the same day, following instructions supplied with the kit. The assay was validated with standard curves, constructed from serial dilutions of 4- to 64-fold for corticosterone and 8- to 200-fold for testosterone (Fokidis, Orchinik & Deviche 2009). This approach enabled us to determine the appropriate dilutions for testing our samples, which was 32-fold for corticosterone and 128-fold for testosterone. Diluted samples were distributed randomly within a 96-well plate for each hormone. The sensitivities of these assays were 32.02 pg mL⁻¹ for corticosterone and 7.81 pg mL⁻¹ for testosterone. Mean coefficients of variation within assays were 5.04% for corticosterone and 8.80% for testosterone ($n = 2$ plates with 36 samples each; one plate for corticosterone and one plate for testosterone).

STATISTICAL ANALYSES

We analysed two types of statistical models. The first type was designed to see whether our method of surgically implanting a temperature logger altered the preferred body temperature of a lizard. The second type was designed to quantify effects of competition on variables of interest: body temperature, distance from heat lamp, total distance moved and hormone concentrations.

Each analysis included a mixture of fixed, continuous and random factors. When modelling preferred body temperature, we treated measurement period (pre-surgery or post-surgery) as a fixed effect, body mass (g) and time of day (h) as covariates, and the identity of the lizard as a random intercept. For the remaining analyses, we included three fixed factors: social rank (dominant or subordinate), treatment (isolation or competition) and treatment order (paired then alone or alone then paired). Temporal block (1 or 2) and body mass (g) were covariates. The identity of the lizard was a random intercept. Because body temperature was measured multiple times within a treatment, we included day of trial (1 or 2) as an additional covariate. Finally, we included a correlation structure for time of day, which accounted for similarities between temperatures or positions recorded closely in time.

When testing hypotheses about competition, we considered the accuracy and the precision of thermoregulation. The accuracy of thermoregulation was estimated by comparing mean body temperatures during experiments to measures of preferred body temperatures taken before experiments. The precision of thermoregulation was estimated from the standard deviation of body temperature for each combination of competition treatment and social rank; a smaller standard deviation would imply that a specific rank of lizards thermoregulated more precisely in a given treatment.

Multimodel inference was used to estimate the most likely values of means and standard deviations. We used the full-average

method, in which a parameter was considered zero when the factor did not appear in a model (Burnham & Anderson 2002). First, we used the procedure described by Zuur *et al.* (2009) to determine the most likely random component of the model. Then, we used the *nlme* library (Pinheiro *et al.* 2012) and the *MuMIn* library (Bartoń 2013) of the R Statistical Software (R Core Team 2015) to fit all possible models of fixed effects and to calculate the Akaike weight of each model (see Tables S1–S5). The Akaike weight estimates the probability that a model describes the data better than other models. Finally, we used Akaike weights to calculate a weighted average of each parameter. The resulting values of parameters were used to calculate the most likely mean for each treatment level. This approach eliminates the need to interpret *P* values because all models (including the null model) contributed to the most likely value of each mean.

Results

When paired, both large males and small males used space differently and thermoregulated less accurately than when alone. As predicted, small males remained an average of 40% farther from the heat source (9.1 ± 6.8 cm; Fig. 1) when paired with large males. By contrast, large males were 31% closer, on average (8.9 ± 3.8 cm) when paired. Consequently, both large and small males thermoregulated less accurately (Fig. 2). Large males had a mean body temperature of 35.7 °C, which exceeded the mean preferred temperature of 34.0 ± 1.4 °C. Small males had a mean body temperature of 32.1 °C, which fell below the preferred temperature (Fig. 2). Surprisingly, only large males decreased their precision of thermoregulation, displaying a greater standard deviation of body temperatures during competition treatment (3.7 vs. 3.2 °C), whereas small males exhibited similar standard deviations during isolation and competition (2.5 and 2.4 °C, respectively). Despite these opposing shifts in body temperature, both large males and small males moved greater distances when paired than when alone (Fig. 3).

