

# Among-Individual Variation in Desert Iguanas (*Squamata: Dipsosaurus dorsalis*): Endurance Capacity Is Positively Related to Home Range Size

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## ABSTRACT

Among species of lizards, endurance capacity measured on a motorized treadmill is positively related to daily movement distance and time spent moving, but few studies have addressed such relationships at the level of individual variation within a sex and age category in a single population. Both endurance capacity and home range size show substantial individual variation in lizards, rendering them suitable for such studies. We predicted that these traits would be positively related because endurance capacity is one of the factors that has the potential to limit home range size. We measured the endurance capacity and home range size of adult male desert iguanas (*Dipsosaurus dorsalis*). Lizards were field captured for measurements of endurance, and home range data were gathered using visual identification of previously marked individuals. Endurance was significantly repeatable between replicate trials, conducted 1–17 d apart ( $r = 0.539$  for log-transformed values,  $N = 23$ ,  $P = 0.008$ ). The log of the higher of two endurance trials was positively but not significantly related to log body mass. The log of home range area was positively but not significantly related to log body mass, the number of sightings, or the time span from first to last sighting. As predicted, log endurance was positively correlated with log home range area ( $N = 21$ ,  $r = 0.408$ , one-tailed  $P = 0.033$ ; for body-mass residual endurance values:  $r = 0.465$ , one-tailed  $P = 0.017$ ). These results suggest that endurance capacity may have a permissive effect on home range size. Alternatively, individuals with larger home ranges may experience training effects (phenotypic plasticity) that increase their endurance.

**Keywords:** behavior, fitness, home range, locomotion, performance, stamina, treadmill.

## Introduction

A key focus of evolutionary physiology is performance capacity, which can be defined as an animal's measurable ability to accomplish an ecologically relevant task when maximally motivated (Bennett and Huey 1990; Irschick and Garland 2001; Husak et al. 2009). In general, selection will act more directly on performance than on lower-level (subordinate) physiological traits, and performance capacities will frequently determine success or failure in various scenarios (see, e.g., Arnold 1983; Watkins 1996; Irschick et al. 2008; Weber 2009; Careau and Garland 2012).

The behavior of an organism may act as a “filter” between selection and performance, determining whether a given performance trait actually affects aspects of Darwinian fitness (Garland and Carter 1994; Garland and Losos 1994; McPeck et al. 1996; Orr and Garland 2017). For example, an animal may use different behavioral strategies for a given situation, such as choosing to hide or bite instead of run when it encounters a predator (e.g., Hertz et al. 1982; Herrel et al. 2007; Vanhooydonck et al. 2011). Performance capacity can also act in a permissive manner (Weber 2009); individuals with better performance can engage in fitness-beneficial behaviors with greater intensity or frequency (Briffa and Sneddon 2007). In some lizards, social dominance (which may lead to better mating opportunities) correlates positively with bite force or locomotor performance capacity (Garland et al. 1990; Robson and Miles 2000; Perry et al. 2004; Peterson and Husak 2006; Lailvaux and Irschick 2007). Furthermore, performance capacity likely enhances foraging abilities and may influence overall patterns of activity, such as microhabitat selection or home range size (Huey and Pianka 1981; Yannicelli et al. 2002; John-Alder et al. 2009).

An animal's home range is classically defined as “the area about its established home which is traversed by the animal in its normal activities of food gathering, mating, and caring for young” (Burt 1940, p. 351). Intraspecific variation in home range size may be attributed to such environmental features as food abundance, water availability, and resource density (Simon 1975; Lucherini and Lovari 1996) or to such individual characteristics as body size and sex/reproductive status (Gompper and Gittleman 1991). However, few studies have attempted to relate home range size to locomotor performance or exercise physiology within a population. Within one population of *Uta stansburiana*, adult males with orange throats had relatively higher endurance, activity, and home

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range size compared with blue- or yellow-throated male morphs, and the former also had greater control over female home ranges (Sinervo et al. 2000). In adult male collared lizards, maximal sprint speed significantly predicted territory size and number of offspring sired (Husak et al. 2006). Interspecific comparisons also suggest a positive relationship between endurance and home range size (Garland 1999; Albuquerque et al. 2015)

Lizards are common research subjects for the examination of locomotor performance and behavioral ecology. In particular, *Dipsosaurus dorsalis*, the desert iguana, has a long history of use in both field and laboratory studies, including some related to locomotion (DeWitt 1967; Berk and Heath 1975; Krekorian 1976, 1983; Gleeson et al. 1980; John-Alder and Bennett 1981); their diurnal nature and calm demeanor make them highly suitable for capture-recapture and observational field studies. We used a free-living population of desert iguanas to test the hypothesis that home range size and endurance capacity are positively related.

