

AN INVASIVE GRASS AND A DESERT ADAPTED RODENT: IS THERE AN
EFFECT ON LOCOMOTORY PERFORMANCE AND IS IT MODIFIED
BY PRIOR EXPERIENCE OR FAMILIARIZATION?

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TITLE: An Invasive Grass and a Desert Adapted Rodent: Is there an Effect on Locomotory Performance and is it Modified by Prior Experience or Familiarization?

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ABSTRACT

An Invasive Grass and a Desert Adapted Rodent: Is there an Effect on Locomotory Performance and is it Modified by Prior Experience or Familiarization?

Camille Delphine Boag

Kangaroo rats (*Dipodomys* spp.) are frequently characterized as keystone species for their role in altering soil characteristics, changing habitat structure through seed consumption and dispersal, and being important primary consumers in their ecosystem. They are arid adapted and known to forage in areas with sparse vegetation. Studies suggests densely vegetated habitat to be unsuitable for kangaroo rats because plants are an impediment to their locomotion and predator avoidance behaviors. This study focuses on an invasive grass, South African Veldt (*Ehrharta calycina*), that converts landscapes with sparse vegetation into dense grassland habitats, and the Lompoc kangaroo rat (*Dipodomys heermanni arenae*) that occupies some of those modified landscapes. I explored the proximate effects of Veldt grass by assessing the locomotion of *D.h. arenae* in three Veldt grass densities. I hypothesized that Veldt grass influences kangaroo rat locomotion, but that performance could also be influenced by experience with the grass. Kangaroo rats with long-term experience with Veldt grass (i.e., those occupying a habitat containing Veldt grass) and short-term experience (two-night habituation in an artificial Veldt grass patch) were tested by pursuing the animals through runways of different grass densities and measuring the amount of time spent crossing the runway, amount of time spent stopped, average velocity, and amount of motivation required to initiate and sustain movement. I also monitored habitat use during the two-night habituation period in order to assess habitat utilization among three Veldt grass density habitat patches. I hypothesized that Veldt grass may influence normal habitat utilization patterns in *D.h. arenae*: specifically, the avoidance of the densest habitats and preference or disproportionate utilization of the most open habitat. I found, when the animals were left alone to forage and explore, they spent significantly more time in habitat patches containing Veldt grass than in a control patch containing zero percent cover. However, in locomotion trials, Veldt grass had a negative effect on locomotory performance. These effects seem to scale with grass density, and were ameliorated to some degree by familiarization: animals from a Veldt grass habitat of origin performed better in novel Veldt grass templates than animals from a non-Veldt habitat of origin; however, both groups performed equally well after two nights' habituation to the templates. These results suggest that learning occurred in two nights and that it increased the kangaroo rats' ability to locomote through the grass when pursued. I note that performance studies often do not take into account the amount of motivation employed to initiate and sustain running of the test animals, and suggest that this be considered in future studies. Furthermore, the learning capacity of a kangaroo rat, as well as a community level perspective that considers neutral or even positive trophic interactions among natives and invasives, must be considered in conservation and management decisions in the future.

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INTRODUCTION

Invasive species and implications for conservation of endemics

Biological invasions have caused more species extinctions than have resulted from human-caused climate change or the changing composition of the atmosphere (D'Antonio and Vitousek 1992). In the United States, invasive species are currently the number one factor impacting threatened species (IUCN 2008). Non-native plant invasions are predicted to become even more common due to climate change and globalization (Dukes and Mooney 1999; Lee and Chown 2009). Therefore, understanding the interactions between invasive flora and native fauna has become increasingly important.

Because non-native plant species often evade their natural herbivores, parasites, and pathogens (D'Antonio and Vitousek 1992), the invasions are often highly successful. Non-native plants often produce or result in a more homogenous (reduced species diversity) and more dense (plant cover) plant community than the previous natural state, as they outcompete the native plants (Vitousek 1986; Gordon 1998). Rodents fulfill important roles in their ecosystems, as both primary consumers and abundant prey items for secondary consumers (Goldingay et al. 1997; Hawkins and Nicoletto 1992; Fields et al. 1999). Rodent diversity and abundance are positively correlated with plant diversity, because heterogeneous habitats provide opportunities for microhabitat segregation among rodent species (Price 1978). High-density cover can be unfavorable for small ground-dwelling vertebrates that are adapted to relatively open habitats, due to its impediment to movement and locomotion (Rosenzweig and Winakur 1969; Rosenzweig 1973). As a result, rodent abundance and diversity often declines in response to plant invasion. For

example, Rowland and Turner (1964) found the abundance of the Chisel-toothed kangaroo rat (*Dipodomys microps*) to be inversely related to the abundance of exotic brome grass in Nye County, Nevada, and speculated that Reynolds' (1950) hypothesis that dense grass interferes with escape from predators depends upon the density of the grass. Similarly, Nelson et al. (2009) found that ungrazed Texas kangaroo rat (*D. elator*) habitat, consisting of invasive Japanese brome (*Bromus japonicas*), a tall, dense growing grass, was rarely used by the kangaroo rats compared to grazed habitat. Most recently, Freeman et al. (2014) found that the abundance and diversity of a small mammal community (including Ord's (*D. ordii*) and Chisel-toothed kangaroo rats) decreased with increasing abundance of invasive cheatgrass in the Great Basin of the western United States. The authors suggest that this correlation is attributed to both indirect and direct effects of the grass, the latter including a reduction in quality of forage and decreased mobility. Furthermore, Germano et al.'s studies (2001, 2012) found dense cover of exotic annual grasses and forbs to have a significant negative effect on the survival of the native animals (Giant kangaroo rats [*D. ingens*], San Joaquin kangaroo rats [*D. nitratoides*] and San Joaquin antelope squirrels [*Ammospermophilus nelsoni*]) of California's San Joaquin valley, and suggest that the structure of the habitats occupied by these species must be kept relatively clear of dense plant growth in order to favor their persistence. Tipton's kangaroo rat (*D. nitratoides nitratoides*) virtually disappeared between 1979 and 1982, when exotic grasses were allowed to dominate the preserve set aside to protect this federally endangered subspecies (Germano et al. 2001). In other taxa, Sammon and Wilkins (2005) found a negative correlation between exotic King Ranch bluestem (*Bothriochloa ischaemum* var. *songarica*) and hispid cotton rat (*Sigmodon hispidus*)

density, and Yensen et al. (1992) found a negative correlation between burrow density of Townsend's ground squirrels (*Urocitellus townsendii*) and cheatgrass (*Bromus tectorum*) and other exotic annuals. It is noteworthy that these studies all demonstrate a trend of decreasing rodent abundance with increasing invasive vegetation that wasn't necessarily obvious: rodents, being small and often nocturnal, are cryptic in nature, and therefore plant invasions can have a substantial but difficult-to-detect impact on this group. As rodents are the most diverse group of mammals (Wilson and Reeder 2005), the sometimes obscure interactions that occur between rodent populations and invasive plants should be given more attention.

Kangaroo rats as keystone species

Kangaroo rats are frequently characterized as ecosystem engineers for their role in altering soil characteristics, changing habitat structure through seed dispersal (primarily due to their seed caching behavior) and seed consumption, and creating expansive burrow networks that are used by many other species (Hawkins and Nicoletto 1992; Fields et al. 1999). Because granivorous rodents compete not only inter-specifically, but also with other seed eaters such as birds and ants, their removal may increase the success of other competing species (Brown and Davidson 1977; Brown et al. 1979). Furthermore, rodents are among the most important primary consumers in arid ecosystems in terms of their numbers, biomass, and species diversity (Goldingay et al. 1997). Consequently, they are largely responsible for supporting substantial populations of mammalian carnivores, snakes, and owls (Goldingay et al. 1997). None of these generalized predators feed exclusively on rodents, let alone kangaroo rats; nevertheless, rodents are quantitatively

important in their diet and a dependable prey item. Well adapted to the harsh environments in which they live, kangaroo rats maintain relatively stable populations and are thus a relatively predictable food source. They may also, then, have significant indirect (trophic cascade) effects on population dynamics of other prey, such as lizards, lagomorphs, and some birds, as well as some predators that can also be prey (Goldingay et al. 1997).

Veldt grass and the Morro Bay kangaroo rat

The Morro Bay kangaroo rat (*D. heermanni morroensis*) was listed as a federally endangered subspecies in 1970 and the last known wild individual was seen in 1991 (USFWS 1999). Many causes have contributed to its decline including habitat reduction, predation by domestic animals, burrow destruction by pedestrians and vehicles, population fragmentation, and alterations to the native plant community via the introduction of invasive species (USFWS 1999). South African Veldt grass (*Ehrharta calycina*) is an invasive species that likely contributed to the decline of the Morro Bay kangaroo rat. Veldt grass was introduced to California in the 1920's as a range improvement crop and erosion control agent (Love 1948), and has since spread rapidly along the state's central coast. Currently, Veldt grass dominates large areas of the central coast dune scrub community, reducing native plant diversity and rapidly shifting open native dune shrub communities toward grassland habitat (FX Villablanca, pers. obs.), as well as ostensibly reducing rodent diversity (FX Villablanca, pers. obs.). Veldt grass eradication efforts are implemented yearly in Central California (USFWS 1999). The management logic is that, without the application of brush management techniques to

“provide optimum kangaroo rat habitat,” the Morro Bay kangaroo rat is “almost certainly doomed to extinction” (Congdon and Roest 1975).

Preference for open habitats in *Dipodomys*

Kangaroo rats (*Dipodomys*) are nocturnal and solitary, live in underground burrows, and are mainly granivorous (reviewed by Brown and Reichman 1983; Genoways and Brown 1993). They are equipped with external cheek pouches and hoard seed that they store either in their burrow or shallow pit caches for future consumption (Brown and Reichman 1983; Genoways and Brown 1993). Decades of literature demonstrate that kangaroo rat prefer habitats with open and low-density vegetation (Howell 1932; Reynolds 1950; Bartholomew and Caswell 1951; Rosenzweig and Winakur 1969; Price 1978; O’Farrel and Uptain 1987; Price et al. 1994; Cypher 2001; Jones et al. 2003; Waser and Ayers 2003; Nelson et al. 2009). Rosenzweig (1973) directly tested for habitat choice in Merriam’s kangaroo rat (*D. merriami*) with a “habitat tailoring” experiment. Adding brush litter to experimental plots significantly decreased kangaroo rat abundance over the course of a year. Because the brush was dead, these results clearly demonstrated that the physical structure (and not a biotic effect) was responsible for the decline. Rosenzweig (1973) contributed the kangaroo rats’ active avoidance of the dense habitats to the vegetation’s interference with escape from predators, and inferred that thick grass would have the same effect. This body of literature forms the basis for the hypothesis that dense grass cover (such as Veldt grass) reduces habitat quality and has a negative effect on population sizes of kangaroo rats.

This effect may be either direct (they avoid this habitat type) or indirect (predation reduces their population size).

Adaptations to open habitats

Kangaroo rats are likely more abundant and successful in more open habitats because they are highly specialized to exploit them. Adaptations such as enlarged tympanic bullae that enable the kangaroo rat to sense snakes and owls before they strike (Webster 1962), and dorsally located eyes that allow for constant visual monitoring of the animal's surroundings (Webster 1962), allow for predator detection and avoidance in sparsely vegetated environments. Long hind feet aid in locomotion across loose sandy soils by energetically efficient bipedal saltation, as well as ricochet rapid dodging of predators (Bartholmew and Caswell 1951; Djawdan and Garland 1988). Kangaroo rat locomotion thus favors exploitation of a highly dispersed resource base, predator avoidance, and specialization in open habitats avoided by sympatric rodents.