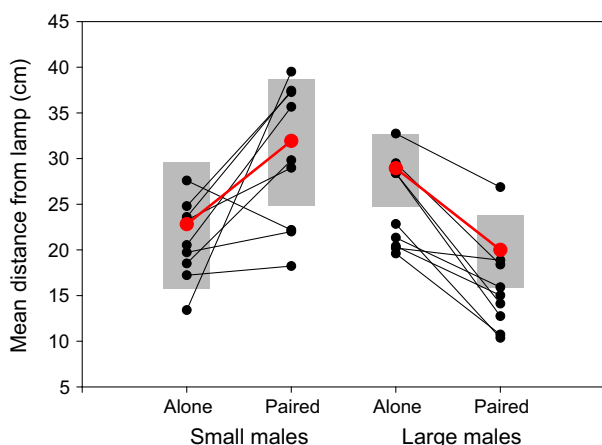


Fig. 1. When paired, large males and small males were closer to and farther from the heat source, respectively, than when alone. Black symbols and connecting lines represent the mean positions of each lizard in a treatment. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.

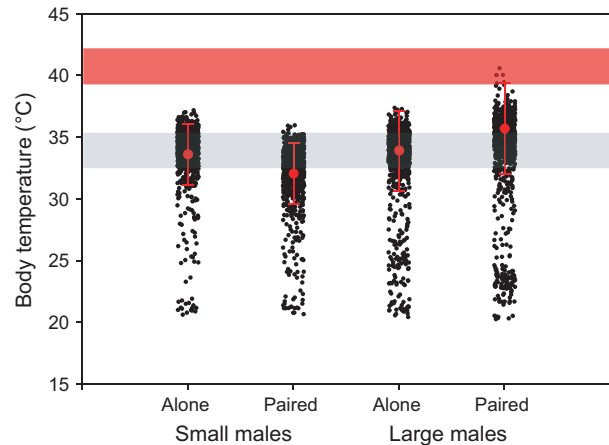


Fig. 2. When paired, body temperatures of large males and small males were higher and lower, respectively, than when alone. Black symbols represent observed body temperatures of lizards in a treatment. Red symbols denote means and standard deviations computed by multimodel averaging. The grey bar and red bar depict the central 68% of preferred body temperatures (34.1 ± 1.4 °C and 41.0 ± 1.3 °C; T. W. Rusch, unpublished data), respectively.

Both large males and small males experienced physiological responses to the presence of a conspecific male. The mean circulating concentration of corticosterone was greater after competition than after isolation for all lizards (Fig. 4), but this effect was almost twice as strong for small males than for large males (44% increase vs. 26% increase). In addition, the competition treatment altered circulating concentrations of testosterone, but in opposite directions between ranks. Large, dominant males increased their mean circulating testosterone by 26%, whereas small, subordinate males decreased their mean circulating testosterone by 26% (Fig. 5). Because circulating testosterone

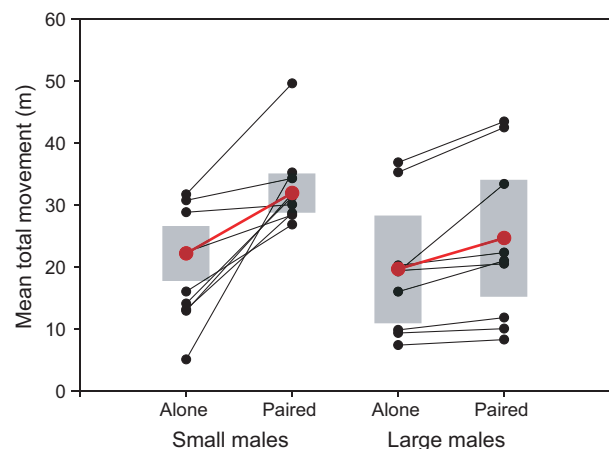


Fig. 3. When paired, both large and small males moved greater distances than when alone. Black symbols and connecting lines represent the total distance moved by each lizard in a treatment. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.