## Methods

Twenty-four male desert iguanas were captured by hand or by noose from August to October 2014 and from May to July 2015 from a population located near Palm Springs, California (Riverside County). Three of these individuals were measured for endurance and home range in both years, but values for their second year were excluded to avoid pseudoreplication (ID 37: endurance year 1 = 8.8 min, endurance year 2 = 13.7 min, home range year 1 = 327 m<sup>2</sup>, home range year 2 = 1,030 m<sup>2</sup>; ID 43: endurance year 1 = 15.0 min, endurance year 2 = 27.2 min, home range year 1 = 3,277 m<sup>2</sup>, home range year 2 = 2,186 m<sup>2</sup>; ID 76: endurance year 1 = 17.1 min, endurance year 2 = 14.9 min, home range year 1 = 935 m<sup>2</sup>, home range year 2 = 490 m<sup>2</sup>).

Lizards were individually marked using the colored beading system (Fisher and Muth 1989). This method was chosen over other others (e.g., PIT [passive integrated transponder] tagging, toe clipping) due to the ease of later identification without capture. Once marked, lizards spotted in the field were slowly approached to a distance of ~5–10 m and identified by bead color series, and their location was recorded and flagged. In general, lizards seemed undisturbed by approaches to this distance. The field site (22,500 m<sup>2</sup>) was gridded with a series of wooden or plastic stakes every 10 m to form a 150 × 150-m grid. Locations were catalogued by lizard ID, time/date, distance (cm) and compass direction (degrees) from stake, and GPS data.

Endurance measurements were performed in September 2014 and from May to June 2015. Desert iguanas were captured from the field site using lizard noosing techniques and transported to a laboratory at Bonnie Bell, California, for performance testing. Lizards were heated for 1 h in individual cloth bags in an insulated chamber until body temperatures reached ~40°C, which is approximately the midpoint between body temperatures as measured in the laboratory in a thermal gradient (38.5°C; DeWitt 1967) and in the field for active lizards (42.0°C; Norris 1953).

Endurance capacity was measured as time to exhaustion at 1.0 km/h using a motorized treadmill with an effective belt surface area of 2,160 cm<sup>2</sup> (108 cm × 20 cm). During trials, lizard body

temperature was maintained by means of overhead heat lamps. Previous research has found that the maximal rate of oxygen consumption ( $\dot{V}O_2$  max) occurs at a walking speed of ~1.0 km/h at 40°C in *Dipsosaurus* (John-Alder and Bennett 1981). This speed has also been used for comparative studies of a variety of other species of lizards (Garland 1994). Following standard protocols, lizards were placed on the treadmill immediately after removal from the heated chamber and encouraged to walk/run continuously, using taps and gentle pinches on the hind legs or upper portion of the tail (Garland 1984, 1999). Exhaustion was identified as the point where a lizard failed to respond or maintain belt speed and was confirmed by inverting the lizard in the operator's hand and observing a weak or absent righting response. At exhaustion, the trial was stopped, time and body mass were recorded, and the lizard was confined to a bag and returned to the field on the same day. At the end of the endurance trials, the degree of cooperativity was noted, and animals judged as uncooperative were excluded from statistical analysis. Animals judged as uncooperative included those that tried to escape from the treadmill multiple times, appeared to refuse to run, or held their breath. Lizards were recaptured at a later date within the same season, and endurance testing was repeated. One individual was excluded from subsequent analyses because of a lack of cooperation during either trial.

Home range area was defined as the area within animal locations/sightings from a given season, not including single points well outside of the rest of the home range (Burt 1943; Hayne 1949). These locations were judged to be "excursions" or potential misidentifications and were therefore removed before calculation of home range size. One previous study in a nearby area used a minimum of six sightings (Krekorian 1976). In our study, examination of home ranges for all individuals suggested that a minimum of six locations was necessary to obtain a reasonable estimate of home range area, so we included only animals with at least this number of locations, which turned out to be justified by the lack of correlation with number of sightings (see "Results and Discussion").

