

## Lizards perceived abiotic and biotic stressors independently when competing for shade in terrestrial mesocosms

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### ABSTRACT

Hormones such as glucocorticoids and androgens enable animals to respond adaptively to environmental stressors. For this reason, circulating glucocorticoids became a popular biomarker for estimating the quality of an environment, and circulating androgens are frequently used to indicate social dominance. Here, we show that access to thermal resources influence the hormones and behavior of male lizards (*Sceloporus jarrovi*). We exposed isolated and paired males to different thermal landscapes, ranging from one large patch of shade to sixteen smaller patches. Both the presence of a competitor and the patchiness of the thermal environment influenced hormone concentrations and movement patterns. When shade was concentrated in space, paired lizards competed more aggressively and circulated more corticosterone. Even without competitors, lizards circulated more corticosterone in landscapes with fewer patches of shade. Conversely, shifts in circulating testosterone depended only on the relative body size of a lizard; when paired, large males and small males circulated more and less testosterone, respectively. Furthermore, isolated males moved the farthest and covered the most area when shade was concentrated in a single patch, but paired males did the opposite. Because the total area of shade in each landscape was the same, these hormonal and behavioral responses of lizards reflect the ability to access shade. Thus, circulating glucocorticoids should reflect the thermal quality of an environment when researchers have controlled for other factors. Moreover, a theory of stress during thermoregulation would help ecologists anticipate physiological and behavioral responses to changing climates.

### 1. Introduction

The spatial distributions of food, mates, shelter, and even microclimates determine how animals perceive and use their environment (Duvall and Schuett, 1997; Fisher, 2000; Kronfeld-Schor and Dayan, 2003; Robinson and Holmes, 1982; Sears and Angilletta, 2015; Sears et al., 2016). When multiple resources are concentrated in space, an animal can satisfy its needs while moving very little (Dunning et al., 1992; Taylor et al., 1993). However, different resources often occur in different locations, forcing animals to spend more time and energy to satisfy their needs (Houston and McNamara, 2014; Possingham, 1989; Schoener, 1971). Furthermore, the extent to which disparate resources are close together or far apart depends on the time of day or year. For instance, preferred microclimates (e.g., shade) shift predictably as the sun moves across the sky, whereas food and mates shift in more complex ways (Ims, 1995; Lima and Bednekoff, 1999; Pyke et al., 1977). Therefore, behavioral and physiological patterns will likely reflect the spatial distributions of resources.

To further complicate matters, members of a species often compete for the same resources. In territorial species, larger, faster, or more aggressive individuals exclude others from places of limited resources (Connell, 1961; Pianka, 1981; Žagar et al., 2015). This phenomenon has been studied intensely from the perspective of competition for food, mates, and shelter (Ellis, 1995; Giraldeau and Caraco, 2000; Holbrook and Schmitt, 2002), but less is known about competition for microclimates that enhance thermoregulation (Angilletta, 2009; Downes and Shine, 1998; Rusch and Angilletta, 2017). Interactions between competitors often impose a potent stress, resulting in behavioral and physiological changes in the loser or winner (Creel, 2001; Gladue et al., 1989; Summers, 2002). Typically, both individuals experience elevated concentrations of glucocorticoids such as corticosterone, although losers often experience a greater increase than winners (Øverli et al., 2000; Summers, 2002; Rusch and Angilletta, 2017; but see Moore, 1987). However, changes in glucocorticoids following aggression vary among species and often depend on allostatic load (Creel et al., 2013; McEwen and Wingfield, 2003). These glucocorticoids mobilize energy

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needed to fight or flee (Dallman et al., 2004; Sapolsky, 2002; Wingfield et al., 1997) and may also increase food or heat seeking behaviors (Lohmus et al., 2006; Preest and Cree, 2008). However, elevated glucocorticoids deplete energy (Marra and Holberton, 1998; Sapolsky, 2002) and discourage aggression and courtship (Denardo and Licht, 1993; Moore and Miller, 1984; Morgan et al., 1999), potentially shrinking an animal's home range and access to resources (Denardo and Sinervo, 1994).

Competition also affects circulating androgens, as described by the challenge hypothesis (Hirschenhauser and Oliveira, 2006; Wingfield et al., 1990). More frequent or more intense bouts of aggression often feedback on the HPG axis to increase circulating testosterone (Johnsen and Zuk, 1995; Oyegbile and Marler, 2005; Trumble et al., 2012). Elevated testosterone usually increases aggression and activity (Denardo and Sinervo, 1994; Haenel et al., 2003; Moore, 1988; Schuett et al., 1996). This response should help an individual to defend resources, but at the expense of losing energy or risking mortality (Klukowski et al., 2004; Marler and Moore, 1988; Marler and Moore, 1989). Given this tradeoff, the loser of an aggressive encounter may decrease its circulating testosterone (or remain at a low level) while the winner increases its circulating testosterone (or remains at a high level) (Johnsen and Zuk, 1995; Oyegbile and Marler, 2005; Rusch and Angilletta, 2017; but see Moore, 1987 and Wingfield et al., 1987). In this way, only individuals that benefitted from behaving aggressively in the past are most likely to behave aggressively in the future.