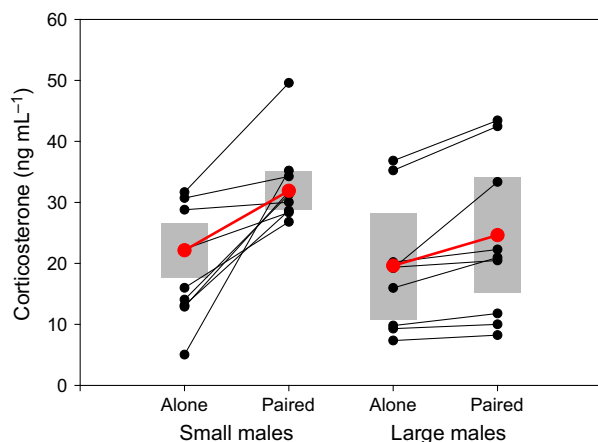


Fig. 4. When paired, both large and small males circulated higher concentrations of corticosterone than when alone. This effect was noticeably greater on small males. Black symbols and connecting lines represent the concentrations of corticosterone in lizards following each treatment. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.

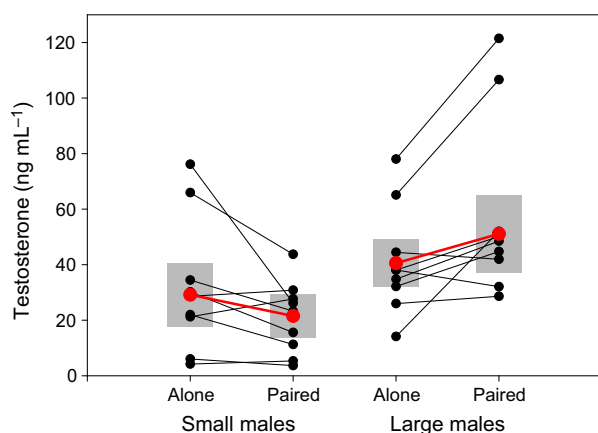


Fig. 5. When paired, large males and small males circulated higher and lower concentrations of testosterone, respectively, than when alone. Black symbols and connecting lines represent concentrations of testosterone in lizards following each treatment. Red symbols and grey bars denote means and standard deviations computed by multimodel averaging.

varied considerably among individuals, the estimated magnitudes of these effects should be interpreted cautiously.

Discussion

Consistent with our theoretical perspective, male lizards competed for limited thermal resources, altering thermoregulatory performance according to social rank. Surprisingly, however, dominant males thermoregulated less accurately and less precisely than did subordinate males during competition, presumably by overexploiting limited thermal resources. On average, the larger male in a pair remained closer to the heat source and thus exceeded preferred temperatures more frequently (lower accuracy of

thermoregulation), resulting in a broader range of body temperatures (lower precision of thermoregulation). In fact, dominant males often warmed well beyond their preferred range of temperatures (see Fig. 2), presumably while defending a heat source, sometimes approaching the mean critical thermal maximum for the species (41.0 ± 1.3 °C; T. W. Rusch, unpubl. data). Thus, larger lizards pushed themselves to their thermal limits during competition. This result accords with an unreplicated observation by Regal (1971), who noticed that a male lizard fixated on a source of heat in the presence of another male, and then basked less after the intruder was removed. More recently, Downes & Shine (1998) reported that larger geckos occupied warm burrows in the evening, forcing smaller geckos to rest under cooler rocks or remain on the surface. Similar patterns have been documented for fish when competing for access to thermal resources in heterogeneous waters (Beitinger & Magnuson 1975; Beitinger & Fitzpatrick 1979; Magnuson, Crowder & Medvick 1979). For example, small male bluegills were forced to occupy cooler or warmer water than preferred when paired with a large male (Beitinger & Magnuson 1975; Beitinger *et al.* 1975). Fish incur little risk of overheating through dominance because water warms slowly throughout the day. However, terrestrial animals such as lizards experience rapid changes in environmental temperatures throughout the day, which creates a potential physiological cost of guarding a heat source.

