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Individual Variation in Corticosterone, Locomotor Endurance, and Home Range Size in the Lizard *Dipsosaurus dorsalis*

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolution, Ecology, and Organismal Biology

by

Jennifer Marie Singleton

December 2018

Dissertation Committee:
    Dr. Theodore Garland, Jr., Chairperson
    Dr. Wendy Saltzman
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Jennifer Marie Singleton
December 2018

The Dissertation of Jennifer Marie Singleton is approved:

Committee Chairperson

University of California, Riverside

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Chapter 1 of this dissertation is a previously published work of which I was a major contributor. This chapter is available in volume 91 (2018) Physiological and Biochemical Zoology, pages 725-730.

This dissertation is dedicated to

Tommy Mooney

And

Jack Edward Mooney

ABSTRACT OF THE DISSERTATION

Individual Variation in Corticosterone, Locomotior Endurance, and Home Range Size in the Lizard *Dipsosaurus dorsalis*

by

Jennifer Marie Singleton

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, December 2018
Dr. Theodore Garland, Jr., Chairperson

The morphology-performance-behavior-fitness paradigm provides an integrative framework within which to examine the functional and adaptive relevance of traits at different levels of biological organization. Variation in morphological or other subordinate traits result in differences in organismal performance abilities. In turn, performance capacities constrain behavioral options, thus influencing the success of an individual during tasks that impact Darwinian fitness. These connections are frequently investigated in the context of locomotion, as locomotor abilities and behaviors are frequent determining factors in survival and/or reproductive success.

Chapter One examines the relationship between endurance capacity and home range size in free-living adult male desert iguanas over two seasons. Individual endurance capacity positively predicted the home range size of adult male desert iguanas.

Chapter Two describes the results of corticosterone manipulation via hormone implants with adult male desert iguanas in a laboratory setting. Neither circulating corticosterone levels nor treadmill endurance differed significantly between treatment groups.

Chapter Three examines the home range of free-living desert iguanas in relation to endurance capacity, circulating corticosterone levels, and body mass, as well as ecological variables quantified for each home range. Corticosterone, endurance capacity, and home range size were not significantly related. Home range size was significantly negatively related to shade plant density.

Chapter Four describes the results of corticosterone manipulation via hormone implants (modified from those used in Chapter 2) with free-living adult male desert iguanas and relationships with endurance capacity and home range size. Desert iguanas that received corticosterone implants had significantly larger home ranges, but not higher endurance, compared with those that received saline implants. Home range size was again significantly negatively related to shade plant density. No relations between corticosterone, endurance capacity, or home range size were significant.

Chapter Five presents an estimate of Darwinian fitness using number of offspring sired by free-living adult male desert iguanas studied in two different years. Offspring number was calculated using DNA microsatellite analysis of paternity. In one year, home range size was a significant negative predictor of number of offspring when included in a multiple regression with corticosterone and endurance capacity. This study was limited due to small sample sizes.

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INTRODUCTION

Evolutionary physiology is a relatively new field (Garland, Jr. and Carter 1994; Feder et al. 2000). Early physiological studies focused on descriptions of functional biology, while evolutionary biologists were lacking a strategy to quantify the fitness relevance of physical traits (Kingsolver and Huey 2003). In 1983, Steven J. Arnold presented the disparities between these two study areas and proposed a statistical framework for future research programs. The connection between individual variation in a low-level (subordinate) trait and Darwinian fitness can be examined within the morphology-performance-fitness paradigm (Arnold 1983). "Morphology" in this context represents any low-level morphological, physiological, or biochemical trait. The adaptive significance of a subordinate trait can be examined as a continuum between the trait itself, the physical relevance of the trait for the organism, and how the effect relates to the Darwinian fitness of that individual as compared with others in a population. The relevant physical effects of a character within this framework are measured in evaluations of performance, defined succinctly as the ability to perform a biologically relevant task (Arnold 1983; Irschick and Garland, Jr. 2001; Careau and Garland, Jr. 2012). In later years, a fourth level of examination was added: that of behavior (Garland, Jr. and Carter 1994; Garland, Jr. and Losos 1994). Behavior determines how the performance of an individual relates to components of Darwinian fitness, such as survival and reproductive success. For example, although an individual may have a high maximum sprint running speed, it does not necessarily follow that it will use its maximum speed as a primary defense against predators (Irschick et al. 2005; Husak 2006a); the individual may be more likely to use crypsis or aggression depending on the context (Crowley and Pietruszka 1983). Performance itself is not necessarily a target of selection (Irschick et al. 2008). In addition, the performance abilities of an individual may influence behaviors on a larger scope, such as habitat choice, forage selection, or home range size. Behavioral studies can be used to further understand the connection between performance traits and Darwinian fitness.

Hormones and Behavior

Hormonal control of behavior has been heavily investigated in endothermic vertebrates. For example, melatonin levels of hedgehogs control the seasonal testes recrudescence; testosterone production from the testes promotes reproductive behavior (Fowler 1988). The “rattle” in songs of male Barn Swallows is positively correlated with circulating androgen levels (Galeotti et al. 1997). Human male college students who are administered intranasal oxytocin are significantly more likely to trust an “investor” in a social trust experiment (Kosfeld et al. 2005).

Individual variation in behavior is often the most direct focus of natural and sexual selection (Garland, Jr. and Kelly 2008, and references therein). A significant portion of variation in behavior may be the result of connections between behavior and multiple elements of the endocrine system; therefore, variation in hormone production and regulation may be one way that behavior is molded across generations in response to selection (Adkins-Regan 2012; Goodson et al. 2012; Garland, Jr. et al. 2016). The endocrine patterns of different species, populations, and individuals correlate with behavioral differences and as such should be investigated when examining individual and evolutionary variation (Rhen and Crews 2002; Amdam et al. 2007; Williams 2008; Careau and Garland, Jr. 2012).

For many years, endocrinology was primarily a laboratory science. Complex assay procedures, surgical hormone control, and technological limitations rarely made field work feasible. With the invention of competitive-binding assays, biologists were able to compare the endocrine functions of individuals with adequate accuracy to test for correlations with other traits (Nelson 2011). However, until field endocrinology developed as an area of research, the ability to relate these results to ecological or behavioral data was lacking (Walker et al. 2005; Fusani 2008). Production and release of hormones is extremely contingent on circumstances; variation in weather, season, recent social interactions, etc. will all contribute to variation in hormone levels (Greenberg and Crews 1990; Tokarz et al. 1998; Moore et al. 2002; Carsia and John-Alder 2003). Therefore, behavioral endocrinology studies should be conducted in the field to the greatest extent possible, and comparisons among species and populations will be fraught with inaccuracy due to the difficulty of a raising animals in a "common garden" (Garland, Jr. and Adolph 1991). In addition, individual variation is the raw material on which natural and sexual selection act (e.g., see review in Careau and Garland, Jr. 2012), and variation in basal hormone levels, even within normal physiological ranges, can have direct effects on individual fitness (Zera et al. 2007). Field examinations of individual variation in endocrine production will contribute important evidence in discussion of the hormonal regulation of behavior (Williams 2008).

Studies of individual variation act as an invaluable portion of the evaluation of hormonal impacts on behavior (Williams 2008). However, to draw causational relationships, experimental manipulation of hormone levels is the preferred method for whole-organism study. A great number of studies have used manipulative approaches to the study of behavioral endocrinology; the introduction of cultivated and synthetic hormones allowed for greater precision in evaluating hormonal effects, and the use of hormonal implants allowed for long-term release of hormones to more closely mimic basal hormone production. Hormonal implants have been used in endocrine studies within a variety of taxa, including lizards (Wingfield and Silverin 1986; Marler and Moore 1988; Astheimer et al. 1992; DeNardo and Licht 1993; DeNardo and Sinervo 1994a; Morici et al. 1997; Bush et al. 2003; Miles et al. 2007; John-Alder et al. 2009; O'Connor et al. 2011)

One frequently studied and easily manipulated hormone in lizards is testosterone. Studies examining testosterone activity in lizards have primarily focused on aggression and reproductive function. Testosterone is an androgen product of the Hypothalamic-Pituitary-Gonadal Axis, produced in the testes in response to gonadotropin signalling. It influences many aspects of behavior and physiology, including skeletal muscle growth (Bhasin et al. 2009; Huyghe et al. 2010), immune response (Marler and Moore 1988; Oppliger et al. 2004), and sexually dimorphic growth (Cox and John-Alder 2005; Cox et al. 2009). Testosterone also is implicated in many behavioral characters of both male and female animals, most frequently with aggressive behavior (Wingfield et al. 1987), and squamates are no exception (Moore and Marler 1987; Marler and Moore 1988; Greenberg and Crews 1990; While et al. 2010).

A number of lizard studies have used hormone implants to further explore these relationships. Restoration of testosterone levels in castrated individuals via implants restores sexually dimorphic growth patterns in males (Cox et al. 2005). The aggressive displays of males decrease and increase concurrently with circulating testosterone (Crews et al. 1978; Tokarz et al. 2002; Weiss and Moore 2004). In addition, experimentally elevated levels of testosterone increase endurance capacity (John-Alder et al. 1996, 2009; Klukowski et al. 1998; Sinervo et al. 2000), home range size (DeNardo and Sinervo 1994b; Sinervo et al. 2000), and position in a dominance hierarchy (Fox et al. 1981).

Corticosterone, a glucocorticoid product of the hypothalamic-pituitary-adrenal axis, is another frequently manipulated hormone. It is produced in the adrenal cortex in response to adrenocorticotropic hormone from the anterior pituitary. Corticosterone and other glucocorticoids are typically investigated as stress hormones. Although cortisol is the primary stress-related hormone in human beings, corticosterone is the common stress hormone in mice and most rodents, birds, and squamates (Nelson 2011).

Increased basal plasma corticosterone levels may be elicited by "constant" levels of stress (Tokarz et al. 1998); however, basal corticosterone also naturally fluctuates in circadian and seasonal cycles for many animals (Beletsky et al. 1992; Carsia and John-Alder 2003; Malisch et al. 2008). Corticosterone levels influence a great number of physiological processes, including bone growth, weight gain, and glucose availability (Li et al. 1996; Jessop et al. 2003; Singleton and Garland, Jr. 2018). In addition, variation in corticosterone levels is implicated in a wide variety of behaviors, including wheel running (house mice: Singleton and Garland, Jr. 2018), exploration (Great Tit nestlings; Martins et al. 2007), food caching (Mountain Chickadees; Pravosudov 2003), and dispersal (Screech Owls; Belthoff and Dufty 1998).

Corticosterone has been a frequent component of hormonal manipulations in many species, including lizards. Induced increases in corticosterone levels in *Uta stansburiana* are correlated with reduced aggressive behavior 5 days after manipulation (DeNardo and Licht 1993). Administration of corticosterone-synthesis blockers reduces the ability of *Anolis* to habituate to an aggressive video (Yang and Wilczynski 2003), while corticosterone implants in the same species result in decreased aggressive displays (Tokarz 1987). Studies using hormone implants have found that high levels of corticosterone act as a testosterone antagonist in *Uta stansburiana* (Tokarz 1987; DeNardo and Sinervo 1994b; Husak et al. 2007) and supplemental testosterone can negatively impact corticosterone levels (O'Connor et al. 2011).

Manipulations of corticosterone have also been found to impact characters related to locomotor performance and behavior. Four days of corticosterone implants cause muscle wastage and decreased body mass in tree sparrows (Astheimer et al. 2000). Adrenalectomized rats subsequently administered corticosterone resumed voluntary wheel running levels and increased running with increased corticosterone (Lin et al. 1988, 1989, p. 19). However, house mice that received supplemental corticosterone showed reduced wheel running and activity in home cages (Singleton and Garland, Jr. 2018). Corticosterone implants caused an increase in endurance capacity over a 4 week period in *Uta stansburiana* (Miles et al. 2007). However, long-term increases in basal corticosterone via implants in *Uta stansburiana* caused a decrease in activity levels and home range size (DeNardo and Sinervo 1994a).

Locomotor Performance

The ability of an individual to accomplish a biologically relevant task when maximally motivated is termed the "maximal performance capacity"(Arnold 1983; Lailvaux and Husak 2014; Storz et al. 2015); when evaluating the locomotor behavior of an individual in terms of functionality, the term "performance" is appropriate. Documentation of individual variation in locomotor abilities would suggest other variation at many physiological levels, because locomotor abilities occur as a "middle step" between proximate physiological traits (such as muscle fiber type) and behavioral-scale traits, such as predator evasion (Careau and Garland, Jr. 2012). In lizards, individual variation in such lower-level physiological traits as enzyme activity and relative organ mass predict variation in endurance capacity (Garland, Jr. 1984; John-Alder 1984; Garland, Jr. and Else 1987). In addition, manipulation experiments have frequently found an increase in endurance and bite force after an artificial increase in testosterone *(Uta stansburiana* and two *Sceloporus* sp.; Klukowski et al. 1998; Sinervo et al. 2000; John-Alder et al. 2009).

Locomotor performance will likely impact behavioral traits of both species and individuals. Foraging style (active searching vs. sit-and-wait) is correlated with expected performance variation between closely-related species of lacertid lizards: endurance is higher in active searchers, whereas burst speed is higher in sit-and wait (quick seizure) species (Huey et al. 1984). With phylogenetic comparison among 15 lizard species, lab measurements of endurance are positively correlated with measurements of field movements (% time moving, daily movement distance; Garland, Jr. 1999). Endurance capacity is positively correlated with natural activity levels in *Lacerta vivipara* (Clobert et al. 2000). Temperature-dependent locomotor performance variation may also determine defense tactics; Leopard lizards will run or fight depending on (temperature-dependent) locomotor ability (Crowley and Pietruszka 1983). In studies of performance relative to Darwinian fitness, several have found clear connections between high levels of ability and reproductive success or survival. The sprint speed of adult Collared Lizards predicts both territory size and number of offspring (Husak 2006a; Peterson and Husak 2006), whereas sprint speed of hatchlings predicted survivorship over 1 year (Husak 2006b). In addition, the endurance capacity of *Anolis cristatellus* predicts success in dyadic dominance "contests" (Perry et al. 2004), which presumably would lead to greater reproductive success, and winners of similar contests exhibited significantly higher sprint speeds in *Sceloporus occidentalis* (Garland, Jr. et al. 1990).

Home Range

A home range was originally defined as the area about its established home that is traversed by an animal in its normal activities of food gathering, mating, and caring for young (Burt 1940). Further examination of home range has moved to exclude areas encompassed during migrations or dispersal. As the home range is the site of so many activities intrinsically tied to components of Darwinian fitness, characteristics of an individual's home range can and should be examined in behavioral ecology, physiological ecology, and evolutionary physiology. One simple characteristic, home range size, has been studied in both within and among species. Among species, home range size is correlated with body size, diet, food and water availability, and mating system (Milton and May 1976; Gittleman and Harvey 1982; Gaulin and FitzGerald 1988; Fisher and Owens 2000). Among species of lizards, home range size is positively correlated with body size (in males more than females) and carnivorous lizards typically have larger home ranges than herbivores (Perry and Garland, Jr. 2002). Though studies examining home range variation among individuals within species are less common, the available studies show patterns similar to those observed among species. In general, individual home range size is directly affected by the availability of resources (Ruby and Dunham 1987); higher resource availability is typically associated with smaller home range size. Home range size of individuals may also be affected by body size, individual diet, habitat type, and sex/reproductive status (Ferner 1974; Gompper and Gittleman 1991; Mikesic and Drickamer 1992; Lucherini and Lovari 1996; Tufto et al. 1996; O'Brien and Kinnaird 1997; Haenel et al. 2003; Schradin et al. 2010). A large home range can be beneficial by including a large number of foraging sites or other resources (Krekorian 1976; Lucherini and Lovari 1996) and/or a large amount of overlap with potential mates (Haenel et al. 2003). However, an individual must have the energy and physical ability (e.g., endurance capacity) to traverse the home range area. In addition, population density will typically impact home range size within a population, especially if some amount of resource defense is occurring. A defended area is referred to as a territory; more specifically, territoriality is the exclusion of a specific class from part or all of an individual's home range (Maher and Lott 1995). A territory is contained within a home range, but must be defended in some manner to qualify as such.

The most frequently described characteristics that determine home range size are environmental factors; however, a number of physiological and locomotor traits of individuals are correlated with variation in home range size. Morphs of *Uta stansburiana* with higher circulating testosterone maintain larger home ranges than those with lower testosterone levels (Sinervo et al. 2000). With hormone implants, it was found that administration of testosterone causes increases in activity and home range size, while corticosterone implants result in decreased home range size (DeNardo and Sinervo 1994b, 1994a). *Uta stansburiana* which hold larger territories also have larger relative dorsal cortical volumes of the telencephalon in comparison with small and non-territory holders (LaDage et al. 2009).

Among species of lizards, endurance is correlated with time spent moving and daily movement distance (Garland, Jr. 1999), likely factors in home range size. A larger home range size also increases the chance of encounters with predators, and it is feasible that higher sprint speed will facilitate predator escape. Finally, a larger home range will typically increase overlap with individuals of the opposite sex and thus may increase reproductive success.

Desert Iguanas

The subfamily Iguaninae is a clade characterized by herbivorous or mostly herbivorous lizards in the Neotropical and Nearctic regions who exhibit varying levels of social behavior (Burghardt 2004). Within this clade, the Desert Iguana (*Dipsosaurus dorsalis*) is a smaller member found in the American Southwest and Baja California. Desert iguanas in the northern majority of their range are typically found in low-lying areas associated with sandy hillocks and creosote bushes, though in southern portions of their range they can be found in semi-arid tropical scrubland (Norris 1953). Desert iguanas are mainly herbivorous, feeding on the flowers and leaves of desert perennials and annuals (in Coachella

Valley: *Larrea divaricata*, *Coldenia* sp., *Psorothamnus emoryi*; Norris 1953). They will also consume feces of rabbits and their own species, and capture insects, though these items make up a small portion of their diet (Norris 1953; Minnich and Shoemaker 1970).

In previous studies, desert iguanas have been hypothesized to centralize their home ranges around creosote bushes (*Larrea divaricata*; Norris 1953; Krekorian 1984), which provide a springtime food source in the form of flowers, and are used season-long as shade and a refuge from predators. However, it is likely that other factors within a habitat may affect a desert iguana's home range as much or more than the presence of creosote. Desert iguanas in Coachella Valley will frequently use smaller plants as shade and retreat, such as the thorny *Psorothamnus*; these plants provide sufficient shade and are less likely to harbor predators, such as Coachwhips (*Masticophus flagellus*; personal observation). Desert iguanas are also expected to select home ranges including as wide a range of plant species as possible, based on the fact that desert plant species are rarely blooming at the same time and a wider variety would provide a more consistent food source (Alberts 1993). Creosote bushes and other desert plants are also frequently used as a shaded retreat from sun and the heated sand. Desert iguanas use burrows for shelter overnight, during the highest heat of the day, and during hibernation (October – March) and egg-laying (June-July; Norris 1953)(June-July; Norris 1953; Muth 1977). These burrows may be self-constructed or co-opted from other lizards or animals, and may be shared with other iguanas (Krekorian 1976, 1984).

Desert iguanas have frequently been used as a model organism for the study of thermal ecology and physiology in reptiles. They have a high thermal body preference for any vertebrate, averaging 38.5 °Celsius when active in the field, and are active at temperatures approaching 44 °C (Norris 1953). Previous studies have found that they have a 50% preferred temperature range in a laboratory thermal gradient of 37-39.5 °C, and they regulate their body temperature within this range using a variety of thermoregulatory behaviors in both the lab and the field (Norris 1953; DeWitt 1967; DeWitt et al. 1967). Desert iguanas were also one of the first ectotherms found to behaviorally increase their body temperature in response to infection, functionally inducing a "fever" (Vaughn et al. 1974). With experimental manipulation of body temperatures after bacterial infection, it was found that increased body temperature significantly improved survivorship of the host iguana (Bernheim and Kluger 1976).

Field research on social behavior of desert iguanas has been successful, though the scope of topics investigated has previously been limited. Their population structure is divided by size and sex into 5 classes (Mayhew 1971). Full-size adult males are >114 mm in snout-vent length (SVL), while females are considered full size at 110 mm SVL. Iguanas under these sizes are sexually immature juveniles, but sex identification continues to be mostly possible until under 60 mm, below which they are considered hatchlings or yearlings. Early behavioral research included descriptions of the typical behavior observed in courtship and aggressive displays (Carpenter 1961). Desert iguanas display aggressive behaviors typical of other iguanids, such as "push-ups" and dorsal arching (Martins and Lamont 1998; Lacy and Martins 2003), which make identification of aggressive interactions relatively simple. Male desert iguanas also occasionally engage in combat via tail-whipping and lateral biting (Norris 1953; Carpenter 1961). Home ranges are occasionally defended in this way, but researchers in the Coachella Valley, Riverside Co. California have found a high degree of home range overlap in areas of high population density (Krekorian 1976; Glinski and Krekorian 1985). The home range overlap of *Dipsosaurus dorsalis* is not limited to the mating period, but has been observed over the entire activity season. Extensive home range overlap implies a lack of home range defense (territoriality; Maher and Lott 1995). Desert iguanas are assumed polygynous, like many members of Iguanidae; however, mating systems vary within Iguanidae and between populations (Brattstrom 1974; Carothers 1984).

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Table 0.1. Sample sizes for analysis within variables, seasons, years, and chapters.

Season	Variable	Sample Size	Ch. 1	Ch. 2	Ch. 3	Ch. 4	Ch. 5
Non-Mating 2014	endurance capacity home range	11 25	X X				
Mating 2015	corticosterone	15			X		X
	endurance capacity	19	X		X		X
	home range size	21	X		X		X
	food plant density	21			X		X
	shade plant density	21			X		X
	soil compactibility	21			X		X
	soil density	21			X		X
	DNA samples	47					X
Non-Mating 2015	corticosterone	7			X		
	endurance capacity	8			X		
	home range size	6			X		
	food plant density	6			X		
	shade plant density	6			X		
	soil compactibility	6			X		
	soil density	6			X		
	hatchling DNA samples	31					X
Mating 2016	corticosterone	9			X		
	endurance capacity	16			X		
	home range size	10			X		
	food plant density	10			X		
	shade plant density	10			X		
	soil compactibility	10			X		
	soil density	10			X		
Non-mating 2016	corticosterone	7			X		
	endurance capacity	6			X		
	home range size	3			X		
	food plant density	3			X		
	shade plant density	3			X		
	soil compactibility	3			X		
	soil density	3			X		
LAB 2016	corticosterone	16		X			
	endurance capacity	16		X			
Mating 2017	hormone implants	42				X	X

	corticosterone	26				X	X
	maximum endurance capacity	28				X	X
	home range size	22				X	X
	food plant density	22				X	X
	shade plant density	22				X	X
	soil compactibility	22				X	X
	DNA samples	39					X
Non-mating 2017	hatchling DNA samples	23					X

CHAPTER 1

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 as measured on a motorized treadmill is positively related to daily movement distance and time spent moving. 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 may play a permissive role in establishment of a home range of a given 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; home range data were gathered using visual identification of previously marked individuals. Endurance was significantly repeatable between replicate trials, conducted 1-17 days apart ($r = 0.539$ for log-transformed values, $N = 23$, $P = 0.008$). The higher of two endurance trials was positively but not significantly related to log body mass. The log of home range area was not significantly related to 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 ($N = 21$, $r = 0.408$; 1-tailed $P = 0.033$: for body-mass residual endurance values, $r = 0.465$, 1-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.

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; McPeek 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 or resource density (Simon 1975; Lucherini and Lovari 1996) or individual characteristics such as body size or 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 range size as 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.

Materials & Methods

Twenty-four male desert iguanas were captured by hand or by noose in August-October 2014 and May-July 2015 from a population located near Palm Springs, CA (Riverside Co.). 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^2, home range year 2 = 1,030 m^2; ID 43, endurance year 1 = 15.0 min, endurance year 2 = 27.2 min, home range year 1 = 3,277 m^2, home range year 2 = 2,186 m^2; ID 76, endurance year 1 = 17.1 min, endurance year 2 = 14.9 min, home range year 1 = 935 m^2, home range year 2 = 490 m^2).

Lizards were individually marked using the colored beading system (Fisher and Muth 1989). This method was chosen over other others (e.g., PIT-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 meters (m), identified by bead color series, and their location recorded and flagged. In general, lizards seemed undisturbed by approaches to this distance. The field site (22,500 m^2) was gridded with a series of wooden or plastic stakes every 10 meters to form a 150 x 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 May-June 2015. Desert iguanas were captured from the field site using lizard noosing techniques and transported to a laboratory at Bonnie Bell, CA for performance testing. Lizards were heated one hour in individual cloth bags in an insulated chamber until body temperatures reached ~40° Celsius, which is approximately the midpoint between body temperatures as measured in the laboratory in a thermal gradient (38.5°; DeWitt 1967) and in the field for active lizards (42.0°; Norris 1953).

Endurance capacity was measured as time to exhaustion at 1.0 km/hr using a motorized treadmill with an effective belt surface area of 2,160 cm^2 (108 cm by 20 cm). During trials, lizard body temperature was maintained by overhead heat lamps. Previous research has found that the maximal rate of oxygen consumption ($V0_2max$) occurs at a walking speed of ~1.0 km/hr at 40° 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 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 recorded, and the lizard was confined to a bag and returned to the field on the same day. At the end of endurance trials, 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 due to 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 only included animals with at least this number of locations, which turned out to be justified by a lack of correlation with number of sightings (see Results & Discussion).

Compass direction was converted to a measure of angle on an X/Y plane, then distance (measured in cm) 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 Ltd.) 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 grams, with a mean of 70.0 (S.D. = 13.0). The first and second values for endurance (log transformed) were significantly positively correlated (Fig. 1.1: $N = 23$, $r = 0.539$, $P = 0.008$), 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 minutes, with a mean 21.4 (S.D. = 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 (Fig. 1.2: $N = 23$, $r^2 = 0.087$, $P = 0.171$). A positive relationship has been reported in previous studies, both within (Garland and Else 1987; van Berkum et al. 1989; Garland 1994) and among species of lizards (Garland 1994), 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^2, though this value varied greatly among individuals (N = 22, min = 143, max = 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). Though 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^2, 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. 1.3) or time span (mean = 80 days, range = 41-132 days, 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. 1.4).

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

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Figure Legends

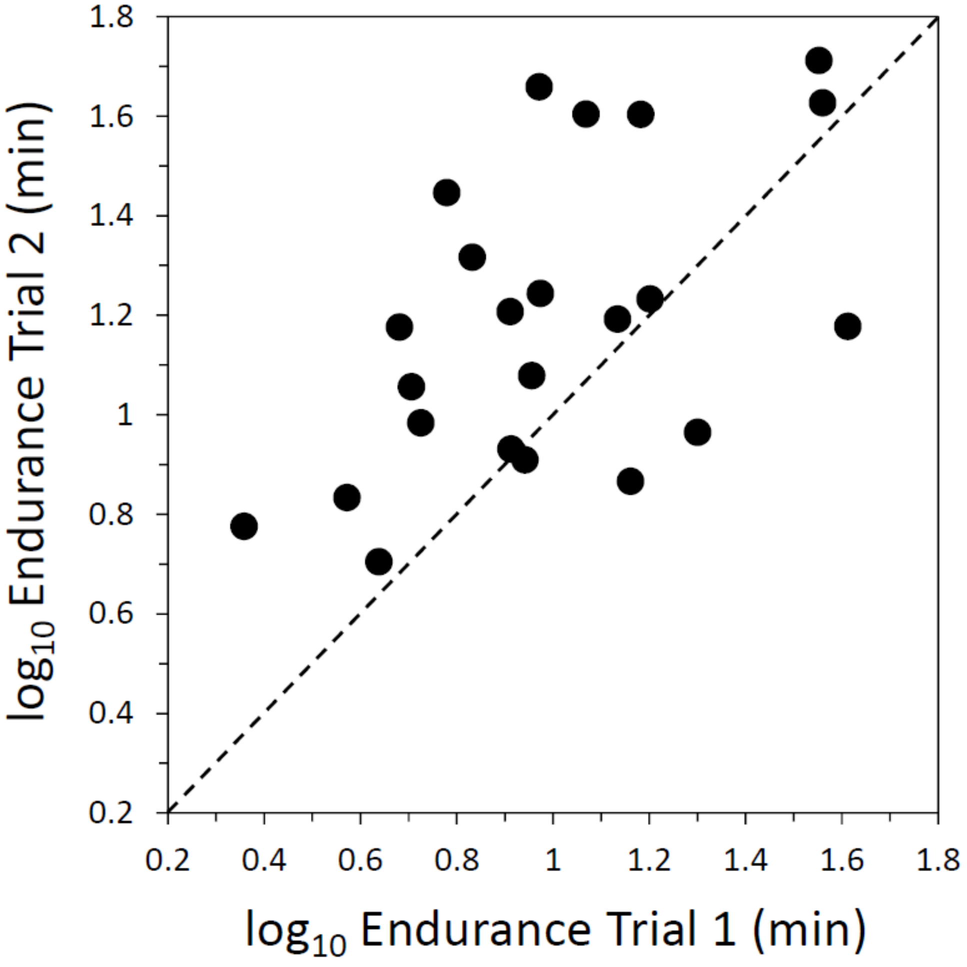
Figure 1.1. Repeatability of endurance between trials ($N = 23$, $r = 0.539$, $P = 0.008$). Dashed line indicates equal endurances between trials; on average, animals had higher endurance at the second trial (paired $t = 3.17$, $P = 0.004$).

Figure 1.2. Neither log-transformed values of the higher of two endurance measurements (top panel) nor log-transformed home range area (bottom panel) was significantly related to log-transformed body mass.

Figure 1.3. Lack of relation between home range area and number of sightings ($N = 22$, $r = 0.291$, $P = 0.188$).

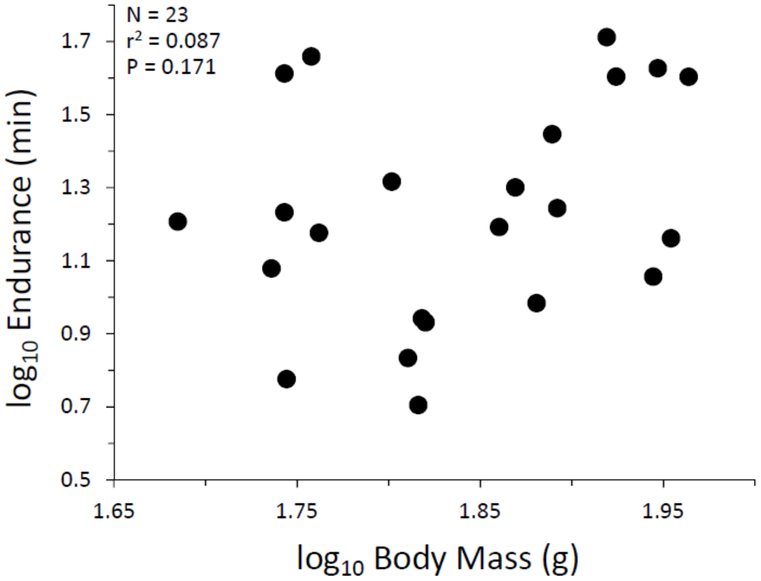
Figure 1.4. Log-transformed values for individual home range size were significantly positively correlated with log-transformed endurance (top panel) and endurance residuals (bottom panel: see text).

Figure 1.1

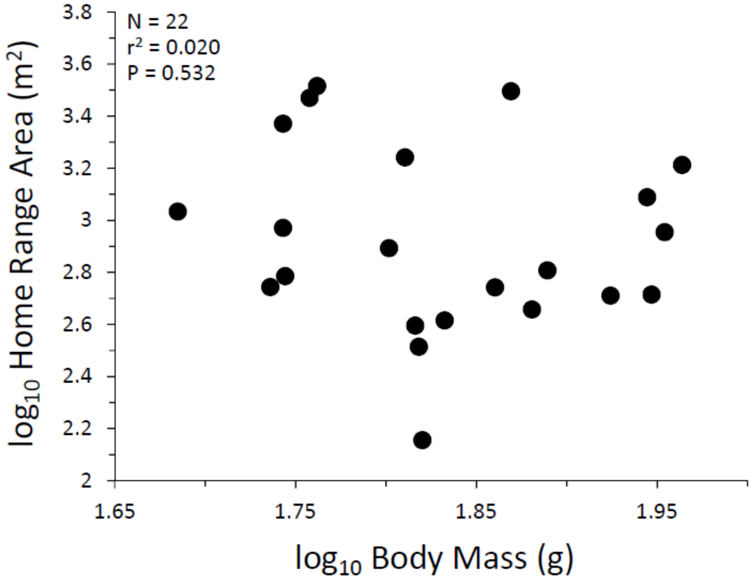


1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
log10 Endurance Trial 2 (min)
log10 Endurance Trial 1 (min)

Figure 1.2

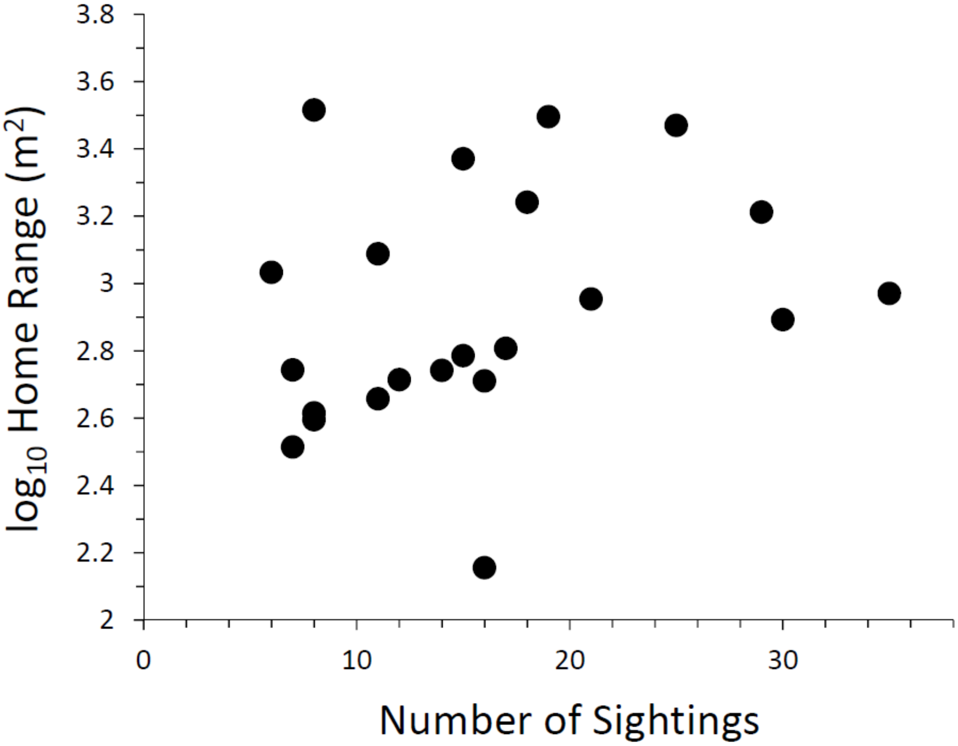


N = 23
r^2 = 0.087
P = 0.171
0.5
0.7
0.9
1.1
1.3
1.5
1.7
1.65
1.75
1.85
1.95
$\log_{10}$ Endurance (min)
$\log_{10}$ Body Mass (g)



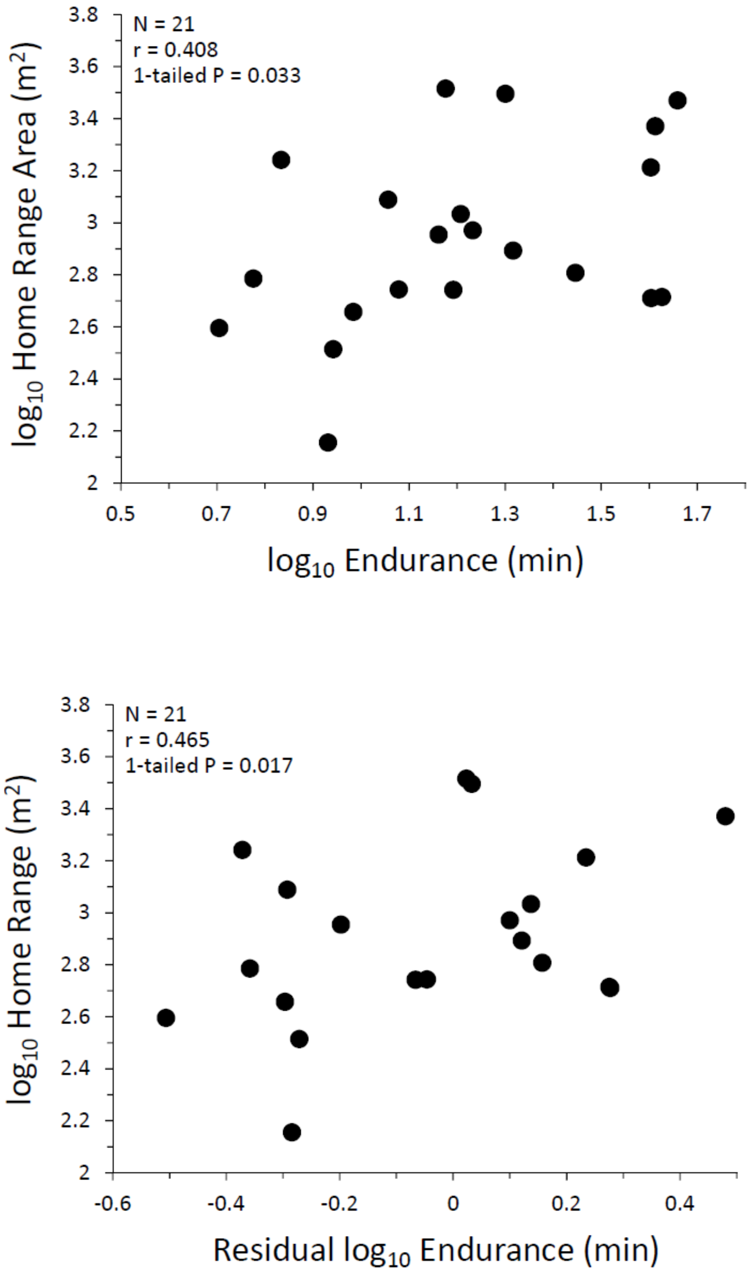
N = 22
r^2 = 0.020
P = 0.532
2
2.2
2.4
2.6
2.8
3
3.2
3.4
3.6
3.8
1.65
1.75
1.85
1.95
$\log_{10}$ Home Range Area (m^2)
$\log_{10}$ Body Mass (g)

Figure 1.3



$\log_{10}$ Home Range (m^2)
3.8
3.6
3.4
3.2
3
2.8
2.6
2.4
2.2
2
0
10
20
30
Number of Sightings

Figure 1.4


N = 21
r = 0.408
1-tailed P = 0.033
$\log_{10}$ Home Range Area (m^2)
3.8
3.6
3.4
3.2
3
2.8
2.6
2.4
2.2
2
0.5
0.7
0.9
1.1
1.3
1.5
1.7
$\log_{10}$ Endurance (min)
N = 21
r = 0.465
1-tailed P = 0.017
$\log_{10}$ Home Range (m^2)
3.8
3.6
3.4
3.2
3
2.8
2.6
2.4
2.2
2
-0.6
-0.4
-0.2
0
0.2
0.4
Residual $\log_{10}$ Endurance (min)

CHAPTER 2

Corticosterone and Endurance Capacity in Captive Desert Iguanas (*Dipsosaurus dorsalis*) Administered Corticosterone Implants

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Abstract

Whole-organism performance traits may directly affect the relationship between behaviors and Darwinian fitness; these same performance traits can be investigated as the product of multiple lower-level morphological and physiological traits. Endocrine function and hormone levels are a class of lower-level traits that have far-reaching physiological effects, yet are not frequently discussed in the context of their contributions to whole-organism performance. As one example, circulating corticosterone and other glucocorticoids interact with numerous physiological systems and are related to skeletal muscle growth, activity levels, and multiple traits relevant to locomotor behavior, yet the connections between basal circulating corticosterone concentrations and locomotor performance are unclear. To further examine the connections between corticosterone and locomotor performance, 16 male desert iguanas were captured in Riverside Co., CA and given corticosterone implants containing a soluble corticosterone complex of either 35.06 and 17.53 mM corticosterone in saline or sterile saline only (N = 6, 5, and 5 respectively). Desert iguanas were tested for endurance capacity and blood samples taken prior to implants and then 1 week, 3 weeks, and 5 weeks post-surgery, followed by dissections. Implants did not significantly increase circulating corticosterone levels in either treatment group. Endurance capacity was significantly repeatable during the two trials conducted at each week, and endurance was significantly greater post-surgery, but it did not differ among treatment groups. These results may be explained by failure of the corticosterone implants.