The need for experimental studies testing mechanistic hypotheses

A negative correlation between kangaroo rat abundance and vegetation density has been thoroughly documented (Howell 1932; Reynolds 1950, Bartholomew and Caswell 1951; Rosenzweig and Winakur 1969; Rosenzweig 1973; Price 1978; O'Farrel and Uptain 1987; Price et al. 1994; Cypher 2001; Jones et al. 2003; Waser and Ayers 2003; Nelson et al. 2009) leading to the conclusion that high vegetation density habitat is unsuitable for kangaroo rats. Specialized adaptations that allow kangaroo rats to exploit open habitats, but may be detrimental in densely vegetated habitats, are cited as the

mechanisms behind the negative correlation (Webster 1962). Few studies, however, have experimentally tested this hypothesis. Much of the supportive evidence behind kangaroo rat preference for open habitat is based on correlation and not causation; few experimental studies testing *mechanistic* explanations have been conducted. If the hypothesis that specialized adaptations are what allow for survival in open habitats is correct, then dense invasive grasses such as Veldt grass should have a disproportionate effect on species such as kangaroo rats with such adaptations.

Rieder et al. (2010) tested a mechanistic explanation for higher survival in open habitat when they included the Ord's kangaroo rat in a study that assessed the effects of invasive cheatgrass (*Bromus tectorum*) on small vertebrate sprint velocity. They found that, under a perceived risk of predation, a homogenous and dense stand of cheatgrass hindered kangaroo rat locomotion by decreasing sprint velocity and disrupting fluid bipedal movement. However, this study may have underestimated velocity, as the presumably non-linear path the animal took as it crossed the grass runway was not taken into account in velocity calculations. Furthermore, the experimenters did not take into account the amount of variation in motivation used to encourage different individuals to move. These are, therefore, results that can be improved upon, however, they are useful in the context of the additional work I do here.

Schooley et al. (1996) found that impediment of locomotion by increased vegetative cover increased rates of predation in the Townsend ground squirrel, also a desert rodent. Based on this and Rieder et al.'s (2010) study, this suggests that effective predator avoidance may be one of the fundamental mechanisms that make high-density habitat unsuitable for kangaroo rats. Kangaroo rats depend on rapid and continuous

bipedal movement away from a perceived risks to escape predation (Bartholomew and Caswell 1951). It can be speculated, then, that circumventing obstacles such as cheat grass or Veldt grass tussocks may increase total distance traveled to the safety of the animal's burrow. This increase in distance to safety can be translated to increased time of escape and therefore increased exposure to potential predators. Furthermore, I would predict that avoiding obstacles negatively affects the animals' velocity, and, by interrupting fluid movement, increases time spent stopped. Obstacles may also limit the movement options thereby reducing the potential number of evasive moves, and increasing vulnerability to predation.

***D.h. arenae*, and evidence of high survivorship in dense Veldt grass**

Interestingly, there is evidence that contradicts the logic that dense vegetation is detrimental to kangaroo rat survivorship. In a five-year mark-release-recapture study in the Guadalupe-Nipomo dunes, California, FX Villablanca and J Trunzo (unpublished data) sampled over 2000 kangaroo rats. In this study, even though invasive Veldt grass substantially increased vegetative cover, no negative relationship was found between grass density and survivorship of the endemic Lompoc kangaroo rat (*Dipodomys heermanni arenae*) across three Veldt grass densities. Likewise, there was no negative quantitative effect on population sizes across the Veldt grass densities. In this study I examined *D.h. arenae*, the closest geographic and genetic relative to the Morro Bay kangaroo rat (Villablanca 2007), in an effort to scrutinize factors that led to the latter's decline and illuminate possible steps toward its recovery. Villablanca and Trunzo's (FX Villablanca and J Trunzo, unpublished data) results present a paradox that begs an

explanation. Here, I address this paradox via a manipulation study of *D.h. arenae* locomotion performance in varying densities of Veldt grass, combined with an examination of habitat utilization in different densities of Veldt grass.

Hypotheses and Predictions

Locomotion in Veldt grass

In this study, I assess the locomotion performance of *D.h. arenae* in varying densities of invasive Veldt grass. My study is similar to that of Reider et al. (2010) who assessed sprint velocity of *D. ordii* in cheatgrass by running the animals through a “raceway” of a monotypic stand of cheatgrass and timing their run. In order to elicit maximal running performance, the animals in that study were pursued with a padded yardstick. As previously discussed, Rieder et al. (2010) did not thoroughly account for three potentially important factors: a) non-linear running path (such that measurements of velocity as assessed by raceway distance/time rather than path distance/time would potentially underestimate velocity), b) the magnitude (type, frequency, etc.) of the “motivation tactic,” or pursuit with the padded yardstick, each animal received, and c) the possibility of habituation to a habitat patch and therefore loss of the detrimental effects imposed by the grass on running performance over time. In my study, I implemented a raceway design similar to Rieder et al. (2010) in order to assess kangaroo rat locomotion in dense grass; however, I address the aforementioned issues by: a) using a marker on the animal combined with digital imaging software to quantify path length and estimate velocity more accurately; b) quantifying the amount and nature of motivation used by the experimenter to initiate and maintain running, and c) testing for the possibility of

acclimation to a habitat patch by assessing running performance in both novel and familiar Veldt grass habitats. Furthermore, I measure running performance in different densities of the invasive grass, and measure several response variables beyond velocity, to better quantify performance. Finally, I ask if an animal's previous experience with Veldt grass influences its running performance; i.e., does habitat of origin (a non-Veldt habitat versus a Veldt habitat) have an effect on running performance?

I hypothesize that kangaroo rat running performance is influenced by Veldt grass density in both novel and familiar habitat patches. I tested kangaroo rats in different densities of novel habitat patches of Veldt grass, as well as in different densities of familiar habitat patches of Veldt grass. The familiar patches consisted of templates of Veldt grass tussocks identical to those that were novel, but became familiar after each rat spent two days in them. Because a kangaroo rat may encounter novel habitat patches under two different ecologically critical circumstances, i.e., as a juvenile during dispersal from its nest burrow, and as a male in search of a mate, I explored the effects of a Veldt grass patch on running performance when it is completely novel. I therefore used running performance in novel habitat as an analogy for running performance during a dispersal phase. However, a kangaroo rat in an established home range encounters familiar habitat patches regularly (high spatial cognition has been demonstrated in kangaroo rats [Langley 1994; Sherry et al. 1992; Barkley and Jacobs 1998; 2007], suggesting they have high cognizance of the physical landscape in their home ranges). Therefore I also explored kangaroo rat performance in Veldt grass in a familiar setting, as a proxy for running performance in an individual's home range.

I predict that in both novel and familiar Veldt patches the time to travel the length of a three-meter runway and the amount of time spent stopped will increase with increasing density of Veldt grass (from 0% to 20% to 40% grass cover). I predict that maximum and average velocity will decrease with increased density of Veldt grass. Furthermore, I predict that animals will require more motivation to cross the runway with increasing density of Veldt grass.

I predict grass density that in both novel and familiar settings grass density will have equal effects (as predicted above) on animals, regardless of their habitat of origin. Based on the literature demonstrating negative correlations between dense vegetative cover and kangaroo rat abundance and persistence (Howell 1932; Reynolds 1950, Bartholomew and Caswell 1951; Rosenzweig and Winakur 1969; Rosenzweig 1973; Price 1978; O'Farrel and Uptain 1987; Price et al. 1994; Cypher 2001; Jones et al. 2003; Waser and Ayers 2003; Nelson et al. 2009), a habitat patch consisting of dense tussock cover should negatively impact running performance of both Veldt and non-Veldt animals (i.e., regardless of experience with the grass itself). I predict no interaction between habitat of origin and the Veldt grass density treatment, however, I do predict a trend of amelioration in performance from field (unfamiliar habitat patch) to lab trials (familiar habitat patch) for kangaroo rats of both habitats of origin. Based on spatial cognition studies on kangaroo rats (Langley 1994; Sherry et al. 1992; Barkley and Jacobs 1998; 2007), the animals should learn the landmarks in their environment and be able to navigate more efficiently through them with experience.

Utilization among habitats

In addition to assessing locomotion performance, I also explored kangaroo rat foraging behavior when the animals were given the choice of three different naturally occurring (FX Villablanca, unpublished data) densities of Veldt grass. I hypothesized that Veldt grass may influence normal habitat utilization patterns in *D.h. arenae*: specifically the avoidance of the densest habitats and preference or disproportionate utilization of the most open habitat. In order to test this hypothesis I measured behavior during the two-day familiarization period with the Veldt grass runways under laboratory conditions. I ask if Veldt grass density a) influences the amount of time spent in a given habitat, b) influences the order in which seed patches are visited, and c) alters the predicted seed-hoarding behavior characteristic of *D.h. arenae*. I predict, based on the prior well-demonstrated preference for open habitat (Howell 1932; Reynolds 1950, Bartholomew and Caswell 1951; Rosenzweig and Winakur 1969; Rosenzweig (1973); Price 1978; O'Farrel and Uptain 1987; Price et al 1994; Cypher 2001; Jones et al 2003; Waser and Ayers 2003; Nelson et al 2009), that when placed in an arena composed of the three Veldt grass densities (0%, 20% and 40% cover), kangaroo rats will spend the greatest amount of time in 0% Veldt grass cover, and the least amount of time in 40% cover. I predict, by this same logic, that when given a seed patch at the end of each runway, kangaroo rats will first choose to visit the seed patch in the 0% cover runway. Finally, I predict, based on the amount of seed in each patch and the ability of the animal to consume and/or cache this amount, there will be no difference in the total seed depletion across the different grass density treatments.

Because kangaroo rats are a keystone species (Hawkins and Nicoletto 1992; Fields et al. 1999), if an invasive plant can influence their survivorship and thus abundance, it is highly probable the implications will transcend species boundaries and affect the entire community. However, if these populations of *D. h. arenae* are largely unaffected by the invasive plant by way of acclimatization to the change in habitat structure, then the community would be more resilient to the effects of an invasion. The relative trophic effects (in the case of Veldt having detrimental effects) versus resiliency (in the case that it does not) would have important implications for habitat management, Veldt grass eradication, and dune restoration decisions.

MATERIALS AND METHODS

Field sites

Five field sites in the Central Coast region of California, USA, were chosen for their evidence of kangaroo rat activity and presence or absence of Veldt grass. Sites Black Lake Non-Veldt (BLNV), Black Lake Veldt (BLV), and Callender Veldt (CV) are located near Highway 1 and Callender road in Arroyo Grande, California (Fig. 1). Sites Oceano Dunes State Vehicular Recreational Area Non-Veldt (ODSVRANV), and Oceano Dunes State Vehicular Recreational Area Veldt (ODSVRAV) are located directly east of the off-road vehicle area in Oceano, California (Fig. 1). In this sand dune ecosystem, the habitat is comprised of (besides Veldt grass at Veldt sites) shrub and herb species including mock heather (*Ericameria ericoides*), dune lupine (*Lupinus chamissonis*), coastal buckwheat (*Eriogonum latifolium*) and sand verbena (*Abronia villosa*).

Trapping

Seasonality and collection

A two-month trapping session in February and March of 2014 assessed the distribution and abundance of *D.h. arenae* across the five sites. Trapping for running trials was initially conducted during a six-week period from May 1st, 2014 to June 7nd, 2014. Trapping and runway trials occurred over three-day sessions and including paired Veldt and non-Veldt sites. A non-Veldt site contained zero density Veldt grass, and a Veldt site contained approximately 50% or higher density Veldt grass cover. To increase sample size, I performed more trials for six nights over June and July of 2014 (6/6, 6/7,

6/26, 6/29, 7/6, 7/10), predominately at Veldt areas, and again for two nights in October of 2014 (10/16, 10/18) at both Veldt and non-Veldt sites (Table 1). Twenty of the kangaroo rats used in field running trials were brought into captivity in the Villablanca lab at California Polytechnic University, San Luis Obispo, California. The animals were chosen in order to balance the sample size for habitat of origin and sex, and to avoid reproductive (pregnant or lactating) females. Eight captive kangaroo rats were female (two Veldt and seven non-Veldt) and 11 were male (five Veldt and six non-Veldt).