For dominance to be adaptive during thermoregulation, the net benefit of high temperatures experienced by a dominant male must outweigh the net benefit of low temperatures experienced by a subordinate male. Although high temperatures increase energy expenditure and water loss (Congdon, Ballinger & Nagy 1979), they might simultaneously enhance sensory and locomotor performances (Huey 1982; Angilletta, Hill & Robson 2002). Access to thermal resources could help a male attract mates, which would explain why large lizards monopolized the heat source in the presence of a smaller conspecific. By contrast, subordinate males likely saved energy but might have captured prey or evaded predators less effectively (Bennett 1980; Angilletta 2001; Angilletta, Hill & Robson 2002). However, small males likely endured a minimal loss of performance because rates of performance decline gradually when a lizard drops below its optimal temperature (Huey & Stevenson 1979; Martin & Huey 2008). And by giving up regular access to heat, a small male probably avoided aggression from a larger competitor, minimizing its loss of energy and risk of injury. Because dominant males periodically left the area under the infrared lamp, small males could attain preferred body temperatures some of the time (see Fig. 2).

Most males moved more in the presence of a competitor, likely because of aggressive interactions around the thermal resource. Although we did not quantify aggression, dominant males frequently paced and displayed to subordinates, occasionally leading to chasing and fighting.

Such behaviours are expected when a lizard defends a resource from a competitor (Greenberg & Crews 1990; Žagar *et al.* 2015). Aggressive interactions over thermal resources have been documented in crocodiles (Seebacher & Grigg 2000). Small crocodiles emerged from cool waters to bask, but were chased back into water by larger males. Consequently, small crocodiles could not warm to their preferred body temperature before fleeing, and returned to land less frequently afterwards. Presumably, these ectotherms compete for thermal resources for the same reason that lizards in our study did: by preventing a subordinate from accessing a limited thermal resource a dominant male gains a physiological advantage that enables him to monopolize food, space and mates. However, the small spatial scale of our thermal arenas might have exaggerated the impact of aggression because a subordinate male could not escape the range of the dominant male. Indeed, small lizards spent time along the edges of the arenas, attempting to escape by jumping. This behaviour surely affected the thermoregulatory performance of lizards because they could not simultaneously thermoregulate and avoid aggressive interactions. Other studies in artificial environments revealed minimal effects of competition for thermal resources, even when a subordinate could not escape the presence of a dominant. For example, *Anolis bimaculatus* outcompeted *Anolis watsi* for perch sites, forcing the *A. watsi* to occupy hotter microclimates; however, *A. watsi* did not grow slower, reproduce less or eat different prey (Rummel & Roughgarden 1985). Similarly, large skinks excluded small ones from optimal microclimates, but the smaller skinks still maintained preferred temperatures by shuttling between other microclimates (Langkilde, Lance & Shine 2005). Thus, the structure and complexity of the thermal landscape likely plays a role in thermoregulatory performance (Basson *et al.* 2016; Sears *et al.* 2016), with more complex environments potentially ameliorating the negative thermoregulatory effects of competition. Nonetheless, males of *S. jarrovi* in natural environments establish territories around the home ranges of females (Ruby 1978). Thus, territories of multiple males often overlap with that of a single female when she is receptive to mating. This spatial arrangement leads to regular aggressive interactions during the breeding season, especially in high density populations (Ball & Wingfield 1987; Marler & Moore 1988).