Compass direction was converted to a measure of angle on an X/Y plane, and then distance (measured in centimeters) was used to provide a precise point for each location via the minimum convex polygon method (Mohr 1947). This method is commonly used to calculate home range size in lizards and is appropriate for animals that occupy horizontal space (Tinkle et al. 1962; Krekorian 1976; Rose 1982; Sinervo et al. 2000; Perry and Garland 2002). The minimum convex polygon method also preserves location points that would otherwise be lost in some other types of home range sampling (de Solla et al. 1999) and so is appropriate for sampling of short time periods and/or limited quantity. Ranges 9 (Anatrack) was used to calculate the home range area. Statistical analysis was conducted with IBM SPSS statistical software.

## Results and Discussion

Body mass was highly repeatable between trials ( $N = 22$  [two individuals were only weighed once],  $r = 0.967$ ,  $P < 0.0001$ ).

Mean body mass ( $N = 24$ ) ranged from 48.4 to 92.0 g, with a mean of 70.0 (SD = 13.0). The first and second values for endurance (log transformed) were significantly positively correlated ( $N = 23$ ,  $r = 0.539$ ,  $P = 0.008$ ; fig. 1), a level of repeatability that is typical for locomotor performance measurements in squamates (Garland and Else 1987; van Berkum et al. 1989; Garland et al. 1990; Austin and Shaffer 1992; Robson and Miles 2000; Peterson and Husak 2006). On average, lizards had higher endurance on the second trial (paired  $t = 3.17$ ,  $P = 0.004$ ). The higher of two measurements of individual endurance ( $N = 23$ ) ranged from 5.1 to 51.5 min, with a mean 21.4 (SD = 14.5), and was positively skewed. Both body mass and endurance values are comparable to those previously reported for adult desert iguanas (John-Alder and Bennett 1981; John-Alder 1984; Garland 1994).

With body mass as a covariate, we found no significant difference in log endurance capacity by year ( $F = 1.303$ ,  $P = 0.266$ ), so we combined the two years for analysis. Log-transformed endurance was positively but not significantly related to log body mass ( $N = 23$ ,  $r^2 = 0.087$ ,  $P = 0.171$ ; fig. 2). A positive relationship has been reported in previous studies, both within (Garland and Else 1987; van Berkum et al. 1989; Garland 1994) and among (Garland 1994) species of lizards, and generally in vertebrates (Bennett 1991). Given this expected relationship, we used both log endurance and residual log endurance as potential predictors of home range size. Whether absolute or residual endurance would be more ecologically relevant is unclear (e.g., see Van Damme and Van Dooren 1999).

Mean home range size was 1,142 m<sup>2</sup>, although this value varied greatly among individuals ( $N = 22$ , minimum = 143,

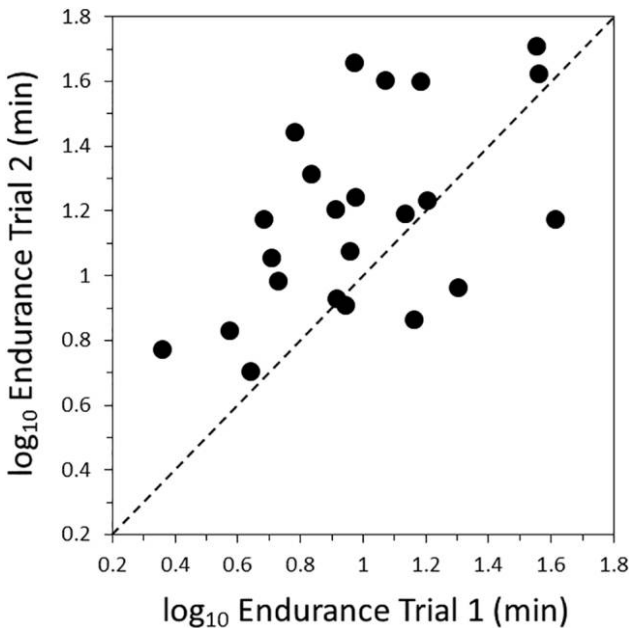


Figure 1. Repeatability of endurance between trials ( $N = 23$ ,  $r = 0.539$ ,  $P = 0.008$ ). The dashed line indicates equal endurance between trials; on average, animals had higher endurance at the second trial (paired  $t = 3.17$ ,  $P = 0.004$ ).