Trap sessions and sample size

During the February/March distribution and abundance survey I used a trap grid approach (plots of 5 traps \times 5 traps or 6 traps \times 6 traps), or occasionally trap lines due to difficult topography, with Sherman XL traps and rolled oats for bait. Trap nights during this period exceeded 2,700. Traps were set just before dusk and checked early the following morning. All captured *D.h. arenae* were sexed and ear-tagged with numbered fingerling tags (National Band & Tag Company, Newport, KY) for identification purposes. The aim of this trapping session was to gain knowledge on the animals' distribution in order to design a balanced study and increase trapping efficiency during the data collection phase of running trials.

During running trials, trapping at each site targeted animals that were previously found at that site in the February/March survey. Sites were spot-trapped (six traps per spot) at trap stations where animals were previously found and ear marked. Trap nights for the running trials period exceeded 1,100, with a total of 43 kangaroo rats captured, yielding a 4 % trap success rate for *D.h. arenae*. Due to the low trapping success

(especially at Veldt sites), mishaps in protocol implementation, and the eventual exclusion of juveniles from the study, final sample size for field running trials was 38, of which 25 were from a non-Veldt habitat of origin, and 13 were from a Veldt habitat of origin. Total, I tested 17 females and 21 males: 12 males and 13 females in the non-Veldt population, and nine males and four females in the Veldt population.

Runway Design

Six identical runways were constructed for field trials (Fig. 2). Three runways were set up at each of two field sites: BLNV and ODSVRV. Runways at BLNV were used for all animals captured at Callender and both Black Lake NV and V sites, while runways at ODSVRV were used for both ODSVRA NV and V sites. The three runways represented the three Veldt grass density treatments (see below) of the study.

Runways were 300 cm long \times 60 cm wide \times 60 cm tall, with a 20 cm \times 60 cm wooden transfer box at each end (Fig. 2). Runway walls were constructed with corrugated plastic sheets (Coroplast model # CP4896S, Home Depot) and cut into three 1.2 meter \times 60 cm sections for easy transportation. Wall sections were spray painted a dull tan color (Rust-Oleum Specialty model # 1917830, Home Depot) to better match field conditions than the original glossy white, and connected in the field with large binder clips both at the bottom and top of the slightly overlapping walls. Runway length was confirmed after set up and before trials. The runway walls were placed directly on the sand substrate so that the “floor” space between the walls was sand. The wooden boxes were placed at either end of the runway, one as a “holding box” for the animal prior to its run, and the other as the “receiving box” to collect the animal on the other end.

To provide the appearance of an escape route and therefore encourage sustained sprinting across the runway, the backs of the boxes were constructed of wire mesh. The fronts of the boxes were fitted with a sliding aluminum door that dropped and lifted vertically.

All vegetation was completely removed from the runway location leaving only bare sand. A template with holes to indicate where Veldt grass tussocks were to be placed was laid down between the runway walls. The templates ensured that both runway set-ups at BLNV and ODSVRAV field sites were identical. Treatments consisted of 16 tussocks (40% cover, or “dense” treatment), 8 tussocks (20% cover, or “medium” treatment), or no tussocks (“control” treatment). Tussocks were collected from a Veldt area within a quarter-mile of the runway site, and chosen to approximate 15 cm in diameter, and 30-50 cm in height. Tussocks were placed only in the last two meters of the runway; the first meter of the runway was devoid of any grass to allow the animal to accelerate easily. Hemp string tied off the top portion of each tussock in order to reduce visual obstruction for both the animal (so that it could see us pursuing it) and the observers (when quantifying response variables).

Field performance trials

I carried out running trials both in the field and in the lab. Based on a prior study (Djawdan and Garland 1988) that found no difference in running performance between night and day, all trials were conducted during the day. The field experiment simulated a situation in which a dispersing kangaroo rat might encounter a predator while exploring or occupying a new habitat patch. For both non-Veldt and Veldt animals, the templates of

Veldt grass they encountered in the runways were completely novel, and therefore all animals were naïve to these particular habitat patches.

Marker and image capture

Kangaroo rats were brought to the runways in their traps. Those captured from non-Veldt sites were described as coming from a non-Veldt habitat of origin, because Veldt grass was absent from an area one could presume to represent their home range (Shier and Randall 2004). Similarly, kangaroo rats from Veldt sites were from a Veldt habitat of origin, as the site included some Veldt grass cover. After removal from traps the animals were handled minimally; ear tag identity was noted and a 6 cm x 10 cm marker made from white poster board was placed on the animals back with double-sided desk tape. The marker was used for downstream digitized data capture. Radio collars weighing 2.2-2.8 g (significantly heavier than our markers) have previously been used on *D. spectabilis*, and collared animals were observed to be capable of normal, rapid movement (Shroder 1979), leading me to believe that the transmitters did not significantly alter normal running behavior. The kangaroo rats in the present study seemed similarly unaffected by the mass of the marker or its presence. Furthermore, the marker's location high on the animal's back did not obstruct movement of its limbs. I was not concerned, therefore, about the marker confounding the animals' performance in running trials.

All trials were filmed with a GoPro Hero 3 White Edition camera mounted on a telescopic aluminum pole (Unger model # 962760, Home Depot) and secured at the end of a plastic pliable arm piece overhanging the runway (Fig. 4b). I confirmed that the

runway was completely within the frame of view of the camera by using the GoPro application for iPhone (GoPro App version 2.6.3 [470]), which transmitted a preview of the footage to the phone via a bluetooth connection built into the camera. The camera was also controlled via this application.

Trial protocol

At the start of each trial, the kangaroo rat was placed in the holding box at the beginning of a runway (order of the three treatments, or runways, was randomized *a priori*), and left for one minute. Trials began by opening the sliding aluminum door of the holding box and motivating the animal to run by hitting and brushing the wire mesh along the back of the box with a long-handled plastic bristled brush (Quickie original deluxe bowl brush Model #301RM-22, Home Depot). Similar rodent running performance studies have used a padded yardstick (Rieder et al. 2010 with *D. ordii*), a small broom, or even a domestic dog (Schooley et al. 1996 with Townsend's ground squirrels) as stimuli. I found the visual and auditory stimulus from the plastic bristled brush against the wire mesh was quite effective, and the different stimuli employed throughout the running trial to be easily quantifiable (in order to account for the amount of motivation the animals required). If, after several minutes, the brushing and hitting the wire mesh did not suffice, the top of the box was opened enough for the brush to be inserted to follow the animal until it exited into the runway. Once the animal was in the runway, I continued constantly to motivate it as needed until it reached the receiving box on the other side. Due to dramatic differences among animals, no consistent motivational technique could be applied. The amount of motivation employed for each animal was

therefore quantified and included in analyses (see analytical methods below). Motivation tactics specifically included waving the plastic brush in quick horizontal sweeping movements behind the animal, flicking sand onto it, banging the ground or runway walls behind it, touching or prodding it, or, if the animal willingly ran, following as closely behind as possible and emulating a constant chase. Each kangaroo rat was tested in each runway twice in succession for a total of six runs per animal. Each animal had approximately one minute of rest between subsequent trials. The animals were moved among runways in the wooden end boxes between trials to reduce direct handling. Sex, mass and reproductive condition were recorded post testing. If an animal was not brought into captivity for runway trials (see below), it was released at the location where it was trapped.

Lab habitat use and performance trials

Animal husbandry and test arena

Twenty of the *D.h. arenae* I captured and tested in the field were brought into captivity for further study and housed in a small ventilated room used exclusively for this purpose in the biology building at California Polytechnic University, San Luis Obispo. Light conditions were set to simulate daylight from 8:00 to 20:00, with one 25-watt light bulb on at night to simulate moonlight. Of these twenty animals, 13 were from a non-Veldt habitat of origin, and 7 were from a Veldt habitat of origin. Because animals were brought into captivity at different times, and tested in the lab at different times, the duration in captivity varied among animals (Table 2). Animals were housed in forty-gallon glass tanks, each equipped with a nest jar made of a 16oz mason jar inside of a

black PVC pipe and fitted with a T-shaped PVC pipe exit (Fig. 3). Approximately 4-5 cm of sand, collected from the field sites, covered the bottom of the tank. Animals received 6 grams of lettuce (3 grams leaf and 3 grams mid-vein) and a quarter cup of seed cocktail (oats, millet and sunflower seed), daily. In order to test for effects of potential acclimation to Veldt grass on running performance in differing Veldt grass densities, we housed each kangaroo rat in a Y-shaped arena for two nights (Fig. 4a). The arena consisted of the nest jar (emptied of any previous seed caches from its lab housing and fitted with a triple-prong PVC pipe exit piece so that the animal could see all arms simultaneously from inside the exit portal) centered in a triangular middle area (60 cm each side), and three two-meter long arms branching out from this area. Arm walls were 1.2 meters high to minimize escape by jumping and made of hardboard panel board (Thrifty White Model # 709106, Home Depot) to minimize escape by chewing. Arms consisted of the same Veldt grass templates the animals encountered in field running trials (40%, 20% and 0%). Sand gathered from the field sites covered the bottom of the arena to a depth of 2-4 cm. Lab surroundings were hidden from view of the focal animal by brown paper drop cloth (EcoDrop Model # 02104/6HD, Home Depot) surrounding the arena. Three grams of hulled sunflower seed and six grams of lettuce were placed in sifted sand in each of three shallow plastic dishes, one at the end of each runway, creating equal motivation to, and reward for, visiting each arm. Seed and lettuce were replenished daily prior to each animal's nocturnal bout of activity. Animals were allowed to use this artificial habitat patch for two consecutive nights.

All sand was removed following each kangaroo rat's two-night stay in the arena, and floors and seed pans were cleaned with Dr. Bronner's Magic Soap and water to

minimize traces of urine or scent marking. We randomized which arm contained which grass density template for each animal, to minimize any effect of arm location on spatial cue use. Each animal received fresh sand from the field and was placed in the center of the arena in its nest jar.

Habitat use monitoring

All lights in the room of the arena operated on timers, with white fluorescent ceiling lights scheduled to turn on at 8:15 and off at 20:15, to match the captive conditions under which the animals were housed. Four 25-watt red light bulbs (one located at the end of each runway and one positioned above the arena center) were scheduled to turn on at 20:05 and off at 23:15. The camera was fastened to a ceiling beam above the center of the Y-arena to capture the entire arena. The camera was connected to a GoPro scheduler (CamDo PS-003 Programmable Scheduler), which began video recording at 20:10 and ended recording at 23:10 nightly. A single 25-watt white light bulb faced upward in the corner of the room and stayed on constantly to simulate moonlight at night.

The order in which kangaroo rats were tested in the Y arena was randomized. Three hours of video were recorded each night for each of two nights, for a total of six hours of footage per kangaroo rat, with the exception of one animal, who escaped from the arena in the first hour of its night one. The rat was recaptured and its second night was filmed. The first three hours after the white lights turned off were recorded, as studies demonstrate high foraging behavior in the initial hours of the night (Schroder 1979).