Competition for thermal resources should stress dominant and subordinate males disproportionately, as does competition for other resources (Greenberg & Crews 1990; Blanchard *et al.* 1995; Schuett *et al.* 1996). Compared to dominant males, subordinate males often circulate more corticosterone following aggressive interactions (Greenberg, Chen & Crews 1984; Blanchard *et al.* 1993; Sapolsky 2002). This hormonal state can be beneficial, as elevated corticosterone mobilizes energy and has positive effects on metabolism (Sapolsky, Romero & Munck 2000; Sapolsky 2002; Summers 2002). For instance, side-blotched lizards (*Uta stansburiana*) displayed greater stamina, slower

resting metabolism and faster recovery from anaerobic activity when corticosterone was elevated experimentally (Miles, Calsbeek & Sinervo 2007). If the same responses occur in *S. jarrovi*, elevated corticosterone during competition could enhance an individual's stamina for fighting or fleeing, as well as its recovery from this activity. Furthermore, a slower metabolism from elevated corticosterone would conserve energy and potentially enhance survival during the breeding season, a time when males patrol territories more frequently and forage less frequently (Simon 1975; Ruby 1978). Conversely, elevated levels of corticosterone can impose costs, such as reduced aggression or courtship. For example, Schuett *et al.* (1996) found that male copperheads (*Agkistrodon contortrix*) circulated more corticosterone after staged fights, with losers increasing more than winners. However, only losers ceased displaying to both rival males and receptive females, often retreating to a corner of the terrarium. Thus, submissive behaviours of subordinate male *S. jarrovi* possibly resulted from the circulating concentration of corticosterone reaching a threshold, which dominant males did not reach (Moore & Mason 2001). Given our experimental design, we cannot distinguish whether corticosterone levels increased because of competition for thermal resources or simply from the presence of a conspecific. Nonetheless, elevated concentrations of corticosterone could reduce the fitness of a male spiny lizard, which has a short window of opportunity for breeding each year (Ramírez-Bautista, Ramos-Flores & Sites 2002).

Multiple studies found direct effects of elevated corticosterone on thermoregulatory behaviour (Belliere & Clobert 2004; Preest & Cree 2008; Cull *et al.* 2015). For instance, geckos basked more frequently and maintained higher temperatures when their levels of corticosterone were experimentally increased (Preest & Cree 2008). Thus, the elevated concentrations of corticosterone exhibited by dominant males of *S. jarrovi* might explain why they basked more frequently during competition in our experiment. If this were true, however, subordinate males should have also maintained higher temperatures during competition. Instead, subordinates were farther from the heat lamp and had lower temperatures during competition (see Figs 1 and 2). Possibly, subordinate males tried to bask more frequently, as evidenced by their greater movement during competition, but were deterred from approaching the heat lamp by dominant males. A connection between corticosterone and thermoregulation would be important because body temperature strongly affects biochemical reactions and organismal performance.

Following competition, most of the large males circulated more testosterone, whereas most of the small males circulated less testosterone or remained at low baseline levels. This pattern seemingly contradicts a pattern reported by Moore (1987), who found no clear change in testosterone levels following a staged encounter between males. The discrepancy between these results could reflect differences in experimental design. We tested sampled the

blood of each lizard before and after 2 days of interactions, whereas Moore (1987) only sampled lizards after a brief staged encounter. In Moore's design, variation among individuals could obscure changes within individuals; changes within individual might have been detected had Moore also sampled blood before staged encounters. Moreover, the longer durations of interactions in our experiment enabled one male to establish dominance over the other, which correlates with shifts in testosterone (Greenberg & Crews 1990; Blanchard *et al.* 1993; Sapolsky 2005). Elevated testosterone causes animals to patrol, display, fight and court more than usual, in the laboratory (Zielinski & Vandenberg 1993; Klukowski, Ackerson & Nelson 2004; Mills *et al.* 2009) and the field (Marler & Moore 1988; Wingfield & Hahn 1994; John-Alder *et al.* 2009). Although these behaviours enhance access to resources, they can also deplete energy, cause injury or attract predators (Marler & Moore 1988, 1989; Wingfield *et al.* 1990). Therefore, elevated testosterone likely results in a trade-off between the short-term costs of greater energy expenditure and reduced feeding with the long-term benefit of maintaining a territory during the breeding season (Goldberg 1972; Marler & Moore 1991; Marler *et al.* 1995). Again, this trade-off makes sense in light of our results because dominant males are already large and consequently benefit more from reproduction than from growth. Conversely, subordinates would benefit from either a low baseline or temporary reduction in testosterone, which discourages costly interactions with larger males (Marler & Moore 1988, 1989; Dufty 1989; Summers 2002). If low testosterone suppresses aggression, a subordinate male would either become submissive to a dominant male (Greenberg & Crews 1990) or attempt to establish a territory elsewhere. Either behaviour would reduce the risk of injury and loss of energy associated with high testosterone levels (Marler & Moore 1989; Wingfield *et al.* 1990), ultimately helping them become dominant in future breeding seasons. Further work with a larger sample would help to better understand these trends and reduce the observed variability.