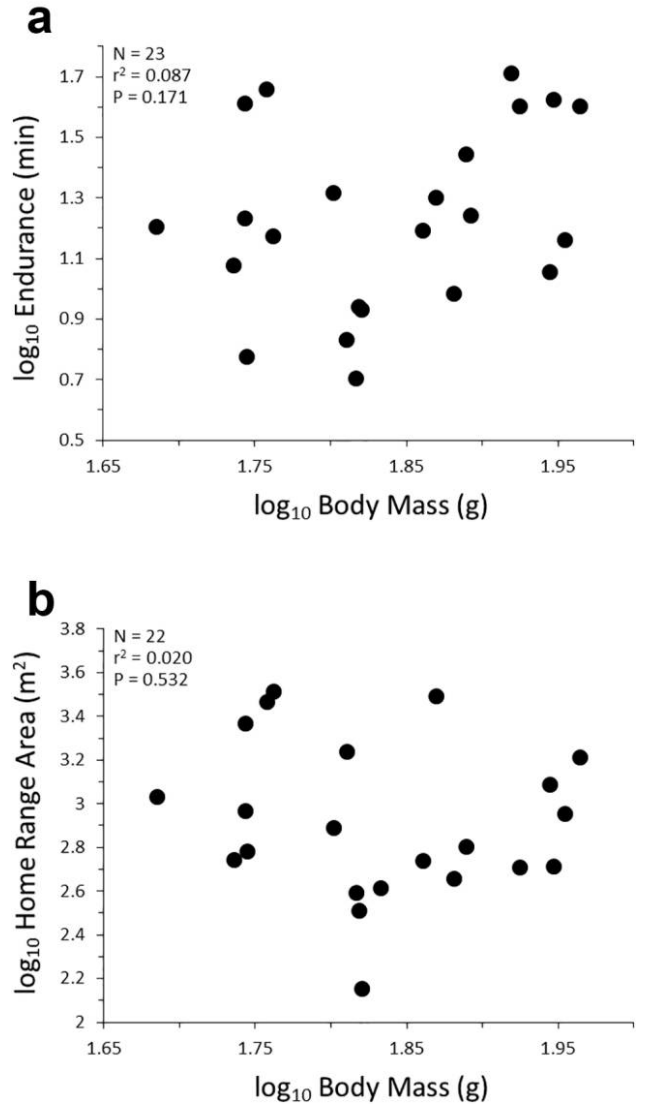


Figure 2. Neither log-transformed values of the higher of two endurance measurements (a) nor log-transformed home range area (b) was significantly related to log-transformed body mass.

maximum = 3,277, SD = 959). Home range size was not significantly different between the two years ( $P = 0.343$  for raw values and  $P = 0.520$  for log values). Although some lizards show changes in home range size between seasons due to variations in territoriality, desert iguanas are not highly territorial and show a great deal of home range overlap (our observations as well as Krekorian 1976). Krekorian found an average home range size of 552 m<sup>2</sup>, but this value is not comparable to ours because it was conducted over a shorter time interval (time between first and last sighting) and used a different method of area calculation (Jennrich and Turner 1969) that may not be suitable for terrestrial lizards (Rose 1982). In our study, log home range size was not significantly correlated with log body mass ( $N = 22$ ,  $r = -0.141$ ,  $P = 0.532$ ), number of sightings (mean = 15.8, range = 6–35,  $r = 0.291$ ,  $P = 0.188$ ; fig. 3), or time span (mean = 80 d, range = 41–132 d,  $r = 0.287$ ,  $P = 0.195$ ). Consistent with our

a priori hypothesis, log home range size was significantly positively related to both log endurance and residual log endurance (fig. 4).

Our prediction of a positive relationship between endurance capacity and home range size was supported by the data for among-individual variation in adult male desert iguanas. Consistent with our result and the study by Sinervo et al. (2000) mentioned in the introduction, a previous field study of *Lacerta vivipara* found a positive correlation between endurance capacity and activity level (as indicated by recapture probability; Clobert et al. 2000). The causality of these sorts of relationships is unclear. Inherent endurance capacity might play a permissive role for home range size or activity levels. On the other hand, an individual that grows up in a habitat with scarce resources and hence has to move relatively long distances to find food, shelter, or mates might “self-train” and develop a higher endurance capacity as it moves around on a daily/weekly/monthly basis. However, laboratory training studies have produced varied results for lizards, and no such studies have been conducted with desert iguanas (Gleeson 1979; Garland and Else 1987; O’Connor et al. 2011; Husak et al. 2015).