Lab performance trials

The lab performance trials simulated a situation in which a kangaroo rat might encounter a predator in its home territory, or a familiar habitat patch. Trials were conducted on the second morning in the same arms the kangaroo rat had familiarized itself with over the past two nights (Table 2). With the addition of a 1 m extension piece, covered also with 2-4 cm of sand but void of grass, the arena dismantled into three runways similar to those used in the field (Fig. 4b) (except for the construction materials, height of sides, and location [lab vs. field]). Holding and receiving boxes were placed at the ends of each runway, which had hinged doors at each end to allow for the placement of the boxes. The protocol followed that of the field running trials (see above). One animal refused to run and was excluded from the analyses, yielding a sample size of 19 for lab trials: 12 non-Veldt and seven Veldt animals.

Data extraction from video recordings

Runway trials

Data were extracted from the video camera footage of both field and lab running trials in the same manner. Both responses of the animal and motivation tactics employed by the experimenter were quantified. Each response variable was recorded by one or two viewers. If two viewers recorded one variable, any discrepancies between viewer counts were mediated by averaging the two counts. Dependent variables were transit time (seconds) across the runway from the time the rat exited the holding box to its entrance in the receiving box, amount of time spent stopped (seconds) during its transit, and average

and maximum velocity (meters/second). Motivation tactics were individually recorded and later consolidated into one composite variable for analysis (see Data Analysis). I quantified several motivational methods: number of sweeping motions, flicking motions, flicking which caused sand to kick up on or towards the animal, impacts to the runway wall, and each instance of physical contact between the plastic bristled brush and the animal during its transit.

Average and maximum velocity achieved by the animals were extracted via the digital image tracking software program Peak Motus (Vicon Peak Motus, Denver, Co), which picked up the white marker on the kangaroo rat's back and traced it for the duration of the trial.

Habitat use quantification

Video footage of habitat use by kangaroo rats was used to quantify total time (seconds) spent in each runway per night, and time (seconds) from start of trial until the first visit to each seed pan ("latency time" to seed pan). Animals varied widely in how much time they spent out of the nest jar during the three-hour filming period; therefore, time spent in each arm was calculated as a ratio of the total amount of time in the arm divided by the total amount of time spent in all arms combined. Time to reach each pan was recorded from when the animal left its nest jar for the first time to its first visit to each pan. Additionally, each morning the pans were collected, the sand sifted, and the amount of seed remaining (grams) was weighed to quantify total seed depletion in each density treatment. A total of 117 hours of video was used for data extraction.

Data analysis

Statistical analyses were performed with JMP v. 11.1.1 (SAS Institute, 1986). I used an alpha of 0.05, and sequential Bonferroni corrections for multiple tests (Rice 1989). I used Tukey's HSD to assess significance in response variables amongst grass density treatments if there was a significant main effect of treatment.

Running trials

For running trials in both lab and field conditions, responses were averaged across the two consecutive runs in each density, yielding one average response value per density treatment. Data from one run of a non-Veldt animal tested in the dense treatment were excluded as values were greater than two standard deviations away from the global mean; therefore, this animal's performance in the dense treatment was from just one run. Response variables were $(\text{value} + 1)$ log transformed to satisfy normality and homogeneity of variances. Similarly, because many scores for the composite motivation tactic variable were negative, I added "2" to all score values before log transformation.

I used mixed model GLM to compare running performance of individuals from different habitats of origin and in different grass densities separately for field and lab trials. Individual nested within habitat of origin was a random effect and the fixed effects were grass density and habitat of origin. Mass and sex were covariates in the model. I found no interactions between covariates and main effects, therefore satisfying the assumption of homogeneity of slopes (Engqvist 2005) and was able to exclude these interactions from the model. Because the grass density \times habitat of origin interaction was marginally significant in some cases, I chose to keep it in the final model.

Response variables included total transit time across a runway, amount of time spent stopped in a runway, maximum and average velocity, and amount of motivation an animal required to begin, and/or continue running. The motivation variable was created by performing a principal components analysis (PCA) from the five motivation tactics we scored from the video footage (described above). For field trials, the first principal component explained 48.4% of the variation across the five motivation types included in the analysis, combined (loadings: sand flicking: 0.742, flicking: 0.782, runway hitting: 0.458, sweeping: 0.650, touches: 0.791). In the lab, the first principal component explained 60.76% of the variation across the five motivation types, combined (loadings: sand flicking: 0.687, flicking: 0.803, runway hitting: 0.694, sweeping: 0.874, touches: 0.822). Because of the limited sample size in this study, I wished to minimize the number of independent variables in the model. The first principle component loaded fairly high and even, therefore I kept only the first principal component as a composite variable. This variable encompasses the response of the experimenter to the kangaroo rat's running behavior, and is thus an indirect response of the kangaroo rat to the grass. Principal component one (PC1) scores represent the magnitude of combined motivation tactics the animals received. Scores along this component's axis were tested for significant differences across grass density treatments, and habitat of origins.

I also statistically explored a comparison of field and lab trials for the 19 animals that performed both. I ran a mixed model GLM, again with individual nested in habitat of origin as a random effect, and looked for effects of location (lab versus field), habitat of origin, grass density, and their interactions, on the same locomotion performance response variables (see above). I also included mass and sex as covariates. Interactions

between covariates and the main effects were not significant so they were excluded from the final model (Engqvist 2005).

For running performance trials I had five response variables, therefore in each analysis I corrected for five tests using sequential Bonferroni (Rice 1989; see Tables 7, 8 and 9 for corrected alpha values).

Habitat use

I used mixed model GLM to look for main effects of grass density, night, and habitat of origin on the habitat utilization behaviors of time spent in each runway and latency time to seed pan. As in the running performance analysis, individual nested within habitat of origin was a randomized main effect. All response variables were log transformed to meet normality and homogeneity of variances, with the exception of time spent in each runway, which was square root transformed. Because of a sample size of 19, there were unfortunately not enough degrees of freedom to include any interactions among these main effects in the final model. I would have liked to include them as, by default, we are attributing significance only to the remaining variables, however I did not have sufficient power. In each analysis I corrected for two tests (total time spent and latency time to seed pan) using sequential Bonferroni (Rice 1989). For the seed depletion analysis I only used non-zero data (i.e., if there was seed left behind; $n = 11$). Because of such a small sample size, only the effect of grass density was assessed.

RESULTS

Running trials

Field trials: assessing running performance in a novel habitat

In field trials, for animals from both habitats of origin pooled (N=38), Veldt grass density had significant effects on performance variables transit time and time spent stopped (Table 7). The animals took significantly longer to cross the dense treatment than the medium and the control, and longer to cross the medium than the control (Tukey's HSD; Fig. 5a and Table 4 for averages). Animals spent more time stopped in the dense treatment than in either the medium (Tukey's HSD) or control (Tukey's HSD; Fig. 5c and Table 4 for averages). Time spent stopped in the medium and in the control was not significantly different from each other (Tukey's HSD).

Habitat of origin was also a significant predictor of performance, with Veldt animals crossing all three runways more quickly than non-Veldt animals (Fig. 5a, Table 7, Table 5 for averages). Likewise, Veldt animals spent less time stopped than non-Veldt animals (Fig. 5c, Table 7, Table 5 for averages).

Maximum velocity was not affected by Veldt grass density or habitat of origin. This would be expected if maximum velocity reflects an anatomical or physiological limit. Post data collection and analysis we realized the possible limits of interpreting maximum velocity as a valid proxy for locomotion, when an animal's fundamental limit in how fast it can travel could lie below a threshold affected by our treatments. In contrast, average velocity was predicted to be impacted because of the interruption of sustained running in the Veldt grass runways, and indeed it was (Table 7). Average velocity was higher in the control treatment than in either the medium (Tukey's HSD) or

dense treatments (Tukey's HSD; Fig. 5e and Table 4 for averages). Average velocity in the medium was not significantly different from the average velocity in the dense treatment.

The amount of motivation used to get, or keep, an animal running, was described using a principal component analysis (see Methods). The component scores were tested for significant differences across grass density treatments, and habitats of origin. Grass density had a significant effect on amount of composite motivation needed (Table 7). More intense motivation was required in the dense treatment than in both the medium (Tukey's HSD) and the control treatments (Tukey's HSD), and more in the medium than the control (Tukey's HSD; Table 4 for averages). Furthermore, animals from a non-Veldt habitat of origin required more motivating than those from a Veldt habitat of origin (Fig. 6, Table 7, Table 5 for averages).

In summary, when exposed to a novel runway with Veldt grass, all animals performed more poorly (as measured by transit time and average velocity) in the dense treatment and best in the control treatment. All animals required more motivation to cross runways containing Veldt grass than to cross runways with no Veldt grass. In addition, animals from a Veldt habitat of origin required less motivation, took less time in transit, and stopped less than animals from a non-Veldt habitat of origin. Because I found no significant interaction between habitat of origin and grass density across all response variables (Table 7), Veldt and non-Veldt animals did not perform differently in any one density. In addition, mass and sex were not significant (both $p > 0.05$) in any analysis.

Lab trials: assessing running performance in a familiar habitat

In lab trials, with all kangaroo rats pooled (N= 19), Veldt grass density had a significant effect on transit time (Table 8). Animals took more time to travel across the dense treatment than either the medium (Tukey's HSD) or the control treatments (Tukey's HSD; Fig. 5b, Table 4 for averages). Transit time was not significantly different between medium and control treatments (Fig. 5b).

Although there was no effect of grass density or habitat of origin on maximum velocity, as might be expected, average velocity was lower in the dense treatment than in both the medium and control (Tukey's HSD for both; Fig. 5f, Table 4 for averages). The average velocity in medium was not significantly different from that of the control.

When comparing animals across the two habitats of origin, there was no longer any difference between Veldt and non-Veldt animals on any response variables that were previously affected in field trials: transit time, time spent stopped, and amount of motivation (Table 8, Table 5 for averages). Also, grass density no longer had an effect on how much motivation all animals pooled required (Fig. 6, Table 8). The interaction between habitat of origin and grass density was not significant in any analysis (Table 8), nor were mass and sex (both $p > 0.05$).

Comparing running performance of animals tested in both field and lab trials

In a qualitative comparison between field and lab trials, performance (as measured by average velocity and transit time) increased in lab trials. For average velocity, a shift in significant comparisons among grass densities indicates that, in lab trials, performance in the medium treatment was more similar to performance in the

control (Fig 5e & f). That is, in a familiar habitat patch, the medium grass density treatment seemed to have less of an effect than it did when the habitat patch was novel. Average transit times across a familiar lab habitat were considerably shorter than in the field when the patch was wholly novel (Fig. 5a & b). There was also a significant difference in comparisons of transit times amongst density treatments: all three transit times were significantly different across all three treatments in the field (Fig. 5a), whereas in the lab, the control and medium treatments were not significantly different from each other, though they were different from the dense (Fig b). In the lab trials there was no longer (relative to field trials) an effect of grass density (Fig. 5d) or habitat of origin (Fig. 5d) on the amount of time spent stopped (Table 8).

Statistically, when comparing field and lab trials, there was a significant effect of the two days' experience with the grass templates (i.e., field versus lab trials) on the average velocity of the 19 animals who were tested in both field and lab conditions (Table 9), with average velocity being significantly higher in lab. There were no significant effects of the two days' experience on other running performance response variables; however, grass density did have a significant effect on both transit time and average velocity in this group (Table 9). The field/lab \times habitat of origin interaction, at $p = 0.024$, had a near significant (at an alpha of 0.0125) effect on transit time, suggesting that the Veldt animals that were tested in both the field and lab did not significantly increase in performance after the two days familiarization with the grass templates, whereas the non-Veldt animals did. Mass and sex were not significant in any analysis (both $p > 0.05$).

While there is qualitative and statistical evidence of amelioration of the detrimental effects of Veldt grass density and habitat of origin effects on running performance after two days' experience with the Veldt grass habitat patches, the data still demonstrate a general trend of reduced running performance in runways containing Veldt grass compared to runways without it, especially in the densest treatment. Thus, ameliorating effects, at least those acquired over the two-night familiarization period, did not entirely compensate for the detrimental effects of dense Veldt grass.