Introduction

Locomotor behavior is intrinsically tied to Darwinian fitness in numerous facets of an organism's life; from avoiding predators to foraging and mate-finding, the majority of animals owe their daily and lifetime success to their capacity to perform some form of locomotion (Arnold 1983; Bennett 1991; Irschick et al. 2008). For example, a lizard may quickly jump from a basking spot to avoid a predation attempt from a hawk. This behavior increases the likelihood of survival of the lizard; at the same time, the jumping ability of the lizard may constrain its behavior. This ability or capacity to perform a task while maximally motivated is term the performance capacity (Arnold 1983; Lailvaux and Husak 2014; Storz et al. 2015). Performance capacity is typically measured in a laboratory setting with assumed maximal motivation (John-Alder and Bennett 1981; Bennett and Huey 1990; Garland, Jr. and Losos 1994), and are considered a reliable proxy measurement for the highest level of performance observed in the field (Hertz et al. 1988; Irschick and Losos 1998).

Locomotor performance capacity results from the interactions of multiple subordinate traits and is a key focus of evolutionary physiology (Bennett and Huey 1990; Garland, Jr. and Carter 1994; Feder et al. 2000). For example, the amount of fast-twitch, Type I muscle fiber in the thigh muscle may directly contribute to the jumping ability of a given lizard. The evolutionary contribution of individual variation in endocrine function has been rarely investigated from the perspective of subordinate traits that may affect locomotor abilities (Breuner et al. 2008; Garland, Jr. et al. 2016). However, the multiple mechanisms for change in the endocrine system as well as the wide-ranging effects of hormones in the body make the endocrine system a good candidate for study from the perspective of subordinate traits.

One hormone that has been investigated in the context of muscular and locomotor performance is testosterone. Testosterone is typically thought of as regulating strictly sexual development and function; however, it is involved with skeletal muscle development and other factors that contribute to successful locomotion (Husak et al. 2009; O'Connor et al. 2011). Castrated mice, for example, show reduced heart mass, muscle mass, and overall body mass (Hooper et al. 1986). In human men, a decrease in circulating testosterone due to aging is associated with decreased muscle mass and physical performance (Brill et al. 2002), and supraphysiological doses of testosterone causes increases in muscle mass and muscle strength (Bhasin et al. 2009).

Another hormone, corticosterone, is frequently maligned as only a "stress" hormone. However, corticosterone is involved in a variety of characters related to locomotion, including skeletal muscle growth, bone growth, and glucose mobilization (Coderre et al. 1992; Li et al. 1996; Jessop et al. 2003). Corticosterone can also be associated with muscle wastage and fat deposition (Gray et al. 1990; Astheimer et al. 1992; Karatsoreos et al. 2010). In lines of mice bred for high voluntary wheel running, both endurance capacity and circulating corticosterone levels are significantly higher than in mice from non-selected control lines (Malisch et al. 2007, 2008; Singleton and Garland, Jr. 2018a).

Some studies have attempted to replicate natural increases in corticosterone levels with the use of corticosterone implants or other forms of supplementation. Zebra finches that received mealworms dosed with corticosterone significantly increased their perch-hopping behavior for the 30 minutes after feeding (Breuner et al. 1998; Breuner and Wingfield 2000). *Uta stansburiana* that received corticosterone implants had a significantly increased endurance capacity over the subsequent 4 weeks (Miles et al. 2007). In contrast, corticosterone administered in drinking water caused decreased growth rates, activity levels, and maximal oxygen consumption in mice from lines bred for high voluntary wheel running as well as in non-selected control lines (Singleton and Garland, Jr. 2018a).

The purpose of the present study was to examine the effects of supplemental corticosterone on endurance capacity in desert iguanas, *Dipsosaurus dorsalis*. Desert iguanas are diurnal, herbivorous lizards found in the southwestern United States and Northern Mexico. Their relatively large body size facilitates blood sampling and physiological studies, and they have been used in a variety of laboratory studies of locomotor performance (John-Alder and Bennett 1981; Gleeson and Harrison 1988; Swoap et al. 1993; Jayne and Irschick 1999; Singleton and Garland, Jr. 2018b). The endurance capacity of desert iguanas is biologically relevant in free-living individuals, as it is positively related to home range size (Singleton and Garland, Jr. 2018b). As corticosterone implants have previously caused increased endurance capacity in *Uta stansburiana* (Miles et al. 2007), we hypothesized that elevation of circulating corticosterone in desert iguanas could lead to increased endurance capacity.

Methods

Sixteen adult male desert iguanas were captured via noosing from public lands in North Palm Springs, CA in late September 2016. Sex and approximate age were determined via SV length and sexually dimorphic characters. Lizards were transported to the University of California, Riverside after capture and placed in cages (55-gallon storage containers with mesh tops) in the vivarium. Desert iguanas were given food (mixed fruit and green vegetables, dried mealworms) and water ad libitum, two hiding areas, and kept four individuals per cage. Group housing is acceptable in this species, as desert iguanas from this population live in high density (Krekorian 1976, 1983, 1984) and exhibit little intrasexual aggression outside the mating period (April-July; Mayhew 1971). During the course of the experiment we saw no fighting nor any evidence of fighting between individuals.

After two weeks of acclimation, each male was tested for endurance capacity at a fixed speed treadmill. Individual lizards were taken from enclosures and placed on a small motorized treadmill (108 cm x 20cm) running at 1.0 km/hr. This speed has been previously estimated to induce maximal oxygen consumption at 40°C in desert iguanas (John-Alder and Bennett 1981) and was also used in a large comparative study of lizards(Garland, Jr. 1994). Lizards were encouraged to maintain activity via gentle taps on the tail and hind limbs (Garland, Jr. 1984, 1999). We were not concerned about autotomy, as desert iguanas are "reluctant" to lose tails. Endurance capacity was measured as the amount of time in seconds that an individual lizard was able to maintain position on the treadmill. The trial was concluded once a lizard could not maintain position on the treadmill after 10 taps in rapid succession. After conclusion, exhaustion was verified via the righting response, where a lizard is placed belly-up on the palm of the researcher to evaluate the effort of the lizard to right itself (1-3: little to no response, some response, full response). At this time I also rated the quality of the run itself based on the encouragement necessary and if the lizard attempted escape (1-5: terrible – great). Endurance capacity was measured once on each of two successive days, and the higher of the two measurements was used to test for treatment effects (Garland, Jr. 1984, 1999; Garland, Jr. et al. 1987).

One day after the second endurance measurement, blood samples were taken from individuals to measure circulating corticosterone. Individuals were quietly removed from their enclosures, taking all the individuals from one cage in succession in order not to disturb the whole captive population. Bleed delay time started at the moment the enclosure top was removed and continued until the blood sample was collected, with sampling attempts terminated at 3 minutes if not complete. Three minutes from first handling to sample is a generally accepted time for obtaining baseline blood samples (Romero and Reed 2005). Blood samples were taken via syringe from the ventral caudal vein. This method allows for repeated sampling from the same individual without the risk of eye injury via retro-orbital puncture, and is commonly used in veterinary practice.

One week after the first set of endurance measurements and the first blood sample, lizards received hormone/saline implants. Implants were constructed using 1 cm sections of 3 mm diameter medical-grade silastic tubing. Corticosterone implant tubes were sealed on one end using silicone and filled with 2.12 mL of a water-soluble corticosterone complex (preformed water-soluble complex of corticosterone and 2-hydroxypropyl-β-cyclodextrin) dissolved in sterile saline (DeNardo and Sinervo 1994; Miles et al. 2007; John-Alder et al.

2009). Two concentrations of corticosterone were used: 35.06 and 17.53 mM. Saline implants were constructed similarly but without the corticosterone complex, and all implants were sealed on the second end with silicone.

For implant surgery, individual animals were anesthetized using isoflurane (Fig. 2.1) administered as 5% atmosphere until movement ceases and reactions to gentles pinches cease (Eatwell 2010). The isoflurane administration continued via a slow intermittent administration system for the full time of surgery. Following anesthesia, 37.5 uL 1% lidocaine solution was administered via local infiltration to the lateral area of the lower abdomen(Mosley 2005; Eatwell 2010). After administration, the surgical site was disinfected and a 1 cm vertical incision into the peritoneum was made 1 cm left of the midline and 2 cm above pelvis to avoid abdominal arteries. The implant was inserted into the abdominal cavity and the incision closed with a combination of horizontal mattress suture stitches and tissue glue. After surgery, animals were placed into a small terrarium under a heat lamp to enhance recovery from anesthesia. All animals recovered from anesthesia to the point of walking and awareness within 20 minutes of surgery completion and showed no signs of pain (e.g. rolling, arched back, pressing of head into corner, tail slapping; Mosley 2006) in the 24 hrs post-surgery.

Eight days post-surgery, lizards were tested twice on subsequent days for endurance capacity, followed by a blood sample on the third day. Two weeks later this process was repeated, and two weeks after these two final measurements of endurance capacity and a final blood sample were taken before sacrifice and dissection (Fig. 2.2). At dissection, lizards were decapitated, with time to decapitation measured from the instant of enclosure lid removal.

Blood samples, two hematocrit measures, liver mass, heart mass, and thigh muscle mass were taken. Plasma was stored at -80°C. These procedures were approved by the California Department of Fish and Wildlife under permit# sc12669. Procedures were also approved by the Institutional Animal Care and Use Committee of the University of California at Riverside under animal use protocol number 20160005.

The extracted samples were assayed using the K-014 Corticosterone DetectX® EIA kit from Arbor Assays. The established protocol for plasma with this kit includes a 1:100 dilution step combined with the application of dissociation reagent in order to separate corticosterone from binding proteins. This amount of dilution raised concern that the resulting concentrations would fall outside the limits of detection for the assay. On recommendation of the arbor Assay technicians, prior to assays corticosterone was separated from binding proteins using a steroid liquid extraction procedure specifically recommended for DetectX® Immunoassay kits from Arbor Assays. In brief, plasma samples were combined with ethyl acetate, vortexed, and frozen in an ethanol bath. The top-level solvent solution (unfrozen) was poured off and dried using a centrifugal evaporator with organic solvent capabilities.

For statistical analysis, SPSS was used to conduct one-way ANOVAs comparing the initial body mass and SV length of individuals among intended treatment groups (Appendix I). Paired *t*-tests and Pearson correlations were used to compare endurance measurements for repeatability. SAS PROC MIXED was used to generate a repeated-measures ANOVA to examine the effects of implant type on endurance capacity, corticosterone levels, and body mass over the course of the experiment (Appendix II). SPSS was used to generate One-way

ANCOVAs to examine organ mass and hematocrit differences among groups, with body mass as the covariate for organ mass.

Results

Neither body mass nor snout-vent length differed significantly among groups prior to surgery (N = 16; Body Mass: F = 1.460, P = 0.268; SV length: F = 0.337, P = 0.720). The mean value for corticosterone for all desert iguanas prior to implant surgery was 7,217 picograms per mL plasma (N = 16; Range: 2,477-26,511 pg/mL; SD = 6,072). The mean of the higher of two initial endurance capacity trials prior to implant surgery was 7.57 minutes (N = 16; Range: 4.0-16.0 min; SD = 3.67). $\log_{10}$ corticosterone and endurance were unrelated before implant surgery (N = 16; R = 0.130; P = 0.632).

Endurance capacity was generally repeatable within pairs of trials (Fig. 2.3), as indicated by Pearson correlations (trials 1 and 2 (pre-surgery), N = 16, R = 0.449, 2-tailed P = 0.081; trials 3 and 4, N = 14, R = 0.469, P = 0.091; trials 5 and 6, N = 15, R = 0.670, P = 0.006; trials 7 and 8, N = 15, R = 0.475, P = 0.074). A paired t-test indicated that the values of trials 1 and 2 were significantly different (t = 2.412; d.f. = 15; P = 0.029). After surgery, there was no significant difference between the average values of trials 3 and 4 (t = 0.223; d.f. = 13; P = 0.827), 5 and 6 (t = -1.694; d.f. = 14; P = 0.112), and 7 and 8 (t = -0.104; d.f. = 14; P = 0.919).

In a repeated-measures ANOVA, body mass was not significantly different among implant groups over the course of the experiment (Table 2.1). Body mass did change significantly over the course of the experiment, being somewhat higher at week 3 (Fig. 2.4), but this pattern did not differ among groups (interaction P = 0.2205).

In a repeated-measures ANOVA with time between disturbance and blood sample included as a covariate, circulating corticosterone levels did not significantly differ by implant type (Table 2.2; Fig. 2.5), nor was there a difference over time overall or for specific groups over time. In specifically examining the two corticosterone values before and after surgery, they were not affected by either implant type (F = 0.72; P = 0.5038) or surgery (F = 0.00; P = 0.9983), with no interaction (F = 0.26; P = 0.7789).

In a repeated-measures ANOVA with $\log_{10}$ body mass as a covariate, there was no significant effect of implant type on endurance capacity over the course of the study (Table 2.3; Fig. 2.6; F = 2.33; P = 0.1360). Endurance capacity overall did change significantly over the course of the study (F = 8.94; P = 0.0001) but this difference did not vary between implant type (interaction F = 0.81; P = 0.5669). In further repeated-measures analysis of specifically before and after surgery, the higher of endurance trials 3 and 4 (days 8 and 9 after surgery) was significantly higher than endurance measured before surgery (F = 35.75; $P < 0.001$), and this difference was not affected by implant type (interaction F = 0.41; P = 0.6756).

At dissection, implant type did not impact $\log_{10}$ body mass in a simple ANOVA model (F = 1.505; P = 0.261) or when including $\log_{10}$ circulating corticosterone as a covariate (F = 1.725; P = 0.223). In ANCOVAs, both liver and heart mass were significantly positively related to body mass, as expected (Fig. 2.7). Results of these ANCOVAs are presented in Table 2.4. Body-mass adjusted liver mass did not vary significantly among implant types (F = 1.047; P = 0.383), including when circulating corticosterone levels were added as a covariate (F = 0.997; P = 0.403). Heart mass was not significantly different among implant types, both without (F = 0.414; P 0.671) and with circulating corticosterone as a covariate (F = 0.419; P = 0.669). Thigh muscle mass was not different among implant types without (F = 0.825; P = 0.464) or with corticosterone as a covariate (F = 0.701; P = 0.519). Hematocrit was not significantly different among implant types, either without (F = 0.467; P = 0.638) or with circulating corticosterone as a covariate (F = 0.428; P = 0.662).

Discussion

Endurance capacity of desert iguanas was not significantly affected by corticosterone implants (Table 2.3, Fig. 2.6). However, endurance increased between week 1 and week 3. This may have been attributable to familiarization with the testing protocol, acclimation or possibly training (physical conditioning: (Husak et al. 2015, but see Garland, Jr. et al. 1987)), although the latter seems unlikely from just two treadmill sessions that occurred two weeks earlier .

Corticosterone implants did not significantly affect liver mass or thigh muscle mass (with body mass as a covariate), or heart mass (Table 2.4; Fig. 2.7). Hematocrit at dissection was also not affected by implant type. Overall, the only physical change detected during the course of the experiment was a decrease in body mass, though that effect did not vary among implant types (Fig. 2.4).

The corticosterone implants did not achieve the desired results of significantly increasing circulating corticosterone levels (Table 2.1, Fig. 2.5). The lack of effect on plasma corticosterone may be explained in several ways. First, the captivity of free-born desert iguanas may have induced higher corticosterone in all lizards used in the experiment. The values for plasma corticosterone before surgery (Mean: 7,217 pg/mL; Range: 2,477-26,511 pg/mL) were significantly higher ($t = -2.170$; $P = 0.040$) than those found for free-living desert iguanas in the same population in the same season (mean: 3,376 pg/mL; range: 682-9,929 pg/mL; see chapter 4). Hence, differences in corticosterone by treatment group may have been obscured by an overall increase.

Alternatively, the corticosterone implants themselves may have failed shortly after surgery. If the integrity of the implant seals was compromised, then the corticosterone may have been released shortly after surgery, with any supplemental corticosterone long metabolized before the first post-surgery blood sample 10 days later. When implants were inspected post-dissection, 12 of 13 recovered implants showed signs of leakage, i.e., a pink coloration inside the tube or visible seal breakdown. Uncertainty regarding the structural integrity of the implant seals informed a secondary, improved plan for construction of corticosterone implants for subsequent studies (see chapter 4). In addition, corticosterone implants do not always have a direct linear effect on circulating corticosterone (in birds; Torres-Medina et al. 2018).

The present results suggest an additional need to perform studies of individual variation in endocrinology in free-living populations (Williams 2008), especially in the investigation of hormones that can vary considerably with individual conditions. Long-term captivity has been found to result in increased baseline corticosterone in Red-spotted Newts (Berner et al. 2013), White-crowned Sparrows (Marra et al. 1995; Romero and Wingfield 1999), and White-throated Sparrows (Marra et al. 1995). These changes could have considerable impacts on related organismal and behavioral functions, and hence interfere with physiological research. The examination of the relationship between corticosterone and endurance is continued in chapter 4 of this dissertation on a free-living population of male desert iguanas outside northern Palm Springs, California.

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Table 2.1. Significance levels from repeated-measures analysis of body mass in 16 captive, free-born male Desert Iguanas, *Dipsosaurus dorsalis*. Body mass was measured twice on successive days at experimental weeks 1 (before implant surgery), 3, 5, and 7 (post-surgery), and the $\log_{10}$ value of mean mass (of the paired masses) was used for analysis. Main effects were implant type, week, and implant type * week interaction. Inspection of the figure indicates that body mass was somewhat lower at week 4, though this decrease did not differ among groups.

Effect	df	F	Sig.
Implant Type	2, 13	2.03	0.1704
Week	3, 37	8.84	0.0002
Implant Type * Week	6, 37	1.46	0.2205

Table 2.2. Results of repeated-measures analysis of circulating plasma corticosterone levels in 16 captive, free-born male Desert Iguanas, *Dipsosaurus dorsalis*. Corticosterone was measured at experimental weeks 1 (before implant surgery), 3, 5, and 7 (post-surgery), and the $\log_{10}$ value of pg/mL was used for analysis. Main effects were implant type, week, and implant type * week interaction. Time from disturbance to completion of blood sample (bleed delay) was included as a covariate.

Effect	df	F	Sig.
Implant Type	2, 13	1.55	0.2482
Week	3, 34	1.26	0.3028
Implant Type * Week	6, 34	0.82	0.5643
Bleed Delay	1, 34	0.14	0.7128

Table 2.3. Results of repeated-measures analysis of endurance capacity in 16 captive, free-born male Desert Iguanas, *Dipsosaurus dorsalis*. Endurance capacity was measured twice on successive days at experimental weeks 1 (before implant surgery), 3, 5, and 7 (post-surgery), and the $\log_{10}$ value of the higher measurement (of the paired trials) was used for analysis. Main effects were implant type, week, and implant type * week interaction. Log_{10} body mass was included as a covariate. Inspection of the figure indicates that endurance was somewhat higher at week 3, though this increase did not differ among groups.

Effect	df	F	Sig.
Implant Type	2, 13	2.33	0.1360
Week	3, 36	8.94	0.0001
Implant Type * Week	6, 36	0.81	0.5669
Body Mass	1, 36	0.01	0.9324

Table 2.4. Results of ANCOVA analysis of organ masses and hematocrit in 15 captive, free-born male Desert Iguanas, *Dipsosaurus dorsalis*. Log_{10} body mass was included as a covariate for comparisons of heart mass, muscle mass, and thigh mass.

Variable	Trans form	Covariate	F	P	Treatment	LS Mean	SE
Liver Mass (g)	log_{10}	log_{10} Body Mass	1.047	0.383	saline	0.184	0.035
					Low	0.198	0.034
					High	0.133	0.031
Liver Mass (g)	log_{10}	lo_{10} CORT log_{10} Body Mass	0.997	0.403	saline	0.184	0.037
					Low	0.200	0.036
					High	0.132	0.032
Heart Mass (g)		log_{10} Body Mass	0.414	0.671	saline	0.082	0.003
					Low	0.085	0.003
					High	0.085	0.003
Heart Mass (g)		log_{10} CORT log_{10} Body Mass	0.419	0.669	saline	0.081	0.004
					Low	0.086	0.003
					High	0.085	0.003
Thigh Mass (g)	log_{10}	log_{10} Body Mass	0.825	0.464	saline	-0.017	0.053
					Low	-0.086	0.050
					High	0.001	0.045
Thigh Mass (g)	log_{10}	log_{10} CORT log_{10} Body Mass	0.701	0.519	Saline	-0.017	0.055
					Low	-0.086	0.053
					High	0.001	0.048
Hematocrit (%)			0.467	0.638	saline	0.444	0.006
					Low	0.441	0.005
					High	0.436	0.005
Hematocrit (%)		log_{10} CORT	0.428	0.662	saline	0.444	0.006
					Low	0.441	0.006
					High	0.436	0.005

Figure 2.1. Diagram of simple anesthesia device for small reptiles; diagram provided by Diana Hews of Indiana State University on December 3 2015. Setup includes A: squeeze bottle with internal straw cut to half-length; B: isoflurane; C: vinyl tubing at a length short as possible, but allowing for maneuverability; D: squeeze bottle with internal straw removed and bottom cut off; E: thick rubber band; F: latex (i.e., cut latex glove) with small hole cut in the middle.

The animal's head is placed through the hole in the latex (F). The isoflurane-containing bottle (A) is squeezed a few times to pump isoflurane-containing air into the second bottle (D) and expose the animal to the anesthetic. Periodically (every couple minutes), the bottle should be squeezed again to replace the air. As the vaporization of isoflurane is temperature dependent, do not use this apparatus during at extremely high environmental temperatures (i.e., > 100 °F). Doing so can lead to anesthetic overdose.

Figure 2.2. Experimental timeline.

Figure 2.3. Scatterplot of the repeatability of endurance measurements at week 1, 3, 5, and 7 (A, B, C, and D respectively). Log_{10} values are compared for subsequent days of testing. Measurements of repeatability were correlated, but this correlation only reached significance on measurements 5 and 6 (week 5).

Figure 2.4. Simple groups means and standard errors of $\log_{10}$ body mass at week 1, 3, 5, and 7. Body mass decreased over the course of the experiment for individuals ($F = 8.84$; $P =$

0.0002). In a repeated-measures ANOVA with blood sampling time as a covariate, group means did not significantly differ among treatment groups (F = 1.87; P = 0.1896); body mass did vary across weeks, but the effect did not vary among implant types (F = 1.46; P = 0.2205).

Figure 2.5. Simple groups means and standard errors of $\log_{10}$ circulating corticosterone levels at week 1, 3, 5, and 7. Corticosterone levels did not change within subjects during the course of the experiment (F = 1.26; P = 0.3028). In a repeated measures ANOVA, groups means did not significantly differ among treatment groups (F = 1.55; P = 0.2482), and the effect of time did not vary among implant types (F = 0.14; P = 0.7128).

Figure 2.6. Simple groups means and standard errors of $\log_{10}$ higher endurance measurements at week 1, 3, 5, and 7. In a repeated measures ANOVA with body mass as a covariate, endurance capacity changed significantly by week over the course of the experiment (F = 8.94; P = 0.0001). However, groups means did not significantly differ between implant types (F = 2.33; P = 0.1360), and the effect of time did not vary among implant types (F = 0.81; P = 0.5669). Week 3 measurements of endurance capacity were significantly greater than those of week 1 (F = 35.75; P < 0.001); however, groups means did not significantly differ between implant types (F = 0.94; P = 0.4153)

Figure 2.7. Liver, heart, and thigh muscle masses and hematocrit and their relationship to $\log_{10}$ body mass for high, low, and saline implant treatment groups. Values for liver and thigh muscle masses were also log-transformed. Heart mass was significantly different between

implant types with both body mass (F = 17.653; P < 0.001) and body mass and corticosterone as covariates (F = 12.530; P = 0.001).

Figure 2.1.

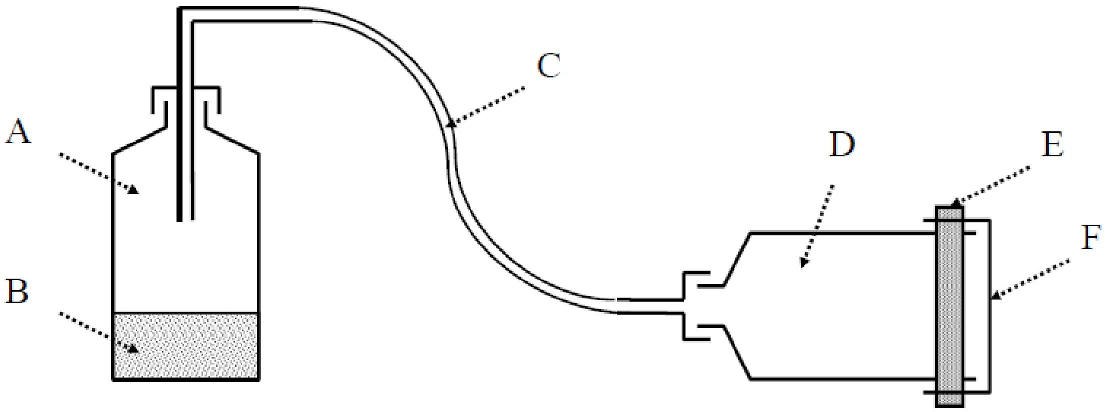


Figure 2.2.

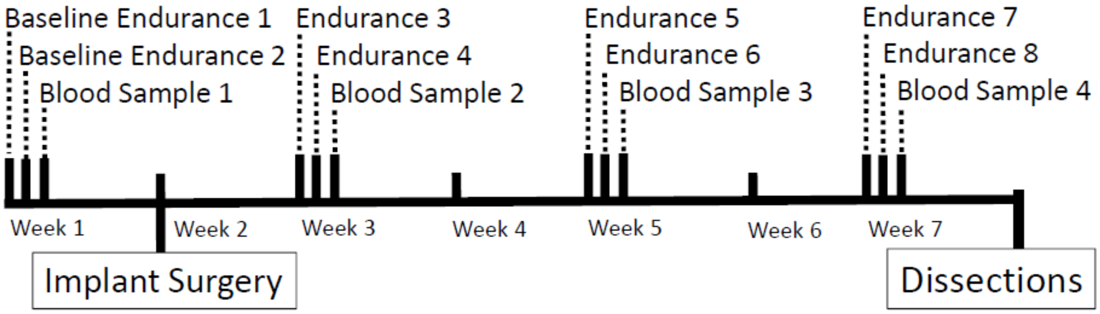

Baseline Endurance 1
Baseline Endurance 2
Blood Sample 1
Endurance 3
Endurance 4
Blood Sample 2
Endurance 5
Endurance 6
Blood Sample 3
Endurance 7
Endurance 8
Blood Sample 4
Week 1
Week 2
Week 3
Week 4
Week 5
Week 6
Week 7
Implant Surgery
Dissections

Figure 2.3.

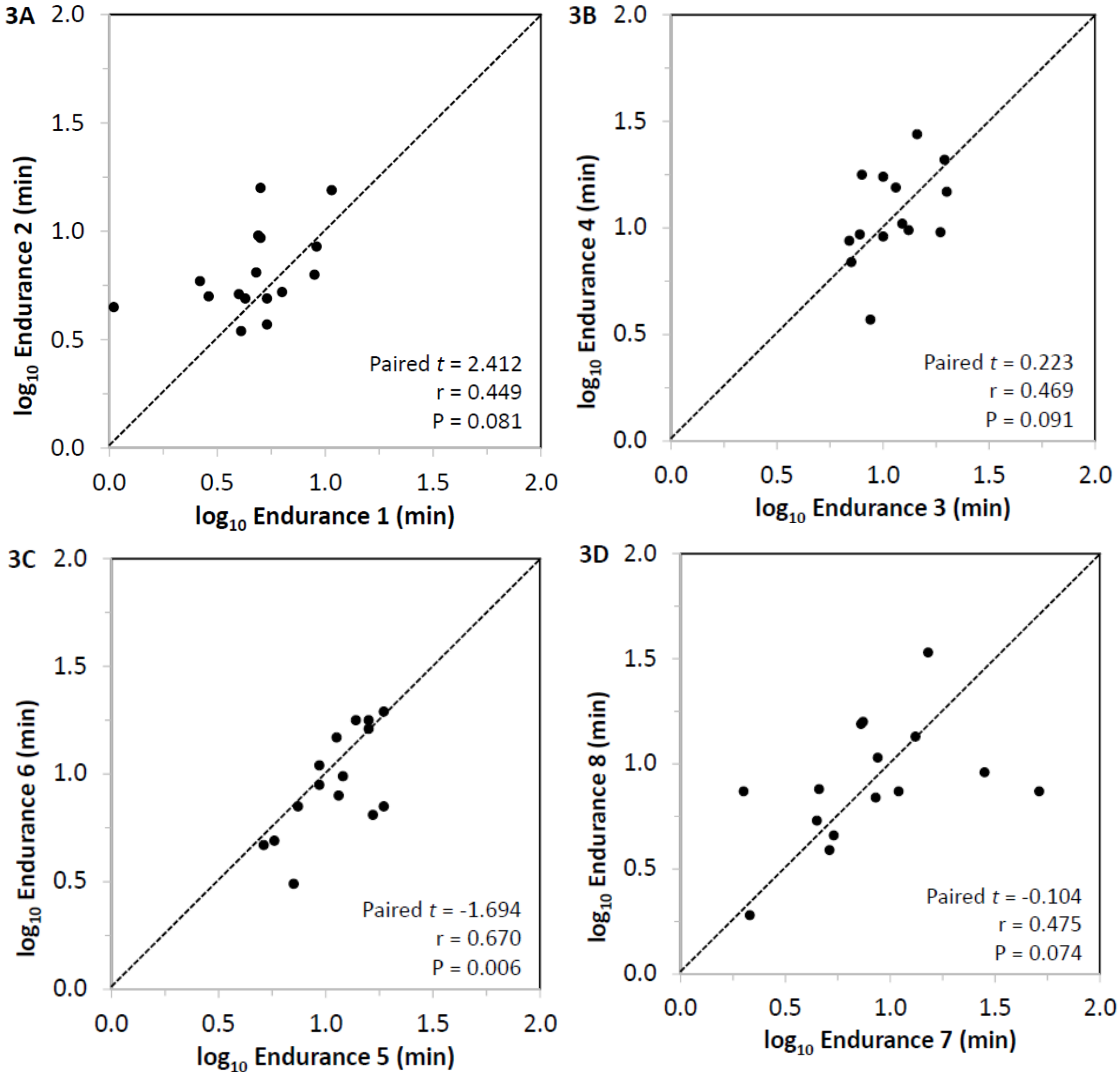
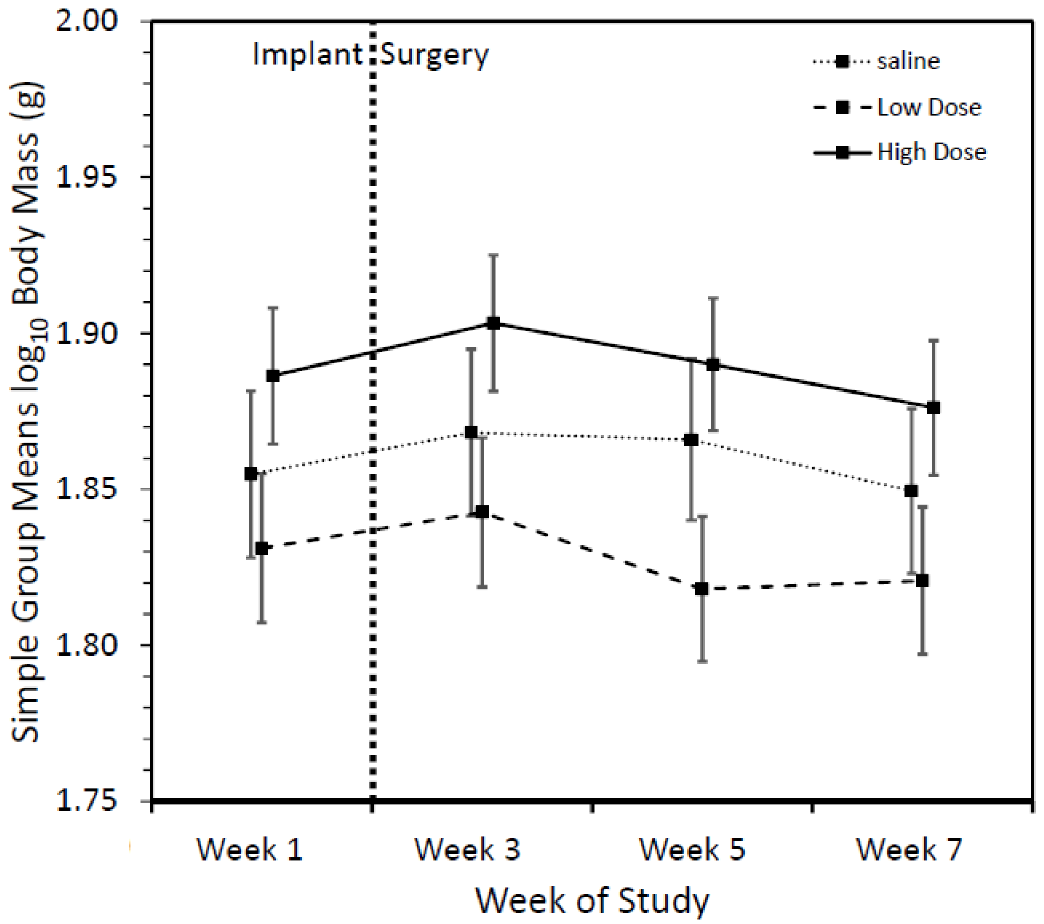
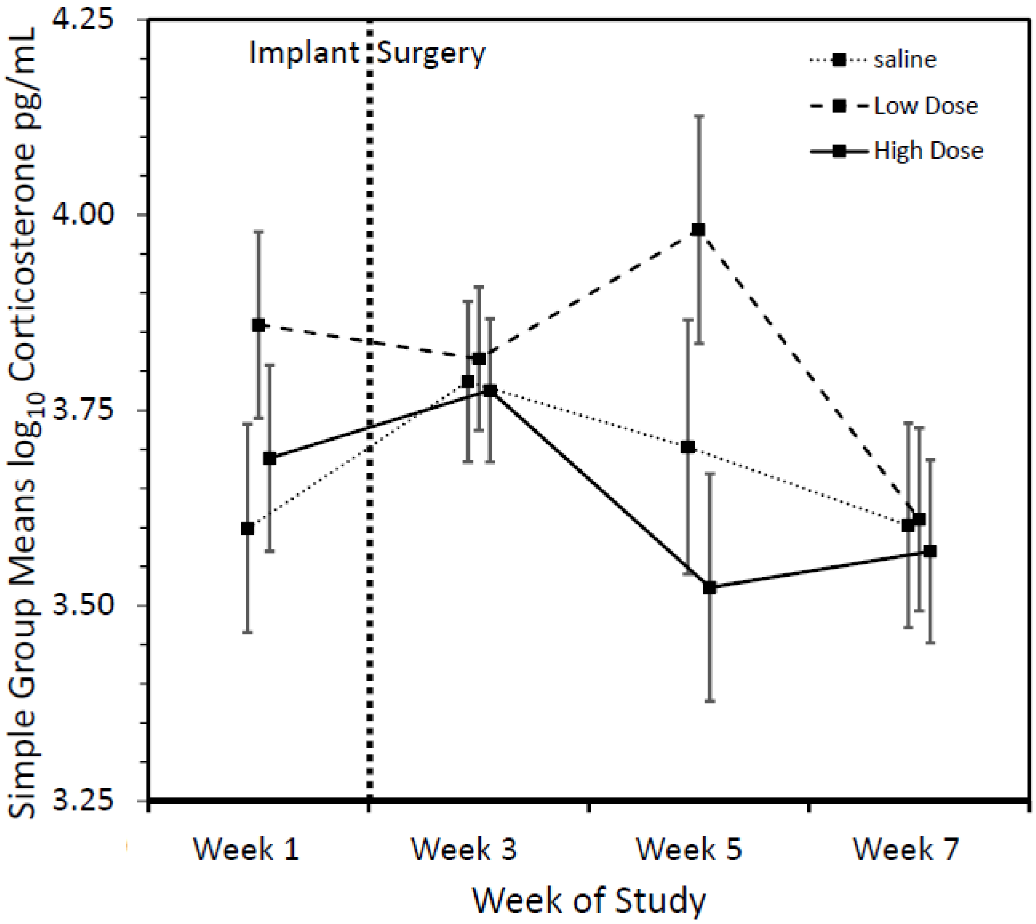

3A
log10 Endurance 2 (min)
log10 Endurance 1 (min)
0.0
0.5
1.0
1.5
2.0
Paired *t* = 2.412
r = 0.449
P = 0.081
3B
log10 Endurance 4 (min)
log10 Endurance 3 (min)
0.0
0.5
1.0
1.5
2.0
Paired *t* = 0.223
r = 0.469
P = 0.091
3C
log10 Endurance 6 (min)
log10 Endurance 5 (min)
0.0
0.5
1.0
1.5
2.0
Paired *t* = -1.694
r = 0.670
P = 0.006
3D
log10 Endurance 8 (min)
log10 Endurance 7 (min)
0.0
0.5
1.0
1.5
2.0
Paired *t* = -0.104
r = 0.475
P = 0.074

Figure 2.4.