Whatever the cause of a positive association between endurance capacity and home range size, a larger home range may be advantageous for desert iguanas for a number of reasons, including simply containing more resources. A larger home range is likely to encompass greater resource heterogeneity, which increases the potential number of food items for an herbivore (Norris 1953), especially in an arid climate (Saïd et al. 2005). A larger home range typically equals more access to potential mates because, in male lizards, a larger home range size is correlated with higher overlap of female home ranges (Simon 1975; Schoener and Schoener 1982; Salvador et al. 1995; Perry and Garland 2002; Haenel et al. 2003). In desert iguanas, females and males maintain overlapping home ranges for the majority of the active season (Krekorian 1976, 1983), so larger male home ranges likely do lead to more

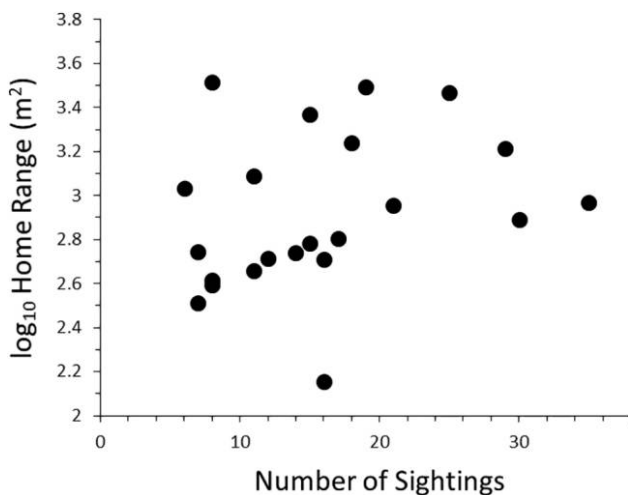


Figure 3. Lack of relation between home range area and number of sightings ( $N = 22$ ,  $r = 0.291$ ,  $P = 0.188$ ).

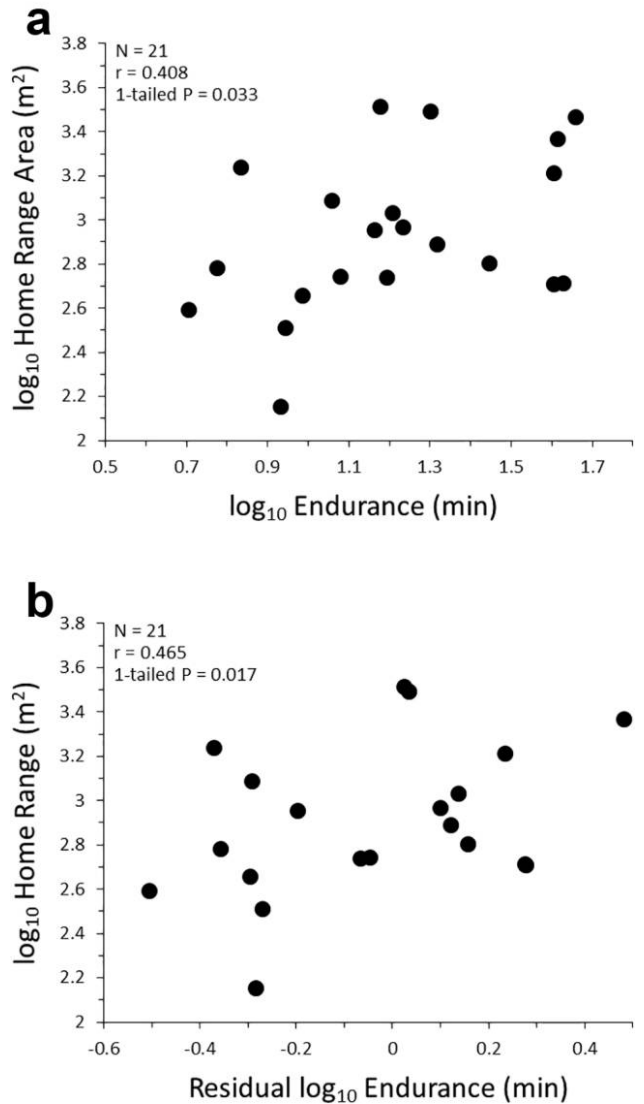


Figure 4. Log-transformed values for individual home range size were significantly positively correlated with log-transformed endurance (a) and endurance residuals (b; see text).

potential mates and hence higher reproductive success, a prediction that we will test in future studies.

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