Style of movement

Qualitative observations of running performance in both field and lab settings confirmed not only the greater difficulty of navigating through the dense treatment, but the different modes of locomotion employed. In the control and often in the medium densities, kangaroo rats tended to travel in one fluid motion with very few pauses from one end of the runway to the other. Most animals moved in a sustained bipedal gait, consisting of short hops occasionally punctuated by long ground-covering jumps, especially when startled. It is noteworthy that both control and medium treatments offered at least one visually unobscured path to the other side; the animals could, therefore, have potentially seen the simulated escape route the wire mesh backing on the receiving box provided. In contrast, animals in the dense treatment exhibited much more stop-and-go movement, comprised more commonly of repeated, short quadrupedal advances, occasionally punctuated by halting collisions with a grass tussock or a bound entirely over one.

I also observed that the kangaroo rats needed more motivation (i.e., higher PC1 scores) to traverse the dense treatment, as supported by correlations with each dependent variable (Fig. 7). There could be concern regarding the correlation between composite motivation tactics and running performance, if, for example, high motivation correlated with high average velocity, low transit time or low amount of time spent stopped. However, this was not so. High motivation correlated with low velocity, high transit time, and high amount of time spent stopped, i.e., the better an animal performed, the less I had to motivate it; the more it hesitated, the more I motivated it. Therefore, performance was not a function of the amount of motivation delivered; rather the amount of motivation delivered was a function of performance.

Habitat use during acclimation to runways in captivity

Although there was no difference in total time spent in each arm of the Y arena between animals of different habitats of origin, both grass density and night had an effect (Fig. 8, Table 11). More specifically, when both nights and all animals were pooled, grass density (arm of arena) had a significant effect. There is evidence of kangaroo rats spending similar amount of time in the dense and medium treatment arms of the arena, but more time in the dense than in the control (Tukey's HSD), and in the medium than in the control (Tukey's HSD; Fig. 8, Table 6 for averages). Further, with grass densities and all animals pooled, kangaroo rats spent more time out of their nest jar during night 1 than during night 2 (Table 11, Table 6 for averages). There was no effect of grass density, habitat of origin, or night on latency time from lights out to leaving the nest jar and traveling to a seed pan (Table 11). There was also no significant difference in amount of

seed left in seed pans (in all three Veldt densities), when animals left seed (Table 11). Eleven of the 20 rats did leave seed on either night; the others, as predicted, depleted all seed patches both nights. When seed was left, it was not left more often in any one habitat patch, that is, it was left with equal *frequency* among the habitat patches (a qualitative assessment). Furthermore, when seed was left, there was no significant difference in the *amount* left among the three habitat patches (a quantitative assessment). In summary, few significant differences were found while monitoring habitat use, with the exception of kangaroo rats spending the least amount of time in the control arm, and less time out of their nest jar the second night.

DISCUSSION

Summary of main results

Consistent with my hypothesis, Veldt grass density had significant negative effects on several measures of running performance both in field and lab trials, with a consistent trend of decreasing running performance with increasing grass density. Habitat of origin had several effects on performance in the field (contradictory to my predictions), as Veldt animals performed significantly better than non-Veldt animals. However, no differences in performance were observed between Veldt and non-Veldt animals after two days of lab experience with varied grass densities. This suggests that the main effects on performance are modified through experience.

The most surprising result from the two-night habitat trials was the non-random use of habitat: kangaroo rats spent more time in the habitat patches that contained Veldt grass (both medium and dense treatments) than in the control patch that contained none. However, no difference was seen in depleting the seed patch in one density over another, or choosing to visit one seed patch in one density first over another. Therefore, the difference in habitat use across densities did not seem to be associated with seed harvesting per se.

Running performance

The effect of grass density and its amelioration with experience

Field running trials represented running performance in a novel habitat, and had the most robust sample size. Veldt grass density, as predicted, was a highly significant predictor of kangaroo rat running performance. These results suggest that *D.h. arenae*

were either reluctant to move or impeded from moving efficiently in the denser Veldt grass. Whereas these effects were reduced in lab running trials (performance was *less* affected by Veldt grass density), higher grass density tended to still correlate with poorer running performance. These results are similar to those found by Rieder et al. (2010), who found a monotypic stand of dense invasive cheatgrass to have negative effects on *D. ordii* running performance. This consistency in results suggests an overall tendency for introduced grasses to impede the locomotion of native kangaroo rats.

I predicted that running performance would be ameliorated in lab trials compared to field trials (i.e., in a familiar habitat patch compared to an unfamiliar habitat patch). This prediction was supported by the trend towards amelioration of almost all response variables of performance for all kangaroo rats, between field and lab trials. The amount of time spent stopped remained roughly the same; in lab trials the animals actually appeared to spend more time stopped in each of the runways. In lab trial average velocity, however, was higher across all three runways, and transit times were lower. This suggests that, in lab (i.e., familiar habitat patches), during the periods in which the animals were in motion they were running faster than in field trials (i.e., novel habitat patches). This highlights the importance of familiarization for these animals; they were able to travel significantly faster once familiar with the habitat, even when stopping for more time.

Time spent stopped as a response variable, however, is also difficult to interpret as a performance variable and could have alternative interpretations. For example, the animals could have been stopping because they did not know how best to proceed, they could have been stopping because they felt safe in the grass and were using it as cover, or they could have been stopping because they felt unsafe and were being vigilant. In

several studies that look at the effects of invasive plants on native rodents (Rowland and Turner 1964; Congdon and Roest 1975; Yensen et al. 1992; Schooley et al. 1996; Germano et al. 2001; Sammon and Wilkins 2005; Nelson et al. 2009; Rieder et al. 2010, Freeman et al. 2014), the plants, like Veldt grass, offer substantial cover. However, especially in those studies with kangaroo rats (Rowland and Turner 1964; Congdon and Roest 1975; Germano et al. 2001; Nelson et al. 2009, Rieder et al. 2010, Freeman et al. 2014), the invasive plants imposed overall negative effects. Specifically, these studies found that the cover created by invasive plant species created often impenetrable thicket for desert-adapted kangaroo rats that rely on open ground to forage and avoid predation (Bartholomew and Caswell 1951; Price 1978; Goldingay et al. 1997), and resulted in a decline of kangaroo rat abundance. My results similarly demonstrate negative effects, specifically pertaining to locomotion. These findings, together with the results of previous studies (Rowland and Turner 1964; Congdon and Roest 1975; Germano et al. 2001; Nelson et al. 2009, Rieder et al. 2010, Freeman et al. 2014), suggest that any benefits provided by the increase in cover do not make up for other detrimental aspects associated with the vegetation, such as impediment to locomotion.

The trend of amelioration of running performance with experience suggests a diminution of the density effect after spending time in the habitat. Spatial cognition is presumably responsible for the amelioration of the poor prior performance by all animals. Cognition can be described as the neuronal processes concerned with the acquisition, retention, and use of information (Dukas 2004). Specifically, the animals in this study were likely to have registered and remembered their surroundings by use of landmarks (Langley 1994, Barkley and Jacobs 1998), or an absolute location in space (Jacobs 2003;

Jacobs & Schenk 2003). This behavior has been well demonstrated (Langley 1994, Sherry et al. 1992, Barkley and Jacobs 1998, 2007) in seed caching kangaroo rats, like *D.h. arenae*, when retrieving seed caches. My results suggest that kangaroo rats were better able to navigate through grass tussocks (when pursued) after having sufficient time to learn the tussock locations. This is an important result as it suggests that the prevailing view that Veldt grass makes for poor kangaroo rat habitat (because of the increased vegetative cover it provides--Howell 1932; Reynolds 1950, Bartholomew and Caswell 1951; Rosenzweig and Winakur 1969; Price 1978; O'Farrel and Uptain 1987; Price et al. 1994; Cypher 2001; Jones et al. 2003; Waser and Ayers 2003; Nelson et al. 2009) does not give the animals enough credit. Their spatial cognition ability may provide the means for them to accommodate to some increase in plant cover.

One could argue that because of differences among trial settings (lab versus field), timeline (pre versus post captivity), and seasonality (spring/summer versus winter), the statistical comparison of lab and field performance depicts more correlation than causation. That is, factors other than just the two nights' experience with the templates resulted in the differences observed between field and lab trials. However, if the differences in performance found between field and lab trials were due to these other factors and not the two nights' experience, the results should be equal for both Veldt and non-Veldt animals; this is not the case. Non-Veldt animals significantly ameliorated in performance, while Veldt showed very little amelioration. Furthermore, an argument could be made that the covariates of age and effects of time spent in captivity likely *negatively* impacted performance instead of improving it. The effect of age should decrease performance (Knechtle et al. 2011), as the animals were all already adults in

field trials and older in subsequent lab trials. Time in captivity, especially with an *ad libitum* food and in a confined space, as was implemented here, should increase fat mass and decrease muscle mass (Boonyarom and Inui 2006). Therefore, both age and time in captivity should result in a neutral or even negative effect on running performance. Yet, this is contrary to what was observed. Increased performance, then, was most likely due to the chief difference between field and lab trials: i.e., acclimation time to the otherwise identical Veldt grass templates. In fact, in an exploratory analysis, I tested for an effect of time in captivity by looking for performance differences between captive “cohorts,” or animals that spent between 10-17 weeks in captivity and animals that spent 2-7 weeks in captivity before lab trials, and found none (Table 10).

In the statistical comparison between field and lab trials a marginally non-significant interaction between habitat of origin and field/lab suggests that two days experience with the templates may have had a differential effect on non-Veldt versus Veldt animals. That is, when Veldt grass-naïve, learning not only the Veldt grass tussock positions, but also some knowledge of the grass itself, was beneficial to the non-Veldt animals. The gain in performance by non-Veldt animals was greater than by Veldt animals, presumably due to this new familiarization with the Veldt grass.

The effect of habitat of origin on running performance

Veldt animals almost always outperformed non-Veldt animals in the novel field studies, but not in the familiar environment of the lab. This result was contrary to my predictions. If the difference is attributed solely to spatial cognition (i.e., the non-Veldt animals learned the physical locations of the tussocks) (Langley 1994; Sherry et al. 1992;

Barkley and Jacobs 1998; 2007), Veldt and non-Veldt performance should have also been the same in the field, since the particular templates of Veldt grass they encountered were novel to both groups. In other words, both groups should exhibit equal levels of spatial cognition. However, in the field, this outperformance of Veldt animals over non-Veldt animals suggests knowledge of or experience with the grass tussock itself to be beneficial. Based on the comparison of which effects were significant across field and lab trials, I can confidently conclude that experience (even short-term) with Veldt grass, in and of itself, improved the performance of non-Veldt animals. It is worth asking whether the same response would occur with a different form of cover; i.e., do the kangaroo rats learn something about Veldt itself, or just “cover?” Given that cover exists in the field where non-Veldt kangaroo rats were collected, I hypothesize that experience with Veldt, and not just experience with cover, is the relevant factor. However, more research on animal behavioral flexibility to increased plant cover is needed to support this hypothesis.

Veldt animals required significantly less motivation than non-Veldt animals to run. This suggests that the Veldt animals were somehow more able or willing to navigate through the grass than the non-Veldt animals. However, in the lab (in a familiar habitat) this difference disappeared. Because the habitat of origin effect was assessed over the three densities of grass pooled, the difference in the field was perhaps not due to grass *density*, as much as something, again, about the grass itself and the kangaroo rat’s experience with it (or lack thereof). Experience may have a) increased willingness by making the landscape less daunting because the animals were aware of the achievability of navigating through it (difficult to prove), and/or b) increased ability by giving the

animals physical practice navigating through it (similar to a rat's increase in spatial location performance in a maze [Morris 1981]).