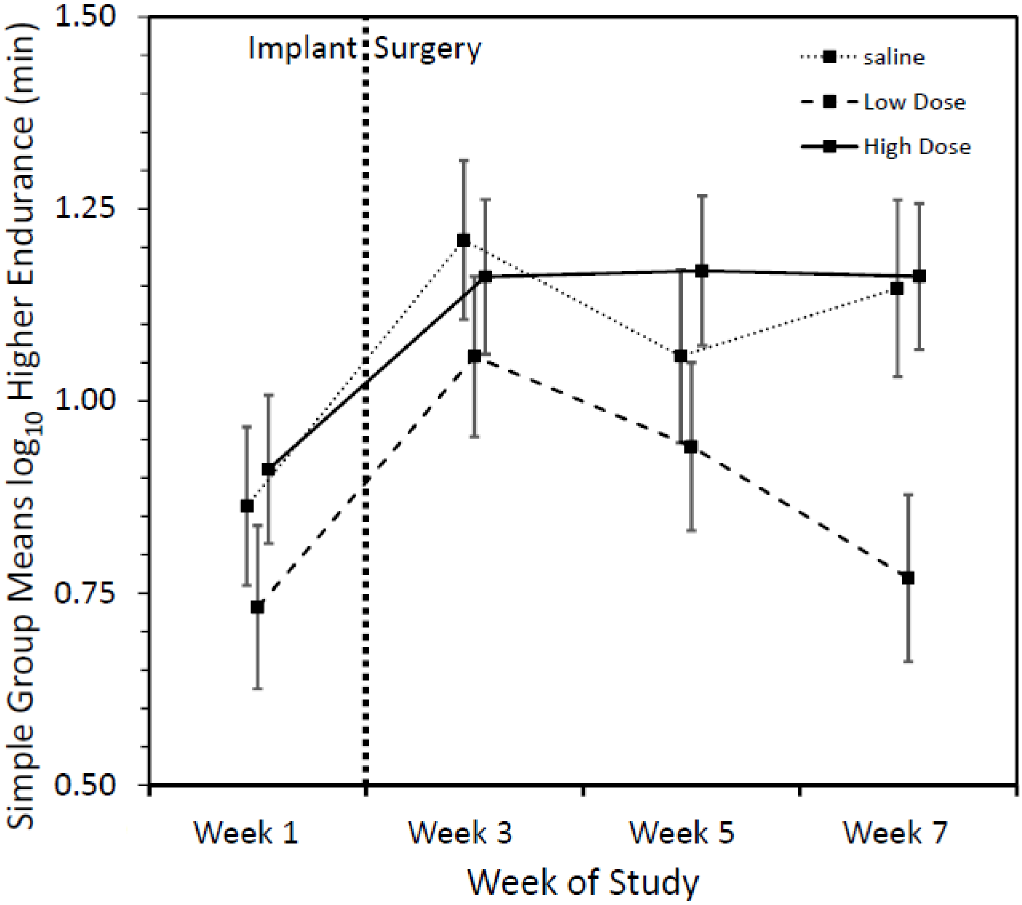
2.00
1.95
1.90
1.85
1.80
1.75
Simple Group Means $\log_{10}$ Body Mass (g)
Implant Surgery
saline
Low Dose
High Dose
Week 1
Week 3
Week 5
Week 7
Week of Study

Figure 2.5.



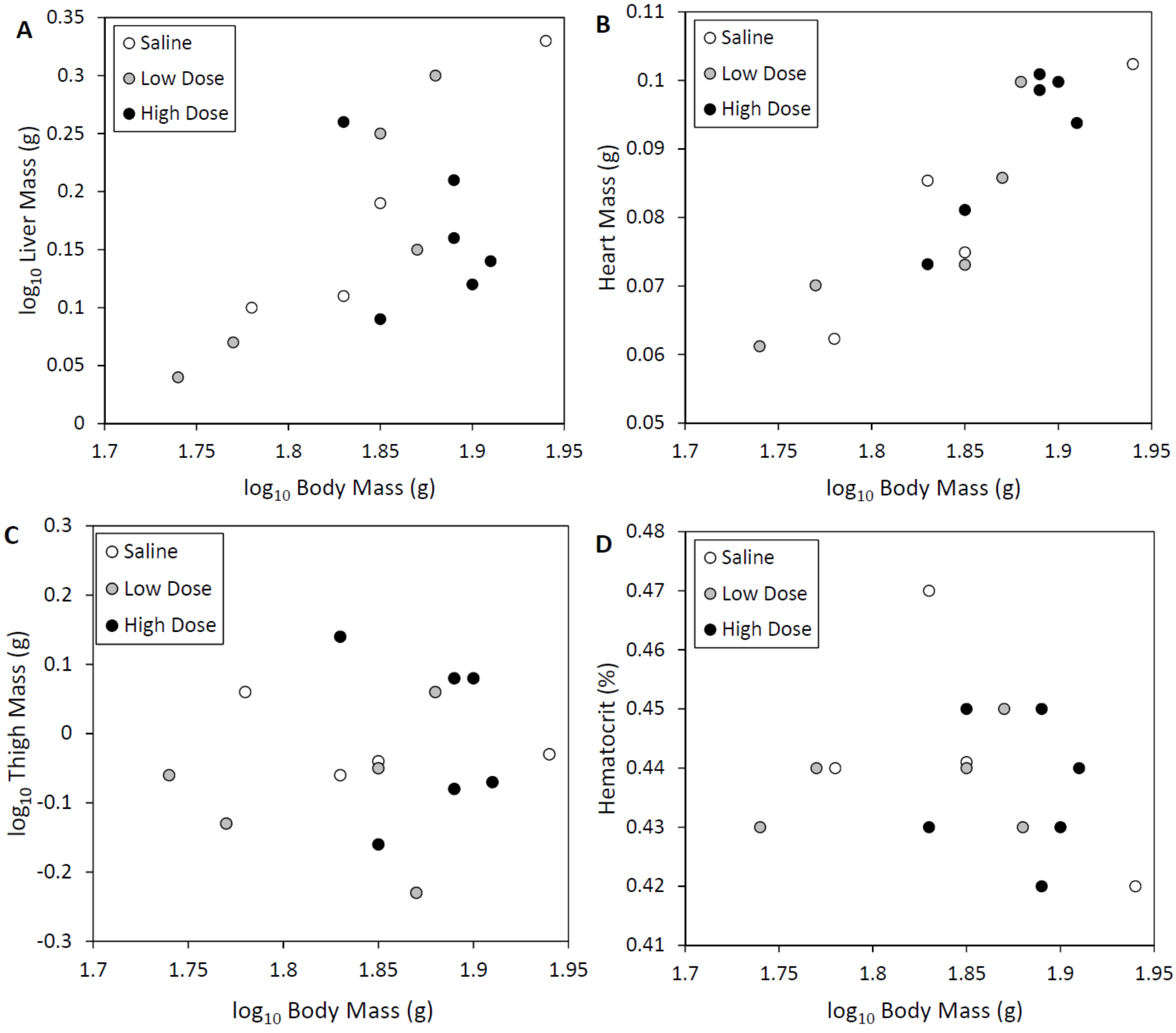
Simple Group Means $\log_{10}$ Corticosterone pg/mL
4.25
4.00
3.75
3.50
3.25
Implant Surgery
saline
Low Dose
High Dose
Week 1
Week 3
Week 5
Week 7
Week of Study

Figure 2.6.



Simple Group Means $\log_{10}$ Higher Endurance (min)
1.50
1.25
1.00
0.75
0.50
Implant Surgery
saline
Low Dose
High Dose
Week 1
Week 3
Week 5
Week 7
Week of Study

Figure 2.7.


A
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
$\log_{10}$ Liver Mass (g)
○ Saline
● Low Dose
● High Dose
1.7
1.75
1.8
1.85
1.9
1.95
$\log_{10}$ Body Mass (g)
B
0.11
0.1
0.09
0.08
0.07
0.06
0.05
Heart Mass (g)
○ Saline
● Low Dose
● High Dose
1.7
1.75
1.8
1.85
1.9
1.95
$\log_{10}$ Body Mass (g)
C
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
$\log_{10}$ Thigh Mass (g)
○ Saline
● Low Dose
● High Dose
1.7
1.75
1.8
1.85
1.9
1.95
$\log_{10}$ Body Mass (g)
D
0.48
0.47
0.46
0.45
0.44
0.43
0.42
0.41
Hematocrit (%)
○ Saline
● Low Dose
● High Dose
1.7
1.75
1.8
1.85
1.9
1.95
$\log_{10}$ Body Mass (g)

Appendix I.

```
*************Body Mass and SV before
Implants*********************************.
GET
FILE='C:\Singleton\Dipsosaurus\lab_study\Labstudy_Implants_endurance_bloodsample_diss
ections_CORT_v1.sav'.

ONEWAY E12MassX BY ImpType
  /MISSING ANALYSIS.
ONEWAY E12SVX BY ImpType
  /MISSING ANALYSIS.

*****************Endurance and CORT before implants************************.
GET
FILE='C:\Singleton\Dipsosaurus\lab_study\Labstudy_Implants_endurance_bloodsample_diss
ections_CORT_v1.sav'.
REGRESSION
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT LE12H
```

```
  /METHOD=ENTER LgCORT1.


**********REPEATABILITY*******.
GET FILE
='C:\Singleton\Dipsosaurus\lab_study\Labstudy_Implants_endurance_bloodsample_dissectio
ns_CORT_v1.sav'.
SELECT IF ID NE 16.
EXECUTE.


T-TEST
  PAIRS =  LE2end WITH LE1end (PAIRED)
  /CRITERIA=CIN(.95)
  /MISSING=ANALYSIS.
T-TEST
  PAIRS = LE4end  WITH LE3end (PAIRED)
  /CRITERIA=CIN(.95)
  /MISSING=ANALYSIS.
T-TEST
  PAIRS = LE6end  WITH LE5end (PAIRED)
  /CRITERIA=CIN(.95)
  /MISSING=ANALYSIS.
T-TEST
```

```
 PAIRS = LE8end  WITH LE7end (PAIRED)
 /CRITERIA=CIN(.95)
 /MISSING=ANALYSIS.



**************ENDURANCE AND BODY MASS*************************.
GET FILE
='C:\Singleton\Dipsosaurus\lab_study\Labstudy_Implants_endurance_bloodsample_dissectio
ns_CORT_v1.sav'.
DESCRIPTIVES VARIABLES=E12X E12H E34X E34H E56X E56H E78X E78H
 /STATISTICS=MEAN STDDEV MIN MAX.

REGRESSION
 /MISSING LISTWISE
 /STATISTICS COEFF OUTS R ANOVA
 /CRITERIA=PIN(.05) POUT(.10)
 /NOORIGIN
 /DEPENDENT LE12H
 /METHOD=ENTER LE12Mass.

REGRESSION
 /MISSING LISTWISE
```

```
  /STATISTICS COEFF OUTS R ANOVA

  /CRITERIA=PIN(.05) POUT(.10)

  /NOORIGIN

  /DEPENDENT LE34H

  /METHOD=ENTER LE34Mass.


REGRESSION

  /MISSING LISTWISE

  /STATISTICS COEFF OUTS R ANOVA

  /CRITERIA=PIN(.05) POUT(.10)

  /NOORIGIN

  /DEPENDENT LE56H

  /METHOD=ENTER LE56Mass.


REGRESSION

  /MISSING LISTWISE

  /STATISTICS COEFF OUTS R ANOVA

  /CRITERIA=PIN(.05) POUT(.10)

  /NOORIGIN

  /DEPENDENT LE78H

  /METHOD=ENTER LE78Mass.
```

*****Conclusion: No relationship between endurance and body mass. This is not wildly different from previous results.

```
**************CORT***DISSECTIONS*****************************************.

GET FILE ='C:\Singleton\Dipsosaurus\lab_study\Labstudy_Implants_endurance_bloodsample_dissections_CORT_v1.sav'.
COMPUTE LLiver = LG10(Liver).
Execute.
COMPUTE LThigh = LG10(thigh).
Execute.
SELECT IF ID NE 16.
Execute.

**Livers.

UNIANOVA LLiver BY ImpType WITH LgCORT4 LE78Mass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /CRITERIA=ALPHA(0.05)
  /DESIGN=LgCORT4 ImpType LE78Mass.
```

```
*F = 2.256; DF = 4, 10; P = 0.135.

UNIANOVA LLiver BY ImpType WITH LE78Mass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /CRITERIA=ALPHA(0.05)
  /DESIGN=ImpType LE78Mass.

**Heart.

UNIANOVA Heart BY ImpType WITH LgCORT4 LE78mass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /CRITERIA=ALPHA(0.05)
  /DESIGN=LgCORT4 ImpType LE78mass.

UNIANOVA Heart BY ImpType WITH LE78mass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /CRITERIA=ALPHA(0.05)
  /DESIGN=ImpType LE78Mass.
```

```
**Thigh.
GRAPH
  /SCATTERPLOT(BIVAR) = LE78Mass WITH Thigh BY id (IDENTIFY)
  /MISSING=LISTWISE.
GRAPH
  /SCATTERPLOT(BIVAR) = LE78Mass WITH Lthigh BY id (IDENTIFY)
  /MISSING=LISTWISE.
GRAPH
  /SCATTERPLOT(BIVAR) = LE78Mass WITH Lthigh BY imptype BY id (IDENTIFY)
  /MISSING=LISTWISE.

UNIANOVA Lthigh BY ImpType WITH LgCORT4 LE78Mass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /CRITERIA=ALPHA(0.05)
  /DESIGN=LgCORT4 LE78Mass ImpType.


UNIANOVA LThigh BY ImpType WITH LE78Mass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /CRITERIA=ALPHA(0.05)
```

```
  /DESIGN=LE78Mass ImpType.


***********HEMATOCRIT***************.


UNIANOVA Hemat BY ImpType
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /CRITERIA=ALPHA(0.05)
  /DESIGN=ImpType.
UNIANOVA Hemat BY ImpType WITH LgCORT4
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /CRITERIA=ALPHA(0.05)
  /DESIGN=LgCORT4 ImpType.
```

Appendix II.

```
options ls=80 pagesize=400;


libname test spss
'c:\Singleton\Dipsosaurus\lab_study\Labstudy_Implants_endurance_bloodsample_dissections
_CORT_v1.sys';
data trash;
set test._first_;
```

For comparisons of body mass between implant types over the course of experiment:

```
PROC GLM;
  CLASS imptype;
  MODEL LE12mass LE34mass LE56mass LE78mass = imptype;
  repeated LEmass 4;
  LSmeans imptype / stderr;


RUN;
quit;
```

For comparisons of corticosterone levels between implant types before and after surgery:

```
PROC GLM;
  CLASS imptype;
  MODEL LgCORT1 LgCORT2 = imptype;
  repeated LgCORT 2;
```

```
  LSmeans imptype;
RUN;
quit;
```

For comparisons of corticosterone levels between implant types over the course of experiment:

```
PROC GLM;
  CLASS imptype;
  MODEL LgCORT1 LgCORT2 LgCORT3 LgCORT4 = imptype;
  repeated LgCORT 4;
  LSmeans imptype / stderr;
RUN;
quit;
```

For comparisons of endurance between implant types before and after surgery:

```
IF WEEK > 3 THEN DELETE;

PROC MIXED RATIO IC;
  CLASS Imptype WEEK ID;
  MODEL Lend = Imptype WEEK Imptype*WEEK Lmass
                  /SOLUTION OUTPRED = JUNK;
              REPEATED /TYPE=AR(1) SUB=ID;
LSMEANS  Imptype WEEK Imptype*WEEK  /PDIFF;
```

For comparisons of endurance between implant types over the course of experiment:

```
PROC MIXED RATIO IC;
  CLASS Imptype WEEK ID;
  MODEL Lend = Imptype WEEK Imptype*WEEK Lmass
                    /SOLUTION OUTPRED = JUNK;
                REPEATED /TYPE=AR(1) SUB=ID;
LSMEANS  Imptype WEEK Imptype*WEEK  /PDIFF;
```

Appendix III.

Excel data files:

Singleton\Dipsosaurus\lab_study\AssayIDs_TO_IDS.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_BloodsampleI_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_BloodsampleII_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_BloodsampleIII_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_BloodsampleIV_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_Dissections_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_EnduranceI_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_EnduranceII_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_EnduranceIII_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_EnduranceIV_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_EnduranceV_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_EnduranceVI_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_EnduranceVII_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_EnduranceVIII_v1.xlsx

Singleton\Dipsosaurus\lab_study\Labstudy_Implants_v1.xlsx

SPSS syntax and data files:

Singleton\Dipsosaurus\assays\3_30_18_assayreadsmerged_tomerge.sav

Singleton\Dipsosaurus\lab_study\Labstudy_Implants_endurance_bloodsample_dissections_CORT_v1.sav

Singleton\Dipsosaurus\lab_study\Dipsosaurus_Labstudy_v2.sps

Singleton\Dipsosaurus\lab_study\Labstudy_Implants_endurance_bloodsample_dissections_CORT_v1.sys

SAS syntax files:

Singleton\Dipsosaurus\lab_study\repeatedmeasures_LEmass

Singleton\Dipsosaurus\lab_study\repeatedmeasures_LendH_12vs34

Singleton\Dipsosaurus\lab_study\repeatedmeasures_LendH

Singleton\Dipsosaurus\lab_study\repeatedmeasures_LgCORT_1vs2

Singleton\Dipsosaurus\lab_study\repeatedmeasures_LgCORT

CHAPTER 3

Basal Corticosterone, Endurance Capacity, and Home Range Area in Free-living Desert Iguanas (*Dipsosaurus dorsalis*)

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Riverside, California 92521

Abstract

Locomotor behavior is constrained by lower-level performance traits and influenced by environmental factors. One indexof a locomotor behavior is home range size, or the size of the area in which an animal conducts feeding, movements, and reproductive activities. Home range size can be impacted by environmental factors (e.g., resource density) that influence the amount of space needed by an individual, but can also be related to locomotor performance traits, such as endurance capacity. In turn, such performance traits as endurance capacity are directly impacted by numerous lower-level morphological and physiological traits, potentially including the basal plasma concentration of corticosterone. I conducted blood sampling, endurance testing, and measurement of home range size in a population of free-living desert iguanas near North Palm Springs, CA. Adult males from the population were individually marked, and measurements were taken in the mating and non-mating seasons of 2015 and 2016. As desert iguanas are herbivores that use burrows for nightly shelter, the soil density, soil compactibility, food plant density, and shade plant density within individual home ranges were also measured as potential factors influencing home range size. Circulating corticosterone varied significantly by year (N = 38; F = 14.07; P = 0.001) and season (mating vs. non-mating; F = 4.39; P = 0.044). Endurance capacity was significantly different between years (N = 49; F = 11.40; P = 0.002) and between seasons (F = 5.00; P = 0.031). Home range did not vary between years (N = 40; F = 0.281; P = 0.559) or seasons (F = 0.023; P = 0.881). Circulating corticosterone concentration was not significantly related to either endurance capacity (N = 26; R = 0.094; 1-tailed P = 0.648) or home range size (N = 23; R = -0.012; 1-tailed P = 0.958). Endurance was not significantly correlated with home range

size (N = 32; R = -0.171; P = 0.174). Home range size was not significantly predicted in a multiple regression with corticosterone and endurance (N = 21; R = 0.226; P = 0.607). Among the environmental variables, home range size was significantly negatively related to shade plant density (N = 38; R = 0.388; P = 0.038). The finding of environmental predictors of home range size may inform future conservation efforts for desert reptiles.

Introduction

Individual variation in behavior is often a direct target of selection in nature. Behavior acts as a "filter" between selection and lower-level traits, such as locomotor performance or hormone levels, as behavior determines which traits are relevant in a given situation where selection may occur (Garland, Jr. and Carter 1994; Careau et al. 2013).

Locomotor behavior may be an important target of selection because it impacts multiple facets of an organism's life that are crucial to Darwinian fitness, from finding mates to foraging to evading predators (Bennett and Huey 1990). Locomotor behavior is constrained by performance abilities (Bennett 1989). Performance is defined as an organism's ability to perform a task when maximally motivated (Careau and Garland, Jr. 2012; Lailvaux and Husak 2014). An organism's ability to perform a certain task may constrain its behavior in a fitness-relevant situation (Bennett and Huey 1990; Bennett 1991); for example, a lizard with lower body temperature than preferred body temperature (and hence, a lower ability to sprint away) may choose to bite an attacker instead of attempting escape (Crowley and Pietruszka 1983).

The maintenance of a home range is one key aspect of locomotor behavior. A home range is traditionally 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). As this area includes all normal necessary activities (feeding, etc.), the size of a home range is influenced by environmental factors (Lucherini and Lovari 1996; Tufto et al. 1996), but it may also be constrained by performance capacities, such as locomotor endurance (Garland, Jr. 1999; Singleton and Garland, Jr. 2018a).

Performance capacities are themselves complex traits, as numerous physiological and morphological traits may contribute to them (Swoap et al. 1993; Vervust et al. 2008). For example, fin dimensions in some fish directly affect their fast-start swimming acceleration (Langerhans 2009). Circulating hormones are rarely considered as subordinate traits affecting either performance capacities or locomotor behavior, despite the far-reaching and rapid effects of some on multiple body systems (Breuner et al. 2008; Husak et al. 2009; Garland, Jr. et al. 2016).

One such hormone with far-reaching effects, corticosterone, is used as a measure of "stress," (Dunlap and Wingfield 1995; Jessop et al. 2003; Cockrem 2007; Romero and Wikelski 2010). However, corticosterone circulates at low levels in the plasma of most vertebrates under non-stress conditions (Nelson 2011) and affects numerous processes known to impact locomotion such as glucose mobilization, muscle maintenance, and fat storage (Li et al. 1996; Jessop et al. 2003). In the Common Side-blotched Lizard (*Uta stansburiana*), corticosterone implants caused an increase in endurance capacity (Miles et al. 2007). Furthermore, corticosterone may be involved with higher-level aspects of locomotion or locomotor motivation leading to locomotor behavior, such as activity levels or spatial memory (Breuner et al. 1998; Pravosudov 2003; Garland, Jr. et al. 2016). Corticosterone implants caused a reduction in both activity levels and home range size in *Uta stansburiana* (DeNardo and Sinervo 1994a, 1994b). In house mice from lines selectively bred for high wheel running, as well as non-selected control lines, supplemental corticosterone added to drinking water resulted in decreased activity levels and decreased maximal oxygen consumption during forced treadmill exercise (Singleton and Garland, Jr. 2018).

The desert iguana (*Dipsosaurus dorsalis*) is a medium-sized herbivorous lizard that occupies desert spaces in the southwestern United States and northern Mexico. It is terrestrial and typically found in low-elevation areas with sandy soil which is used for burrow construction (Norris 1953). Desert iguanas consume the flowers and leaves of a variety of desert plants, in addition to feeding opportunistically on arthropods and the feces of other herbivores (Minnich and Shoemaker 1970). These lizards maintain the highest active body temperature of any vertebrate in North America (42° C; Norris 1953), but this temperature is tightly regulated (DeWitt 1967), with wild lizards using a combination of open shade and burrows to thermoregulate (Norris 1953; DeWitt et al. 1967). The burrows of desert iguanas act as refugia from both excessive heat and crepuscular/nocturnal predators.

Studies of desert iguanas have examined aspects of locomotor performance, behavior, and endocrine function (e.g. Krekorian 1976; John-Alder and Bennett 1981; John-Alder 1984; Hancock and Gleeson 2005; Singleton and Garland, Jr. 2018a). Their relatively large size and docile demeanor allows blood collection and other physiological measurements to be performed easily, while their tolerance to observation in the field enables monitoring of individual behavior over time. In a previous study, the endurance capacity of free-living desert iguanas was measured repeatedly and found to positively correlate with home range size (Singleton and Garland, Jr. 2018a). In the present study, we have expanded the focus of this research to include lower-level traits that may contribute to endurance capacity, such as circulating plasma corticosterone, body mass, and body size. We also measured environmental characteristics to examine their correlation with home range size.

Methods

Individual desert iguanas were captured using a "noosing" technique(e.g., see García-Muñoz and Sillero 2010 and references therein). This capture technique involves using thin thread or fishing line suspended in a loop with a slip knot from a long pole. The researcher slowly approaches the lizard until within range of the pole, then positions the loop over the head of the lizard and pulls upward, closing the loop and lifting the lizard into the air where it can then be captured by hand. This technique is useful for most small to medium-sized lizards.

Lizards larger than 100 mm snout-vent length (SVL) were given unique identifying markers consisting of a series of colored beads (the colors correspond to numbers) on a length of stainless steel wire (Fisher and Muth 1989). The wire was run under the skin of the dorsal proximal tail and the ends were twisted together to secure (Fig. 3.1). This method provides advantages over other methods of permanent marking for lizards such as toe-clipping or the use of PIT-tags, the most significant of which for this study is the ability to identify an individual lizard from a distance without recapture. In the pilot study for this marking method, 357 *Uma inornata* were beaded and retained the markings for >2 years, with only ~5% requiring repairs to the beading over time (Fisher and Muth 1989).

Field Site

The study area was located in the northern Coachella Valley outside Palm Springs, CA within the Whitewater Floodplain Preserve (1,230 acres), established in 1984 and managed by Bureau of Land Management (Alagona and Pincetl 2008). The area is characterized as a windblown ephemeral sandfield region in the Colorado Desert. Other lizard species present include the Zebra-tailed Lizard (*Callisaurus draconoides*), Coachella Valley Fringe-toed lizard (*Uma inornata*), and Flat-tailed Horned Lizard (*Phrynosoma mcallii*). Predators of lizards in this area include ravens, several species of raptors, Red Racers (*Masticophis flagellum*), Sidewinder rattlesnakes (*Crotalus cerastes*), Long-nosed Leopard Lizards (*Gambelia wislizenii*), and coyotes (pers. obs). The field site is 150 m by 150 m (fig. 3.2), marked every 10 m with wooden or plastic stakes on a North-South and East-West axis for a grid of 256 total stakes.

Home Range

Data for desert iguana locations were collected from May to September 2015 and 2016. Collecting times each year were divided into "mating season" and "non-mating season," May to early July and August to September, respectively for this species (Mayhew 1971; Krekorian 1984). In 2015 I observed what appeared to be two gravid females in September, suggesting instances of second clutches for some females potentially resulting from an unusually rainy August. However, for our purposes we have maintained the differentiation between mating and non-mating season regularly expected and previously described for this population.

A location for an individual desert iguana was given as the precise location that an iguana was first spotted within the field site. A researcher, upon seeing an adult desert iguana, would slowly approach until able to identify the colors of the individual's beading by plain sight or binoculars. The researcher would then approach and place a field flag at the location. At the end of the field day, locations were measured as the distance (in cm) and compass direction from the nearest stake. Global Positioning System (GPS) coordinates were also recorded but not ultimately used for analysis, as the GPS unit rarely achieved precision of less than ± 15 m.

To use locations for analysis, I converted the compass direction (degrees from North) into radians (for SPSS) and then into an angular direction using the stake as the origin. I used this angle and the distance from the given stake to give a precise XY location (in cm) from the stake and combined these measurements with the set XY coordinates of each stake (southwest corner (0,0), northeast corner (15000,15000)) to give precise coordinates for each location within the field site.

Locations were graphically depicted for individual lizards using the program Ranges 9 (Anatrack, Dorset, UK). Each set of locations was examined for location points well outside others, with widely disparate points removed. Removed points were thought to represent either the "occasional forays outside the home range"(Burt 1940) or a potential misidentification. Home range size was calculated using the Minimum Convex Polygon (MCP) function in Ranges (see Rose 1982 on lizard methods). This method is acceptable for a species that occupies only horizontal space (desert iguanas are rarely found >1 meter off the ground; Perry and Garland, Jr. 2002) and is the most common method used to assess home range size in lizards (Tinkle et al. 1962; Krekorian 1976; Fox et al. 1981; Rose 1982; Dubas and Bull 1992; DeNardo and Sinervo 1994a, 1994b; Bull and Baghurst 1998; Fair and Henke 1999; Civantos 2000; Haenel et al. 2003a, 2003b; Anderson 2013; Singleton and Garland, Jr. 2018).

Endurance

Lizards were captured from the field and transported by car to a location in Bonnie Bell, CA for endurance capacity testing (within 12 h of capture). Endurance capacity was measured as the amount of time a lizard was able to maintain position on a 1 km/hr fixed-speed treadmill (108 cm x 20 cm). Prior to endurance testing, lizards were incubated at 40 °C until internal body temperature approached 40 °C (as measured by thermocouple). Desert iguanas running at 40 °C attain maximal oxygen consumption at 1 km/h (John-Alder and Bennett 1981), though their natural movements typically involve more intermittent locomotion (Hancock and Gleeson 2005)Subjects were then placed on the moving treadmill and encouraged to continuously move via gentle taps on the tail and hind legs (Garland, Jr. 1994, 1999). The trial was terminated when a lizard failed to maintain position on the treadmill after 10 successive taps. Immediately after the trial, exhaustion was estimated by rating the strength of the “righting response,” or a lizard’s response to being inverted; the response was rated 1-3 with 1 as little-no attempt to right and 3 as immediately self-righted. Lizards that scored a 3 (no exhaustion) were returned to the treadmill in order to achieve full exhaustion. The trial was also rated by the researcher as to the tractability and “effort” of the subject; the trial was rated 1-5 with 1 as an unsuccessful trial (numerous escape attempts or refusal to walk/run) and 5 as an excellent trial. Trial rating was recorded as additional information to determine exclusions in analysis; however, no lizards had to be excluded from this study because of trial rating.

Following the endurance trial, morphometric measurements and body mass were taken and lizards were allowed to recover before being transported back to the field site and being released at the location of capture. Lizards were recaptured at a later date (>24 h after trial 1) for a second measurement of endurance capacity and to assess repeatability (Garland Jr. 2010). No lizards were taken for endurance capacity measurement the day of or <48 hrs after a blood sample was taken, to prevent potential effects of reduced hematocrit.

Blood Samples

Blood samples were taken from marked adult male desert iguanas once per season. The blood sampling procedure was as follows: three assistants systematically walked through the field site together, passing through each 10 m x 10 m section one time. This system insured that lizards were disturbed only once during the sampling attempts. Once an adult-sized lizard was sighted, a stopwatch was started and two people tried to catch the lizard via noosing while one person identified the sex and ID number of the lizard and checked the notebook to determine whether a blood sample was needed. When the lizard was caught, a 100 uL sample was taken via syringe from the ventral caudal vein. The stopwatch was stopped when the blood sample was complete. All samples were taken (from sighting to finish) in <5 minutes. If 5 minutes elapsed, the sampling process was terminated. Five minutes is well under the time in which a stress-induced corticosterone response has been detected in other reptiles (Romero and Reed 2005). Blood samples were not taken if the lizard had been tested for endurance capacity on the previous day, as the circulating corticosterone levels could retain some increases due to the the effects of the prolonged handling associated with endurance testing. Blood samples were transferred to a heparinized tube, stored on ice packs in the field and centrifuged <6 h after collection. Plasma was stored at -80°C. Prior to assays, corticosterone was separated from binding proteins using a steroid liquid extraction procedure specifically recommended for DetectX® Immunoassay kits from Arbor Assays (Ann Arbor, MI). The extracted sample was assayed using the K-014 Corticosterone EIA kit from Arbor Assays.

Ecological Characteristics

I measured a number of ecological variables expected to impact the usage and size of the home range of desert iguanas. Plant density was evaluated by counting the number of individual plants within 1.5 m of each stake, with counts taken monthly and averaged within the mating and non-mating seasons (May and June for mating, August and September for non-mating). This number was then evaluated from two perspectives: food plant density and shade plant density.

Food plant density was used to evaluate the density of plants that can act as food items for desert iguanas. The list of plants consumed by desert iguanas is taken from Minnich and Shoemaker (1970) and personal observation. Desert iguanas will consume the flowers of some plants and the leaves and flowers of other plants, and will selectively consume the flowers of some plants when they are present and consume the leaves when flowers are not present. Hence, plants counted were further separated into the categories of flowering, leafed or bare. Each consumable plant was given a score of 0, 1 or 2, depending on whether it had 0, 1 or 2 edible components. For example, a plant that has both edible (for desert iguanas) flowers and edible leaves, such as Fanleaf Crinklemat (*Tiquilia plicata*), would have a score of 2, whereas a plant with only edible flowers, such as Creosote (*Larrea tridentate*), would have a score of 1. Bare plants received a score of 0, as they could not be considered a food source. The score per plant species was multiplied by the number of plants per stake and this product for each species was summed to obtain a total food plant score associated with each stake. To estimate food plant density for individual desert iguana home ranges, the total food plant scores for each stake within a desert iguana's home range were summed and then divided by the home range area (m^2).

Shade plant density is not a typical environmental descriptor used to characterize a microhabitat or home range. However, it was included as a descriptor for this study due to the obvious ecological importance of shade areas for a desert lizard with diurnal activity (Norris 1953). Desert iguanas in the field maintain activity at body temperatures approaching 42°C (DeWitt 1967; DeWitt et al. 1967), but the sand in the field site in direct sun may reach far higher while desert iguanas are active. Regular stops in shaded areas are a feature of any active periods for desert iguanas.

To evaluate the shade quality, a spherical densiometer (Forestry Suppliers Inc., Jackson MS, model no. 43888) was used to measure the canopy cover for plants on the field site (Daubenmire 1959; Vora 1988). Plants were measured if they had at least 5 cm of space between stalks/branches and the ground available as a potential resting place. Twenty plants of each species were randomly chosen and measured at their area of densest canopy cover, and an average value was taken. Canopy cover of greater than 50% warranted a score of 1 in the shade plant density analysis. Plants with an average of less than 50% canopy cover received a score of 0. The score per plant species was multiplied by the number of plants per stake and this product for each species was summed to obtain a total shade plant score associated with each stake. To estimate shade plant density for individual desert iguana home ranges, the total shade plant scores for each stake within a desert iguana's home range were summed and then divided by the home range area (m^2).

Measurements of soil characters were also taken as a potential metric of burrow-suitability; though characters that enhance or encourage burrow-building in this species have not been formally researched, this feature has been examined in other burrowing species of lizards (Zaady and Bouskila 2002; Hayes et al. 2007). A pocket penetrometer with adaptor foot (Ctech, Hebei, China, Model# 16-T0171) was used to measure the compactability of the soil at each stake (1 m from the stake in each cardinal direction, then averaged) once per season (mating and non-mating) in both years. Soil samples were taken from 0.5 m from each stake, once per year, and the density of samples was measured (g/ml).

In the 2015 season, insects were collected at each stake via small pitfall traps (~0.5 L volume) for an evaluation of insects as food sources within home ranges. Traps were placed at stakes at 08:00 h, when most desert iguanas began activity, and removed at 15:00 h the same day; this time period was used to obtain an accurate index of insects active during desert iguana active periods. Values for each month portray a mean of 1.29 non-ant insects total (Chapter Appendix II): in essence, the insect presence was not sufficient to use for analysis in any meaningful fashion. Hence, insect numbers were not included in the overall analysis and insects were not collected again in 2016.

For statistical analysis, Paired *t*-tests and Pearson correlations in SPSS software were used to examine the repeatability of endurance trials. Two-way ANCOVAs were used to compare traits between years and seasons (mating vs non-mating). Linear regression was used to generate residual values for further analysis and to examine relationships between traits. Values were log-transformed for normality. Residual value of $\log_{10}$ plasma corticosterone concentrations were calculated with year and season as independent variables. For $\log_{10}$ endurance, residuals were calculated with year, season, their interaction, and $\log_{10}$ body mass as independent variables. For HR, residuals were first calculated with year, season, their interaction, and $\log_{10}$ body mass as independent variables. A second set of home range residuals was calculated with all of those independent variables plus the four ecological variables. The impacts of ecological variables on home range size were calculated using multiple regression, with model reduction based on the significance of partial coefficients.

Some individual lizards were sampled in multiple field seasons (maximum once per season). Upon consideration of sample size and temporal distance between measurements, values for these lizards were included in the analysis. Procedures concerning lizards were approved by the California Department of Fish and Wildlife under permit# sc12669. Procedures were also approved by the Institutional Animal Care and Use Committee of the University of California at Riverside under animal use protocol number 20130015 and 20160005.

Results

The repeatability of first and second endurance trials varied between years and seasons (Table 3.1; Fig. 3.3). In the 2015 mating season, the two measures of endurance capacity were significantly correlated but significantly different in a two-sample t-test, with the second trial averaging longer than the first. In the 2015 non-mating season as well as the mating and non-mating seasons of 2016, the two measures of endurance were not significantly correlated but were not significantly different.

Body mass did not differ significantly between years (Table 3.2; $N = 83$; $F = 3.113$; $P = 0.082$) or between seasons (mating vs. non-mating; $F = 0.117$; $P = 0.675$) with no significant year*season interaction ($F = 1.474$; $P = 0.228$). Snout-vent length also did not differ significantly between years (SVL; $N = 75$; $F = 0.018$; $P = 0.893$) or between seasons ($F = 0.391$; $P = 0.534$). Body mass was also not significantly different between years ($F = 2.261$; $P = 0.137$) or seasons ($R = 0.822$; $P = 0.368$) when SVL was included as a covariate.

Mean circulating corticosterone concentration for all male desert iguanas was 2.41 ± 0.38 ng/mL (SE; Range: 0.53-10.81 ng/mL). Values of $\log_{10}$ circulating corticosterone levels were not significantly correlated with blood collection delay time ($N = 38$; $R = -0.107$; $P = 0.552$). In a 2-way ANOVA, corticosteronelevel were significantly higher in 2015 than 2016 (Fig. 3.4A; $N = 38$; $F = 14.087$; $P = 0.001$) and significantly higher in the non-mating season vs. the mating season ($F = 4.389$; $P = 0.044$), with no interaction ($F = 0.400$; $P = 0.531$; Fig. 3.4A). Further results are available in Tables 3.3 and 3.4.