In conclusion, we have shown that lizards compete for thermal resources in the way that earlier researchers have proposed (Magnuson, Crowder & Medvick 1979). Thus, competition for a thermal resource can be viewed in the same way as competition for shelter, food or mates, which could result in physiological stress. These considerations underscore the need to better understand how abiotic and biotic factors interact to determine an organism's performance. If social hierarchies determine access to thermal resources, physiological performance will depend on the distribution of these resources in relation to the size of a territory (Huey & Slatkin 1976; Sears & Angilletta 2015; Sears *et al.* 2016). As territories of male lizards often overlap the ranges of several females (Ruby 1978; Haenel *et al.* 2003), subordinate males should have lower quality microclimates within their territories compared to dominant males and females, especially when thermal resources are

rare. Furthermore, our results are important when assessing current and future threats of climate change because climatologists predict continued warming on a global scale (Walther *et al.* 2002; Edenhofer *et al.* 2014). Such anthropogenic warming could limit the abundance of preferred microclimates (Sinervo *et al.* 2010; Sears *et al.* 2016), exacerbating competition for space. Whether behavioural thermoregulation will enable animals to compensate for a warming climate will depend not only on the presence of thermal heterogeneity (Clusella-Trullas & Chown 2011; Sears, Raskin & Angilletta 2011; Buckley, Ehrenberger & Angilletta 2015) but also on the ecological interactions within and among species.

Authors' contributions

T.R. and M.A. Jr conceived the ideas and designed methodology together. T.R. collected and analysed the data, and led the writing of the manuscript. M.A. Jr contributed significantly to writing and editing the manuscript. Both authors contributed critically to the revisions and gave final approval for publication.

Acknowledgements

We thank Andrew Cronin, Colton Smith and David Belohlavek for collecting data. We also thank Scott Davies and Pierre Device for help with running and interpreting ELISA assays. And lastly, we thank Sevilleta National Wildlife Refuge and the University of New Mexico for allowing us to conduct these experiments on their premises. All procedures were approved by the Animal Care and Use Committee of Arizona State University (Protocol 15-1392R). Collection of animals was approved by Arizona Department of Game and Fish (LIC# SP719140). There was no conflict of interest related to this study.

Data accessibility

All raw data have been archived at the Dryad Digital Repository <https://doi.org/10.5061/dryad.3bc74> (Rusch & Angilletta 2017). All R scripts will be made available upon request.

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Received 9 August 2016; accepted 7 March 2017

Handling Editor: Anthony Herrel

Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. On average, lizards preferred the same body temperatures before and after surgical implantation of temperature loggers.

Table S1. A ranking of mean distance from heat lamp models based on the likelihood of being the best model.

Table S2. A ranking of body temperature models based on the likelihood of being the best model.

Table S3. A ranking of total movement models based on the likelihood of being the best model.

Table S4. A ranking of corticosterone models based on the likelihood of being the best model.

Table S5. A ranking of testosterone models based on the likelihood of being the best model.

Table S6. Coefficients and standard errors for the model of distance from heat lamp, based on full model averaging.

Table S7. Coefficients and standard errors for the model of body temperatures, based on full model averaging.

Table S8. Coefficients and standard errors for the model of total movement, based on full model averaging.

Table S9. Coefficients and standard errors for the model of corticosterone, based on full model averaging.

Table S10. Coefficients and standard errors for the model of testosterone, based on full model averaging.

Table S11. Outline of experimental design indicating when specific events occurred.