Overall, Veldt animals outperformed non-Veldt animals in the field, yet they did not outperform them disproportionately in any one grass-density treatment. This lack of significant interaction between grass density and habitat of origin was predicted; an interaction would have suggested an advantage of Veldt animals in what was predicted to be an equally detrimental situation for all. Considering the overall superiority in performance in the field of Veldt animals, their superior performance in the dense treatment, for example, would not have been surprising. The lack of interaction, however, again supports the idea that the overall differences observed between animals from Veldt and non-Veldt habitat of origins were not due to grass density as much as simply the grass itself and experience with it. To my knowledge, no studies that assess the effects of invasive plants on native rodents (Rowland and Turner 1964; Congdon and Roest 1975; Yensen et al. 1992; Schooley et al. 1996; Germano et al. 2001; Sammon and Wilkins 2005; Nelson et al. 2009; Rieder et al. 2010, Freeman et al. 2014) have looked at the effects of different densities of the plant; instead they have looked only at the effects of presence/absence of the plant. This is an area in which further study is needed, especially when an invasive is extremely difficult to fully eradicate and the realistic result of management efforts is a thinner distribution of the invader rather complete removal of it. To this end, my results of the differential effects of different Veldt grass densities on the locomotion of *D. h. arenae* are also relevant. In both the field and lab, the dense treatment (40% grass cover) had significantly greater effects than both the control (0%) and medium (20%) treatments on locomotion. For Veldt grass and *D.h. arenae*, this

suggests a possible density threshold under which the animals are less adversely affected; this knowledge could contribute to future management decisions.

It is noteworthy that I predict that the lab locomotion trials of my study, though carried out in an artificial setting, are more indicative of what is occurring naturally in the wild than the field locomotion trials. This is because kangaroo rats occupy home territories that they become familiar with, and therefore testing their locomotory performance in novel habitat patches does not realistically reflect their performance in familiar territories. This, again, highlights the need for a period of familiarization in performance studies of kangaroo rats. I would extend this to also include behavioral studies of kangaroo rats, and, further, to perhaps all species that exhibit some spatial cognition of their surroundings.

Implications of dense Veldt grass for kangaroo rat movement

Overall inexperience may have caused non-Veldt animals to run more poorly in a novel Veldt habitat, but higher densities of Veldt grass were nonetheless having significant effects on the locomotion of all kangaroo rats. These results are consistent with the wealth of literature arguing that open habitat characterized by sparse vegetative cover is the most suitable habitat for *Dipodomys* species (Howell 1932; Reynolds 1950; Bartholomew and Caswell 1951; Rosenzweig and Winakur 1969; Rosenzweig 1973; Price 1978; O'Farrel and Uptain 1987; Price et al 1994; Cypher 2001; Jones et al 2003; Waser and Ayers 2003; Nelson et al. 2009). Many of these studies involve highly controlled, experimentally manipulated designs and thus offer robust conclusions (see Introduction). Some authors have speculated on possible mechanisms behind this trend.

Reynolds (1950), Rosenzweig and Winakur (1969) and Rosenzweig (1973) postulated that dense grass interferes with kangaroo rat escape efficiency and ability to detect predators; Lemen and Rosenzweig (1978) credit low kangaroo rat abundance in habitats of dense vegetation partially to their preference of foraging in open bare ground and availability therein of their preferred resource-- dense seed clumps (Reichman 1977). None of these studies, however, have experimentally tested the speculated mechanisms. My study offers an experimental, controlled and mechanistic explanation of the well-established trends; that is, kangaroo rat abundance may be lower in high vegetative cover habitat specifically because of reduced ability to locomote efficiently through it when pursued.

In a long-term habitat restoration study, Cosentino et al. (2014) recently found that *D. spectabilis* density increased in experimentally reduced shrub areas, but the response lagged by a decade or more. Dispersal constraint was responsible for the time lag, and they suggested that a mosaic of attainable and suitable (i.e., lower vegetation density) habitat is the right approach to restoration of the species. It is clear that *Dipodomys* inhabit and prosper in sparsely vegetated habitats, and interconnectedness of local populations is vital to metapopulation success, especially in highly varied environments of irregular quality. Furthermore, Price et al. (1994) found unvegetated corridors to be very important in maintaining interconnectedness of local populations of *D. stephensi*. This study further demonstrates that cover consisting specifically of tussock grass impedes locomotion in a kangaroo rat's home range and especially in unfamiliar corridors used during the dispersal phases of juveniles and males, and that different percentages of density cover have different effects. Therefore, the mechanism behind

decreased persistence of *Dipodomys* populations in unsuitable (high vegetation density) habitat may extend to densely vegetated dispersal corridors among populations.

Spatial cognition and its application to overall fitness

My results demonstrate that familiarization to the grass/habitat dampens the detrimental effects of the grass on the animal's locomotion. Based on previous spatial cognition studies (Langley 1994; Sherry et al. 1992; Barkley and Jacobs 1998; 2007), I suspect that the animals in my study learned the components of their habitat. This learning process seems to occur quickly, and could have significant utility in the wild. It can be especially advantageous when animals are exposed to frequent and unpredictable environmental perturbations, such as a changing habitat due to invasive species (as reviewed in Sih et al. 2011; Tuomainen and Candolin 2011). Acquiring information (i.e., learning), such as the location of grass tussocks in a home habitat, is valuable when it leads to behavioral changes that enhance fitness. Learning has thus been shown to be adaptive (Gould 1974; Stephens 1989; Dall et al. 2005). Based on my results showing the amelioration of locomotory performance through Veldt grass when given time to learn its distribution, I predict that the learning that is occurring in *D.h. arenae* is an adaptive trait.

The familiarization to Veldt grass that I saw in the lab may occur in specific cases in the wild, mitigating at least some of the impediments Veldt grass has on locomotion. When a juvenile kangaroo rat disperses from its nest burrow, or when a male leaves his territory in search of mates, the novel habitat they come across (whether in a dispersal corridor or new home territory) may contain Veldt grass, and if the animal is pursued by a predator during this time, the Veldt grass would impede their locomotion

during escape. The animal may thus have a higher probability of being preyed upon in novel Veldt areas. However, due to learning, the animals improved in their locomotor performance. Increased locomotory abilities can be translated to greater successful predator evasion (Schooley et al. 1996), a direct fitness benefit. I predict this same interpretation for any type of change in vegetative cover due to plant succession and plant invasion.

As demonstrated here, a juvenile kangaroo rat could quickly become familiar with its new home territory, and acclimation to its new landscape would lessen the effects the vegetation in the new habitat have on escape locomotion. A mate-seeking male would presumably be traveling through novel habitat more frequently (Daly et al. 1990; Price and Kelly 1994); this effect of novel grass on its locomotion may be a mechanistic explanation for why this segment of the population in some species of kangaroo rats is most vulnerable to predation (Daly et al. 1990; also see Zuk and Kolluru 1998). Therefore, I predict mate-seeking males to be the most vulnerable to the effects of Veldt grass on locomotion. This possibility leads to several other interesting predictions: a) longer-lived males (presumably with more spatial knowledge) should have higher survivorship, b) mate finding and monitoring may be less risky in open habitats, and c) roads or trails might be more easily learned and therefore preferentially used by males. The last observation is consistent with the observations made by Consentino et al. (2014) and Price et al. (1994, discussed above).

Habitat use

Effect of density on time spent in habitat patches

While monitoring the Lompoc kangaroo rat's habitat use over three hours per night and across a two-night period, the most intriguing result was the apparent preference for Veldt habitat (medium or dense) over the control. Having predicted that the kangaroo rats would spend more time in the Veldt-free runway, I can only speculate why they chose to spend significantly more time in the Veldt grass runways across both nights. Considering the natural landscape of these animals' home territories-- open dune habitat dotted with endemic shrub and herbaceous cover (FX Villablanca, unpublished data)-- the absence of cover may have represented a risky environment. Although abundant literature suggests low kangaroo rat abundance in densely vegetated habitat, no study (to the extent of my knowledge) has compared zero vegetation habitat to light vegetation habitat. I therefore have little precedent to draw upon. Alternatively, perhaps the Veldt landscape simply offered more perceived possibility of a seed source. Or perhaps the long narrow runways, surrounded by tall walls on every side, were simply not an adequate representation of natural habitat to interpret these results.

Effect of time (night 1 versus night 2) on time spent in habitat patches

My study animals spent more time exploring their habitat during the first three hours of the first night than during the first three hours of the second night. I can hypothesize that the animals, while having started with zero seed cached in their nest jars on night 1, had established some stores by night 2, and were therefore less motivated by the second night to leave the safety of their nest jar to forage. However, some exploratory

analyses found no difference between night 1 and night 2 on amount of seed taken, suggesting that the first three hours of the night may not have been representative of the animals' activity over the entire night.

Effect of density on seed left, and Giving Up Density

As predicted, kangaroo rats did not preferentially deplete one seed patch (in one density arm of the arena) more than another. Kangaroo rats are seed hoarders; they fill their cheek pouches and deposit reserves in pit caches or back in their burrows (see reviews in Brown and Reichman 1983 and Genoways and Brown 1993). When given seed *ad libitum*, kangaroo rats have been found to remove as much as possible, even if they are unable to consume it all (Daly et al. 1992; Jenkins et al. 1995; Price and Correl 2001). The 1g of seed presented in each patch in the present study could have easily been carried in one trip based on measurements of *D.h. arenae* cheek pouch volumes (J. Trunzo, unpublished data). Therefore, the observation that seed was most often fully depleted in all three habitat patches, and when it wasn't, no preference was shown for one seed patch, is not surprising, even with the addition of medium to dense Veldt grass tussocks in the habitat.

No significant difference in amount of seed remaining among the three Veldt grass densities can be further explained in the context of an optimal foraging model (Charnov 1976) for kangaroo rats. This model suggests that the amount of seed remaining at a seed patch when the forager leaves ("giving up density," or GUD [Brown 1988]) provides quantitative information on fitness costs and benefits (Brown 1988; 1992; 1999; Brown et al. 1994). Assuming the seed patch represents 100% reward, at some point

during foraging the percent reward remaining becomes equal to the predation risk. Continuing to forage on a lower amount of seed than this threshold percent is not adaptive (Brown 1992). However, if predation risk is not perceived, then, under this hypothesis, the forager would continue to deplete the patch until the full 100% reward is attained. This hypothesis allows me to predict risk perceived in the habitat patches of varying densities of Veldt grass, based on where the greatest amount of seed remained. I found no significant difference in the amount of seed remaining among habitat patches; therefore, it is possible that the animals in my study perceived no difference in predation risk among the three Veldt grass densities. Noteworthy also is that sample size in this analysis (N= 11) may have been too small to have sufficient power; this is a likely explanation for not finding an effect if there was one indeed to be found.

Effect of density on latency time to pan

The animals also did not prefer to visit one seed patch first over the others; seed patches in the control, medium and dense treatments were visited in no apparent order. Consistent with my prediction that most animals would spend more time in the control runway, I predicted that most animals would visit the seed patch in the control runway first. However, despite spending more time in the medium and dense runways than in control, the animals did not preferentially choose to visit the medium and dense seed patches first. The random order of seed patch visitation along with the random pattern of seed depletion from them suggests no effect of Veldt grass tussocks on preference of foraging location.