Mean endurance capacity was 19.46 ± 1.65 min (range: 4.22-51.50 min). Values of $\log_{10}$ endurance capacity were positively correlated with body mass, though the relationship was not significant (N = 49; R = 0.157; P = 0.282). Endurance capacity was also not significantly correlated with SVL (N = 49; R = 0.035; P = 0.810). Endurance capacity with body mass as a covariate was significantly higher in 2015 than 2016 (Fig. 3.4B; N = 49; F = 11.398; P = 0.002) and higher in the mating season than the non-mating season (F = 4.997; P = 0.031). Additionally, the year*season interaction was significant, as the difference between the mating and non-mating season was apparent in 2015 but not in 2016 (F = 5.022; P = 0.030; Fig. 3.4B). Further results are available in Tables 3.5, 3.6, and 3.7.

Mean home range size was 954 ± 124 m^2 (range: 157-3131 m^2). Values of $\log_{10}$ home range size were nearly significantly correlated with body mass (N = 40; R = 0.311; P = 0.051), but not with SVL (N = 35; R = 0.248; P = 0.150). Number of location points used for home range calculation and squared z-scores of location number were significant predictors for $\log_{10}$ home range size (R square = 0.298; number of points: B = 0.051, P = 0.001; squared z-score locations: B = -0.101, P = 0.021). In a multiple regression, home range size (with location point number, z-transformed point number squared, and body mass as covariates) was not significantly different between years (Fig. 3.4C; N = 40; F = 0.278; P = 0.601) nor between seasons (F = 0.021; P = 0.885); the interaction between year and season was also non-significant (F = 1.135; P = 0.294; Fig. 3.4C). Further results are available in Tables 3.8, 3.9, and 3.10. In this ANCOVA, the relation of $\log_{10}$ home range size to $\log_{10}$ body mass was not significant (F = 0.231; P = 0.634), while the relation to number of location points was significant and the relation to z-scored number of location points squared was positive and close to significance (Table 3.9).

Residual corticosterone concentration was not significantly correlated with residual endurance capacity (Fig. 3.5; N = 26; R = 0.094; P = 0.647) or with residual home range size (Fig. 3.6; N = 23; R = 0.139; P = 0.526). Endurance residuals were not significantly correlated with residual home range size (Fig. 3.7; N = 32; R = -0.168; P = 0.358). Residual home range was not significantly predicted in a multiple regression with residual corticosterone and residual endurance (N = 21; R = 0.270; P = 0.487). In further analysis of factors predicting home range size, additional home range residuals were calculated including the ecological variables shade plant density as well as year, season, location point number, z-transformed point number squared and body mass. These home range residuals were also not significantly correlated with endurance residuals (N = 32; R = -0.286; P = 0.112) or corticosterone residuals (N = 23; R = 0.072; P = 0.743). Secondary home range residuals were not significantly predicted in a multiple regression on residual corticosterone and residual endurance (N = 21; R = 0.242; P = 0.565).

Soil compactibility within home ranges was not significantly different between seasons (F = 1.068; 0.307) or years (F = 1.751; P = 0.192). In the analysis of ecological variables and their relationship to home range, the initial model included all available ecological measurements (Table 3.11: soil compactibility, soil density, food plant density, and shade plant density) as well as body mass, number of location points, z-transformed point number squared, year, mating season, and the year*mating season interaction (Table 3.12). Of the ecological independent variables, only shade plant density had a significant partial regression coefficient, and it was negative (N = 40; d.f. = 1, 29; partial F = 7.456; B = -0.386; P = 0.011). Number of location points was also significant (B = 0.055; P = 0.001). In further analysis, non-significant variables were removed from the model in sequence (with the exception of body mass); the resulting model included body mass, shade plant density, year, season, year*season interaction, number of location points, and z-transformed number of points squared (Table 3.13). The resulting model was highly significant (Adjusted R square = 0.411; P = 0.001) and shade plant density remained significant (partial F = 9.441; B = -0.370; P = 0.004).

Discussion

Body masses of male desert iguanas did not vary significantly between the mating season and the non-mating season, though males in the mating season were slightly heavier on average than those in the non-mating season (Table 3.2). *Dipsosaurus* males are typically heavier in the spring than the summer (May vs. August; Minnich 1971), though it is unclear whether this difference is due to stored fat or hydration levels.

The mean circulating corticosterone concentration obtained in the present study (2.41 ng/mL) was similar to those for other iguanas and members of the Suborder Iguania (4 - 16.3 ng/mL; DeNardo and Licht 1993; Dunlap and Wingfield 1995; Hanley and Stamps 2002; Romero and Wikelski 2002; Robertson et al. 2011; Hews and Abell Baniki 2013). In a previous study examining circadian rhythm in desert iguanas, the mean corticosterone between 08:00 h and 12:00 h was 26.9 ng/mL (as compared with 2.41 ng/mL in this study; Chan and Callard 1972). The previous study used captive females and did not comment on the disturbance of individuals prior to blood sampling; these differences in study design may explain variation in results for basal corticosterone values in *Dipsosaurus*. My values for corticosterone in adult males were significantly different between seasons, with higher circulating corticosterone levels occurring during the non-mating season as compared with the mating season. The timing of peak corticosterone on a yearly cycle varies in reptiles; though in many species high basal corticosterone coincides with reproductive activity (Eikenaar et al. 2012; reviewed in Moore and Jessop 2003), in other species this is not the case (Tokarz et al. 1998; Amey and Whittier 2000; Ott et al. 2000). As the non-mating season corresponds with the hottest part of the dry season in the Mojave desert (August-mid-September), increased circulating corticosterone may also be the result of environmental stressors (Wingfield et al. 1997; Kitaysky et al. 2001).

Endurance capacity also varied between the mating and the non-mating season, with higher endurance capacity seen during the mating season (spring-early summer: Table 3.5). This difference agrees with previous literature on this species. In a study examining seasonal variation in a number of physiological traits in desert iguanas, endurance capacity (males and females combined) was found to peak in spring (early June), with a decrease in late summer (September; John-Alder 1984).

Home range size did not vary significantly between seasons for free-living adult male desert iguanas. This contrasts with male lizard seasonal behavior in other species (Stamps 1983); for example, in *Sceloporus undulatus*, male home range size decreases significantly after the mating season (Ferner 1974). For many terrestrial male lizards, the maintenance of a large home range is a benefit when it increases reproductive fitness but an unnecessary energy expenditure otherwise. Desert iguanas may require home ranges of a given size throughout the active season due to resource needs (Norris 1953; Krekorian 1976), as herbivores in seasonal environments (such as the rainy/dry season in a desert) require greater resource heterogeneity to ensure consistent food sources (Saïd et al. 2005). Alternately, the potential for second clutches during the year (with mating occurring in August; pers. obs.) may motivate a strategy of long-term home-range maintenance.

The relationships between circulating corticosterone, endurance capacity, and home range size are complex and may be impacted by numerous factors beyond the scope of the present research. Circulating corticosterone measurements were especially vulnerable to variation, as the lizards were free-living and any combat, predator evasion, or other stress-inducing occurrence not directly witnessed could not be accounted for in the measurements. Previously, we reported a significant positive correlation between endurance capacity and home range size in desert iguanas of this population in Fall 2014 and Spring 2015 (Singleton and Garland, Jr. 2018a). However, that relationship was not apparent in the present study. Desert iguanas are known to use intermittent locomotion in nature, a combination of motion and rests that can maximize endurance beyond that described in a laboratory setting (Hancock and Gleeson 2005).

The negative relationship between shade plant density and home range size found in this study is, to our knowledge, a novel finding, though numerous previous studies have found similar relationships between plant food density and home range size in mammalian herbivores (Lucherini and Lovari 1996; Tufto et al. 1996; Relyea et al. 2000; Saïd et al. 2005; Schradin et al. 2010). In principle, the less of a given resource available in an area, the larger the home range would need to be in order to fulfill the needs of an individual. In other lizard studies (typically done with insectivorous lizards), home range size is not negatively related to food density (Ruby and Dunham 1987), and experimental increases in food resources have not changed home range size (Waldschmidt 1983; Dubas and Bull 1992 [herbivorous lizard]). In a previous study of desert iguanas in Thousand Palms, CA, home range size increased significantly after a 5 day sandstorm that decimated the vegetation in the area (Krekorian 1976); however, that study did not quantify plant abundance or status as food plants. For a diurnal ectotherm in a thermally extreme environment, plants as thermal refugia may be a more crucial aspect of microhabitat than even food.

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Table 3.1. Repeatability of first and second endurance capacity trials for free-living adult male desert iguanas during the mating and non-mating seasons of 2015 and 2016. * indicates statistical significance at $p < 0.05$. The significant difference between trials in the mating season of 2015 reflects an increase from first to second endurance trial.

		Pearson Correlation		Paired-*t* test		
Season	N	R	P	Paired-*t*	P	Direction of Change
Mating 2015	19	0.699	*0.001	2.242	*0.038	Increase
Non-mating 2015	8	0.412	0.310	0.119	0.909	---
Mating 2016	16	0.140	0.605	-1.138	0.273	---
Non-mating 2015	6	0.202	0.702	0.411	0.698	---

Table 3.2. Descriptive statistics for $\log_{10}$ body mass (g).

Descriptive Statistics

Dependent Variable: $\log_{10}$ Corticosterone

Year	Season	N	Mean	Std. Deviation
2015	Non-mating	15	1.9099	0.05549
	Mating	31	1.8999	0.05720
	Total	46	1.9032	0.05623
2016	Non-mating	15	1.8724	0.04992
	Mating	22	1.8930	0.05385
	Total	37	1.8847	0.05259
Total	Non-mating	30	1.8912	0.05525
	Mating	53	1.8970	0.05541
	Total	83	1.8949	0.05509

Table 3.3. Descriptive statistics for $\log_{10}$ circulating corticosterone (ng/mL).

Descriptive Statistics

Dependent Variable: $\log_{10}$ Corticosterone

Year	Season	N	Mean	Std. Deviation
2015	Non-mating	7	0.5586	0.29812
	Mating	15	0.2991	0.26881
	Total	22	0.3817	0.29810
2016	Non-mating	7	0.1414	0.33400
	Mating	9	0.0023	0.23457
	Total	16	0.0632	0.28115
Total	Non-mating	14	0.3500	0.37331
	Mating	24	0.1878	0.29097
	Total	38	0.2476	0.32845

Table 3.4. ANOVA of $\log_{10}$ circulating corticosterone (ng/mL) with factors of year and season (mating vs. non-mating).

Tests of Between-Subjects Effects

Dependent Variable: $\log_{10}$ Corticosterone

Source	Type III Sum of Squares	df	Mean Square	F	P
Corrected Model	1.337[a]	3	0.446	5.709	0.003
Intercept	2.164	1	2.164	27.718	0.000
Year	1.100	1	1.100	14.087	0.001
Season	0.343	1	0.343	4.389	0.044
Year *season	0.031	1	0.031	0.400	0.531
Error	2.654	34	0.078		
Total	6.321	38			
Corrected Total	3.991	37			

a. R Squared = 0.335 (Adjusted R Squared = 0.276)

Table 3.5. Descriptive statistics for $\log_{10}$ endurance capacity (minutes).

Descriptive Statistics

Dependent Variable: $\log_{10}$ Endurance

Year	Season	N	Mean	Std. Deviation
2015	Non-mating	8	1.2965	0.28383
	Mating	19	1.2974	0.27127
	Total	27	1.2972	0.26951
2016	Non-mating	6	.8613	0.17190
	Mating	16	1.2036	0.17001
	Total	22	1.1103	0.22810
Total	Non-mating	14	1.1100	0.32356
	Mating	35	1.2546	0.23229
	Total	49	1.2132	0.26632

Table 3.6. ANCOVA of $\log_{10}$ endurance capacity with factors of year and season (mating vs. non-mating) and $\log_{10}$ body mass as a covariate.

Tests of Between-Subjects Effects

Dependent Variable: $\log_{10}$ Endurance

Source+	Type III Sum of Squares	df	Mean Square	F	P
Corrected Model	0.935[a]	4	0.234	4.163	0.006
Intercept	0.044	1	0.044	0.777	0.383
Log_{10} Body Mass	0.000	1	0.000	0.000	0.995
Year	0.640	1	0.640	11.398	0.002
Season	0.280	1	0.280	4.997	0.031
Year*season	0.282	1	0.282	5.022	0.030
Error	2.470	44	0.056		
Total	75.531	49			
Corrected Total	3.405	48			

a. R Squared = 0.275 (Adjusted R Squared = 0.209)

Table 3.7. Estimated marginal means for $\log_{10}$ endurance capacity in an ANCOVA with factors of year and season (mating vs. non-mating) and $\log_{10}$ body mass as a covariate. Because the effect of body mass was nil, these numbers are virtually identical to those in Table 4.

Estimated Marginal Means

Dependent Variable: $\log_{10}$ Endurance

Year	Season	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
2015	Non-mating	1.297[a]	0.084	1.127	1.466
	Mating	1.298[a]	0.055	1.187	1.408
2016	Non-mating	0.861[a]	0.100	0.659	1.063
	Mating	1.204[a]	0.059	1.084	1.323

a. Covariates appearing in the model are evaluated at the following values: Log_{10} Body Mass = 1.9019.

Table 3.8. Descriptive statistics for $\log_{10}$ home range size (m^2).

Descriptive Statistics

Dependent Variable: $\log_{10}$ Home Range Size

Year	Season	N	Mean	Std. Deviation
2015	Non-mating	6	2.9043	0.41210
	Mating	21	2.8113	0.31090
	Total	27	2.8320	0.32949
2016	Non-mating	3	2.5543	0.16989
	Mating	10	2.9711	0.39787
	Total	13	2.8749	0.39615
Total	Non-mating	9	2.7876	0.37944
	Mating	31	2.8628	0.34306
	Total	40	2.8459	0.34796

Table 3.9. ANCOVA of $\log_{10}$ home range size (m^2) with factors of year and season (mating vs. non-mating) and covariates of $\log_{10}$ body mass, number of location points used for home range calculation, and z-scores of location points squared.

Tests of Between-Subjects Effects

Dependent Variable: $\log_{10}$ Home Range Size

Source	Type III Sum of Squares	df	Mean Square	F	P
Corrected Model	1.766[a]	6	0.294	3.286	0.012
Intercept	0.019	1	0.019	0.213	0.648
Year	0.025	1	0.025	0.278	0.601
Season	0.002	1	0.002	0.021	0.885
Year*season	0.102	1	0.102	1.135	0.294
Log_{10} Body Mass	0.021	1	0.021	0.231	0.634
Location points for HR	0.545	1	0.830	9.269	0.005
$(\text{Zscore Location points})^2$	0.319	1	0.319	3.563	0.068
Error	2.956	33	0.090		
Total	328.693	40			
Corrected Total	4.722	39			

a. R Squared = 0.374 (Adjusted R Squared = 0.260)

Table 3.10. Estimated marginal means of $\log_{10}$ home range size (m^2) from an ANCOVA with factors of year and season (mating vs. non-mating) and covariates of $\log_{10}$ body mass, number of location points used for home range calculation, and squared z-scores of location points.

Estimated Marginal Means

Dependent Variable: $\log_{10}$ Home Range Size

Year	Season	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
2015	Non-mating	2.923[a]	0.128	2.662	3.184
	Mating	2.764[a]	0.068	2.625	2.903
2016	Non-mating	2.851[a]	0.192	2.460	3.241
	Mating	2.971[a]	0.097	2.774	3.168

a. Covariates appearing in the model are evaluated at the following values: $\log_{10}$ Body Mass = 1.9046, location points in home range = 12.5500, squared Z-score of location points = 0.000.

Table 3.11. Correlation matrix of environmental variables (soil compactibility, soil density, food plant density, and shade density). Significant correlations are in bold. (N = 40).

		Shade Plant Density	Soil Density	Soil Compactibility
Pearson Correlation	Food Plant Density	**0.379**	0.300	0.106
	Shade Plant Density		**0.330**	-0.098
	Soil Density			-0.056
Sig. (2-tailed)	Food Plant Density	**0.016**	0.060	0.106
	Shade Plant Density		**0.037**	0.546
	Soil Density			0.730

Table 3.12. Results of regression analysis of $\log_{10}$ home range size in all years/seasons with ecological variables as predictors: soil compactibility, soil density, shade plant density, and food plant density (N = 40). Model also includes year, season, year*season interaction, $\log_{10}$ body mass, number of location points used for home range calculation, and squared z-scores of location points.

Partial Regression Coefficients^{a}

Model	Unstandardized Coefficients		Standardized Coefficients	t	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	0.0012	4.183		0.003	0.998	-8.543	8.567
Log_{10} Body Mass	-0.009	0.901	-0.001	-0.010	0.992	-1.852	1.834
Soil Compactibility	-0.303	0.352	-0.118	-0.863	0.395	-1.023	0.416
Soil Density	1.576	2.303	0.109	0.684	0.499	-3.134	6.285
Food Plant Density	-0.016	0.034	-0.068	-0.473	0.640	-0.085	0.053
Shade Plant Density	-0.386	0.141	-0.434	-2.731	0.011	-0.675	-0.097
Location Point Number	0.055	0.015	1.045	3.597	0.001	0.024	0.087
Squared z-score of points	-0.091	0.046	-0.565	-1.991	0.056	-0.184	0.002
Year	0.076	0.236	0.103	0.321	0.750	-0.407	0.558
Season	-0.123	0.146	-0.149	-0.840	0.408	-0.421	0.176
Year*season	0.241	0.261	0.303	0.924	0.363	-0.292	0.774

a. Dependent Variable: $\log_{10}$ home range area   R squared = 0.540 (Adjusted R squared = 0.381)

Table 3.13. Results of regression analysis of $\log_{10}$ home range size in all years/seasons with shade plant density (N = 40). Reduced model also includes year, season, year*season interaction, $\log_{10}$ body mass, number of location points used for home range calculation, and z-scores of location points squared.

Partial Regression Coefficients[a]

Model	Unstandardized Coefficients		Standardized Coefficients	t	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	2.344	1.655		1.416	0.166	-1.027	5.716
Log10 Body Mass	0.073	0.871	0.012	0.084	0.934	-1.701	1.848
Shade Plant Density	-0.370	0.120	-0.416	-3.073	0.004	-0.615	-0.125
Location Point Number	0.053	0.014	1.008	3.671	0.001	0.024	0.083
Squared Z-score of points	-0.078	0.041	-0.485	-1.902	0.066	-0.161	0.006
Year	0.025	0.207	0.034	0.122	0.904	-0.397	0.448
Season	-0.179	0.134	-0.218	-1.338	0.190	-0.451	0.093
Year*season	0.306	0.234	0.386	1.307	0.201	-0.171	0.784

a. Dependent Variable: $\log_{10}$ home range size R squared = 0.517 (adjusted R squared = 0.411)

Figure Legends

Figure 3.1. A) Illustrated diagram of the beading procedure, reproduced from Fisher and Muth (1989). B) Photograph of tail beading on *Dipsosaurus dorsalis*, taken by Jennifer Singleton. White-red-red translates to unique identification number 0-1-1 or 11.

Figure 3.2. Aerial photo of field site screen-captured from GoogleMaps October 31st 2015, with boundaries and size indicated.

Figure 3.3. Repeatability of first and second endurance capacity measurements made for individual free-living desert iguanas from northern Palm Springs, CA, separated by year and season (mating vs. non-mating season). Endurance trials in the mating season of 2015 (**A**) were significantly correlated (N = 19; R = 0.699; P = 0.001), while values for the non-mating season of 2015 (**B**) as well as the mating and non-mating seasons of 2016 (**C** and **D**, respectively) were not significantly correlated (2015NM: N = 9, R = 0.412, P = 0.310; 2016M: N = 16, R = 0.140, P = 0.605; 2016NM: N = 6, R = 0.202, P = 0.702). Endurance trials in the mating season of 2015 were significantly different (t = 2.242; p = 0.038). Values for individuals in the 2015 non-mating season as well as the mating and non-mating seasons of 2016 were not significantly different (2015 NM: t = 0.119, p = 0.909; 2016M t = -1.138, p = 0.273; 2016NM t = -0.411, p = 0.698).

Figure 3.4. Estimated marginal means $\pm$ SE of (A) $\log_{10}$ circulating corticosterone (ng/mL), (B) $\log_{10}$ endurance capacity (min; covariate of body mass), and $\log_{10}$ home range size (m^2; covariates of body mass, number of location points used for home range calculation, and z-scores of location points squared) during the mating and non-mating seasons of 2015 and 2016 in *Dipsosaurus dorsalis* in northern Palm Springs, CA. Some lizards were measured for variables in more than one season.

Figure 3.5. Scatterplot of $\log_{10}$ circulating corticosterone (ng/mL) and $\log_{10}$ endurance capacity (min; covariate of body mass) during the mating and non-mating seasons of 2015 and 2016 in *Dipsosaurus dorsalis* in northern Palm Springs, CA. The relationship between circulating corticosterone and residual values of endurance capacity was not significant ($N = 26$; $r = 0.094$; $P = 0.324$).

Figure 3.6. Scatterplot of $\log_{10}$ circulating corticosterone (ng/mL) and $\log_{10}$ home range size (m^2; covariates of shade plant density, body mass, number of location points used for home range calculation, and z-score of number of points squared) during the mating and non-mating seasons of 2015 and 2016 in *Dipsosaurus dorsalis* in northern Palm Springs, CA. The relationship between circulating corticosterone and residual values of home range size was not significant ($N = 23$; $r = -0.075$; $P = 0.367$).

Figure 3.7. Scatterplot of $\log_{10}$ endurance capacity (min; covariate of body mass) and $\log_{10}$ home range size (m^2; covariates of shade plant density, body mass, number of

location points used for home range calculation, and z-score of number of points squared) during the mating and non-mating seasons of 2015 and 2016 in *Dipsosaurus dorsalis* in northern Palm Springs, CA. The relationship between residual values of endurance capacity and residual values of home range size was not significant (N = 32; r = r = -0.112; P = 0.367).

Figure 3.1.

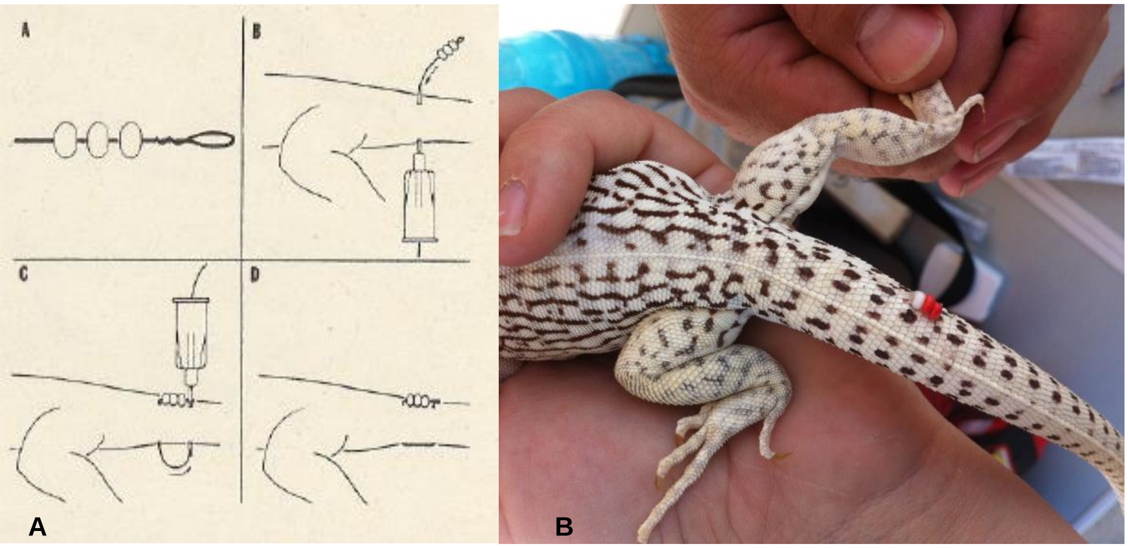


Figure 3.2.


150 m
Google
Imagery ©2015 Google, Map data ©2015 Google Terms Privacy

Figure 3.3.

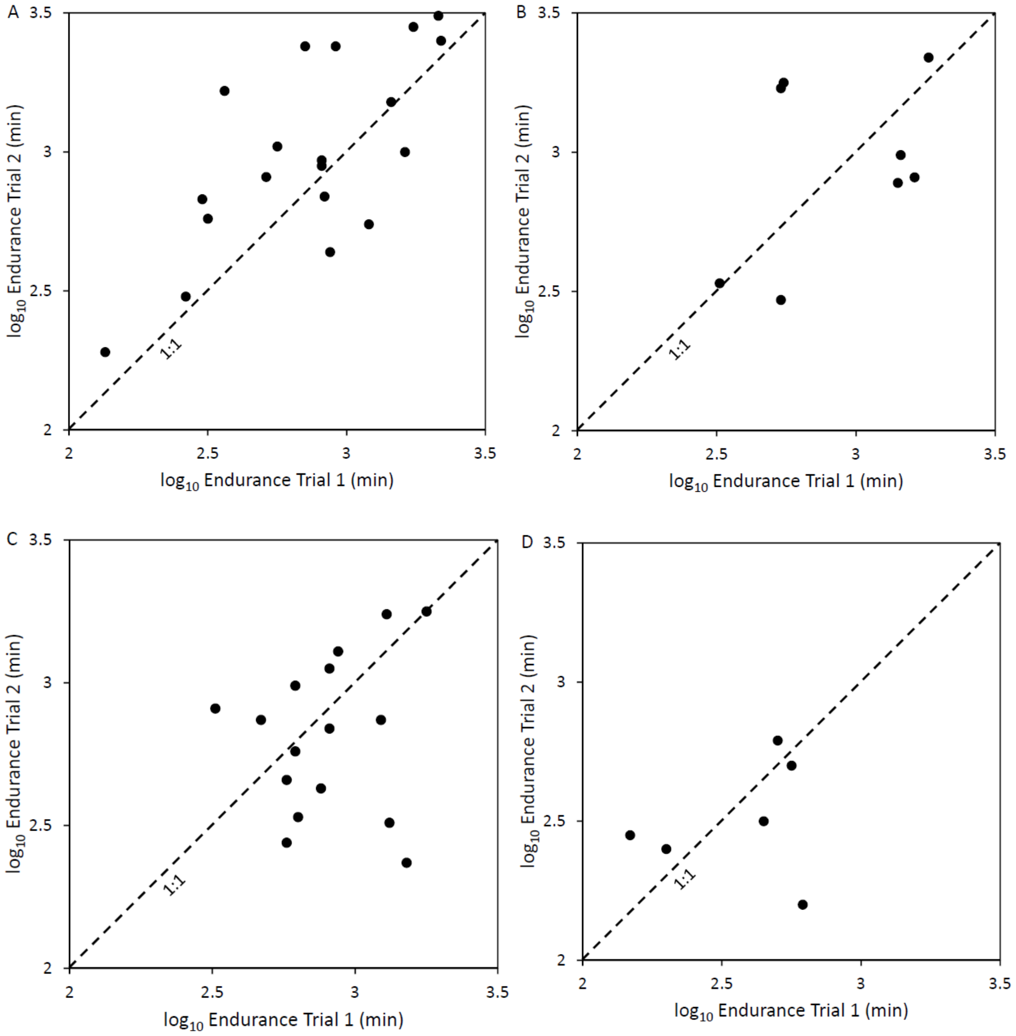

A
B
C
D
3.5
3
2.5
2
2.5
3
3.5
1:1
$\log_{10}$ Endurance Trial 2 (min)
$\log_{10}$ Endurance Trial 1 (min)

Figure 3.4.

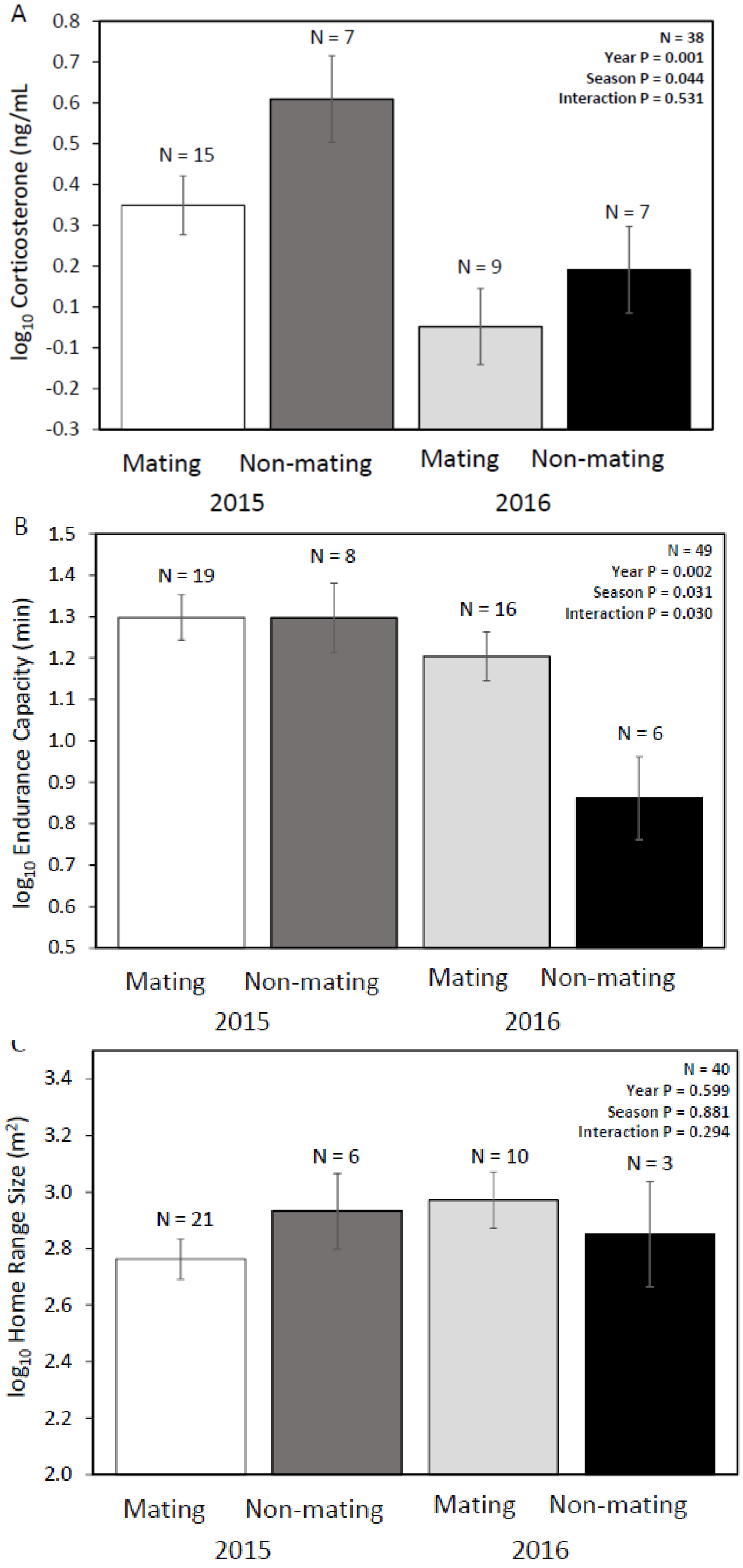

A
log$_{10}$ Corticosterone (ng/mL)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
-0.1
-0.2
-0.3
N = 15
N = 7
N = 9
N = 7
N = 38
Year P = 0.001
Season P = 0.044
Interaction P = 0.531
Mating
Non-mating
Mating
Non-mating
2015
2016
B
log$_{10}$ Endurance Capacity (min)
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
N = 19
N = 8
N = 16
N = 6
N = 49
Year P = 0.002
Season P = 0.031
Interaction P = 0.030
Mating
Non-mating
Mating
Non-mating
2015
2016
C
log$_{10}$ Home Range Size (m^2)
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
N = 21
N = 6
N = 10
N = 3
N = 40
Year P = 0.599
Season P = 0.881
Interaction P = 0.294
Mating
Non-mating
Mating
Non-mating
2015
2016

Figure 3.5.

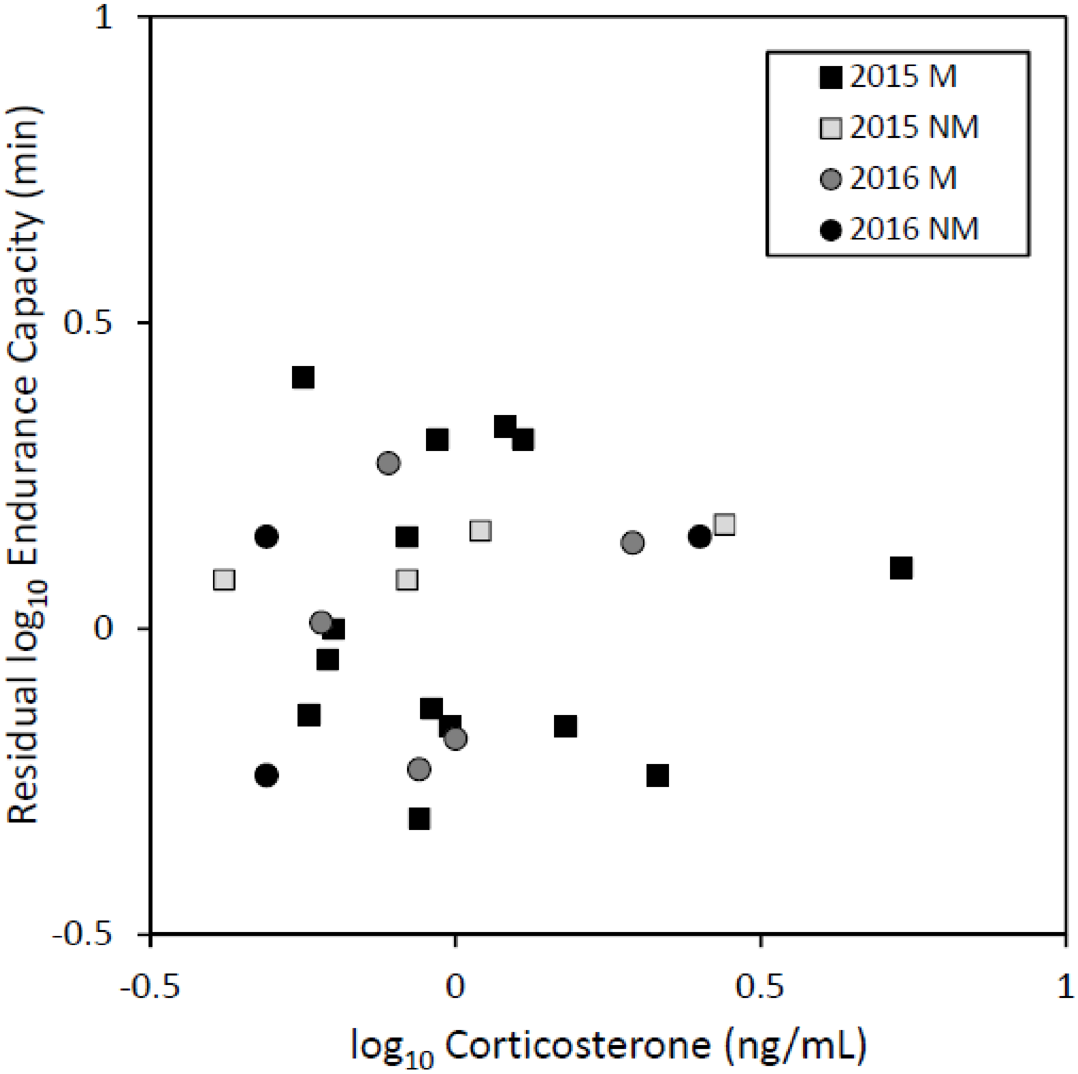

■ 2015 M
□ 2015 NM
● 2016 M
● 2016 NM
1
0.5
0
-0.5
-0.5
0
0.5
1
Residual log10 Endurance Capacity (min)
log10 Corticosterone (ng/mL)

Figure 3.6.