The intensity of competition, and thus the magnitude of stress, should depend on the quality of the environment. When resources are rare or aggregated, competition should be intense (Dubois and Giraldeau, 2005; Dunham, 1980; Emlen and Oring, 1977; Schoener, 1983), presumably increasing both an animal's activity level and its circulating glucocorticoids (Ancona et al., 2010; Rusch and Angilletta, 2017). Based on this reasoning, we predicted that animals would compete more intensely for thermal resources when preferred microclimates are concentrated in space. If competition impedes behavioral thermoregulation, an ectothermic animal would experience suboptimal temperatures when the distribution of resources exacerbates competition (Downes and Shine, 1998; Regal, 1971; Rusch and Angilletta, 2017). By contrast, when preferred microclimates are dispersed in space, multiple animals can access these resources without moving great distances or occupying large areas (Basson et al., 2017; Sears and Angilletta, 2015; Sears et al., 2016). Therefore, we expected the intensity of competition to decline as the thermal landscape became patchier.

We tested our hypotheses (above) about competition for thermal resources by measuring the hormones and behaviors of male spiny lizards (*Sceloporus jarrovi*) in controlled thermal landscapes. We expected lizards to move greater distances and circulate more corticosterone when thermoregulating in a landscape with fewer patches of shade. Additionally, we expected smaller males to circulate more corticosterone during competition than would larger males, which can

monopolize thermal resources. We also measured aggression and testosterone to infer the effects of body size on competition for space in different thermal landscapes. Based on a previous study of *S. jarrovi* (Rusch and Angilletta, 2017), we expected competing lizards to establish a dominance hierarchy in which the large male circulates more testosterone than the small male does.

## 2. Methods

### 2.1. Collection and husbandry of animals

In August of 2012, we captured 24 adult males of *Sceloporus jarrovi* in the Chiricahua Mountains of Arizona (1500–2500 m). These lizards were transported to the Sevilleta Field Station in New Mexico. Upon arrival, each lizard was weighed (mean = 26.8 g, SD = 5.1 g) and toe-clipped for identification (Dunham et al., 1988).

Lizards were housed individually in plastic terraria (30 × 26 × 13 cm) lined with paper towels. Terraria were heated from below at one end using Flex Watt heat tape (Big Apple Pet Supply, Inc., Delray Beach, FL, USA) to create a thermal gradient, enabling lizards to attain a body temperature between 23° and 42 °C, a range that includes the preferred temperature of 34.1 ± 1.4 °C (Rusch and Angilletta, 2017); the operative environmental temperatures along this gradient were determined by hollow copper models of a lizard (Bakken and Gates, 1975). A cardboard wall between terraria prevented adjacent lizards from viewing each other. Every other day, lizards were offered food—adult crickets (*Acheta domestica*) and larval beetles (*Tenebrio morio*)—coated with a powder of vitamins and calcium (Rep-Cal, Los Gatos, CA, USA). Water was provided at the time of feeding by misting the sides of the terraria. Animals were maintained this way for two weeks before our experiment to ensure that individuals were in good condition. Because lizards ate regularly and maintained weight, none were excluded from the study.

### 2.2. Experimental design and treatments

We recorded spatial positions and hormone levels of lizards when alone and when paired in controlled thermal environments. To manipulate the thermal environment, we used outdoor thermal arenas (Fig. 1) described by Sears et al. (2016). Each of the nine arenas (20 × 20 m) consisted of sheet metal walls (0.5 mm thick, buried 20 cm below the surface, and extending 71 cm above the surface) and a canopy of shade cloth (Greenhouse Megastore, Georgetown, IL) that blocked approximately 80% of solar radiation. Shade cloth was suspended 1.2 m above the ground by steel cables (diameter = 0.4 cm) running between regularly spaced iron posts (5 cm × 5 cm × 2 m) outside the arena. The total area of shade (36% of the 400 m<sup>2</sup>) was the same in all arenas, but the distribution of shade followed one of three spatial designs (Fig. 1): 1 large patch (12 × 12 m), 4 medium patches (6 × 6 m), or 16 small patches (3 × 3 m). Given the nine arenas, we

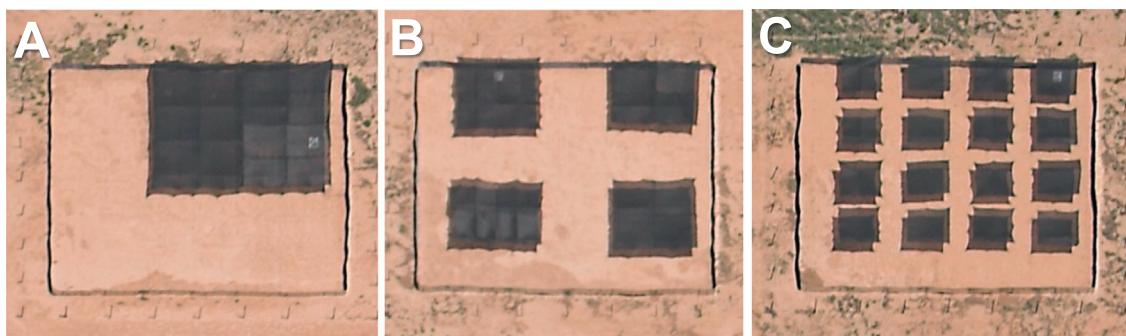


Fig. 1. Large, outdoor arenas (400 m<sup>2</sup>) were used to manipulate the thermal landscape. Each arena contained one of three levels of patchiness; (a) 1 patch, (b) 4 patches, or (c) 16 patches.

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