Drought and kangaroo rat trap success

It is noteworthy to mention that during this study there was a noticeably low Lompoc (*D.h. arenae*) kangaroo rat live-trapping success rate, particularly at Veldt sites. Trap success rate is defined as the number of kangaroo rats captured per 100 traps set in the field. Previous trap success rates (Dec 2012 and Dec 2013) at the OSDVRA and Callendar sites, for example, ranged between 20% and 40% (FX Villablanca, pers. comm.); I had a 1.5% success rate at these same sites, from May 2014 to July 2014 (Table 1). Total trap success (6.2%) across all non-Veldt sites was also low compared to previous years, but was higher than total trap success across all Veldt sites at 2.1%. Trapping at these locations has been ongoing for several years, with rates ranging as high as 80% (FX Villablanca, pers. comm.). I can speculate on causes for this discrepancy; an obvious candidate would be the concurrent record-setting drought in California (NIDIS 2015). California experienced its warmest winter in 2013-2014, and lowest precipitation during 2013, in 118 years of record keeping (NOAA/NCDC 2015). Record-warm days, months and multi-month periods, with temperature records broken by a margin as much as an entire degree Fahrenheit (NOAA/NCDC 2015), have contributed to perceivable effects statewide.

The drastic drought may be affecting kangaroo rat population sizes. In a two-year study which included one year of below-average rainfall, Price and Kelly (1994) found that, for Stephen's kangaroo rat, the length of the breeding season, average number of litters per female, and the fraction of first-year females breeding were much greater in the year of higher rainfall. Jones et al. (2003) created a model of Merriam's kangaroo rat abundance in relation to ground cover, precipitation, fire and grazing based on their field

studies in southeastern Arizona. In their model, highest kangaroo rat abundance was correlated with low percent ground cover, high grazing and fire regimes, and ~ 15 inches annual precipitation. Below this ideal amount of rainfall, kangaroo rat abundance dropped drastically; from 15 inches to 0 inches kangaroo rat abundance dropped by half. San Luis Obispo received only 4.56 inches of precipitation in 2013, and 9.51 inches from the Jan-October period of 2014 during which our study was performed, compared to the normal of 19 inches of annual rainfall for this region (NOAA/NCDC 2015). Cypher (2001) also found precipitation to impact Heermann's and Short-nosed kangaroo rat populations, both of which declined following the unusually wet, cold conditions in the winter of 1994-1995 in the Elk Hills of California. An ideal range of rainfall, then, seems to be instrumental in maintaining kangaroo rat population size.

The significant decrease in Lompoc kangaroo rat population size in the Oceano dunes is potentially a textbook example of bottom-up population regulation (as in Baez et al. 2006). In comparing to Jones et al.'s (2003) study (although this pertained to a related species in a different area), a general principal may emerge given the adaptations of this genus to extremely arid conditions. *Dipodomys* are highly adapted for arid environments, both physiologically and morphologically (Schmidt-Nielsen et al. 1948; Schmidt Nielsen and Schmidt Nielsen 1951,1952; Kenagy 1973); however, the plants on which they forage may not be. This might be especially true in California's Oceano Dunes, where the habitat is comprised of (besides Veldt grass) such shrub and herb species as mock heather (*Ericameria ericoides*), dune lupine (*Lupinus chamissonis*), coastal buckwheat (*Eriogonum latifolium*) and sand verbena (*Abronia villosa*), none of which are particularly arid-adapted plants. I postulate that drought conditions are affecting the local

flora more directly than the kangaroo rats themselves. Drought imposes major difficulties in executing normal physiological functions in plants, like flower and seed production (Lisar et al. 2012) and can ultimately lead to complete desiccation and death. A decrease in vegetation or seed production equates to a decrease in kangaroo rat food supply, and could impact the abundance of this and other herbivores (Brown and Ernest 2002).

Regarding the lower trap success rate at Veldt sites compared to non-Veldt sites, it would be convenient to conclude that Veldt grass areas represent unsuitable habitat for kangaroo rats and therefore cannot support large populations. Veldt areas may act as sinks in the metapopulation, such that kangaroo rat populations are characterized by greater deaths than births, and greater immigration than emigration (Andrewartha and Birch 1954, 1984). However, FX Villablanca and J Trunzo's (unpublished data) survivorship study found equal survivorship at sites of 40% Veldt grass density when comparing across densities of 0%, 20% and 40%. In this study, I found 40% Veldt grass density to decrease locomotion performance, regardless of life-long or two-day experience with the grass. However, the survivorship study suggests that these negative effects may be mitigated by other factors. Recently J Trunzo and FX Villablanca (unpublished data) found that Lompoc kangaroo rats in the Oceano Dunes were not only collecting and caching Veldt grass seed, but also consuming it. The use of Veldt grass as a food source may mitigate the negative effects that it imposes on their locomotion. A 40% Veldt grass density cover may significantly reduce running performance but offer plentiful seed. Veldt grass, like the other plants in the community, is likely suffering in terms of vegetative growth and seed set due to the drought. The combination of fewer

seeds and impediment of locomotion could have contributed to low population numbers and poor trap success rates at Veldt sites in this study.

Veldt grass as an invasive species

There is an increasing body of evidence showing that native species are able to respond adaptively to the presence of invaders either through phenotypic plasticity responses (Ortega et al. 2013; Latta et al. 2007) or evolutionary processes (Oduor 2013; Goergen et al. 2011). Over time, these adaptive changes in natives may diminish impacts of invaders and promote coexistence between invaders and natives (Strauss et al. 2006). In the Carrizo Plains (CA, USA), giant kangaroo rats (*D. ingens*) have a mutualistic relationship with exotic weeds such as *Erodium cicutarium* and *Bromus madritensis*, as the kangaroo rats depend on the plants for food, and the plants depend on the kangaroo rats to disturb their habitat continually as the animals dig tunnels, clip plants and cache seed (Schiffman 1994). In other taxa, black-capped chickadees (*Poecile atricapillus*) in western Montana have shifted their foraging behavior in a way that allows them to exploit larvae of the exotic insect *Urophora* (Ortega et al. 2013). The authors suggest that behavioral flexibility may be used to predict how native species will respond to invasions, particularly the availability of exotic food resources. Soapberry bug (*Jadera haematoloma*) populations in Florida that have co-existed with an introduced plant species (*Koeleria elegans*) have higher fecundity on the introduced host than on its historical native host (*Cardiospermum coridum*; Carroll et al. 1998). Carroll et al. (1998), Schiffman (1994), and Ortega et al. (2013) demonstrate that an invasive plant species may become a valuable food resource for native fauna. This relationship may be

occurring between the Lompoc kangaroo rat and invasive Veldt grass, given that the kangaroo rat has recently been found to be consuming Veldt seed (J Trunzo and FX Villablanca, unpublished data).

Malo et al. (2012) found an invasive plant species (*Rhododendron ponticum*) to increase the abundance of a native mouse (*Apodemus sylvaticus*). The authors recognized, however, that this increase may affect populations of other species within the community, at lower (seed predation and dispersal) and upper (weasel populations) trophic levels. A similar phenomenon could be occurring in the Oceano dunes. I suspect community-level trophic cascades to be present in this ecosystem, in which the Lompoc kangaroo rat's predators (such as great horned and barn owls, coyotes, gopher and rattle snakes) and prey species (native shrubs and grasses) are affected by the impacts of invasive Veldt grass on the kangaroo rat. Such possible interactions should not be ignored when assessing the overall implications of invasive Veldt in this ecosystem.

Conclusions

In conclusion, my study questions the extent of harm an invasive grass poses on an endemic keystone desert-adapted rodent. I have documented detrimental effects of the grass on locomotion of kangaroo rats that were pursued in a simulated predator attack, but also a dampening of these effects when the animals were given time to become familiar with the habitat. I have presented data suggesting no preference for foraging location or seed taken based on grass density, and a preference for spending time in habitat patches containing the grass over a habitat without it. I considered studies that suggest mutualistic, and even positive, effects of invasive flora on native fauna, including

the recent and highly relevant example of *D.h. arenae* feeding on Veldt grass seed. Considering all of this, I hesitate to suggest large-scale management and restoration plans for *D.h. arenae* habitat, but instead suggest further exploratory study at the community level; we must consider the possibility that removing Veldt may reduce habitat quality. I predict that the current focus on the detrimental impacts of invasive plants on native animals will eventually be replaced by a more pluralistic perspective, in which we recognize that some species are negatively impacted, whereas some species benefit, from the presence of the same non-native plants.

I propose that future locomotion studies might benefit from accounting for the motivation tactics employed to force animals to move. Previous studies (Djawdan and Garland 1988; Djawdan 1993; Rieder et al. 2011) found it difficult to motivate kangaroo rats to perform at their maximum capacity, and subsequently used wide-ranging methods beyond simply chasing the animals with padded meter sticks (i.e., in Djawdan and Garland [1988] rattling pieces of cardboard and plastic bags along track walls, clapping, yelling, even “mild electric shock”). To my knowledge, none of these studies quantified these tactics, opening the door for possible criticism that some animals performed better than others because they were motivated more aggressively than others. Ideally, in these types of experiments, a single standardized motivation tactic should be employed. Based on great variability in the animals’ reactions to the motivation tactics I employed, this was not possible in my study, and I predict that it is not possible in general. To attain the most reliable results in running performance analyses, I suggest future studies to at least quantify their motivation efforts, and, as I did, look at correlations between amount of

motivation and running performance to ensure that performance is not simply a measure of motivation.

Administering performance trials after an acclimation period, and not solely drawing conclusions based on performance in novel habitat patches (e.g., Rieder et al. 2010), may illuminate interesting coping abilities of kangaroo rats or other species exposed to non-native plants. Few studies have considered how short and/or long-term experience with an invasive can alter proximate effects on the native animals, such as locomotory abilities. Phenotypic plasticity in the form of learning may provide a fundamental advantage in the face of plant succession, climate change and/or shifting community composition associated with plant invasions. Though I have found a performance effect on locomotion, it seems to scale with grass density, and was ameliorated to some degree by familiarization. The capacity to learn, together with a community level perspective that considers possible neutral or even positive trophic interactions among natives and invasives, must be considered in conservation and management decisions in the future.

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APPENDICES

Appendix A: Tables

Table 1: Dates and distribution of *D. h. arenae* field running trials. The original design involved pairing Veldt and non-Veldt sites; however, after great difficulty finding Veldt animals, trap nights were increased at Veldt sites at the end of the study. BLV and BLNV are Black Lake Veldt and Black Lake Non-Veldt sites, ODSVRVAV and ODSVRANV are Oceano Dune State Vehicular Riding Area Veldt and Oceano Dune State Vehicular riding Area Non-Veldt sites. A trap night is one trap deployed in the field for one night.

Date	Site	Trap Nights	N
5/1/14	BLNV	48	5
5/2/14	BLV	66	3
5/3/14	BLNV	66	2
5/8/14	ODSVRAV, ODSVRANV	36	5
5/9/14	ODSVRAV, ODSVRANV	36	0
5/14/14	BLNV	42	5
5/15/14	BLNV	67	3
5/16/14	BLNV	67	0
5/21/14	CV	20	2
5/22/14	BLNV	28	3
5/23/14	BLNV	25	1
5/24/14	BLNV	25	0
5/29/14	ODSVRANV	18	0
5/30/14	ODSVRAV	36	0
5/31/14	ODSVRAV	36	1
6/6/14	ODSVRAV	18	2
6/7/14	ODSVRAV	24	0
6/26/14	ODSVRAV	51	2
6/29/14	ODSVRAV	121	0
7/6/14	OSDVRAV	121	0
7/10/14	OSDVRAV	121	1
10/16/14	BLNV	60	7
10/18/14	BLV	30	1

Table 2: Timeline for running trials in the field and the lab for captive animals.