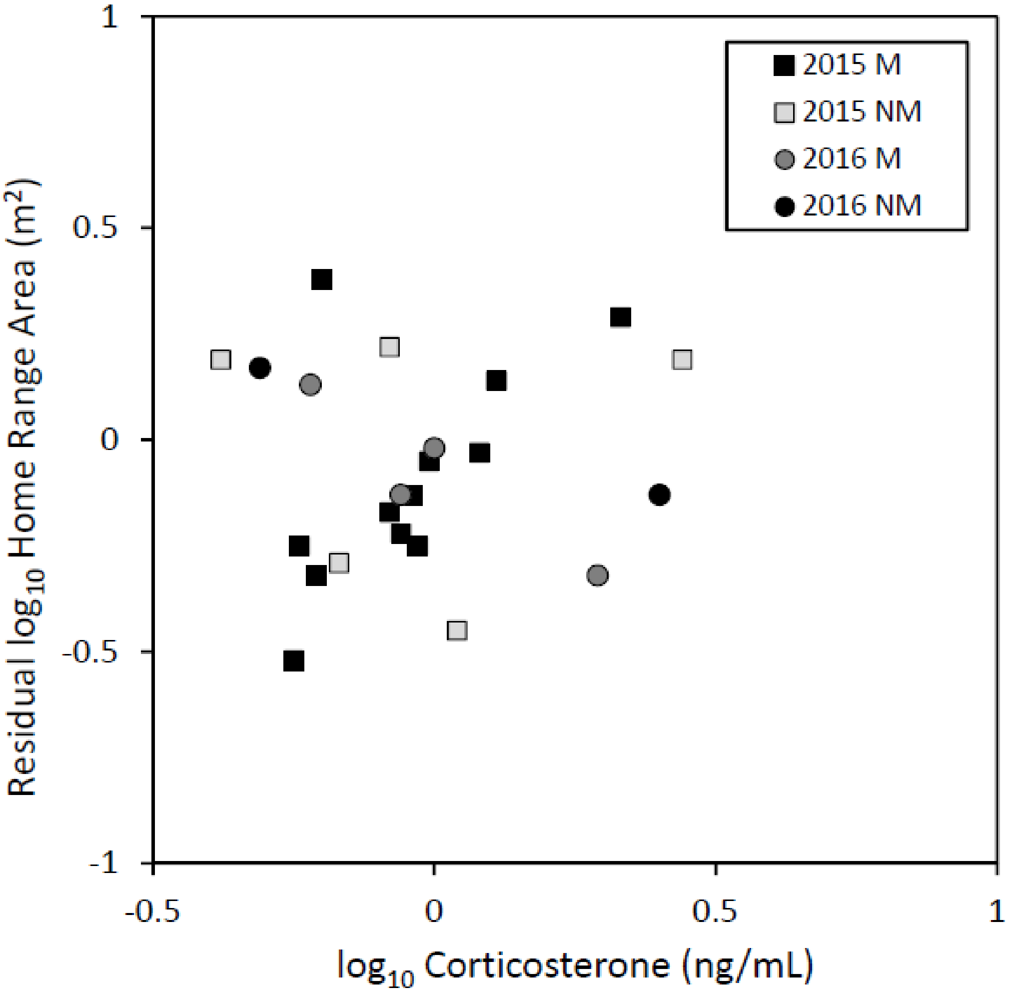
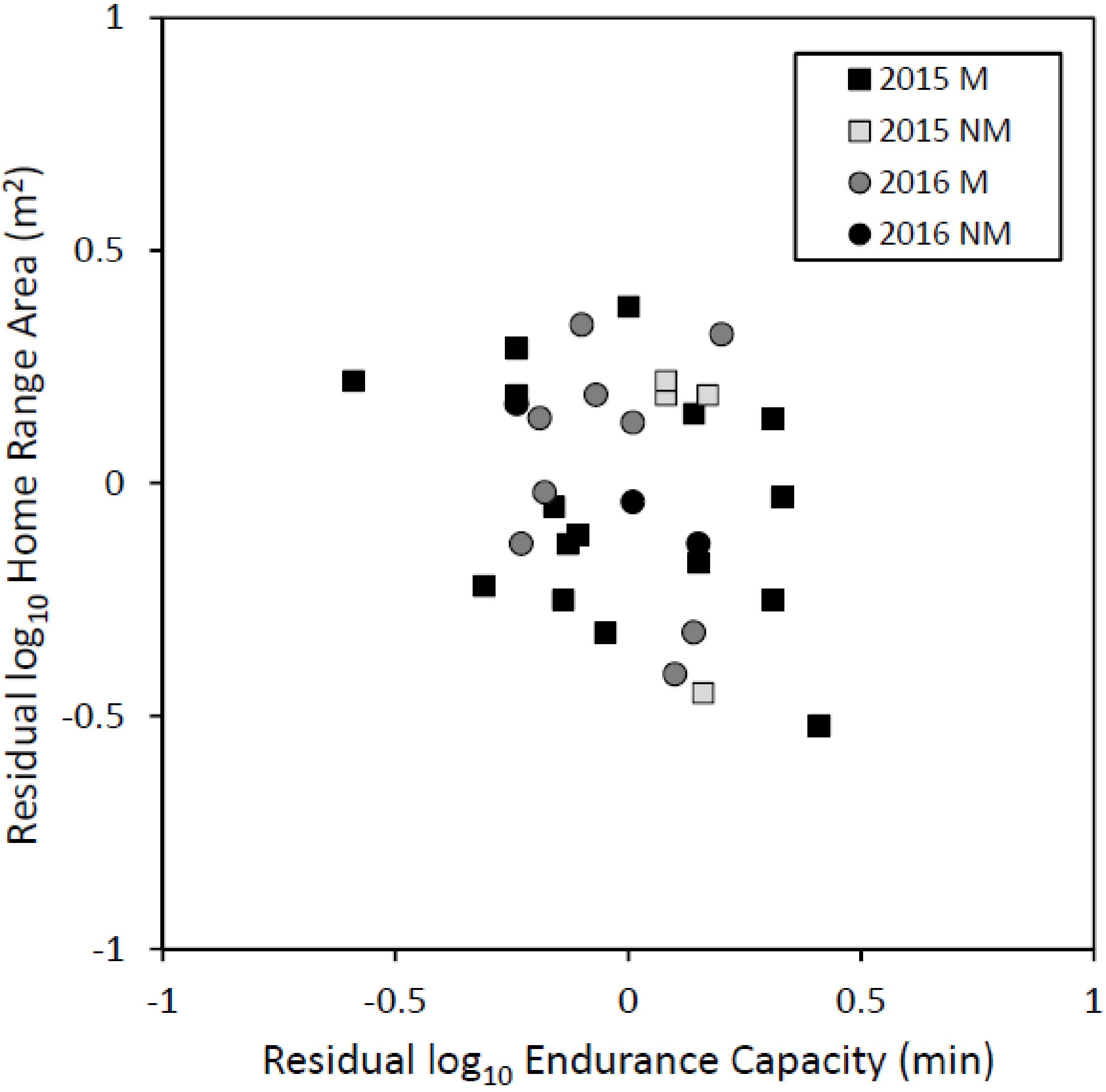

1
0.5
0
-0.5
-1
-0.5
0
0.5
1
Residual log10 Home Range Area (m2)
log10 Corticosterone (ng/mL)
■ 2015 M
□ 2015 NM
● 2016 M
● 2016 NM

Figure 3.7



1
0.5
0
-0.5
-1
-1
-0.5
0
0.5
1
Residual $\log_{10}$ Home Range Area (m^2)
Residual $\log_{10}$ Endurance Capacity (min)
■ 2015 M
□ 2015 NM
● 2016 M
● 2016 NM

		2015						2016						Resource	
Name	**State**	**Mating**			**Non-Mating**			**Mating**			**Non-Mating**			**Food**	**Shade**
Perennials:		Mean	Max	Pct	Mean	Max	Pct	Mean	Max	Pct	Mean	Max	Pct		
Coldenia procumbens	F	0.152	9	10.2	0.035	2	3.1	1.453	27	33.2	0.887	16	23.4	**1**	**0**
	L	0.111	2	10.0	0.076	3	6.1	0.656	16	22.1	0.871	9	31.3	**0**	**0**
	B	0.012	1	1.2	0.033	1	3.3	0.094	4	5.7	0.336	10	18.8	**0**	**0**
Tiquilia plicata	F	0.000	0	0.0	0.002	1	0.2	0.000	0	0.0	0.000	0	0.0	**1**	**0**
	L	0.055	3	3.9	0.006	1	0.6	0.230	40	3.7	0.027	2	2.3	**1**	**0**
	B	0.014	2	0.8	0.000	0	0.0	0.018	5	1.0	0.039	3	2.3	**0**	**0**
Euphorbia polycarpa	F	1.318	43	26.0	0.012	5	0.4	0.121	17	3.1	0.008	2	0.4	**1**	**0**
	L	1.771	32	38.7	1.689	27	34.0	2.377	46	27.7	2.250	40	38.3	**1**	**0**
	B	0.156	17	6.3	0.418	13	21.3	0.074	8	4.3	0.426	15	16.0	**0**	**0**
Petalonyx thurberi	F	0.150	6	9.4	0.205	4	15.0	0.174	4	11.7	0.168	4	12.1	**1**	**1**
	L	0.123	3	9.8	0.102	3	8.0	0.049	12	2.7	0.129	3	10.2	**1**	**1**
	B	0.191	6	14.6	0.232	6	20.1	0.084	1	8.4	0.191	3	17.6	**0**	**0**
Baccharis sarothroides	F	0.000	0	0.0	0.000	0	0.0	0.002	1	0.2	0.000	0	0.0	**0**	**1**
	L	0.059	12	2.3	0.021	3	1.8	0.027	9	1.0	0.012	1	1.2	**0**	**1**
	B	0.051	7	2.5	0.047	2	4.3	0.074	11	2.7	0.156	8	8.2	**0**	**0**
Psorothamnus arborescens	F	0.002	1	0.2	0.000	0	0.0	0.029	3	2.3	0.004	1	0.4	**1**	**0**
	L	0.018	1	1.8	0.010	1	1.0	0.014	2	1.2	0.008	1	0.8	**1**	**0**
	B	0.131	5	5.3	0.084	4	6.8	0.012	1	1.2	0.078	4	5.9	**0**	**0**
Psorothamnus spinosus	F	0.021	1	2.1	0.002	1	0.2	0.160	3	11.3	0.000	0	0.0	**1**	**1**
	L	0.445	5	28.1	0.316	3	21.9	0.082	2	7.0	0.320	3	21.1	**1**	**1**
	B	0.139	11	9.8	0.234	4	17.2	0.082	21	4.1	0.199	3	14.8	**0**	**1**

Larrea tridentata	F	0.025	1	2.5	0.002	1	0.2	0.008	1	0.8	0.000	0	1	**1**	**1**
	L	0.008	1	0.8	0.055	1	0.5	0.014	4	0.4	0.039	1	1	**0**	**1**
	B	0.006	1	0.6	0.012	1	1.2	0.012	1	1.2	0.012	1	1.2	**0**	**1**
Croton californicus	F	0.000	0	0.0	0.000	0	0.0	0.002	1	0.2	0.000	0	0.0	**1**	**1**
	L	0.020	3	1.4	0.000	0	0.0	0.020	5	0.6	0.000	0	0.0	**1**	**1**
	B	0.037	6	1.0	0.000	0	0.0	0.020	7	0.6	0.000	0	0.0	**0**	**0**
Annuals:															
Cryptantha angustifolia	F	0.006	2	0.4	0.000	0	0.0	0.074	13	2.0	0.000	0	0.0	**1**	**0**
	L	0.174	24	5.1	0.000	0	0.0	0.309	91	2.1	0.000	0	0.0	**0**	**0**
	B	5.926	39	75.8	1.805	21	54.9	17.18	160	54.9	7.754	56	72.3	**0**	**0**
Brassica tournefortii	F	0.004	1	0.4	0.000	0	0.0	0.029	6	1.2	0.000	0	0.0	**0**	**0**
	L	0.002	1	0.2	0.000	0	0.0	0.066	21	2.3	0.004	1	0.4	**0**	**0**
	B	0.027	4	1.4	0.004	2	0.2	2.213	35	30.1	1.875	30	28.9	**0**	**0**
Grasses (various species)	F	0.238	25	4.3	0.002	1	0.2	0.010	5	0.2	0.000	0	0.0	**0**	**0**
	L	0.277	36	4.1	0.012	4	0.4	0.150	22	2.7	0.020	5	0.4	**0**	**0**
	B	26.807	97	85.7	18.53	83	85.9	5.738	120	31.3	16.73	83	68.8	**0**	**0**

Appendix I. List of plant species (perennials and annuals) separated by states (F = flowering, L = leafed, B = bare) and the mean number of plants per stake (within 1.5 m diameter of the stake; 256 total stakes), the maximum number per stake section, the median number of plants per stake, and the percent of stake subsections where the plant was present. Numbers presented are mean values of months within the given season (May and June = Mating season, August and September = Non-mating season). Minimum number for each plant was always 0. In addition, the determination for each species/state as either a food or shade resource is indicated.

Appendix II. Results of Arthropod Trapping

Month	**Mean**	**Valid Percent of Frequency of Number of Insects**					
		% = 0	% = 1	% = 2	% = 3	% = 4	% = 5 or greater
April	1.36	41.0	37.1	7.6	7.6	3.8	3.0
May	0.83	59.5	20.6	9.9	4.8	1.6	3.6
June	1.34	46.0	23.0	11.9	8.7	4.8	5.6
Mating Season	1.13						
August	1.70	47.1	17.5	10	6.3	5.8	13.3
Sept	1.24	46.9	26.8	12.6	5.9	1.6	6.4
Non-mating season	1.42						
Overall	1.29						

Appendix III. SPSS syntax

```
GET FILE='C:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl.sav'.

**********BODY MASS*************************************.

GET  FILE='C:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl.sav'.

UNIANOVA Lmass BY year MATE

  /METHOD=SSTYPE(3)

  /INTERCEPT=INCLUDE

  /EMMEANS=TABLES(MATE*year)

  /PRINT=DESCRIPTIVE

  /CRITERIA=ALPHA(.05)

  /DESIGN=MATE*year year MATE.


UNIANOVA LgSV BY year MATE

  /METHOD=SSTYPE(3)

  /INTERCEPT=INCLUDE

  /EMMEANS=TABLES(MATE*year)

  /PRINT=DESCRIPTIVE

  /CRITERIA=ALPHA(.05)

  /DESIGN=MATE*year year MATE.


UNIANOVA Lmass BY year MATE WITH LgSV

  /METHOD=SSTYPE(3)
```

```
 /INTERCEPT=INCLUDE
 /SAVE=RESID ZRESID
 /CRITERIA=ALPHA(0.05)
 /DESIGN=LgSV year MATE year*MATE.


********************CORTICOSTERONE*******************************.
GET  FILE='C:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl.sav'.
*******ID 141 (lIZid 243) has extremely low CORT value, 50% ANY OTHER
VALUE. .
IF  (ID = 141) CORT=$SYSMIS.
IF  (ID = 141) LgCORT=$SYSMIS.
EXECUTE.
UNIANOVA LgCORT BY year MATE WITH blddly
 /METHOD=SSTYPE(3)
 /INTERCEPT=INCLUDE
 /EMMEANS=TABLES(OVERALL) WITH(blddly=MEAN)
 /EMMEANS=TABLES(year) WITH(blddly=MEAN)
 /EMMEANS=TABLES(MATE) WITH(blddly=MEAN)
 /EMMEANS=TABLES(year*MATE) WITH(blddly=MEAN)
 /PRINT=PARAMETER DESCRIPTIVE
 /CRITERIA=ALPHA(.05)
 /DESIGN=blddly year MATE year*MATE.
```

```
*******No relationship before or after removing weird 141.


* Use this = after removing blkeed delay, which showed a bizarre negative relationship above.
UNIANOVA LgCORT BY year MATE
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(year)
  /EMMEANS=TABLES(MATE)
  /EMMEANS=TABLES(year*MATE)
  /PRINT=PARAMETER DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=year MATE year*MATE.

***********************ENDURANCE*********************************.


GET  FILE='C:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl.sav'.
*CONCERN:  ID = 45 (LizID 74) had very low endurance (3.18 min), compared with John-Alder and Bennet (1981)
whose lowest measure at 40 was nearly 6.  Exclude. Can keep other values for this lizard if present.
```

```
IF  (ID = 45) EndminH=$SYSMIS.
IF  (ID = 45) LendminH=$SYSMIS.
EXECUTE.
REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA COLLIN TOL CHANGE Zpp
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT LendminH
  /METHOD=ENTER LMass.
**No relationship, but almost.

UNIANOVA LendminH BY year MATE WITH Lmass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /EMMEANS=TABLES(MATE*year) WITH(Lmass=MEAN)
  /PRINT=DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=MATE*year year MATE Lmass.
```

```
***********************HOME RANGE******************************.
GET  FILE='C:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl.sav'.
SELECT IF ptshrs > 5.
Execute.
REGRESSION
 /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA COLLIN TOL CHANGE Zpp
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT LgHRA
  /METHOD=ENTER Lmass ptsHR SZptsHR.



UNIANOVA lgHRA BY year MATE WITH Lmass ptsHR SZptsHR
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /EMMEANS=TABLES(year*mate) WITH(Lmass=MEAN ptsHR=MEAN
SZptsHR=MEAN)
  /PRINT=DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=year MATE  mate*year Lmass ptsHR SZptsHR.
```

```
**********************************************************.
* Create file with saved residuals for all traits.
GET  FILE='C:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl.sav'.
*******ID 141 (lIZid 243) has extremely low CORT value, 50% ANY OTHER
VALUE. .
IF  (ID = 141) CORT=$SYSMIS.
IF  (ID = 141) LgCORT=$SYSMIS.
EXECUTE.


* This also saves residuals.
*CORT RESIDUALS: THESE ResLgC2 ARE WITH YEAR AND MATE. THERE
ARE NONE WITHOUT BC NO CORR.
UNIANOVA LgCORT BY year MATE
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (RESLgC2) ZRESID (ZRESLgC2)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(year)
  /EMMEANS=TABLES(MATE)
  /EMMEANS=TABLES(year*MATE)
  /PRINT=PARAMETER DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
```

```
  /DESIGN=year MATE year*MATE.
*CONCERN:  ID = 45 (LizID 74) had very low endurance (3.18 min), compared with
John-Alder and Bennet (1981)
whose lowest measure at 40 was nearly 6.  Exclude. Can keep other values for this lizard
if present.
IF  (ID = 45) EndminH=$SYSMIS.
IF  (ID = 45) LendminH=$SYSMIS.
EXECUTE.
*Endurance RESIDUALS: THESE ResLen1 ARE WITH body mass only.
UNIANOVA LendminH WITH Lmass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (RESLEN1) ZRESID (ZRESLEN1)
  /EMMEANS=TABLES(OVERALL) WITH(Lmass=MEAN)
  /PRINT=PARAMETER DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=Lmass.


*Endurance RESIDUALS: THESE ResLen2 ARE WITH Lmass, YEAR AND MATE.
UNIANOVA LendminH BY year MATE WITH Lmass
  /METHOD=SSTYPE(3)
```

```
  /INTERCEPT=INCLUDE
  /SAVE=RESID (RESLEN2) ZRESID (ZRESLEN2)
  /EMMEANS=TABLES(OVERALL) WITH(Lmass=MEAN)
  /EMMEANS=TABLES(year) WITH(Lmass=MEAN)
  /EMMEANS=TABLES(MATE) WITH(Lmass=MEAN)
  /EMMEANS=TABLES(year*MATE) WITH(Lmass=MEAN)
  /PRINT=PARAMETER DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=Lmass year MATE year*MATE.

IF  (ptsHR < 6) HRA=$SYSMIS.
IF  (ptsHR < 6) LgHRA=$SYSMIS.
Execute.
*HOME RANGE RESIDUALS: THESE ResLHR1 ARE WITH Lmass, location points, and z-(location points)^2..
UNIANOVA lgHRA WITH ptsHR SZptsHR Lmass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (RESLHR1) ZRESID (ZResLHR1)
  /PRINT=PARAMETER DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=ptsHR SZptsHR Lmass.
```

*Endurance RESIDUALS: THESE ResLHR2 ARE WITH year, season, Lmass, location points, and z-(location points)^2.

```
UNIANOVA lgHRA BY year MATE WITH ptsHR SZptsHR Lmass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (RESLHR2) ZRESID (ZResLHR2)
  /EMMEANS=TABLES(OVERALL) WITH(ptsHR=MEAN Lmass=MEAN
SZptsHR=MEAN)
  /EMMEANS=TABLES(year) WITH(ptsHR=MEAN Lmass=MEAN SZptsHR=MEAN)
  /EMMEANS=TABLES(MATE) WITH(ptsHR=MEAN Lmass=MEAN
SZptsHR=MEAN)
  /EMMEANS=TABLES(year*MATE) WITH(ptsHR=MEAN Lmass=MEAN
SZptsHR=MEAN)
  /PRINT=PARAMETER DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=ptsHR SZptsHR Lmass year MATE year*MATE.
```

*Home Range RESIDUALS: THESE ResLHR3 ARE WITH Lmass, location points, and z-(location points)^2, and eco.

```
UNIANOVA lgHRA WITH ptsHR SZptsHR Lmass soildens fooddens shaddens penet
```

```
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (ReSLHR3) ZRESID (ZResLHR3)
  /PRINT=PARAMETER DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=ptsHR SZptsHR Lmass soildens fooddens shaddens penet.

*Home range RESIDUALS: THESE ResLHR4 ARE WITH year, season, Lmass,
location points,
* and (z-location points)^2, and eco.

UNIANOVA lgHRA BY year MATE WITH ptsHR SZptsHR Lmass soildens fooddens
shaddens penet
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (ReSLHR4) ZRESID (ZResLHR4)
  /EMMEANS=TABLES(OVERALL) WITH(ptsHR=MEAN Lmass=MEAN
SZptsHR=MEAN)
  /EMMEANS=TABLES(year) WITH(ptsHR=MEAN Lmass=MEAN SZptsHR=MEAN)
  /EMMEANS=TABLES(MATE) WITH(ptsHR=MEAN Lmass=MEAN
SZptsHR=MEAN)
```

```
  /EMMEANS=TABLES(year*MATE) WITH(ptsHR=MEAN Lmass=MEAN
SZptsHR=MEAN)
  /PRINT=PARAMETER DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=ptsHR SZptsHR Lmass year MATE year*MATE soildens fooddens
shaddens penet.

*Home range RESIDUALS (REDUCED MODEL): THESE ResLHR5 ARE WITH year,
season, Lmass, location points,
* and (z-location points)^2, and shade plant density.

UNIANOVA lgHRA BY year MATE WITH ptsHR SZptsHR Lmass shaddens
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (ReSLHR5) ZRESID (ZResLHR5)
  /EMMEANS=TABLES(OVERALL) WITH(ptsHR=MEAN Lmass=MEAN
SZptsHR=MEAN)
  /EMMEANS=TABLES(year) WITH(ptsHR=MEAN Lmass=MEAN SZptsHR=MEAN)
  /EMMEANS=TABLES(MATE) WITH(ptsHR=MEAN Lmass=MEAN
SZptsHR=MEAN)
  /EMMEANS=TABLES(year*MATE) WITH(ptsHR=MEAN Lmass=MEAN
SZptsHR=MEAN)
```

```
  /PRINT=PARAMETER DESCRIPTIVE
  /CRITERIA=ALPHA(.05)
  /DESIGN=ptsHR SZptsHR Lmass year MATE year*MATE shaddens.

SAVE
OUTFILE='C:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl_withresids.sav'
  /COMPRESSED.

****************Environmental variables****************************.
GET  FILE='e:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl.sav'.
SELECT IF (PTSHR > 5).
EXECUTE.

CORRELATIONS
  /VARIABLES = penet soildens fooddens shaddens
  /PRINT=TWOTAIL NOSIG
  /MISSING=PAIRWISE.

* Including year and season.
* All environmental variables forced in.
COMPUTE YEAR01 = 0.
```

```
IF (YEAR = 2016) YEAR01 = 1.

COMPUTE YEARMATE = YEAR01 * MATE.

EXECUTE.

REGRESSION

 /DESCRIPTIVES MEAN STDDEV CORR SIG N

 /MISSING LISTWISE

 /STATISTICS COEFF OUTS CI(95) BCOV R ANOVA

 /CRITERIA=PIN(.05) POUT(.10)

 /NOORIGIN

 /DEPENDENT lgHRA

 /METHOD=ENTER LMASS penet soildens fooddens shaddens ptshr SZptsHR

                    YEAR01 MATE YEARMATE.


REGRESSION

 /DESCRIPTIVES MEAN STDDEV CORR SIG N

 /MISSING LISTWISE

 /STATISTICS COEFF OUTS CI(95) BCOV R ANOVA

 /CRITERIA=PIN(.05) POUT(.10)

 /NOORIGIN

 /DEPENDENT lgHRA

 /METHOD=ENTER LMASS shaddens ptshr SZptsHR

                    YEAR01 MATE YEARMATE.
```

Appendix IV.

Spss Data/Program Pathway for Chapter 3:

Flows from top to bottom. Each syntax is followed by the .sav or excel file it starts with and what it produces.

Each year and season uses the same syntax with a different label in the title (e.g. “2015M”, “2016NM).

Corticosterone:

Reads from assays are read from respective assays. 2015-2016 was more than one plate.

Dipsosaurus\assays\DIPS_CORT_ASSAYS_plate3_v1.sps

C:\Singleton\Dipsosaurus\assays\Results_from_MyAssays_3_30_18_read1_v2.xlsx

C:\Singleton\Dipsosaurus\assays\Results_from_MyAssays_3_30_18_read2_v2.xlsx

C:\Singleton\Dipsosaurus\assays\Results_from_MyAssays_3_30_18_read3_v2.xlsx

C:\Singleton\Dipsosaurus\assays\3_30_18_assayreadsmerged_tomerge.sav

Dipsosaurus\assays\DIPS_CORT_ASSAYS_plate4_v1.sps

C:\Singleton\Dipsosaurus\assays\Results_from_MyAssays_7_31_18_read1_v2.xlsx

C:\Singleton\Dipsosaurus\assays\Results_from_MyAssays_7_31_18_read2_v2.xlsx

C:\Singleton\Dipsosaurus\assays\Results_from_MyAssays_7_31_18_read3_v2.xlsx

C:\Singleton\Dipsosaurus\assays\7_31_18_assayreadsmerged_tomerge.sav

Dipsosaurus\assays\CORT_2015_2016_v2.sps

C:\Singleton\Dipsosaurus\assays\3_3_18_assayreadsmerged_tomerge.sav

C:\Singleton\Dipsosaurus\assays\7_31_18_assayreadsmerged_tomerge.sav

C:\Singleton\Dipsosaurus\assays\2015_2016_CORT_values.sav

Endurance

Dipsosaurus\endurance\2015M\Dipsosarus_endurance_2015M.sps

C:\Singleton\Dipsosaurus\Endurance\2015M\EnduranceCap_2015_M_v1.xls

C:\Singleton\Dipsosaurus\Endurance\2015M\EnduranceCap_2015M_calcs.sav

Dipsosaurus\endurance\2015NM\Dipsosarus_endurance_2015NM.sps

C:\Singleton\Dipsosaurus\Endurance\2015NM\EnduranceCap_2015_NM_v1.xls

C:\Singleton\Dipsosaurus\Endurance\2015NM\EnduranceCap_2015M_calcs.sav

Dipsosaurus\endurance\2016M\Dipsosarus_endurance_2016M.sps

C:\Singleton\Dipsosaurus\Endurance\2016M\EnduranceCap_2016M_v1.xls

C:\Singleton\Dipsosaurus\Endurance\2016M\EnduranceCap_2016M_calcs.sav

Dipsosaurus\endurance\2016NM\Dipsosarus_endurance_2016NM.sps

C:\Singleton\Dipsosaurus\Endurance\2016NM\EnduranceCap_2016NM_v1.xls

C:\Singleton\Dipsosaurus\Endurance\2016NM\EnduranceCap_2016NM_calcs.sav

Dipsosaurus\endurance\End_2015_2016_v1.sps

C:\Singleton\Dipsosaurus\endurance\2015M\endurancecap_2015M_calcs.sav

C:\Singleton\Dipsosaurus\endurance\2015nm\endurancecap_2015NM_calcs.sav

C:\Singleton\Dipsosaurus\endurance\2016M\endurancecap_2016M_calcs.sav

C:\Singleton\Dipsosaurus\endurance\2016NM\endurancecap_2016NM_calcs.sav

C:\Singleton\Dipsosaurus\endurance\endurance_2015M_2015NM_2016M_2016NM.sav

Home Range Size (example for 2015)

Dipsosaurus\field\2015M\Fielddata_2015M_toranges_v1.sps

C:\Singleton\Dipsosaurus\field\2015M\fielddata_2015M_locations_v2.xls

C:\Singleton\Dipsosaurus\field\STKCODE.xls

C:\Users\Jennifer\Documents\Ranges\Dipsosaurus\fielddata_2015M_locations_MALES_gridloc.xls (need excel for ranges)

Dipsosaurus\field\2015M\Fielddata_2015M_fromranges_v1.sps

C:\Singleton\Dipsosaurus\field\2015M\fielddata_2015M_locations_males_gridloc_excluded_xk_nobuffer_100%.xls

C:\Users\Jennifer\Documents\Ranges\Dipsosaurus\2015\fielddata_2015M_locations_males_gridloc_NOTES_1.xlsx

C:\Singleton\Dipsosaurus\field\2015M\fielddata_2015M_locations_males_gridloc_HR_notes.sav

Dipsosaurus\field\HR_2015_2016_v1.sps

C:\Singleton\Dipsosaurus\field\2015M\fielddata_2015M_locations_males_gridloc_HR_notes.sav

C:\Singleton\Dipsosaurus\field\2015NM\fielddata_2015NM_locations_males_gridloc_HR_notes.sav

C:\Singleton\Dipsosaurus\field\2016M\fielddata_2016M_locations_males_gridloc_HR_notes.sav

C:\Singleton\Dipsosaurus\field\2016NM\fielddata_2016NM_locations_males_gridloc_HR_notes.sav

C:\Singleton\Dipsosaurus\field\fielddata_2015M_2015NM_to_merge.sav

C:\Singleton\Dipsosaurus\field\fielddata_2016M_2016NM_to_merge.sav

Penetrometer (example for 2015M)

Dipsosaurus\eco\2015\penetrometer\penetrometer_syntax_2015M_v2.sps

'C:\Singleton\Dipsosaurus\eco\2015\penetrometer\penetrometer_2015_m_v3_coded.xls

C:\Singleton\Dipsosaurus\eco\2015\fielddata_2015M_locations_males_gridloc_excluded.txt

C:\Singleton\Dipsosaurus\field\2015M\fielddata_2015M_locations_MALES_gridloc.sav

C:\Singleton\Dipsosaurus\eco\2015\penetrometer\penetrometer_2015M_ALLMALES.sav

THEN

Dipsosaurus\eco\penetrometer_2015_2016_v1.sps

Food Plant Density (example for 2015M)

Dipsosaurus\eco\2015\plantdensity\ translate_datafile_June2015_v1.sps

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\Plantspeciesdensity_June2015_v3.xlsx

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\order_specnum.xlsx

'C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantspeciesdensity_June2015_B_ready.xls

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantspeciesdensity_June2015_F_ready.xlsx

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantspeciesdensity_June2015_L_ready.xlsx

(these get copy-pasted into a file with different months as pages:

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantdensity_2015M_plantnumbers_v2.xlsx)

Dipsosaurus\eco\2015\plantdensity\plantdensity_2015_scores_numbers_v1.sps

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantdensity_2015M_plantscores.xlsx'

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantdensity_2015M_plantnumbers_v2.xlsx

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantdensity_2015M_MAY_totals.sav

(for each month)

Dipsosaurus\eco\2015\plantdensity\plantdensity_inHRs_2015M_v2.sps

C:\Singleton\Dipsosaurus\eco\2015\fielddata_2015M_locations_MALES_gridloc_excluded_ADJstakes_ALL.sav

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantdensity_2015M_MAY_totals.sav

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantdensity_2015M_June_totals.sav

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantdensity_inHR_2015_to_merge.sav

Shade Plant Density (example for 2015M)

(use same counts as food plants, just different scores)

Dipsosaurus\eco\2015\plantdensity\SHADEplantdensity_2015M_scores_numbers_v1.sps

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\SHADEplantdensity_2015M_plantscores.xlsx'

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantdensity_2015M_plantnumbers_v2.xlsx

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\SHADEplantdensity_2015M_MAY_totals.sav

C:\Singleton\Dipsosaurus\eco\2015\plantdensity\SHADEplantdensity_2015M_JUNE_totals.sav

Dipsosaurus\eco\2015\plantdensity\SHADEplantdensity_inHRs_2015M_v2.sps

C:\Singleton\Dipsosaurus\eco\2015\fielddata_2015M_locations_MALES_gridloc_excluded_ADJstakes_ALL.sav
C:\Singleton\Dipsosaurus\eco\2015\plantdensity\SHADEplantdensity_2015M_MAY_totals.sav
C:\Singleton\Dipsosaurus\eco\2015\plantdensity\SHADEplantdensity_2015M_June_totals.sav
C:\Singleton\Dipsosaurus\eco\2015\plantdensity\SHADEplantdensity_inHR_2015_to_merge.sav

A few other random excel files get merged (like blood sample notes) but we don’t need to go into their process.

Merging of Seasons and Years:

Singleton\Dipsosaurus\Analyze\2015_2016_super_merge_v1.sps
C:\Singleton\Dipsosaurus\field\fielddata_2015M_2015NM_to_merge.sav
C:\Singleton\Dipsosaurus\field\fielddata_2016M_2016NM_to_merge.sav
C:\Singleton\Dipsosaurus\Endurance\endurance_2015M_2015NM_2016M_2016NM.sav
C:\Singleton\Dipsosaurus\assays\2015_2016_CORT_values.sav
C:\Singleton\Dipsosaurus\blood\Bleed_delay_2015_2016_TO_MERGE.sav
C:\Singleton\Dipsosaurus\eco\Penetrometer_inHR_2015_2016.sav
C:\Singleton\Dipsosaurus\eco\soil_density_TO_MERGE.sav
C:\Singleton\Dipsosaurus\eco\2015\plantdensity\plantdensity_inHR_2015_to_merge.sav
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C:\Singleton\Dipsosaurus\eco\2016\plantdensity\plantdensity_inHR_2016M_to_merge.sav
C:\Singleton\Dipsosaurus\eco\2016\plantdensity\plantdensity_inHR_2016N_to_merge.sav
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C:\Singleton\Dipsosaurus\eco\2015\plantdensity\SHADEplantdensity_inHR_2015N_to_merge.sa
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'C:\Singleton\Dipsosaurus\analyze\ALLDATA_2015_2016.sav'

Singleton\Dipsosaurus\Analyze\2015_2016_super_merge_v1
C:\Singleton\Dipsosaurus\analyze\ALLDATA_2015_2016.sav'.
C:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl_vA.sav'

Singleton\Dipsosaurus\Analyze\2015_2016_analysis_v5 (this is the file to use for stats!!)

CHAPTER 4

Effects of Corticosterone Supplementation on Locomotor Endurance and Home Range size in Free-Living Desert Iguanas (*Dipsosaurus dorsalis*)

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Abstract

Baseline circulating corticosterone impacts a variety of traits related to locomotor behavior, including activity levels, endurance capacity, skeletal muscle function, and glucose mobilization. We attempted to manipulate the corticosterone levels of free-living Desert Iguanas (*Dipsosaurus dorsalis*) as part of a series of studies exploring the relationships between baseline corticosterone, endurance, and home range size. Previous observational work on this population has shown a significant positive correlation between endurance capacity and home range size. For the present experiment, adult male desert iguanas received either corticosterone or saline abdominal implants in April 2017 and were released at the point of capture. Lizards were captured for field blood sampling starting four weeks after surgery. Endurance capacity was measured twice during temporary (<1 day) captivity starting two weeks after surgery. Individual locations were recorded May-July (via visual recognition) for home range evaluation. In addition, ecological variables were quantified for individual lizard home ranges. Mean circulating corticosterone averaged higher in lizards that received corticosterone implants, though this difference was not statistically significant (1.95 vs. 4.91 ng/mL; N = 26, F = 3.028, P = 0.095). Mean maximum endurance capacity did not differ between corticosterone- and saline-treated lizards (11.03 vs. 11.60 min; N = 28, F = 0.347, P = 0.561). However, mean home range size was significantly larger for lizards with corticosterone implants (703.5 vs. 346.8 m^2; N = 22, F = 4.755, P = 0.044). Contrary to our *a priori* expectations, no correlations between corticosterone concentrations, endurance capacity, and home range were statistically significant.

Introduction

The study of evolutionary physiology concerns the continuum between relatively simple, lower-level traits (morphological, physiological, etc.), their contributions to specific performance capacity/capacities, and the effects of performance abilities on Darwinian fitness (Bennett and Huey 1990; Garland, Jr. and Carter 1994; Feder et al. 2000). This continuum has been called the morphology-performance-fitness paradigm (Arnold 1983). Behavior has been added to this paradigm as a term between performance and fitness, as behavior can act as a “filter,” determining the extent that performance capacity influences fitness (Garland, Jr. and Carter 1994; Garland, Jr. and Losos 1994). For example, an individual animal may choose to flee from a predator or remain stationary and attempt crypsis; the behavioral choice made determines whether a given performance capacity (such as sprint speed) influences its survival, which is an important component of Darwinian fitness. Conversely, the ability of an individual to perform a task maximally may influence the behavioral choice made; for example, long-nosed leopard lizards (*Gambelia wislizennii*) with lower body temperatures than preferred body temperature (hence lower sprint speeds) are more likely to attack human "predators," whereas individuals at higher body temperature will flee (Crowley and Pietruszka 1983).

Subordinate traits that contribute to performance and behavior include numerous aspects of both morphology and physiology (Garland, Jr. et al. 2016). As a specific example, maximum oxygen consumption impacts endurance capacity (e.g., see John-Alder and Bennett 1981; Rezende et al. 2006b, 2006a). More generally, endocrine function has pervasive effects on physiology and behavior, yet comparatively little research has been done within the evolutionary physiological perspective in relation to hormones as subordinate traits (Breuner et al. 2008; Husak et al. 2009).

One endocrine trait with far-reaching effects is the basal concentration of corticosterone that circulates in the bloodstream. Though much research focuses on stress-induced levels of corticosterone and other glucocorticoids, corticosterone circulates at low levels under baseline conditions in most vertebrates (Nelson 2011). Basal corticosterone impacts numerous traits related to locomotor function, including skeletal muscle growth, muscle maintenance, and glucose mobilization (Astheimer et al. 1992; Coderre et al. 1992; Li et al. 1996; Jessop et al. 2003). In lines of mice bred for high levels of voluntary wheels running, circulating corticosterone is ~2x higher than in non-selected control lines around the circadian cycle (Malisch et al. 2007, 2008; Singleton and Garland, Jr. 2018a). Basal circulating corticosterone also increases in numerous reptile and amphibian species during periods of high physical activity, such as the mating season (Wilson and Wingfield 1994; Romero 2002; John-Alder et al. 2009; Eikenaar et al. 2012).

Studies in numerous vertebrates have evaluated the relationships between corticosterone and performance traits with using experimental manipulations. For example, the endurance capacity of side-blotched lizards (*Uta stansburiana*) significantly increased across four weeks after the lizards received a corticosterone implant (Miles et al. 2007). White-crowned sparrows (*Zonotrichia leucophrys*) that received supplemental corticosterone via meal worms increased perch-hopping behavior for 30 minutes after feeding (Breuner et al. 1998; Breuner and Wingfield 2000). Conversely, supplementation of corticosterone via drinking water causes decreases in activity levels and in maximal oxygen consumption in house mice (Karatsoreos et al. 2010; Singleton and Garland, Jr. 2018a).

External to the morphology-performance-behavior-fitness paradigm, ecological and environmental factors affect behavioral choices (Garland, Jr. and Losos 1994). Home range size is an example of an index of locomotor behavior that is undoubtedly affected by both the performance of an individual and the external environment. The home range of an animal is "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). The ability of an animal to move throughout an area can be affected by performance capacities, but the size of the home range itself is also affected by the needs that it exists to fill. For example, home range size is known to be related to food density or primary productivity (Lucherini and Lovari 1996; Tufto et al. 1996).

Desert iguanas (*Dipsosaurus dorsalis*) are medium-size desert lizards native to the American southwest and northern Mexico. They are terrestrial herbivores most frequently found in low-elevation deserts with primarily sandy soil. Desert iguanas feed on the leaves and flowers of a variety of desert plants as well as the occasional arthropod; they will also consume the feces of other vertebrates such as black-tailed jack rabbits (*Lepus californicus*; Minnich and Shoemaker 1970). Desert iguanas are often active during the hottest portion of the day; their active body temperature is the highest recorded of any vertebrate in North America (42° C; Norris 1953). Though tolerant of such temperatures, the desert iguana actively and closely regulates body temperature through the use of shade plants and burrows (Norris 1953; DeWitt 1967; DeWitt et al. 1967). Desert iguanas dig burrows (and may use those abandoned by other vertebrates) to avoid excessive afternoon heat and associated high rates of evaporative water loss, and as overnight refuges from predators (Norris 1953; Moberly 1963; Krekorian 1984).

Desert iguanas have frequently been used as the subjects of laboratory studies examining a variety of topics, such as chemoreception, locomotor performance, and endocrine function (Chan and Callard 1972; Alberts 1992; Wagner and Gleeson 1996; Hazard 2001; Bealor and Krekorian 2002). Their docile nature and large body size allow blood draws and physiological measurements to be performed with relative ease. Field studies also benefit from these traits, as desert iguanas are easily spotted and fairly tolerant to human observation; much of this fieldwork has taken place with populations near Palm Springs, CA. Desert iguanas in this area tend to live in high-density populations with large amounts of home-range overlap (Krekorian 1976, 1983, 1984). In a previous study of this population, the endurance capacity of adult male desert iguanas was found to be positively correlated with home range size (Singleton and Garland, Jr. 2018b). In the current study, we have used corticosterone implants to examine individual variation in both endurance capacity and home range size in relation to endocrine function. We also measured a number of environmental variables with expected relevance to desert iguanas and quantified their effect on home range size.

Methods

Forty-two adult male desert iguanas were captured via noosing (García-Muñoz and Sillero 2010) from the Whitewater Floodplain Preserve in northern Palm Springs, Coachella Valley, Riverside Co. California in April 2017. This preserve was established in 1984 and is managed by the Bureau of Land Management (Alagona and Pincetl 2008); it is composed of windblown ephemeral sand fields dominated by creosote (*Larrea tridentata*) and smoketree (*Psorothamnus spinosus*). The field site measures 150 x 150 m, with 10 m increments marked by wooden/plastic stakes from north to south and east to west (Singleton and Garland, Jr. 2018b; Fig. 4.1). Lizards were taken from the field site to the University of California, Riverside for implant surgery within 48 hrs of capture.

Corticosterone/saline implants were constructed using 4 mm of 2 mm internal diameter (i.d.) surgical-grade silastic tubing (DeNardo and Licht 1993; DeNardo and Sinervo 1994a, 1994b; Miles et al. 2007; John-Alder et al. 2009). One end of the tube was sealed with a shortened, sterilized (via autoclave) 1/8” i.d. silicone rubber end cap (High Temp Masking Supply, PPCSSC109-50) and the inside was filled with crystalline corticosterone or a saline solution (Fig. 4.2). The second end of the implant was sealed with another silicone end cap. All implants were soaked in sterile saline solution for 24 hrs before use. This implant design is the second version of corticosterone implant employed in desert iguana studies, as a previous version without the silicone endcaps showed a high failure rate upon dissection (Chapter 2). Immediately before surgery, I poked a small hole in the exposed silastic tubing using a sterile 26g hollow needle, as crystalline corticosterone diffuses only a small amount through silastic tubing (H. B. John-Alder, personal communication).

For implant surgery, animals were anesthetized using isoflurane administered as 5% atmosphere until movement ceases and reactions to gentles pinches ceased (Eatwell 2010). Isoflurane administration continued via a slow intermittent administration system for the full duration of surgery (Fig. 4.3). Anesthetized lizards were provided with a unique identifying marker via three colored beads in a unique sequence (Fisher and Muth 1989). Beads were threaded onto stainless steel wire that was run under the skin on the left side of the proximal tail area (Fig. 4.4). This method allowed unique identification over multiple field seasons and allowed for identification without recapture; in the pilot study for this method, 95% of 357 *Uma inornata* retained bead markers for >2 years (Fisher and Muth 1989). Fourteen lizards used in this study were beaded previously.

Following anesthesia, 37.5 uL 1% lidocaine solution was administered via local infiltration to the lateral area of the lower abdomen (Mosley 2005; Eatwell 2010). After administration, the surgical site was disinfected and a 1 cm vertical peritoneal incision was made 2 cm above pelvis and 1.5 cm left of the midline (avoiding significant shallow abdominal arteries). The implant was placed in the abdominal cavity and the incision was closed with a combination of horizontal mattress suture stitches and tissue glue. After surgery animals were placed into a small terrarium under a heat lamp to enhance recovery from anesthesia. All animals recovered from anesthesia to the point of wakefullness and walking within 20 minutes of surgery completion and showed no signs of pain (e.g. rolling, arched back, pressing of head into corner, tail slapping; Mosley 2006) in the 24 hrs post-surgery.

Twenty-four hours post-surgery desert iguanas were released at the individual place of capture at the field site. Following release, location data was collected for implanted desert iguanas from May to mid-July 2017 (Fig. 4.5). Data was collected via sightings; when a desert iguana was sighted, it was slowly approached until it could be identified, and then a flag was placed at the precise location where it was first seen. Later in the day, locations were quantified as the distance (in cm) and direction from the nearest grid point (stake).

To use locations for analysis, I converted the compass direction (degrees from North) into radians (for SPSS) then into an angular direction using the stake as the origin. I used this angle and the distance from the given stake to give a precise XY location (in cm) from the stake and combined these measurements with the set XY coordinates of each stake (southwest corner (0,0), northeast corner (15000,15000)) to give precise coordinates for each location within the field site.

Home range was calculate based on locations starting after the post-surgery release until July 14th, 2017. As previously (Singleton and Garland, Jr. 2018b), home range was graphically represented via the program Ranges 9 (Anatrack). A small number of locations for individuals were excluded due to their distance from the majority of other points for that individual. These points were considered either “occasional forays” or possible misidentifications. Home range size was then calculated using the minimum convex polygon method, the most common method used to assess home range size in lizards (Tinkle et al. 1962; Krekorian 1976; Fox et al. 1981; Rose 1982; Dubas and Bull 1992; DeNardo and Sinervo 1994a; Bull and Baghurst 1998; Fair and Henke 1999; Civantos 2000; Haenel et al. 2003a, 2003b; Anderson 2013).

Blood Sample

To ascertain the functionality of the corticosterone implants, blood samples were taken from lizards in the field in June and early July, between the hours of 09:00 and 13:00. To quantify circulating levels of corticosterone without conflating the measurements with stress-induced corticosterone, the procedure for sampling was as follows: beginning at the northeast corner of the field site, three researchers walked together through the site systematically, east to west and back. This method was used in order to limit blood sampling to the first disturbance by humans on that day. When a desert iguana was sighted, a stopwatch was started. At this, two people began attempting to capture the lizard via noosing while the third person identified the lizard (by beading) and checked the notebook to see if a blood sample was needed. Once the lizard was captured, a 100 uL blood sample was drawn from the ventral caudal vein with syringe and 27 gauge needle. The stopwatch continued running until the sample was fully collected. If the timer reached 4 minutes before the sample was finished, the attempt was terminated. Stress-induced corticosterone responses are not detectable in reptiles until well after 4 minutes (Romero and Reed 2005). Lizards did not have blood drawn if they had been tested for endurance capacity <48 hrs prior, as the prolonged handling associated with endurance testing could result in lingering elevated corticosterone. Blood samples were stored cold in the field and centrifuged <6 hrs after collection. Plasma was stored at -80°C. Prior to assays, corticosterone was separated from binding proteins using a steroid liquid extraction procedure specifically recommended for DetectX® Immunoassay kits from Arbor Assays. The extraction procedure was used due to concerns that the circulating corticosterone concentrations would fall outside of the limits of detection for the assay as a result of an initial dilution with the protein dissociation reagent. In brief, samples were combined 1:5 with ethyl acetate, vortexed for 5 minutes, and frozen in a dry ice bath. The unfrozen fraction was poured off and dried using an organic-solvent-capable centrifugal evaporator. The extracted sample was assayed using the K-014 Corticosterone EIA kit from Arbor Assays. Validation information is available in Dissertation Appendix I.

Endurance

At least 2 weeks post-surgery, lizards were captured from the field site and taken to an IACUC-approved facility at Bonnie Bell, CA (~13 km from field site) to test endurance capacity. As previously (Singleton and Garland, Jr. 2018b), endurance trials were conducted using a fixed speed (1.0 km/h) treadmill (108 cm x 20 cm). Activity at this speed at 40°C has been previously estimated to induce maximal oxygen consumption in desert iguanas (John-Alder and Bennett 1981). Lizards were incubated at 40° C for ~ 1 h, until internal body temperature approached 40° C (as measured with a thermocouple). They were then placed on the running treadmill and encouraged to walk/run at pace via gentle taps and nudges to the tail and hind legs (Garland, Jr. 1984, 1999). Endurance was measured as the length of time that lizards were able to maintain position on the treadmill, with the trial terminating after a failure to maintain pace after 10 taps in rapid succession. At finish, lizards were evaluated for exhaustion by rating the "righting response," or the ability to right after being placed on their dorsal side; the response was rated 1-3, with 1 as little-no response and 3 as the full response (not tired). A lizard that retained full responsiveness would be returned to the treadmill to ensure that full exhaustion was reached. The quality of the run was also rated by the researcher (based on the encouragement necessary and if the lizard attempted escape) as 1-5, with 5 being a perfect run and 1 a run where the lizard was highly reluctant to maintain pace and/or attempted to escape repeatedly. Run quality was recorded to potentially evaluate runs for exclusion due to poor quality, although such exclusions proved unnecessary in the present study). Lizards were returned to the field on the same day as the endurance trial, and were recaptured another day to repeat testing. Endurance capacity trials were not conducted on individuals <48 h after collection of a blood sample. The higher of two measurements for an individual was used as the maximum endurance capacity (Garland, Jr. 1984, 1999; Garland, Jr. et al. 1987).

To quantify the effects of the microhabitat within the home ranges of individuals, a number of ecological variables were measured for each stake within the field site in May and June. For each stake, the number of plants of each species within 1.5 m of the stake were counted in May and June and the average value was taken. This number was used to calculate food plant density and shade plant density. Food plant density and shade plant density were evaluated as described in chapter 3 of this dissertation. Soil compactibility was measured as described in chapter 3, once per stake within the field site.

For statistical analysis of repeatability of endurance trials, paired t-tests and Pearson correlations in SPSS software were used. Regression was used to examine the relationships between traits and expected covariates. The use of specific covariates in further analyses was determined by statistical significance during regression or by expected contribution to the variation of a trait (for example, endurance capacity is known to be associated with body mass, and was therefore included in analysis). ANCOVAs were used to examine differences between groups (implant type). Multiple regression was used to calculate the residuals of traits in order to examine the relationships between traits. Specifically, endurance capacity residuals were calculated with $\log_{10}$ body mass as a covariate. Home range size residuals were calculated with $\log_{10}$ body mass, number of location points used for home range analysis, and squared z-scores of location point numbers; additionally, home range size residuals were calculated without including $\log_{10}$ body mass for comparison, as intraspecific support for this relationship is scant and was not apparent in the current analysis. No covariates were included for corticosterone. The impact of ecological variables on home range size was also examined using multiple regression.

Procedures involving lizards were approved by the California Department of Fish and Wildlife under permit# sc12669. Procedures were also approved by the Institutional Animal Care and Use Committee of the University of California at Riverside under animal use protocol number 20170012.

Results

Mean $\pm$ SE circulating corticosterone concentration (ng/mL) was 3.313 $\pm$ 0.881 ng/mL (Table 4.1; N = 26; range: 0.63-17.59 ng/mL). Circulating corticosterone levels averaged higher for lizards with corticosterone implants (Fig. 4.6B; 4.91 vs. 1.95 ng/mL), but the difference was non-significant (Table 4.2; N = 26; F = 3.028; P = 0.095). Log_{10} circulating corticosterone showed no significant correlation with time from lizard sighting to completion of blood draw (R = -0.183; P = 0.371) or time between implant surgery and blood sample (R = 0.028; P = 0.892).

Mean $\pm$ SE maximum endurance capacity (higher of two measurements per individual) for all lizards was 11.26 $\pm$ 1.33 min (Table 4.3; N = 28; range: 4.0-27.9 min). First and second endurance measurements were significantly correlated (Fig. 4.7; R = 0.521; P = 0.003) and not significantly different on average (paired-t = -1.185; P = 0.246). Log_{10} endurance capacity was not significantly correlated with the mean time period between surgery and endurance measurements (N = 28; R = -0.068; P = 0.730) or $\log_{10}$ body mass (R = 0.023; P = 0.906) and did not differ between treatment groups with body mass as a covariate (Table 4.4, 4.5; Fig. 4.6C; N = 28; F = 0.347; P = 0.561). This difference was also non-significant when body mass was removed as a covariate (F = 0.356; P = 0.556).

The first lizards with implants were released April 10 2017 and the final lizards were released May 1 2017. Thirty-six (of forty-two) implanted individuals were seen again in the field after release, meaning they survived the surgery after release and remained in the area, though a number of these were excluded from home range analysis due to a low number of location points (<6). Mean home range size was 476.5 ± 62.2 m^2 (Table 4.6; N = 22; range: 75 – 1058 m^2). Log_{10} home range size was not significantly correlated with body mass (N = 22; R = -0.060, P = 0.792) or span of time between first and last location sighting (N = 22; R = 0.112; P = 0.621). Home range size was also not significantly correlated with the number of location points used to calculate the maximum convex polygon (N = 22; R = 0.363; P = 0.096) or the squared z-score of location point number (R = 0.194; P = 0.388). Log_{10} home range size with location point number, squared z-score point number, and $\log_{10}$ body mass as covariates was significantly different between treatment groups (Table 4.7; F = 4.755; P = 0.044); desert iguanas with corticosterone implants had larger home ranges (Fig. 4.6A; Table 4.8). This difference remained significant when removing body mass from the analysis (F = 0.5344; P = 0.033).

None of the pairwise Pearson correlations for $\log_{10}$ circulating corticosterone, residual $\log_{10}$ endurance capacity, and residual $\log_{10}$ home range size were statistically significant (Table 4.9, Fig. 8, Fig. 9, Fig. 10). Residual home range (including body mass, number of location points, and squared z-score of points) was not significantly predicted in a multiple regression with residual corticosterone and residual endurance (N = 18; R^2 = 0.117; P = 0.369; partial regression coefficients in Table 4.10). This relationship was also not significant when body mass was removed from residual calculations of home range (R^2 = 0.115; P = 0.376).

Ecological variables (soil compactibility, food plant density, and shade plant density; Table 4.11) were incorporated as covariates in a model to predict $\log_{10}$ home range size, in addition to the above-mentioned covariates of $\log_{10}$ body mass, number of location points used for home range calculation, and z-scored point number squared. In the initial model, shade plant density was the only significant predictor of home range mass (Table 4.12; $N = 22$; $B = -0.101$; $P = <0.001$). Non-significant ecological variables were removed step-wise (while keeping $\log_{10}$ body mass, number of location points, and z-scored point number squared as necessary covariates), with the resulting model including only shade plant density. In this reduced model, shade plant density remained a significant negative predictor of home range size (Table 4.13; $B = -0.91$; $P < 0.001$) and number of location points was also a significant predictor ($B = 0.051$; $P = 0.039$). With the residuals calculated from this model, residual home range (including shade plant density) was not predicted by residual endurance capacity and $\log_{10}$ corticosterone ($N = 18$; multiple $R^2 = 0.019$; $P = 0.856$; partial coefficients available in Table 4.14).

In a second series of models, body mass was removed from the initial model (keeping number of location points, and z-scored point number squared) of ecological variables as predictors of home range size. In the complete model, shade plant density remained the only significant predictor ($B = -0.096$; $P = <0.001$). After removal of non-significant ecological variable, shade plant density and location point number remained significant (shade plant density: $B = -0.087$, $P = <0.001$; location point number: $B = 0.052$, $P = <0.001$). With the residuals calculated from this model, residual home range (including shade plant density) was not predicted by residual endurance capacity and $\log_{10}$ corticosterone ($N = 18$; multiple $R^2 = 0.006$; $P = 0.952$; partial coefficients available in Table 15).

Discussion

Although the difference in circulating corticosterone between lizards receiving corticosterone implants and those with saline implants was not statistically significant, the former had higher average corticosterone levels (Table 4.1). The implants were designed specifically to raise corticosterone to levels that are not above typical physiological ranges, thus precluding pathological effects of continuous excessive corticosterone (Arnaldi et al. 2003; Karatsoreos et al. 2010). The maximum value, 17.58 ng/mL, was higher than the maximum detected previously in this population (10.81 ng/mL; chapter 3), but the average implant value (4.91 ng/mL) was well within that of a range of other iguanas and members of the suborder Iguania ((DeNardo and Licht 1993; Dunlap and Wingfield 1995; Hanley and Stamps 2002; Romero and Wikelski 2002; Robertson et al. 2011; Hews and Abell Baniki 2013).

I did not find a significant correlation between corticosterone plasma concentration and endurance capacity for individual adult desert iguanas, nor was either corticosterone or endurance capacity a significant predictor of home range size. Endurance capacity and home range size were positively but not significantly related in this study. In a previous study with this population in 2014-2015 with a similar sample size, the relationship was found to be positive and statistically significant (Singleton and Garland, Jr. 2018b).

Circulating corticosterone differed between implant types, though this difference was not quite significant (Table 4.2). Implant type did have a significant effect on home range size; supplemental corticosterone significantly increased home range size (Table

4.8). Though this difference was not directly reflected in circulating corticosterone levels, home range size was a product of the movements over the whole period of observation. Corticosterone may have had an early effect on home range size, but not a detectable correlation at the time of blood sampling (27-90 days post-surgery). In some birds, corticosterone implants do not have a direct linear effect on circulating corticosterone (Torres-Medina et al. 2018); Endurance capacity did not differ significantly between implant types; $\log_{10}$ values for the two groups were nearly identical (0.944 vs. 1.008 min; Table 4.5). These results suggest that another factor (not endurance capacity) may modulate the relationship between corticosterone and home range size. Supplemental corticosterone has previously been seen to positively impact activity levels in birds (Breuner et al. 1998; Breuner and Wingfield 2000), though results in mammals and reptiles have been varied (DeNardo and Sinervo 1994a; Singleton and Garland, Jr. 2018a). In general, reptiles tend to have higher levels of corticosterone during periods of high activity, such as the reproductive season (Wilson and Wingfield 1994; Moore and Jessop 2003; Eikenaar et al. 2012). Corticosterone may also play a role in spatial memory; mountain chickadees implanted with corticosterone showed greater food cache recall and spatial memory performance when compared with controls (Pravosudov 2003). Optimum home range usage is achieved through the use of "cognitive maps," built with spatial memory (Spencer 2012); higher corticosterone may allow an individual to retain more information and build a larger cognitive map.

Home range size was significantly and negatively correlated with the density of shade plants within the home range. Although previous studies have found similar results when examining food plant density (Lucherini and Lovari 1996; Tufto et al. 1996; Relyea et al. 2000; Saïd et al. 2005), our study is the first to establish a similar relationships between home range size and shade sources. In theory, the denser a specific limiting resource, the smaller a home range can be. In a previous study on a nearby population, desert iguanas were seen to increase home range size and overlap after a severe 5-day sandstorm that destroyed most of the vegetation in the area (Krekorian 1976). In typical conditions for a diurnal desert ectotherm such as the desert iguana, it may be that the attainment of protection from the sun is of much more immediate importance to survival. Thus, one possible conservation strategy for increasing population density of desert iguanas might be to add artificial shade structures to otherwise suitable habitat, although this could potentially lead to limitations related to food availability.

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Table 4.1. Descriptive statistics for circulating corticosterone (ng/mL).

Descriptive Statistics

Dependent Variable: Corticosterone (ng/mL)

Implant Type	N	Mean	Std. Deviation	Minimum	Maximum
Saline	14	1.9473	1.17660	0.97	5.09
Corticosterone	12	4.9057	6.25351	0.63	17.59
Total	26	3.3127	4.49319	0.63	17.59

Table 4.2. ANOVA of circulating corticosterone (ng/mL) between implant types.

Tests of Between-Subjects Effects					
Dependent Variable: corticosterone (ng/mL)					
Source	Type III Sum of Squares	df	Mean Square	F	P
Corrected Model	56.552[a]	1	56.552	3.028	0.095
Intercept	303.451	1	303.451	16.250	0.000
Implant Type	56.552	1	56.552	3.028	0.095
Error	448.168	24	18.674		
Total	790.040	26			
Corrected Total	504.720	25			
a. R Squared = 0.112 (Adjusted R Squared = 0.075)					

Table 4.3. Descriptive statistics for $\log_{10}$ endurance capacity (minutes).

Descriptive Statistics

Dependent Variable: $\log_{10}$ endurance capacity

Implant Type	N	Mean	Std. Deviation	Minimum	Maximum
Saline	17	0.9441	0.29674	0.60	1.45
Corticosterone	11	1.0079	0.23993	0.65	1.30
Total	28	0.9692	0.27296	0.60	1.45

Table 4.4. ANCOVA of $\log_{10}$ endurance capacity between implant types, with $\log_{10}$ body mass as a covariate.

Tests of Between-Subjects Effects

Dependent Variable: $\log_{10}$ Endurance

Source	Type III Sum of Squares	df	Mean Square	F	P
Corrected Model	0.029[a]	2	0.014	0.181	0.836
Intercept	0.006	1	0.006	0.074	0.788
Log_{10} Body Mass	0.001	1	0.001	0.018	0.893
Implant Type	0.028	1	0.028	0.347	0.561
Error	1.983	25	0.079		
Total	28.311	28			
Corrected Total	2.012	27			

a. R Squared = 0.014 (Adjusted R Squared = -0.065)

Table 4.5. Estimated marginal means for $\log_{10}$ endurance capacity in an ANCOVA between implant types, with $\log_{10}$ body mass as a covariate. Because the effect of body mass was nil, these numbers are virtually identical to those in Table 6.

Estimated Marginal Means

Dependent Variable: Log_{10} Endurance

Implant Type	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
Saline	0.944[a]	0.068	0.803	1.085
Corticosterone	1.008[a]	0.085	0.833	1.183

a. Covariates appearing in the model are evaluated at the following values: Log_{10} Body Mass = 1.7919.

Table 4.6. Descriptive statistics for $\log_{10}$ home range size (m^2).

Descriptive Statistics

Dependent Variable: $\log_{10}$ Home Range Size

Implant Type	N	Mean	Std. Deviation	Minimum	Maximum
Saline	14	2.4654	0.29400	1.88	2.79
Corticosterone	8	2.7814	0.28948	2.23	3.02
Total	22	2.5803	0.32503	1.88	3.02

Table 4.7. ANCOVA of $\log_{10}$ home range size (m^2) between implant types, with covariates of $\log_{10}$ body mass, number of location points used for home range calculation, and z-scores of location points squared.

Tests of Between-Subjects Effects

Dependent Variable: $\log_{10}$ Home Range Size

Source	Type III Sum of Squares	Df	Mean Square	F	P
Corrected Model	0.796[a]	4	0.199	2.377	0.093
Intercept	0.049	1	0.049	0.582	0.456
Log_{10} Body Mass	0.000	1	0.000	0.003	0.960
Location points for HR	0.282	1	0.282	3.370	0.084
(Zscore Location points)^2	0.150	1	0.150	1.791	0.198
Implant Type	0.398	1	0.398	4.755	0.044
Error	1.423	17	0.084		
Total	148.698	22			
Corrected Total	2.219	21			

a. R Squared = 0.359 (Adjusted R Squared = 0.208)

Table 4.8. Estimated marginal means of $\log_{10}$ home range size (m^2) in an ANCOVA (Table 4.7) between implant types, with covariates of $\log_{10}$ body mass, number of location points used for home range calculation, and z-scores of location points squared.

Grand Marginal Means

Dependent Variable: Log_{10} Home Range Size

Implant Type	Mean	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
Saline	2.471[a]	0.080	2.303	2.639
Corticosterone	2.772[a]	0.107	2.545	2.999

a. Covariates appearing in the model are evaluated at the following values: Log_{10} body mass = 1.7973, location points in the home range = 11.64, squared zscore of location points = 0.4680.

Table 4.9. Sample sizes, Pearson correlations, and significance of correlations between $\log_{10}$ corticosterone, $\log_{10}$ endurance capacity , residual $\log_{10}$ endurance capacity, $\log_{10}$ home range area, residual $\log_{10}$ home range size (with residuals of $\log_{10}$ body mass, number of location points, and squared z-score of point number), residual $\log_{10}$ home range size (with residuals of number of location points, and squared z-score of point number), residual $\log_{10}$ home range size (with residuals of ecological variables (soil compactibility, food plant density, shade plant density) $\log_{10}$ body mass, number of location points, and squared z-score of point number), residual $\log_{10}$ home range size (with residuals of ecological variables (soil compactibility, food plant density, shade plant density), number of location points, and squared z-score of point number), residual $\log_{10}$ home range size (with residuals of shade plant density, $\log_{10}$ body mass, number of location points, and squared z-score of point number), and residual $\log_{10}$ home range size (with residuals of shade plant density, number of location points, and squared z-score of point number). Significant correlations ($p < 0.05$) are designated in bold.

		Log$_{10}$ corticosterone			**Log$_{10}$ Endurance**			**Res. Log$_{10}$ Endurance (body mass)**		
		N	R	P	N	R	P	N	R	P
Log$_{10}$ Endurance	Total	23	0.233	0.285						
	Saline	14	0.100	0.733						
	Corticosterone	9	0.207	0.592						
Res. Log$_{10}$ Endurance	Total	23	0.228	0.295						
	Saline	14	0.090	0.740						

(body mass)	Corticosterone	9	0.204	0.598						
Log$_{10}$ HR	Total	19	0.408	0.082	23	0.207	0.343	23	0.206	0.345
	Saline	11	0.505	0.113	14	0.179	0.540	14	0.182	0.534
	Corticosterone	8	0.264	0.527	9	0.210	0.589	9	0.198	0.609
Res. log$_{10}$ HR (mass, points, (z-points)^2)	Total	19	0.206	0.397	23	0.249	0.253	23	0.248	0.254
	Saline	11	0.545	0.084	14	0.196	0.503	14	0.197	0.500
	Corticosterone	8	-0.438	0.278	9	0.362	0.338	9	0.351	0.354
Res. log$_{10}$ HR (points, (z-points)^2)	Total	19	0.179	0.463	23	0.257	0.236	23	0.260	0.232
	Saline	11	0.484	0.132	14	0.196	0.501	14	0.200	0.493
	Corticosterone	8	-0.554	0.154	9	0.415	0.266	9	0.409	0.275
Res. log$_{10}$ HR (mass, points, (z-points)^2, ecological var.	Total	19	-0.073	0.768	23	-0.027	0.901	23	-0.027	0.901
	Saline	11	0.089	0.795	14	-0.107	0.715	14	-0.106	0.719
	Corticosterone	8	-0.534	0.173	9	0.194	0.617	9	0.188	0.628
Res. log$_{10}$ HR (points, (z-points)^2), ecological var.	Total	19	-0.009	0.970	23	-0.023	0.918	23	-0.027	0.903
	Saline	11	0.169	0.619	14	-0.092	0.754	14	-0.093	0.751
	Corticosterone	8	-0.330	0.425	9	0.149	0.702	9	0.137	0.726
Res. log$_{10}$ HR (mass, points, (z-points)^2, shade plants)	Total	19	-0.139	0.571	23	0.037	0.867	23	0.037	0.868
	Saline	11	0.093	0.787	14	-0.096	0.743	14	-0.098	0.740
	Corticosterone	**8**	**-0.810**	**0.015**	9	0.332	0.383	9	0.332	0.382
Res. log$_{10}$ HR (points, (z-points)^2, shade plants)	Total	19	-0.078	0.751	23	0.038	0.864	23	0.034	0.878
	Saline	11	0.188	0.580	14	-0.078	0.791	14	-0.082	0.780
	Corticosterone	8	-0.670	0.069	9	0.296	0.440	9	0.290	0.449

Table 4.10. Results of regression analysis of residual $\log_{10}$ home range size (including shade density as a covariate) with residual $\log_{10}$ endurance capacity and $\log_{10}$ corticosterone as predictor variables (N = 18). Residual home range was not significantly predicted by residual endurance capacity and corticosterone (N = 18; P = 0.369).

Partial Regression Coefficients[a]

Model	Unstandardized Coefficients		Standardized Coefficients	T	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	-0.065	0.098		-0.667	0.515	-0.273	0.142
Residual $\log_{10}$ endurance	0.315	0.271	0.274	1.163	0.262	-0.259	0.889
Log_{10} corticosterone	0.166	0.212	0.185	0.784	0.444	-0.283	0.615

a. Dependent Variable: Residual $\log_{10}$ endurance capacity R squared = 0.11

Table 4.11. Correlation matrix of environmental variables (soil compactibility, food plant density, and shade density). Significant correlations are in bold. (N = 22).

		Food Plant Density	Shade Plant Density
Pearson Correlation	Soil Compactibility	-0.257	-0.278
	Food Plant Density		-0.047
Sig. (2-tailed)	Soil Compactibility	0.248	0.211
	Food Plant Density		0.835

Table 4.12. Results of regression analysis of $\log_{10}$ home range size with ecological variables as predictors: soil compactibility, shade plant density, and food plant density (N = 22). The model also included $\log_{10}$ body mass, number of location points used for home range calculation, and squared z-scored of location points.

Partial Regression Coefficients[a]

Model	Unstandardized Coefficients		Standardized Coefficients	T	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	0.527	2.281		0.231	0.820	-4.334	5.389
Log_{10} Body Mass	1.022	1.262	0.126	0.809	0.431	-1.669	3.713
Soil Compactibility	-0.148	0.128	-0.185	-1.154	0.266	-0.422	0.125
Food Plant Density	-0.061	0.058	-0.185	-1.044	0.313	-0.184	0.063
Shade Plant Density	-0.101	0.020	-0.821	-4.937	<0.001	-0.144	-0.057
Location Point Number	0.046	0.027	0.516	1.708	0.108	-0.011	0.103
Squared z-score of Points	-0.004	0.165	-0.008	-0.025	0.980	-0.356	0.347

a. Dependent Variable: $\log_{10}$ home range size R squared = 0.689 (Adjusted R squared = 0.565)

Table 4.13. Results of regression analysis of $\log_{10}$ home range size with shade plant density as a predictor (N = 22). The reduced model also included $\log_{10}$ body mass, number of location points used for home range calculation, and squared z-scores of location points.

Partial Regression Coefficients[a]

Model	Unstandardized Coefficients		Standardized Coefficients	t	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	0.397	2.230		0.178	0.861	-4.309	5.102
Log_{10} Body Mass	0.981	1.249	0.121	0.786	0.443	-1.654	3.616
Shade Plant Density	-0.091	0.019	-0.745	-4.725	<0.001	-0.132	-0.051
Location Point Number	0.051	0.023	0.577	2.238	0.039	0.003	0.099
Squared z-score of Points	-0.056	0.135	-0.109	-0.416	0.683	-0.341	0.229

a. Dependent Variable: $\log_{10}$ home range size R squared = 0.645 (Ajusted R squared = 0.562)

Table 4.14. Results of regression analysis of residual $\log_{10}$ home range size (including shade density as a covariate) with residual $\log_{10}$ endurance capacity and $\log_{10}$ corticosterone as predictor variables (N = 18). Residual home range was not significantly predicted by residual endurance capacity and corticosterone (N = 18; P = 0.369).

Partial Regression Coefficients[a]

Model	Unstandardized Coefficients		Standardized Coefficients	T	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	0.034	0.065		0.527	0.605	-0.103	0.172
Residual $\log_{10}$ endurance	0.004	0.180	0.005	0.022	0.983	-0.377	0.385
Log_{10} corticosterone	-0.079	0.141	-0.139	-0.560	0.583	-0.377	0.219

a. Dependent Variable: Residual $\log_{10}$ home range size R squared = 0.11

Figure Legends

Figure 4.1. Aerial photo of field site screen-captured from GoogleMaps October 31st 2015, with boundaries and size indicated.

Figure 4.2. Photograph of saline/corticosterone implant: 4 mm of surgical grade silastic tubing with seals composed of trimmed 1/8” i.d. silicone rubber end caps.

Figure 4.3. Diagram of simple anesthesia device for small reptiles; diagram provided by Diana Hews of Indiana State University on December 3 2015. Setup includes A: squeeze bottle with internal straw cut to half-length; B: isoflurane; C: vinyl tubing at a length short as possible, but allowing for maneuverability; D: squeeze bottle with internal straw removed and bottom cut off; E: thick rubber band; F: latex (i.e., cut latex glove) with small hole cut in the middle.

The animal’s head is placed through the hole in the latex (F). The isoflurane-containing bottle (A) is squeezed a few times to pump isoflurane-containing air into the second bottle (D) and expose the animal to the anesthetic. Periodically (every couple minutes), the bottle should be squeezed again to replace the air. As the vaporization of isoflurane is temperature dependent, do not use this apparatus during at extremely high environmental temperatures (i.e., > 100 °F). Doing so can lead to anesthetic overdose.

Figure 4.4. A) Illustrated diagram of the beading procedure, reproduced from Fisher and Muth (1989). B) Photograph of tail beading on *Dipsosaurus dorsalis*, taken by Jennifer Singleton. White-red-red translates to unique identification number 0-1-1 or 11.

Figure 4.5. Experimental timeline for studies conducted in 2017.

Figure 4.6. Mean $\underline{+}$ SE of (A) $\log_{10}$ circulating corticosterone (ng/mL), (B) estimated marginal means of $\log_{10}$ endurance capacity (min; covariate of body mass), and (C) estimated marginal means of $\log_{10}$ home range size (m^2; covariates of body mass, number of location points used for MCP calculation, and z-scores of location points squared) between implant types (saline vs. corticosterone) in an experimentally manipulated population of *Dipsosaurus dorsalis* in northern Palm Springs, CA.

Figure 4.7. Repeatability of first and second endurance capacity measurements made for individual free-living desert iguanas from northern Palm Springs, CA. First and second endurance measurements were significantly correlated ($R = 0.521$; $P = 0.003$) and not significantly different on average (paired-t = -1.185; $P = 0.246$). The higher of two trials was used as the value for maximum endurance capacity.

Figure 4.8. Scatterplot of residual $\log_{10}$ endurance capacity (min; covariate of body mass) and $\log_{10}$ circulating corticosterone (ng/mL) for individual desert iguanas, distinguished by implant type (saline vs. corticosterone). The relationship between

circulating corticosterone and residual endurance capacity was not significant (N = 23; R = 0.228; P = 0.295). The relationship was also non-significant within implant types (saline: N = 14, R = 0.090, P = 0.740; corticosterone: N = 9; R = 0.204; P = 0.598).

Figure 4.9. Scatterplot of residual $\log_{10}$ home range size (m^2; covariates of body mass, number of location points used for home range calculation, and squared z-scores of point number) and residual $\log_{10}$ endurance capacity for individual desert iguanas, distinguished by implant type (saline vs. corticosterone). The relationship between residual home range size and residual endurance capacity was not significant (N = 23; R = 0.248; P = 0.254). The relationship was also non-significant within implant types (saline: N = 14, R = 0.197, P = 0.500; corticosterone: N = 9, R = 0.351, P = 0.354).

Figure 4.10. Scatterplot of residual $\log_{10}$ home range size (m^2; covariates of body mass, number of location points used for home range calculation, and squared z-scores of point number) and $\log_{10}$ circulating corticosterone (ng/mL) for individual desert iguanas, distinguished by implant type (saline vs. corticosterone). The relationship between circulating corticosterone and residual home range size was not significant (N = 19; R = 0.206; P = 0.369). The relationship was also non-significant within implant types (saline: N = 11, R = 0.545, P = 0.084; corticosterone: N = 8, R = -0.438, P = 0.278).

Figure 4.1.

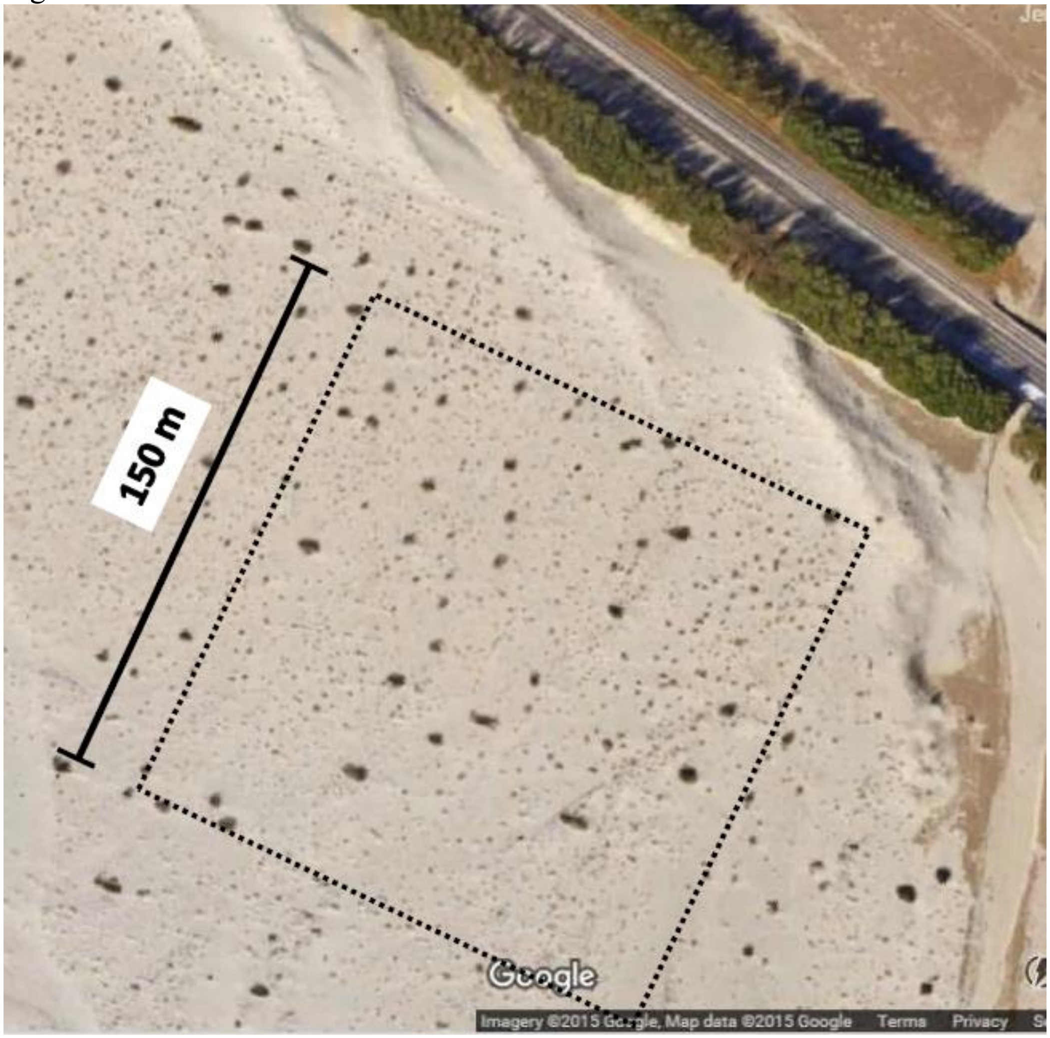

150 m
Google
Imagery ©2015 Google, Map data ©2015 Google Terms Privacy

Figure 4.2.

Figure 4.3.

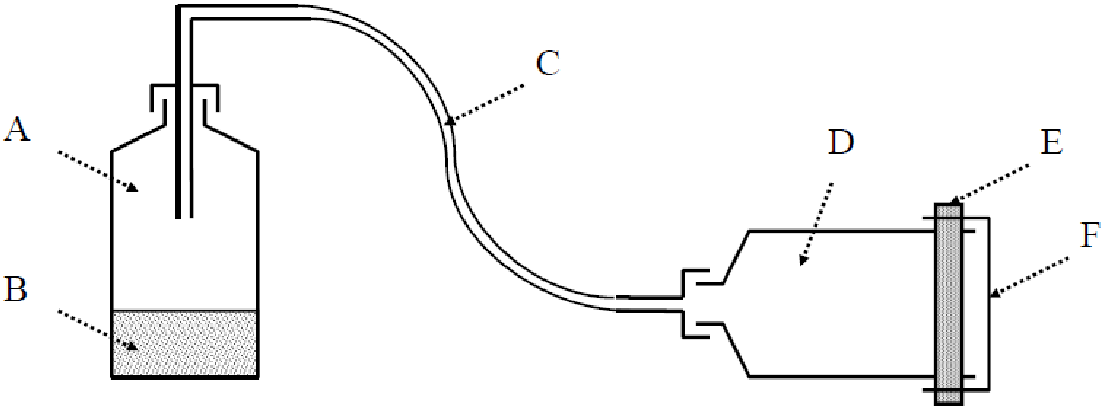


Figure 4.4.

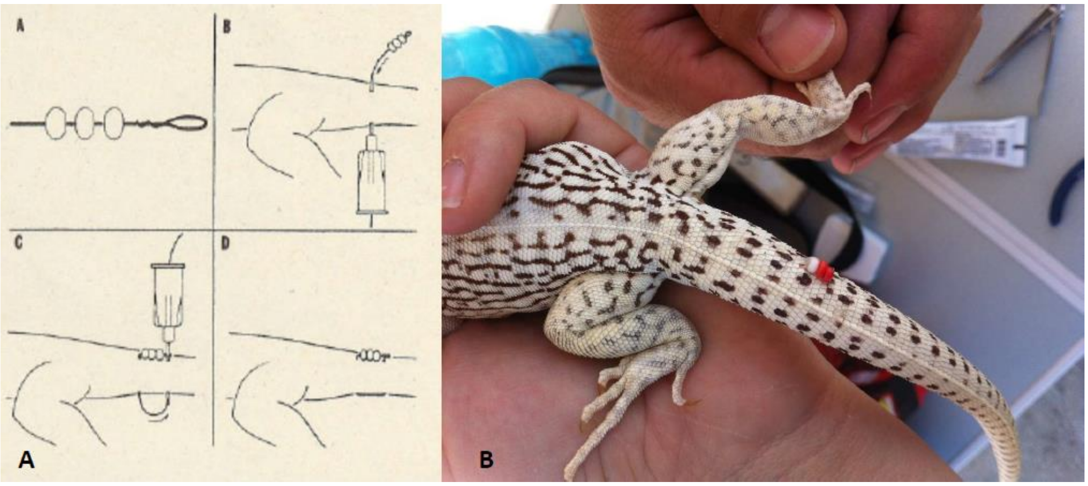


Figure 4.5.

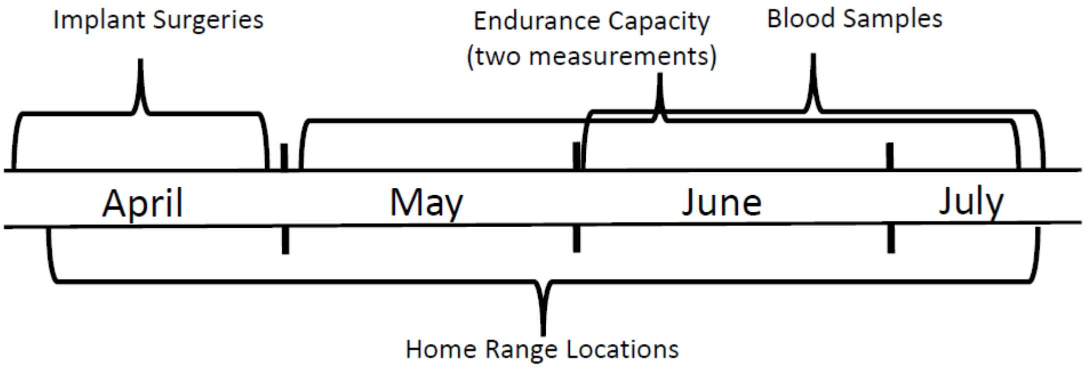

Implant Surgeries
Endurance Capacity
(two measurements)
Blood Samples
April
May
June
July
Home Range Locations

Figure 4.6.

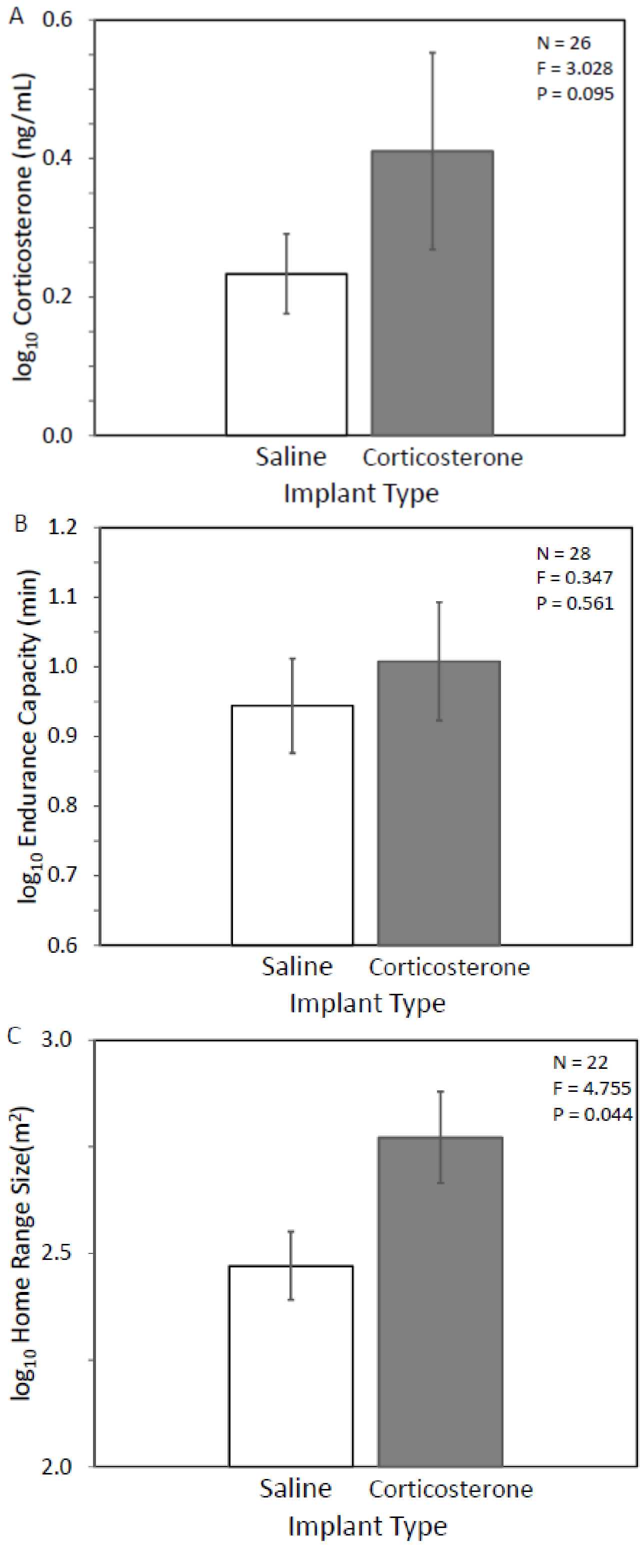
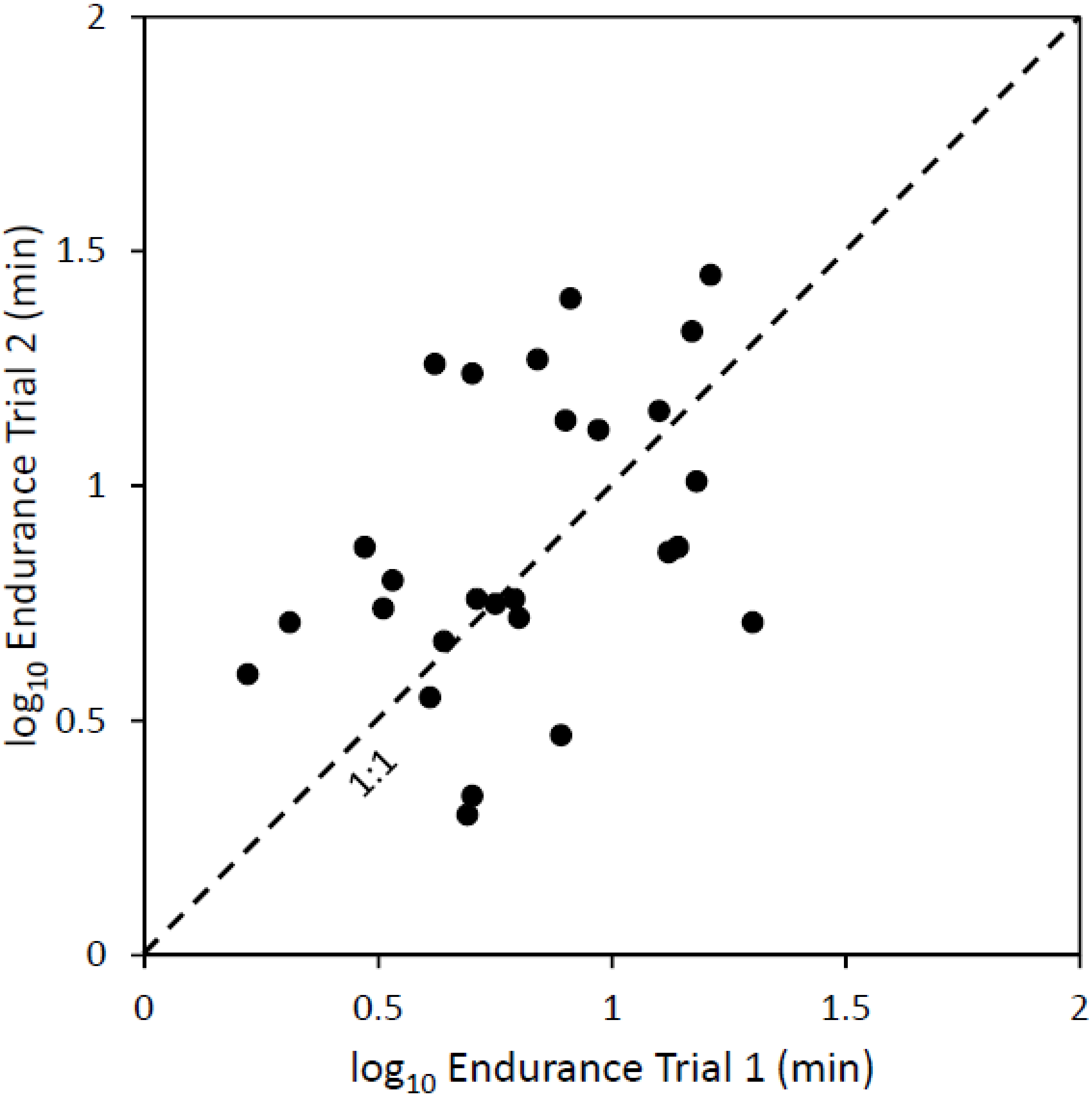

A
0.6
0.4
0.2
0.0
log10 Corticosterone (ng/mL)
N = 26
F = 3.028
P = 0.095
Saline
Corticosterone
Implant Type
B
1.2
1.1
1.0
0.9
0.8
0.7
0.6
log10 Endurance Capacity (min)
N = 28
F = 0.347
P = 0.561
Saline
Corticosterone
Implant Type
C
3.0
2.5
2.0
log10 Home Range Size(m2)
N = 22
F = 4.755
P = 0.044
Saline
Corticosterone
Implant Type

Figure 4.7.



2
1.5
1
0.5
0
0
0.5
1
1.5
2
1:1
$\log_{10}$ Endurance Trial 2 (min)
$\log_{10}$ Endurance Trial 1 (min)

Figure 4.8.

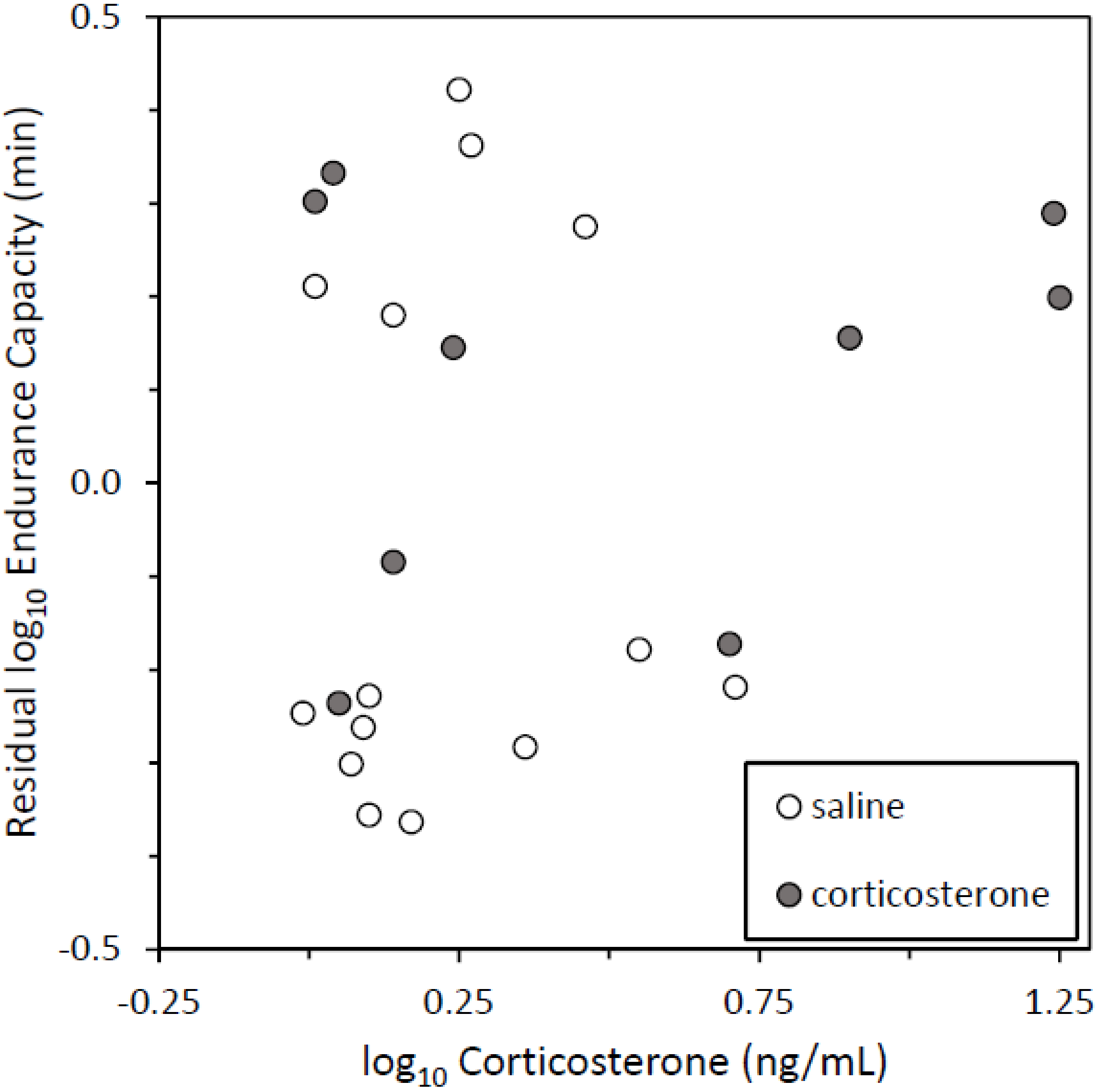

0.5
0.0
-0.5
Residual $\log_{10}$ Endurance Capacity (min)
-0.25
0.25
0.75
1.25
$\log_{10}$ Corticosterone (ng/mL)
○ saline
● corticosterone

Figure 4.9.

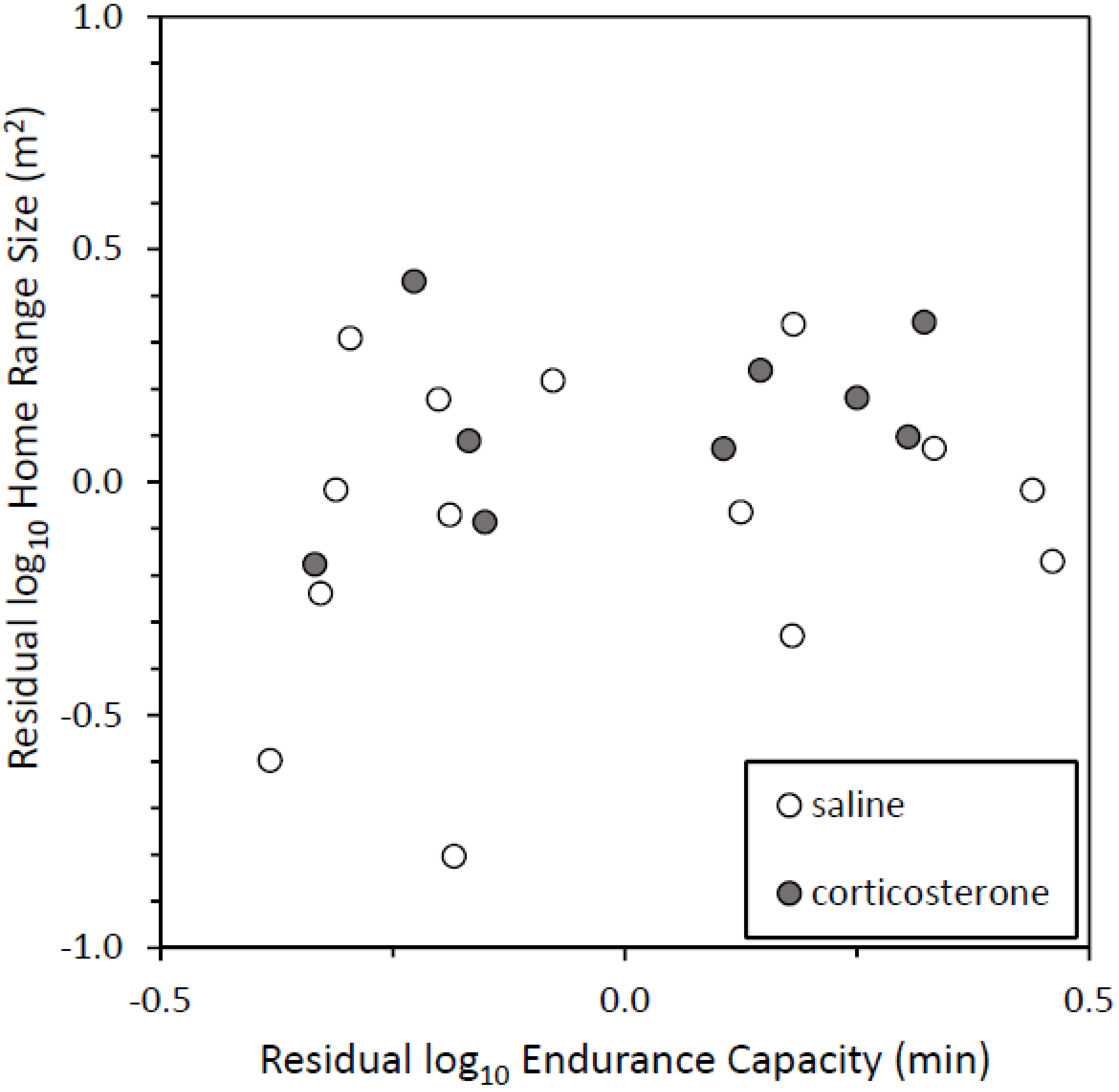
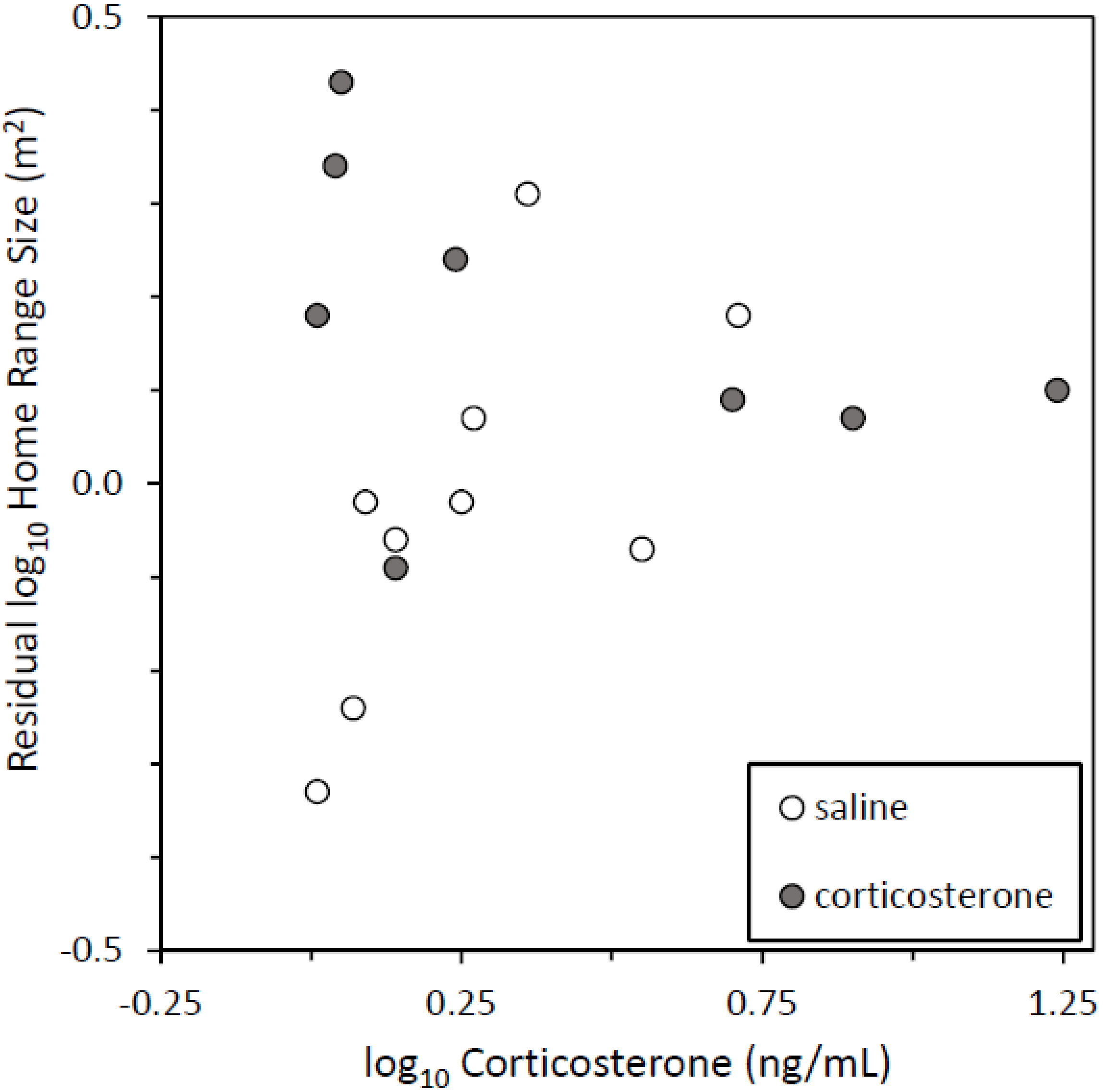

1.0
0.5
0.0
-0.5
-1.0
Residual log10 Home Range Size (m2)
-0.5
0.0
0.5
Residual log10 Endurance Capacity (min)
○ saline
● corticosterone

Figure 4.10.


0.5
0.0
-0.5
Residual $\log_{10}$ Home Range Size (m^2)
-0.25
0.25
0.75
1.25
$\log_{10}$ Corticosterone (ng/mL)
○ saline
● corticosterone

Appendix I. SPSS syntax

```
GET
FILE='C:\Singleton\Dipsosaurus\Implant_Field_study\EnduranceCap_HR_Implants_CORT_BLDnotes_2017.sav'.

*************************ENDURANCE REPEATBILITY FOR LIZARDS WITH IMPLANTS****************************************

GET
FILE='C:\Singleton\Dipsosaurus\Implant_Field_study\EnduranceCap_HR_Implants_CORT_BLDnotes_eco_2017.sav'.
Select IF ENDMINHI > 4.
SORT CASES BY ImpCode(A).
Execute.
LIST Variables IMPCODE LEND2MIN LEND1MIN.

CORRELATIONS
  /VARIABLES = END2MIN END1MIN
  /PRINT=TWOTAIL NOSIG
  /MISSING=PAIRWISE.
```

```
CORRELATIONS
  /VARIABLES = LEND2MIN LEND1MIN
  /PRINT=TWOTAIL NOSIG
  /MISSING=PAIRWISE.


****************HOME RANGE VS. IMPLANT
TYPE***********************************.

SELECT IF locpointa > 5.
Execute.

DESCRIPTIVES VARIABLES = AREA100 LAREA100
  /STATISTICS = MEAN STDDEV MIN MAX SEMEAN SKEWNESS.

MEANS TABLES=area100 BY ImpCode
  /CELLS=MEAN COUNT STDDEV SEMEAN.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA COLLIN TOL CHANGE
```

```
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT LAREA100
  /METHOD=ENTER locpointa SZptsHR hrspan LgBMass
  /RESIDUALS DURBIN
  /CASEWISE PLOT(ZRESID) ALL.

UNIANOVA LAREA100 BY ImpCode WITH LgBMass locpointa SZptsHR
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /EMMEANS=TABLES(ImpCode) WITH(LgBMass=MEAN locpointa=MEAN
SZptsHR=MEAN)
  /PRINT=DESCRIPTIVE PARAMETER
  /CRITERIA=ALPHA(.05)
  /DESIGN=LgBMass locpointa SZptsHR ImpCode.



***************CORTICOSTERONE VS. IMPLANT TYPE*****************.
DESCRIPTIVES VARIABLES = CORT LGCORT  cortng blddelay SectoBld
  /STATISTICS = MEAN STDDEV MIN MAX SEMEAN SKEWNESS.
```

```
MEANS TABLES=CORTng BY ImpCode
  /CELLS=MEAN COUNT STDDEV SEMEAN.


REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA COLLIN TOL CHANGE
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT LgCORT
  /METHOD=ENTER TDifBld blddelay
  /RESIDUALS DURBIN
  /CASEWISE PLOT(ZRESID) ALL.


UNIANOVA CORTng BY ImpCode
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /EMMEANS=TABLES(ImpCode)
 /PRINT=DESCRIPTIVE
 /CRITERIA=ALPHA(0.05)
  /DESIGN=ImpCode.
```

```
UNIANOVA LgCORT BY ImpCode

  /METHOD=SSTYPE(3)

  /INTERCEPT=INCLUDE

  /EMMEANS=TABLES(ImpCode)

  /PRINT=DESCRIPTIVE

  /PLOT=SPREADLEVEL RESIDUALS

  /CRITERIA=ALPHA(.05)

  /DESIGN=ImpCode.



***************ENDURANCE VS. IMPLANT

TYPE******************************.


REGRESSION

  /DESCRIPTIVES MEAN STDDEV CORR SIG N

  /MISSING LISTWISE

  /STATISTICS COEFF OUTS CI(95) R ANOVA COLLIN TOL CHANGE

  /CRITERIA=PIN(.05) POUT(.10)

  /NOORIGIN

  /DEPENDENT LendHmin

  /METHOD=ENTER TDfendX LgBMass

  /RESIDUALS DURBIN
```

```
  /CASEWISE PLOT(ZRESID) ALL.
********No significant correlation with body mass or mean time between implants and endurance.

UNIANOVA LENDHMIN BY ImpCode WITH LgBMass
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /EMMEANS=TABLES(ImpCode) WITH(LgBMass=MEAN)
  /PRINT=DESCRIPTIVE PARAMETER
  /CRITERIA=ALPHA(.05)
  /DESIGN=LgBMass ImpCode.




*****************MAKE FILE WITH
RESIDUALS*********************************.
GET
FILE='C:\Singleton\Dipsosaurus\Implant_Field_study\EnduranceCap_HR_Implants_CO
RT_BLDnotes_eco_2017.sav'.

UNIANOVA LENDHMIN WITH LgBMass
```

```
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (ReSLend) ZRESID (ZResLend)
  /CRITERIA=ALPHA(0.05)
  /DESIGN=LgBMass.

UNIANOVA Larea100 WITH LgBMass  locpointa SZptsHR
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (ReSLHR1) ZRESID (ZResLHR1)
  /CRITERIA=ALPHA(0.05)
  /DESIGN=LgBMass  locpointa SZptsHR.

UNIANOVA Larea100 WITH LgBMass locpointa SZptsHR Xpenet fds2017 sds2017
  /METHOD=SSTYPE(3)
  /INTERCEPT=INCLUDE
  /SAVE=RESID (ReSLHR2) ZRESID (ZResLHR2)
  /CRITERIA=ALPHA(0.05)
  /DESIGN=LgBMass locpointa SZptsHR Xpenet fds2017 sds2017.

UNIANOVA Larea100 WITH LgBMass  locpointa SZptsHR sds2017
  /METHOD=SSTYPE(3)
```

```
 /INTERCEPT=INCLUDE
 /SAVE=RESID (ReSLHR3) ZRESID (ZResLHR3)
 /CRITERIA=ALPHA(0.05)
 /DESIGN=LgBMass locpointa SZptsHR sds2017.


********************************ECOLOGICAL MODELS OF HOME
RANGE*******************.

GET
FILE='C:\Singleton\Dipsosaurus\Implant_Field_study\EnduranceCap_HR_Implants_CO
RT_BLDnotes_eco_2017.sav'.

CORRELATIONS
 /VARIABLES = Xpenet fds2017 sds2017
 /PRINT=TWOTAIL NOSIG
 /MISSING=PAIRWISE.

REGRESSION
 /DESCRIPTIVES MEAN STDDEV CORR SIG N
 /MISSING LISTWISE
 /STATISTICS COEFF OUTS CI(95) BCOV R ANOVA
```

```
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT larea100
  /METHOD=ENTER LgbMASS Xpenet fds2017 sds2017 locpointa SZptsHR.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) BCOV R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT larea100
  /METHOD=ENTER LgbMASS Xpenet sds2017 locpointa SZptsHR.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) BCOV R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT larea100
  /METHOD=ENTER LgbMASS sds2017 locpointa SZptsHR.
```

CHAPTER 5

Corticosterone, Endurance Capacity, Home Range Size, and Reproductive Success in Free-living Desert Iguanas (*Dipsosaurus dorsalis*)

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Riverside, California 92521

Abstract

The relationship of a subordinate trait to the Darwinian fitness of an individual can be measured by reproductive success. I used "DNA fingerprinting" to estimate the number of offspring sired by individual male desert iguanas (*Dipsosaurus dorsalis*) in years 2015 and 2017 at a field site near Palm Springs, CA. I then related this fitness component to body mass, home range size, locomotor endurance capacity, and circulating corticosterone levels. Offspring numbers were calculated through paternity analysis via microsatellite genotyping. For the 2017 data set, offspring number was also compared between two groups with either corticosterone or saline implants. No significant relationships were seen in the 2015 sample. In 2017, offspring number was significantly predicted in a multiple regression with home range, endurance, corticosterone, and implant type ($N = 14$; $R^2 = 0.635$; $P = 0.041$). In this regression, only home range size residuals were statistically significant ($P = 0.008$), and they negatively predicted reproductive success. We speculate that individuals with larger home ranges occupied relatively poor habitat with few females available for mating. Limited sample sizes reduce the reliability of conclusions, but further studies should examine these relationships with greater offspring sampling to gain understanding of fitness correlates in *Dipsosaurus dorsalis*.

Introduction

Darwinian fitness (lifetime reproductive success) is exceedingly difficult to measure in most organisms, especially in the wild. In field studies, survival over a limited period of time is often used as a metric of one fitness component. For example, one may examine organisms in a population for a given feature, then return and see whether survival rates correlate with certain trait values (Clobert et al. 2000; Le Galliard et al. 2004; Romero and Wikelski 2010). The most direct measure of fitness may be the number of offspring produced, though this is not a simple measurement for free-living organisms, especially if one wishes to obtain measures for the entire reproductive lifespan in long-lived organisms (Oli and Armitage 2003; Wikelski and Romero 2003).

The home range of an individual organism typically includes the area used for both foraging and mate-finding (Burt 1943). Hence, home ranges of successful males in polygynous mating systems are either higher-quality or larger, depending on the male strategy (Fox et al. 1981; Salvador et al. 1995; Haenel et al. 2003; Schradin et al. 2010). Other qualities which show variation in males may also confer advantages in a polygynous mating system. Body mass, for example, is often correlated with mating success in lizards (Wikelski et al. 1996; Sinervo et al. 2000; Wikelski and Romero 2003; John-Alder et al. 2009). Larger males are better able to defend females or territories in competition with others.

Similarly, some evidence suggests that animals with higher locomotor performance benefit with greater mating success. Male Collared lizards (*Crotaphytus collaris*) with higher sprint speeds defend females from other potential mates better and sire more offspring (Husak et al. 2006, 2008). Laboratory-measured endurance capacity significantly predicts the “winner” in size-matched male-male aggressive encounters in Puerto Rican Crested Anoles (*Anolis cristatellus*; Perry et al. 2004). Maximum sprint speed was significantly higher for winners in dyadic contests of male *Sceloporus occidentalis* (Garland, Jr. et al. 1990).

Circulating hormones may also impact the outcome of similar contests. Testosterone levels are correlated with contest-relevant traits, such as bite force, in numerous lizards (Husak et al. 2007; Gowan et al. 2010). Though conventional wisdom dictates a trade-off between testosterone and corticosterone, increasing numbers of reptiles and amphibians show positive correlations between testosterone and corticosterone on a yearly cycle, peaking during the reproductive period (Moore and Jessop 2003; Eikenaar et al. 2012), though some studies have found that supplemental cort or testosterone can conflict with each other (Denardo and Sinervo 1994; O’Connor et al. 2011). Circulating corticosterone is thought to facilitate high levels of activity through glucose mobilization (Wingfield et al. 1998; Jessop et al. 2003). High levels of activity may be needed to pursue females, defend territories, and participate in aggressive encounters. In one study, the circulating corticosterone levels of male Eastern Fence Lizards (*Sceloporus undulatus*) were strongly correlated with the number of offspring sired (John-Alder et al. 2009).

Molecular techniques can be used in both captive and free-living animals to estimate paternity (Gullberg et al. 1997; Bateson et al. 2011). One such technique uses microsatellites to determine the levels of relatedness between adults and juveniles in a population (Dierkes et al. 2008; Faria et al. 2010; Olsson et al. 2011). Microsatellites are repetitions of nucleotides that are highly polymorphic and specific to species or closely-related taxa, making them very useful for comparisons between closely related individuals (Kelkar et al. 2010). Microsatellites are among the most popular choices of analysis for population-level genetics (Guichoux et al. 2011).

Desert iguanas (*Dipsosaurus dorsalis*) have been used as a study system to examine a wide range of characters, from muscle physiology and ionic balance to field ecology and social behavior (Berk and Heath 1975; Krekorian 1976; Glinski and Krekorian 1985; Gleeson and Harrison 1988; Alberts 1990; Bealor and Krekorian 2002; Hancock and Gleeson 2005). Desert iguanas are favorable for use in physiological studies due to their large size, allowing greater volumes of blood sampling and ease of handling. This species is also relatively docile and tractable for locomotor studies. In the field, desert iguanas are terrestrial, diurnal, and tolerant of human observation, all qualities which facilitate behavioral studies.

Desert iguanas have a polygamous mating system, though research has not established whether the male guards territory (overlapping with females) from other males, or whether males compete for females in situ with or without elements of female choice (Norris 1953; Carpenter 1961). The regular observance of significant home range overlap in males seems to suggest against true territoriality (Krekorian 1976, 1984; Glinski and Krekorian 1985). Hence, a simple counting of female home range overlap would not be an adequate proxy measurement of fitness. However, females typically lay only one clutch per year which is a product of the same year's mating system, and desert iguanas typically hibernate from October to April (Norris 1953); sperm storage is not known to occur in this species. Hatchlings from year to year do not overlap in size; in this way, the results of the conditions during mating season and the success of males present is directly measurable. Fifteen microsatellite loci have been identified for use in desert iguanas (Valdivia Carrillo et al. 2013), rendering them suitable for field studies of reproductive success.

Methods

DNA samples were taken from adult male desert iguanas at time of first capture during the mating seasons (April-early July) of 2015, 2016, and 2017. Lizards were captured via noosing (García-Muñoz and Sillero 2010) and samples were taken using a pair of nail clippers (cleaned and sterilized with ethanol between uses). Adult samples consisted of 0.5 cm sections of unbroken tail tips, or 0.25 cm sections of regenerated tail tips (as these were blunter and more fleshed). After sampling, pressure was applied to tail tips if needed (rare) until bleeding ceased.

Hatchling samples were collected in September-October 2015, 2016, and2017, as they emerged from natal burrows. Any hatchlings seen within the field site were caught by hand or noosed. Hatchling samples were 1 cm sections of tail tips (hatchling tails are thinner and the distal portion is much thinner and less fleshed). All samples were stored at -20°C.

Considering the number of samples obtained per year, 2015 and 2017 were chosen as the years for analysis. Qiagen D'Neasy Blood & Tissue kits (catalogue #69504) were used for DNA extraction.

Microsatellite primers have been previously described for this species, though in a population from the Baja California Peninsula (Valdivia Carrillo et al. 2013). Fifteen primers have been described, 10 of which were selected for this study based on number of alleles per locus, annealing temperature, and disparate fragment size (advantageous for planned multiplex reactions in a closely-related population). Oligonucleotide primers were ordered from Integrated DNA Technologies Inc. (Skokie IL, USA). Primers were used in polymerase chain reactions (PCR) on 10 individual samples to check amplification for the 10 selected primers within the population. The PCR reaction was adapted from Valdivia Carrillo et al. (2013); in brief: 12.5 uL taq polymerase master mix (Promega Corporation (Madison WI, USA), then Life Technologies Corporation (ThermoFisher Scientific), 9.5 uL nuclease-free water, 0.75 uL of 10uM forward primer, 0.75 uL of 10 uM reverse primer, 1.5 uL DNA. Initial denaturation was 5 min at 95°C, followed by 30 cycles of (1 min at 95°C, 1 min at primer-specific temperature, 1 min at 72°C), with a final extension of 10 min at 72°C.

Following the check for amplification, seven primers were selected for use and fluorescent dye-labelled versions of forward primers were ordered (labeled with 6-FAM fluorescein and HEX as 5' modifications). Five primers were amplified in 10-sample PCR multiplex reactions (3 primers and 2 primers, respectively) with two additional single-loci PCR reactions to examine the allelic diversity and heterozygosity via fragment analysis. Fragment analysis was performed at the Arizona State University CLAS DNA laboratory on a Applied Biosystems (ABI) 3730 capillary sequencer. The size standard ladder was GeneScan 500.

Results from the initial multiplex reactions necessitated a reduction in the number of loci processed to five: Ddor7, Ddor14, Ddor2, Ddor3 and Ddor12 (GeBank accession numbers KC514950, KC514957, KC514945, KC514946, and KC514955, respectively). Owing to concerns about interference between loci, final reactions were single-loci PCR.

Results of fragment analysis were examined used the program Geneious Prime with Microsatellite plugin (Geneious Biologics, NZ). Peaks were called via peak suggestion function and confirmed via visual comparison. Cervus 3.0.7 (Marshall et al. 1998; Kalinowski et al. 2007) was used to assign paternity. Offspring were analyzed separately by years (2015 and 2017). Paternity analysis requires attempted testing of all mature males potentially present during the mating season. Potential fathers were separated by years as follows: all males that were beaded by the end of the field season (September) 2015 were included as potential fathers for 2015 offspring. Males analyzed for paternity for 2017 offspring included those sampled in 2017 as well as adult male iguanas that were 1) sampled in 2015 or 2016 and 2) seen at some time in the year before analysis. For example, a lizard sampled in 2015 but not seen again in 2016 was assumed to not be present in the 2017 mating season.

Offspring were assigned to males at 80% confidence (Marshall et al. 1998; Husak et al. 2006). Simulations required for parentage assignment were run with the following parameters: 10,000 cycles; 90% of candidates sampled; 51 potential fathers; 92% of loci typed, 1% of loci mistyped. It was considered likely that the majority of potential fathers were sampled, as samples were collected throughout the mating season. I used 51 as the number of potential fathers, as this was the maximum number of males seen on a single-day observation period during May-June over a four year-period at a nearby field site of similar size in the area (~500 m East; A. Muth, pers. comm).

Desert iguanas were sampled from a 150 x 150 m field site located outside Palm Springs, CA within the Whitewater Floodplain Preserve (Alagona and Pincetl 2008). Body mass, circulating corticosterone, endurance capacity, and home range size were also examined for adult males in this population in 2015 and 2017 (Table 5.1). All adult lizards captured were given unique identifying markers in the form of a permanent set of colored beads (corresponding to numbers) placed on surgical wire and run under the skin of the tail (details in Chapters 3 and 4) (Fisher and Muth 1989). This system of individual identification allows for recognition at a distance and is mostly permanent over a two year-period (as documented in the pilot study of the method, with *Uma inornata*: only 5% of beading required repairs over time; Fisher and Muth 1989). Adult male desert iguanas were blood-sampled in the field (details in chapters 3 and 4). Lizards were also captured and tested for maximum endurance capacity, then released at point of capture (details in Chapters 1, 3, and 4). From April 30 – July 15, lizard locations in the field were recorded; home range was calculated via the maximum convex polygon method (details in Chapters 1, 3, and 4). In the April of 2017, 42 desert iguanas were captured from the field site and received supplemental corticosterone (or saline) via surgical implants. These lizards were released at point of capture and measurements of corticosterone, endurance capacity, and home range size for the 2017 field season (details in chapter 4). To examine the relationship between home range size and habitat features, several ecological variables were also measured at intervals on the field site and quantified for each home range (food plant density, shade plant density, soil compactibility; details in Chapters 3 and 4).

For statistical analysis, 2015 and 2017 data were analyzed separately. Linear regression was used to generate residual values for further analysis and to examine relationships between traits. Residual values of $\log_{10}$ endurance capacity were calculated using $\log_{10}$ body mass. Residual values of $\log_{10}$ home range size in 2015 were calculated using $\log_{10}$ body mass, number of location points used in home range calculation, and squared z-score of location point number. Alternative home range residuals were also calculated with incorporation of all ecological variables (#2) and only statistically significant ecological variables (#3: shade plant density). Shade plant density was chosen due to its significance in predicting home range size in previous studies with this population (Chapters 3 and 4). Residual values of $\log_{10}$ home range size in 2017 were calculated as above, with additional residuals removing $\log_{10}$ body mass; this was due to the non-significant, negative relationship between body mass and home range size in the 2017 study (details in Chapter 4). Pearson correlations, linear regression, and multiple regression in SPSS software were used to examine relationships between traits and residuals.

Procedures involving lizards were approved by the California Department of Fish and Wildlife under permit# sc12669. Procedures were also approved by the Institutional Animal Care and Use Committee of the University of California at Riverside under animal use protocol number 20130015 and 20170012.

Results

For 2015, the total number of offspring assigned to individual fathers at 80% confidence was 25 (of 31 offspring with DNA data; Fig. 5.1A). Number of offspring was not significantly correlated with $\log_{10}$ body mass, residual $\log_{10}$ endurance, or any residual $\log_{10}$ home range size (Table 5.2). For the purposes of multiple regression, we chose to use the residual values of $\log_{10}$ home range size calculated with $\log_{10}$ body mass, number of location points used for home range calculation, and squared z-score of location number. Number of offspring was not predicted in a multiple regression with residual $\log_{10}$ home range size, residual $\log_{10}$ endurance capacity, and $\log_{10}$ corticosterone ($N = 9$; multiple $R^2 = 0.691$; model $P = 0.318$), with no significant partial regression coefficients (Table 5.3). Reduction of this model did not result in significance or partial coefficient significance. Number of offspring was also not predicted in a multiple regression with soil density, soil compactibility, food plant density, and shade plant density (Table 5.4; $N = 17$, multiple $R^2 = 0.457$, $P = 0.552$).

For the 2017 data set, 15 offspring (of 23 sampled; Fig. 5.1B) were assigned to individual fathers at 80% confidence. Number of offspring was not significantly correlated with $\log_{10}$ body mass, residual $\log_{10}$ endurance, or any residual $\log_{10}$ home range size (Table 5.5). For the purposes of multiple regression, we chose to use the residual values of $\log_{10}$ home range size calculated with number of location points used for home range calculation and squared z-score of location number for the purposes of multiple regression (body mass was excluded as it was non-significantly and negatively related to home range size in this sample). Number of offspring was significantly predicted in a multiple regression of residual $\log_{10}$ home range size, residual $\log_{10}$ endurance capacity, $\log_{10}$ corticosterone, and implant type (N = 14; multiple $R^2 = 0.635$; P = 0.041), with $\log_{10}$ home range residual as a significant partial regression coefficient (Table 5.6; B = -2.584, P = 0.008). Number of offspring was not predicted in a multiple regression with soil compactibility, food plant density, and shade plant density (Table 5.7; N = 22, multiple $R^2 = 0.425$, P = 0.299). Reduction of this model did not result in significance.

Discussion

As expected for a polygynous mating system (Emlen and Oring 1977; Clutton-Brock 1998; Johnstone 2000), including for other species of iguanid lizards (Wikelski et al. 1996; but see Husak 2006), reproductively success was highly skewed, with most males apparently siring no offspring, and a few siring multiple offspring (Fig. 5.1). Within the 2017 data set, adult male desert iguana yearly reproductive success could be significantly predicted in a model that included circulating corticosterone, endurance capacity, home range size, and implant type. In this model, only home range size was statistically significant, and it had a negative relationship with number of offspring. Home range size is known to correlate negatively with resource density in many species; studies of herbivores have found this negative relationship between home range size and food plant density (Tufto et al. 1996; Relyea et al. 2000; Saïd et al. 2005). In essence, the more resource-dense an area is, the smaller a home range needed. In previous studies with this population (see Chapters 3 and 4), the home range size of adult male desert iguanas was significantly negatively related to shade plant density. Though offspring number was not correlated with any ecological variable measured in this study, it is possible that a larger home range may signify a low density of some other resource, also important to females, and/or a low density of females. Unfortunately, we were not able to collect home range data for females and as such could not quantify overlap between ecological variables.

Limitations and Future Directions

Our conclusions are limited by the low number of offspring sampled during the two years, reduced further by the proportion of those genotypes that were successfully assigned to fathers. Desert iguana hatchlings typically appear at the end of August/beginning of September (Norris 1953). Depending on the weather, these hatchlings may be active for as little as 3 weeks before beginning their over-winter hibernation. In addition, desert iguana hatchlings are much warier than adults and much less easily approached by researchers. Noosing of lizards requires approach at least within the length of the pole, and hatchlings are less tolerant of such approaches. Other methods of lizard sampling are not without associated trouble; lethal means, such as shooting, are destructive to the population and highly unlikely to be approved by the California Department of Fish & Wildlife. Similarly, the use of pitfall traps is highly regulated and unlikely to be approved, as the traps can be fatal to other animals that may be caught out in the desert heat (especially small rodents, already a taxon of concern in Southern California). The pitfall traps would need to be placed and removed each day, as sealed pitfall traps may be forced open by ravens seeking an easy meal (C. Barrows, pers. com.). With any method, the number of individuals and time spent actively seeking hatchling samples would need to be greatly increased to achieve a more reliable understanding of the relationships between subordinate traits and Darwinian fitness in this species.

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Table 5.1. Sample sizes for adult male desert iguanas used for trait analysis, genotyping, and paternity in 2015 and 2017.

	Corticosterone	**Endurance Capacity**	**Home Range Size**	**Adult DNA**	**Offspring DNA**	**Offspring Assigned**
2015	15	19	21	47	31	25
2017	26	28	23	39	23	15

Table 5.2. Correlations of offspring number in 2015 with paternal body mass, $\log_{10}$ corticosterone, $\log_{10}$ endurance residuals calculated from linear regressions on body mass, and residual values of home range size calculated with independent variables of $\log_{10}$ body mass, number of location points used for home range calculation, and squared z-score of number of location points. Additional residual values of home range size were calculated with variables above plus multiple measures of environmental variables (soil compactibility, soil density, food plant density, and shade density) or only shade plant density.

		Offspring Number
Log_{10} Body Mass	Pearson Correlation	0.056
	Sig. (2-tailed)	0.796
	N	24
Log_{10} Corticosterone	Pearson Correlation	-0.145
	Sig. (2-tailed)	0.671
	N	11
Res. Log_{10} Endurance Capacity (body mass)	Pearson Correlation	0.090
	Sig. (2-tailed)	0.742
	N	16
Res. Home Range Size (body mass, location points, (z-score loc. pts)^2	Pearson Correlation	0.232
	Sig. (2-tailed)	0.370
	N	17
Res. Home Range Size (body mass, location points, (z-score loc. pts)^2, ecol. var.)	Pearson Correlation	0.340
	Sig. (2-tailed)	0.181
	N	17

Res. Home Range Size (body mass, location points, (z-score loc. pts)^2, shade plants	Pearson Correlation	0.340
	Sig. (2-tailed)	0.181
	N	17

Table 5.3. Results of regression analysis of offspring number in 2015 with $\log_{10}$ corticosterone, residual $\log_{10}$ endurance capacity, and residual $\log_{10}$ home range size (calculated with $\log_{10}$ body mass, number of location points used for home range calculation, and squared z-scores of location points). N = 9.

Partial Regression Coefficients[a]

Model	Unstandardized Coefficients		Standardized Coefficients	t	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	0.620	0.304		2.037	0.097	-0.162	1.401
Res. Log_{10} Home Range	1.040	0.595	0.666	1.747	0.141	-0.490	2.570
Res. Log_{10} Endurance	-0.250	0.687	-0.134	-0.364	0.731	-2.014	1.515
Log_{10} Corticosterone	-0.457	0.930	-0.172	-0.491	0.644	-2.848	1.934

a. Dependent Variable: offspring number R squared = 0.477 (Adjusted R squared = 0.163)

Table 5.4. Results of regression analysis of offspring number in 2015 with ecological variables that characterized the home ranges of males as predictors: soil compactibility, soil density, shade plant density, and food plant density. N = 17.

Partial Regression Coefficients[a]

Model	Unstandardized Coefficients		Standardized Coefficients	t	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	-3.041	15.164		-0.201	0.844	-36.082	29.999
Soil compactibility	2.280	1.348	0.460	1.692	0.116	-0.656	5.217
Soil density	1.780	9.511	0.053	0.187	0.855	-18.943	22.504
Food plant density	-0.139	0.188	-0.223	-0.743	0.472	-0.548	0.269
Shade plant density	1.140	1.224	0.302	0.931	0.370	-1.528	3.807

a. Dependent Variable: offspring number R squared = 0.209 (Ajusted R squared = -0.054)

Table 5.5. Correlations of offspring number in 2017 with paternal body mass, log$_{10}$ corticosterone, implant type (corticosterone vs. saline), log$_{10}$ endurance residuals calculated with body mass, and residual values of home range size calculated with log$_{10}$ body mass, number of location points used for home range calculation, and the squared z-score of number of location points. Additional residual values of home range size were calculated without log$_{10}$ body mass and with variables above plus measures of environmental variables (soil compactibility, soil density, food plant density, and shade density) or only shade plant density.

		Offspring Number
Res. Log$_{10}$ Endurance Capacity (body mass)	Pearson Correlation	0.193
	Sig. (2-tailed)	0.402
	N	21
Log$_{10}$ Corticosterone	Pearson Correlation	-0.213
	Sig. (2-tailed)	0.411
	N	17
Log$_{10}$ Body Mass	Pearson Correlation	0.291
	Sig. (2-tailed)	0.190
	N	22
Implant Type	Pearson Correlation	-0.301
	Sig. (2-tailed)	0.135
	N	26
Res. Home Range Size (body mass, location points, (z-score loc. pts)^2	Pearson Correlation	-0.388
	Sig. (2-tailed)	0.112
	N	18
Res. Home Range Size (body mass, location points, (z-score loc. pts)^2	Pearson Correlation	-0.415
	Sig. (2-tailed)	0.086
	N	18
Res. Home Range Size (body mass, location	Pearson Correlation	-0.238
	Sig. (2-tailed)	0.341

points, (z-score loc. pts)^2, ecol. var.)	N	18
Res. Home Range Size (body mass, location points, (z-score loc. pts)^2, ecol. var.)	Pearson Correlation	-0.197
	Sig. (2-tailed)	0.434
	N	18
Res. Home Range Size (body mass, location points, (z-score loc. pts)^2, shade plants	Pearson Correlation	-0.198
	Sig. (2-tailed)	0.431
	N	18
Res. Home Range Size (body mass, location points, (z-score loc. pts)^2, shade plants	Pearson Correlation	-0.165
	Sig. (2-tailed)	0.513
	N	18

Table 5.6. Results of regression analysis of offspring number in 2017 with $\log_{10}$ corticosterone, implant type (corticosterone vs. saline), residual $\log_{10}$ endurance capacity, and residual $\log_{10}$ home range size (calculated with $\log_{10}$ body mass, number of location points used for home range calculation, and squared z-scores of location points). N = 14.

Partial Regression Coefficients[a]

Model	Unstandardized Coefficients		Standardized Coefficients	t	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	-0.078	0.348		-0.225	0.827	-0.866	0.710
Res. $\log_{10}$ Home Range	-2.584	0.771	-1.097	-3.354	0.008	-4.327	-0.841
Res. $\log_{10}$ Endurance	0.241	0.754	0.075	0.320	0.757	-1.464	1.946
$\log_{10}$ Corticosterone	-0.439	0.470	-0.199	-0.935	0.374	-1.501	0.623
Implant Type	0.836	0.507	0.510	1.650	0.133	-0.310	1.982

a. Dependent Variable: offspring number R squared = 0.635 (Adjusted R squared = 0.473)

Table 5.7. Results of regression analysis of offspring number in 2017 with ecological variables that characterized the home ranges of males as predictors: soil compactibility, soil density, shade plant density, and food plant density. N = 22.

Partial Regression Coefficients^{a}

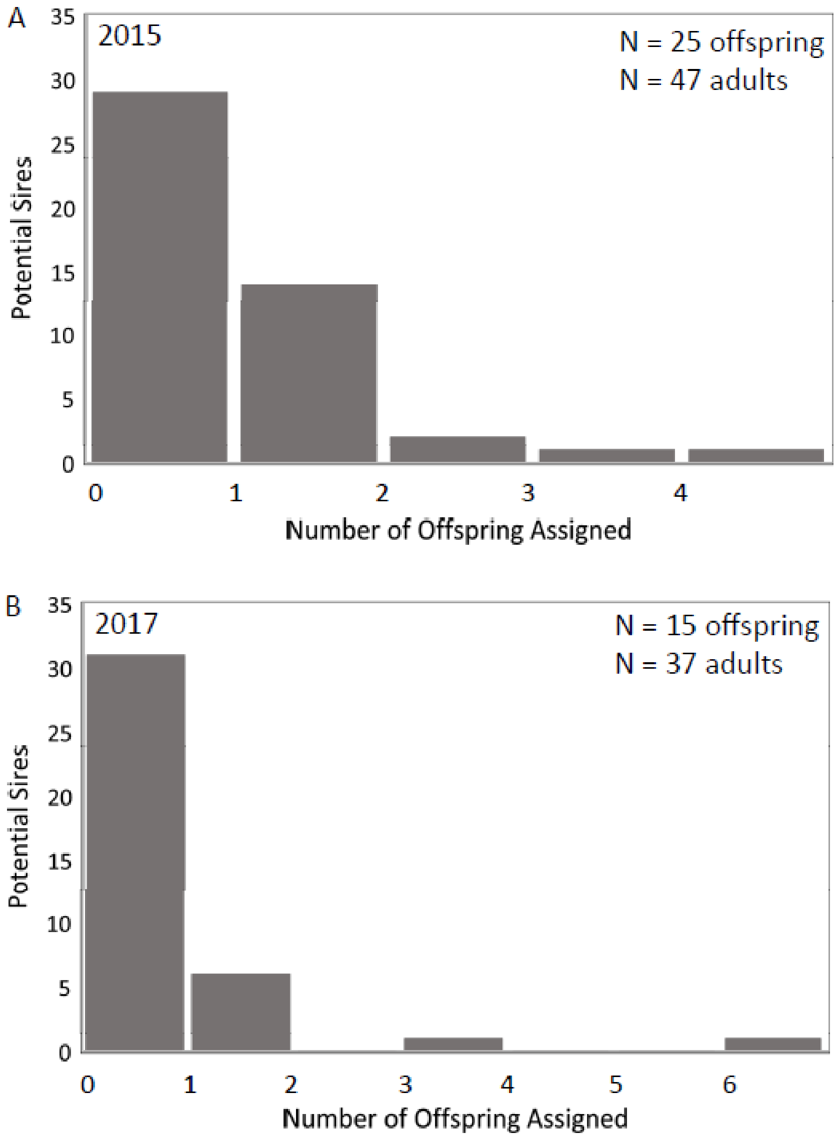
Model	Unstandardized Coefficients		Standardized Coefficients	t	Sig.	95.0% Confidence Interval for B	
	B	Std. Error	Beta			Lower Bound	Upper Bound
(Constant)	0.759	0.640		1.186	0.251	-0.585	2.103
Soil compactibility	-0.794	0.942	-0.193	-0.843	0.410	-2.773	1.184
Food plant density	-0.084	0.133	-0.140	-0.632	0.535	-0.364	0.196
Shade plant density	0.173	0.117	.0326	1.477	0.157	-0.073	0.419

a. Dependent Variable: offspring number R squared = 0.180 (Adjusted R squared = 0.044)

Figure Legends

Figure 5.1. Histogram of (A) 2015 and (B) 2017 offspring assigned to sampled male desert iguanas. Note that most males apparently did not sire any offspring.

Figure 5.1.


A
2015
N = 25 offspring
N = 47 adults
Potential Sires
35
30
25
20
15
10
5
0
0
1
2
3
4
Number of Offspring Assigned
B
2017
N = 15 offspring
N = 37 adults
Potential Sires
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
Number of Offspring Assigned

Appendix I.

```
GET DATA
  /TYPE=XLSX
  /FILE='C:\Singleton\Dipsosaurus\microsats\fitness_2015_2017_v3.xlsx'
  /SHEET=name 'Sheet1'
  /CELLRANGE=RANGE 'A5:I72'
  /READNAMES=ON
  /DATATYPEMIN PERCENTAGE=95.0
  /HIDDEN IGNORE=YES.
EXECUTE.
SAVE OUTFILE='C:\Singleton\Dipsosaurus\microsats\fitness_2015_2017_v3.sav'
  /COMPRESSED.


GET
FILE='c:\Singleton\Dipsosaurus\analyze\COMBINED_2015_2016_noexcl_withresids.sa
v'.
SELECT IF SEASON = 1.
Execute.
SAVE
OUTFILE='C:\Singleton\Dipsosaurus\microsats\COMBINED_2015_2016_noexcl_withr
esids_only2015.sav'
  /DROP=ID
  /COMPRESSED.

GET
FILE='c:\Singleton\Dipsosaurus\microsats\COMBINED_2015_2016_noexcl_withresids_
only2015.sav'.
RENAME VARIABLES (LizID = ID).
Execute.
MATCH FILES /FILE=*
  /FILE='C:\Singleton\Dipsosaurus\microsats\fitness_2015_2017_v3.sav'
  /RENAME (Year = d0)
  /BY ID
  /DROP= d0.
EXECUTE.
COMPUTE propfit = fit15_80/25.
Execute.

* Manually delete the annoying labels.

SAVE OUTFILE=
```

```
'C:\Singleton\Dipsosaurus\microsats\COMBINED_2015_2016_noexcl_withresids_only2
015_fitness_v2.sav'
  /DROP=Fit2015 Fit17_80 Fit2017
  /COMPRESSED.



GET
FILE='C:\Singleton\Dipsosaurus\Implant_Field_study\EnduranceCap_HR_Implants_CO
RT_BLDnotes_eco_2017_resids.sav'.
MATCH FILES /FILE=*
  /FILE='C:\Singleton\Dipsosaurus\microsats\fitness_2015_2017_v3.sav'
  /RENAME (Age Year = d0 d1)
  /BY ID
  /DROP= d0 d1.
EXECUTE.
COMPUTE propfit = fit17_80/25.
Execute.
SAVE OUTFILE=

'C:\Singleton\Dipsosaurus\microsats\EnduranceCap_HR_Implants_CORT_BLDnotes_ec
o_2017_resids_fitness_v2.sav'
  /DROP=Fit2015 Fit15_80 Fit2017
  /COMPRESSED.


*************************************************************************
**************************************************.
* 2015.
*************************************************************************
**************************************************.
*List of Residuals:
ResLgC2 - cort by year, mate
ResLen1 - endurance with body mass only
ResLen2 - endurance with body mass, year, mate
ResLHR1 - HR with mass and points
ResLHR2 - HR with mass, points, year, mate
ResLHR3 - HR with mass, points, eco variables
ResLHR4 - HR with year, mate, mass, points, eco variables
ResLHR5 - HR with mass, points, shade plants
ResLHR4 - HR with year, mate, mass, points, shade plants

GET
```

```
FILE='c:\Singleton\Dipsosaurus\microsats\COMBINED_2015_2016_noexcl_withresids_
only2015_fitness_v2.sav'.
RENAME VARIABLES (Fit15_80 = Fit80).
Execute.

*FOR HISTOGRAM.
*SELECT IF fit80 > -1.
*Execute.
*SELECT IF ID < 260.
*Execute.
*LIST VARIABLES fit80.
*Execute.

* N = 21.
CORRELATIONS
  /VARIABLES=Fit80 ResLHR1 ResLHR3 ReSLHR5
  /PRINT=TWOTAIL NOSIG
  /MISSING=PAIRWISE.

CORRELATIONS
  /VARIABLES=Fit80 Lmass  LgCORT ResLEn1 ResLHR1 ResLHR3 ReSLHR5
  /PRINT=TWOTAIL NOSIG
  /MISSING=PAIRWISE.

GRAPH
  /SCATTERPLOT(BIVAR)=ReSLHR4 WITH Fit80 BY ID (IDENTIFY)
  /MISSING=LISTWISE.

GRAPH
  /SCATTERPLOT(BIVAR)=LgHRA WITH Fit80 BY ID (IDENTIFY)
  /MISSING=LISTWISE.


* Only have 15 cort samples.
REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER ResLHR1 ResLEn1 LgCORT
  /RESIDUALS DURBIN
```

```
  /CASEWISE PLOT(ZRESID) ALL.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER ResLHR1 LgCORT
  /RESIDUALS DURBIN
  /CASEWISE PLOT(ZRESID) ALL.
GRAPH
  /SCATTERPLOT(MATRIX)=Fit80 ReSLHR4 LgCORT BY ID (IDENTIFY)
  /MISSING=LISTWISE.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS  CI(95) R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER penet soildens fooddens shaddens.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS BCOV R ANOVA ZPP
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER penet fooddens shaddens.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS BCOV R ANOVA ZPP
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER penet fooddens.
```

```
**********************************************************************
***********************************************.
* Chapter 4 (2017).
**********************************************************************
***********************************************.
*2017 residuals:
ResLend - endurance with body mass
ResLHR1 - HR with body mass, points
ResLHR2 - HR with points
ResLHR3 - HR with body mass, points, eco
ResLHR4 - HR with points, eco
ResLHR5 - HR with body mass, points, shade
ResLHR6 - HR with points, shade

GET
FILE='c:\Singleton\Dipsosaurus\microsats\EnduranceCap_HR_Implants_CORT_BLDno
tes_eco_2017_resids_fitness_v2.sav'.
RENAME VARIABLES (Fit17_80 = Fit80).
Execute.


CORRELATIONS
  /VARIABLES=Fit80 ReSLend LGCORT LgBmass ImpCode ReSLHR1 ReSLHR2
ReSLHR3 ReSLHR4 ReSLHR5 ReSLHR6
  /PRINT=TWOTAIL NOSIG
  /MISSING=PAIRWISE.


REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER ReSLHR1
  /RESIDUALS DURBIN
  /CASEWISE PLOT(ZRESID) ALL.

* Use this, no body mass.
REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
```

```
  /STATISTICS COEFF OUTS CI(95) R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER ReSLHR2
  /RESIDUALS DURBIN
  /CASEWISE PLOT(ZRESID) ALL.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER ReSLHR2 ReSLend LGCORT ImpCode
  /RESIDUALS DURBIN
  /CASEWISE PLOT(ZRESID) ALL.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER ReSLHR2 LGCORT ImpCode
  /RESIDUALS DURBIN
  /CASEWISE PLOT(ZRESID) ALL.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
  /STATISTICS COEFF OUTS CI(95) R ANOVA
  /CRITERIA=PIN(.05) POUT(.10)
  /NOORIGIN
  /DEPENDENT Fit80
  /METHOD=ENTER ReSLHR2 impcode
  /RESIDUALS DURBIN
  /CASEWISE PLOT(ZRESID) ALL.

REGRESSION
  /DESCRIPTIVES MEAN STDDEV CORR SIG N
  /MISSING LISTWISE
```

```
/STATISTICS COEFF OUTS CI(95) R ANOVA ZPP
/CRITERIA=PIN(.05) POUT(.10)
/NOORIGIN
/DEPENDENT Fit80
/METHOD=ENTER xpenet fds2017 sds2017.
```

CONCLUSION

Summary

In this dissertation, my goal was to examine relationships between basal corticosterone, endurance capacity, home range size, and one component of Darwinian fitness (the number of offspring sired by males in a given season). I did this using the Desert iguana (*Dipsosaurus dorsalis*) over five studies:

Chapter 1

In chapter one, I examined correlations between endurance capacity and home range size in free-living male desert iguanas over two seasons. I found that body mass was positively related to endurance capacity, but not home range size, among individual adult males. Endurance capacity and home range size were positively and significantly correlated. 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.

Chapter 2

In this chapter, I examined the relationship between basal circulating corticosterone and endurance capacity in captive desert iguanas that received surgical implants with using corticosterone or saline vehicle. Corticosterone supplementation did not increase circulating corticosterone or endurance capacity over a 5-week period. Endurance capacity was significantly increased two weeks after implant surgery, but this increase did not differ between treatment groups. These negative results may be explained by failure of the corticosterone implants.

Chapter 3

In chapter three of the dissertation, I characterized relationships between circulating corticosterone, endurance capacity, and home range size in free-living desert iguanas during the mating and non-mating seasons of two years. I also measured ecological variables expected to impact home range size (e.g., soil density, plant food availability) and quantified these for individual home ranges. Circulating corticosterone varied significantly by both year and season, as did endurance capacity, while surprisingly home range did not vary by season or year. I found no significant relationships between corticosterone, endurance capacity, and home range size. Home range size was significantly and negatively related to the density of shade plants within the home range. The importance of shade plants in home range size determination should inform future conservation efforts for desert ectotherms.

Chapter 4

In chapter four, I examined relationships between circulating corticosterone, body mass, endurance capacity, and home range size in free-living desert iguanas using corticosterone implants with improved design. I again measured ecological variables expected to impact home range size and quantified these for individual home ranges. Corticosterone implants seemed to increase circulating corticosterone, though this difference was not statistically significant. Corticosterone was measured once, Desert iguanas with corticosterone implants had significantly larger home ranges than those receiving saline implants, but endurance was not altered. Home range size was also significantly negatively related to the density of shade plants within the home range. Contrary to expectations, no relations between corticosterone, endurance capacity, and home range size were statistically significant, in either bivariate correlations or multiple regressions.

Chapter 5

In chapter five, I estimated the number of offspring sired by free-living male desert iguanas in two years using microsatellite paternity analysis. Number of offspring sired was compared with circulating corticosterone, body mass, endurance capacity, home range size, and potential ecological predictors of home range size. Home range size was a significant negative predictor of offspring number. I speculate that individuals with large home ranges may occupy relatively poor habitat with few females available. Conclusions for this study were constrained by small samples sizes.

Overview

In consideration of this dissertation as a whole, it appears that the relationships between corticosterone, body size, endurance capacity, home range size, and Darwinian fitness are not strong. Although endurance capacity was positively correlated with home range size and supplemental corticosterone increased home range size, basal corticosterone and endurance capacity seem to have no direct relationship in this species of lizard. This result is not inconsistent with various studies in vertebrates that have found mixed effects of supplemental glucocorticoids on physical activity, endurance, aerobic capacity, and home range size (DeNardo and Sinervo 1994; Sandi et al. 1996; Breuner et al. 1998; John-Alder et al. 2009; Singleton and Garland, Jr. 2018). Endurance capacity may allow an individual to maintain a larger home range size; alternately, endurance capacity may be the result of a larger home range size, as the increased daily movements may have a training effect (Husak et al. 2015; but see Garland, Jr. et al. 1987).

Home range size and circulating corticosterone were not generally correlated, though home range size was the product of several months of activity while corticosterone was only measured once. Corticosterone does have a relationship with home range size in desert iguanas, as corticosterone implants significantly increased home range size. This suggests two concepts: A) desert iguana home range size can result from changes to a specific drive or trait (motivation), which can be affected by corticosterone, and 2) desert iguana home ranges are not typically determined by that drive or trait. Several possibilities exist for this missing link between corticosterone and home range size; for example, corticosterone may increase appetite, leading to greater and wider food searching (Sapolsky et al. 2000; Cote et al. 2006; Singleton and Garland, Jr. 2018). Corticosterone may also improve memory and the building of spatial mental maps (Pravosudov 2003; Hajisoltani et al. 2011), allowing an individual lizard to move farther from burrows or refuges with greater confidence (if their home range is deficient in a given resource). Shade plant density was the only significant predictor of home range size for non-manipulated lizards, but I may have failed to measure a different important resource or feature that influences the movements of desert iguanas. Offspring number was also negatively correlated with home range size, though none of the environmental variables were related to offspring number. Female desert iguanas may be more likely to enter a smaller, more thickly vegetated home range, but the shade plant density itself seems irrelevant. Further investigations concentrating on female desert iguanas during their brief active period may further elucidate environmental factors relating to locomotor behavior and Darwinian fitness in this species.

In addition, our finding of a negative relationship between shade plant density and home range size, though not a direct focus of this set of studies, is to our knowledge a novel finding and should be investigated further in other studies and other taxa. Studies of resources within home ranges are biased towards mammals; we should consider that the daily needs of an ectotherm may be considerably different than those of a metabolically demanding endotherm. Indeed, thermoregulation may have a far greater impact on the survival of desert (and other) reptiles than food resources. As conservation studies frequently attempt to quantify the food resources available for species of concern, we should realize that other aspects of the habitat may have even greater impact on survivorship.

Regarding ecological implications, we should consider the elevation of corticosterone, its effect on home range size, and potential implications for conservation. Increases of basal corticosterone in free-living animal populations can be the result of human disturbance, such as logging, habitat alterations, or simply human presence (Tempel and Gutierrez 2003; Lucas et al. 2006; Graham et al. 2017). Although numerous studies report effects of human disturbance on feeding and reproduction (Newcomb Homan et al. 2003; Strasser and Heath 2013; reviewed in Frid and Dill 2002), increased corticosterone may also result in changes to the home range sizes of threatened populations. Home range alterations may potentially expose individuals to greater predation or other sources of mortality, such as roads, human habitats, edges, etc., and should be considered within the possible negative impacts of human disturbance. The examination of long-term physiological responses to human disturbance should be integrated with the study of behavior to better facilitate conservation efforts (Ellis et al. 2012; Cooke et al. 2014; French et al. 2018).

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Appendix I. Assay Validation

As a part of my dissertation research, I performed work to validate the Arbor Assays DetextX Corticosterone Enzyme Immunoassay kit for use in Dipsosaurus dorsalis. I followed previously outlined procedures for determining assay parallelism, precision, and accuracy (Harper and Austad 2000; Good et al. 2003; Chauke et al. 2011; Zhao et al. 2017). A plasma pool was created using the plasma of 5 adult desert iguanas collected under baseline conditions. For assay validation, a limited number of assay plates meant that validation procedures were performed without prior knowledge of initial plasma pool concentrations.

I. To evaluate Parallelism, I diluted the desert iguana plasma pool by 50% in sequence.

Plasma Pool *1
Plasma Pool*0.5
Plasma Pool*0.25
Plasma Pool*0.125
Plasma Pool*0.0625
Plasma Pool*0.03125

Background corrected absorbance values were logit-transformed and plotted against log10 values of concentration. The slope of diluted plasma was compared with the slope of log-logit transformed standard curve from the kit standards assayed on the same plate. Two points from the dilution were removed from analysis due to concentrations below the stated sensitivity limits of the assay. Difference between slopes was not significant (F = 1.245; P = 0.297.)

II. To evaluate intra-assay precision, I calculated the mean coefficient of variation (Standard deviation of reads for a given sample divided by mean of reads for a given sample * 100).

Plate 1: 11.87%

Plate 2: 9.07%

Plate 3: 7.50%

Plate 4: 13.34%

Mean intra-assay CV = 10.45%

III. To evaluate inter-assay precision, the plasma pool was assayed in two samples per plate (in duplicate) for the first three plates, then once (in duplicate) in the fourth (n = 7). The precision is given by the coefficient of variation for the remaining plasma pool readings.

Mean Interassay CV = 11.26%

IV. To evaluate accuracy, I added 10 uL of plasma pool to each standard and compared the resulting concentrations to the expected concentration.

Standard Concentrations:

10,000 pg/mL

5,000 pg/mL

2,500 pg/mL

1,250 pg/mL

625 pg/mL

312.5 pg/mL

156.25 pg/mL

78.125 pg/mL

Accuracy was 34.1 + 20.9% (mean + SE). Expected and observed values per samples were not significantly different (t = -1.250; P = 0.258). Values for spiked standard1 (normal conc. 10,000 pg/mL) were excluded from analysis as they were outside the curve and absorbance could not be verified.

This percent accuracy was much lower than expected, but as is indicates that an aspect of Dipsosaurus plasma interferes with the assay. However, this may have been the result of incorrect procedure with examining accuracy (specifically, a sample volume of 60 uL instead of the directed 50 uL). The next step is to contact the assay manufacturer for guidance about expected outcome of incorrect volume. Following this, the accuracy step may be repeated at a future date.

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Appendix II. Field Observations and Anecdotes

Arthropod Eating

A student was looking for insects for their entomology assignment, and trapped a beetle under a cup then went to get a permanent container. After walking away, a second student observed an adult desert iguana inspecting the cup. The lizard knocked the cup over, seized the insect, and ran.

On more than one occasion, I witnessed a desert iguana jumping into the air to pursue a flying insect.

Creosotes

Desert iguanas used the creosotes extensively starting in the later morning. Lizards jumped into the bush and then would climb to a preferred spot. If flowers were present, they would eat. Otherwise, they would sit. This is theorized to be related to thermoregulation, and did seem to occur (the sitting) during the hottest parts of the day. Desert iguanas also used the larger smoketrees in this way.

Other Vegetation

Desert iguanas would consume some part of most of the plants present on the field site. The smoketree was used for both food (flowers and newer leaves) and shelter. Small ground-plants made up a large portion of the observed diet (sandmat, coldenia, etc.).

Social Interactions

Adult and juvenile desert iguanas of mixed sexes were observed feeding on the same plants, within view of each other, without antagonistic interactions. These groups included groups of fully adult males.

90% of combat situations between adult males happened when a female lizard was present nearby.

The majority of adult males have scars from combat (bite marks on thighs).

Male lizards seemed to rarely display to each other unless engaged in a physical interaction (chasing, combat, etc.) or if surprised (coming around a corner, etc.)

The male desert iguana uses two different forms of displays. One consists of a slow head-bobbing with the arched back and “inflated” torso. The other display is a rapid “vibration” used when pursuing a female.

In male-female interactions, males seem to employ multiple strategies. Males have a courting display, described above. Females may lift the tail to accept mating (FEMALE CHOICE?) Males will also chase females and seize the female by the neck for copulation, leaving visible wounds.

Male lizards have been observed “wiggling” their ventral pelvis region in the sand or on rocks. Relationship to femoral glands?

Predators

The only successful predation attempt I observed was that of a coyote, that chased, caught, and ate whole an adult desert iguana. I observed another attempt by a coyote, where the iguana was chased to a burrow, dug out by a coyote, and pursued to a second burrow where the chase ended (the coyote was unsuccessful).

I observed attempted predation by roadrunners and Red Racers.

Other potential predators (seen on the field site) included sidewinder rattlesnakes, ravens, leopard lizards, and raptors.

Interactions with Researchers:

On at least 5 separate occasions, desert iguanas were found sitting in or on the backpack used for field equipment.

Desert iguanas will readily accept food from people.