Animal ID	Tested in Field	Brought into Captivity	Habitat Trials	Tested in Lab	Days in Captivity prior to Lab Running Trials
3202	5/15/14	5/17/14	9/4/14-9/6/14	9/6/14	110
3213	5/9/14	6/1/14	9/6/14-9/8/14	9/8/14	98
3131	5/22/14	5/24/14	9/8/14-9/10/14	9/10/14	101
3201	5/15/14	5/17/14	9/11/14-9/13/14	9/13/14	117
3267	6/1/14	6/1/14	9/13/14-9/15/14	9/15/14	106
3095	5/2/14	5/25/14	9/15/14-9/17/14	9/17/14	115
3083	5/2/14	5/25/14	9/17/14-9/19/14	9/19/14	117
3119	5/9/14	7/11/14	9/19/14-9/21/14	9/21/14	72
3247	5/9/14	7/11/14	9/21/14-9/23/14	9/23/14	74
3224	5/23/14	9/18/14	10/22/14-10/24/14	10/24/14	36
3303	10/17/14	10/17/14	11/1/14-11/3/14	11/3/14	17
3088	5/2/14	10/17/14	11/3/14-11/5/14	11/5/14	19
3308	10/17/14	10/19/14	11/5/14-11/7/14	11/7/14	19
3302	10/17/14	10/17/14	11/7/14-11/9/14	11/9/14	23
3307	10/17/14	10/17/14	11/9/14-11/11/14	11/11/14	25
3242	5/4/14	10/17/14	11/11/14-11/13/14	11/13/14	27
3305	10/17/14	10/17/14	11/13/14-11/15/14	11/15/14	29
3306	10/17/14	10/17/14	11/16/14-11/18/14	11/18/14	31
3304	10/17/14	10/17/14	11/19/14-11/21/14	11/21/14	34
3301	10/19/14	10/17/14	12/1/14-12/3/14	12/3/14	46

Table 3: Average mass (g) of animals tested in running performance trials, in field and lab.

Field (N= 38)	Lab (N= 19)
61.3 ± 8.4	59.9 ± 6.5

Table 4: Averages of response variables for running performance trials across the three grass density treatments, in both the field and in lab. Maximum velocity was post-hoc regarded as an unreliable performance measure and thus the results are not presented.

	Control		Medium		Dense	
	Field	Lab	Field	Lab	Field	Lab
Mean Transit Time (s)	8.13	5.58	12.45	8.41	16.58	12.57
Mean Time Stopped (s)	0.84	1.33	1.95	2.05	4.5	3.43
Mean Average Velocity (m/s)	0.62	0.92	0.44	0.71	0.42	0.55
Motivation (PC1 score)	-0.59	-0.71	-0.25	0.19	0.141	0.51

Table 5: Averages of response variables for running performance trials across the two habitats of origin, in both the field and in lab. Maximum velocity was post-hoc regarded as an unreliable performance measure and thus the results are not presented.

	Non-Veldt		Veldt	
	Field	Lab	Field	Lab
Mean Transit Time (s)	14.45	8.4	8.59	9.68
Mean Time Stopped (s)	2.95	2.08	0.85	2.61
Mean Average Velocity (m/s)	0.46	0.71	0.56	0.74
Motivation (PC1 score)	0.181	-0.11	-0.644	0.2

Table 6: Averages of total time spent during the two nights of monitoring habitat use. Percent of time in each density is calculated across both nights (i.e., six hours), and represents the amount of time the animal spent in the density as a fraction of the total amount of time the animal was out of its nest jar. Percent of time each night represents the amount of time the animal was out of its nest jar (in any density) as a fraction of the total six hours filmed.

	Total Time Spent (%)
Control	16.62
Medium	23.44
Dense	28.86
Night 1	24.6
Night 2	20.89

Table 7: Field running trials significance tests: the effects of Veldt grass density (0%, 20% or 40%), habitat of origin (Veldt versus non-Veldt), and their interaction, on the response variables transit time, time spent stopped, average and maximum velocity, and amount of motivation required. DFNum is the degrees of freedom in the numerator, which reflects the number of treatments. DFDen is the degrees of freedom in the denominator, which reflects sample size. F and p values are from mixed model GLM with animal ID as a random effect. Significance was judged after Bonferroni correction for multiple tests (see results).

Response Variable	DFNum	DFDen	F	p	alpha
<i>Transit Time</i>					
Density	2	71.19	29.86	< 0.0001	0.0167
Habitat of Origin	1	36	7.88	0.008	0.0167
Density × Habitat of Origin	2	71.19	0.41	0.66	0.025
<i>Time Stopped</i>					
Density	2	71.31	8.79	0.0007	0.025
Habitat of Origin	1	36.02	8.3	0.01	0.01
Density × Habitat of Origin	2	71.31	2.93	0.08	0.01
<i>Average Velocity</i>					
Density	2	73.42	22.15	< 0.0001	0.0167
Habitat of Origin	1	40.75	3.57	0.05	0.025
Density × Habitat of Origin	2	73.42	0.39	0.68	0.05
<i>Maximum Velocity</i>					
Density	2	73.99	1.56	0.23	0.05
Habitat of Origin	1	40.55	0.21	0.61	0.05
Density × Habitat of Origin	2	73.99	0.89	0.42	0.0167
<i>Motivation</i>					
Density	2	70.65	15.69	< 0.0001	0.0167
Habitat of Origin	1	35.49	8.85	0.0034	0.0125
Density × Habitat of Origin	2	70.65	1.32	0.25	0.0125

Table 8: Lab running trials significance tests: the effects of Veldt grass density (0%, 20% or 40%), habitat of origin (Veldt versus non-Veldt) and their interaction, on the response variables transit time, time spent stopped, average and maximum velocity, and amount of motivation required. DFNum is the degrees of freedom in the numerator, which reflects the number of treatments. DFDen is the degrees of freedom in the denominator, which reflects sample size. F and p values are from mixed model GLM with animal ID as a random effect. Significance was judged after Bonferroni correction for multiple tests (see results).

Response Variable	DFNum	DFDen	F	p	alpha
<i>Transit Time</i>					
Density	2	34	12.97	< 0.0001	0.01
Habitat of Origin	1	17	0.003	0.93	0.05
Density × Habitat of Origin	2	34	1.61	0.21	0.01
<i>Time Stopped</i>					
Density	2	34	3.99	0.03	0.0167
Habitat of Origin	1	17	0.01	0.79	0.025
Density × Habitat of Origin	2	34	0.85	0.44	0.0167
<i>Average Velocity</i>					
Density	2	34	11.22	0.0002	0.0125
Habitat of Origin	1	17	0.02	0.89	0.0167
Density × Habitat of Origin	2	34	0.63	0.54	0.025
<i>Maximum Velocity</i>					
Density	2	34	0.33	0.72	0.05
Habitat of Origin	1	17	0.26	0.62	0.01
Density × Habitat of Origin	2	34	0.98	0.39	0.0125
<i>Motivation</i>					
Density	2	34	3.94	0.029	0.025
Habitat of Origin	1	17	0.03	0.97	0.0125
Density × Habitat of Origin	2	34	0.07	0.93	0.05

Table 9: Field versus lab running trials significance tests: the effects of field versus lab trials, Veldt grass density (0%, 20% or 40%) and habitat of origin (Veldt versus non-Veldt) and their interactions on running performance variables of the nineteen animals who were tested in both lab and field. Response variables include transit time, time spent stopped, average and maximum velocity, and amount of motivation required. DFNum is the degrees of freedom in the numerator, which reflects the number of treatments. DFDen is the degrees of freedom in the denominator, which reflects sample size. F and p values are from mixed model GLM with animal ID as a random effect. Significance was judged after Bonferroni correction for multiple tests (see results).

Response Variable	DFNum	DFDen	F	p	alpha
<i>Transit Time</i>					
Field/Lab	1	88.9	4.28	0.04	0.0125
Density	2	86.73	18.15	< 0.0001	0.0125
Habitat of Origin	1	18.97	4.06	0.06	0.01
Density × Habitat of Origin	2	86.73	0.87	0.42	0.0167
Field/Lab × Habitat of Origin	1	87.7	5.25	0.024	0.0125
Field/Lab × Density	2	86.73	0.116	0.89	0.0167
<i>Time Stopped</i>					
Field/Lab	1	88.65	3.53	0.063	0.0167
Density	2	86.45	2.66	0.076	0.25
Habitat of Origin	1	18.57	0.5	0.49	0.05
Density × Habitat of Origin	2	86.45	0.17	0.84	0.025
Field/Lab × Habitat of Origin	1	87.43	1.96	0.165	0.025
Field/Lab × Density	2	86.45	0.13	0.88	0.0125
<i>Average Velocity</i>					
Field/Lab	1	87.3	18.48	< 0.0001	0.01
Density	2	85.44	17.54	< 0.0001	0.0125
Habitat of Origin	1	18.44	3.12	0.094	0.0125
Density × Habitat of Origin	2	85.44	1.28	0.28	0.0125
Field/Lab × Habitat of Origin	1	86.65	3.6	0.061	0.0167
Field/Lab × Density	2	85.49	0.11	0.89	0.0167
<i>Maximum Velocity</i>					
Field/Lab	1	87.75	0.36	0.55	0.025
Density	2	86	0.41	0.67	0.05
Habitat of Origin	1	18.18	2.3	0.15	0.0167

Density × Habitat of Origin	2	86	1.57	0.21	0.01
Field/Lab × Habitat of Origin	1	87.1	0.003	0.96	0.05
Field/Lab × Density	2	86.08	0.04	0.96	0.05
<i>Motivation</i>					
Field/Lab	1	88.59	0.006	0.94	0.05
Density	2	86.41	7.04	0.0015	0.0167
Habitat of Origin	1	18.72	2	0.17	0.025
Density × Habitat of Origin	2	86.41	0.047	0.95	0.05
Field/Lab × Habitat of Origin	1	87.38	5.29	0.024	0.0125
Field/Lab × Density	2	86.41	0.69	0.5	0.01

Table 10: Captive cohorts' time in captivity significance tests: comparing the running performance of lab animals of “cohort 1,” or animals who had spent between 2-7 weeks in captivity before running trials, and “cohort 2,” animals who had spent between 10-17 weeks in captivity before running trials. Time in captivity was not a significant indicator of running performance across all response variables. Significance was judged after Bonferroni correction for multiple tests (see results).

	DFNum	DFDen	F	p	alpha
Transit Time	1	14	1.54	0.23	0.01
Time Stopped	1	14	1.3	0.27	0.0125
Motivation	1	14	0.2	0.66	0.05
Average Velocity	1	14	0.24	0.63	0.025
Maximum Velocity	1	14	0.31	0.59	0.0167

Table 11: Habitat use significance tests: the effects of Veldt grass density (0%, 20% or 40%), habitat of origin (Veldt versus non-Veldt), and night (one or two), on the response variables total time spent in a grass density runway, latency time from first leaving nest jar to first visit to a seed pan in a grass density runway, and amount of seed remaining in a seed pan in each grass density runway, when seed remained. Because of limited sample size, only the effects of grass density were assessed for amount of seed remaining. DFNum represents the degrees of freedom in the numerator, which reflects the number of treatments. DFDen represents the degrees of freedom in the denominator, which reflects sample size. F and p values are from mixed model GLM with animal ID as a random effect. Significance was judged after Bonferroni correction for multiple tests (see results).

Response Variable	DFNum	DFDen	F	p	alpha
<i>Total Time Spent</i>					
Density	2	93.74	13.06	< 0.0001	0.025
Habitat of Origin	1	17.82	0.016	0.9	0.05
Night	1	96.13	6.45	0.0127	0.025
<i>Latency Time to Seed Pans</i>					
Density	2	94.37	0.58	0.56	0.025
Habitat of Origin	1	18.51	0.04	0.84	0.025
Night	1	96.57	1.33	0.25	0.05
<i>Seed Remaining</i>					
Density	2	25.49	0.86	0.44	0.05

Appendix B: Figures

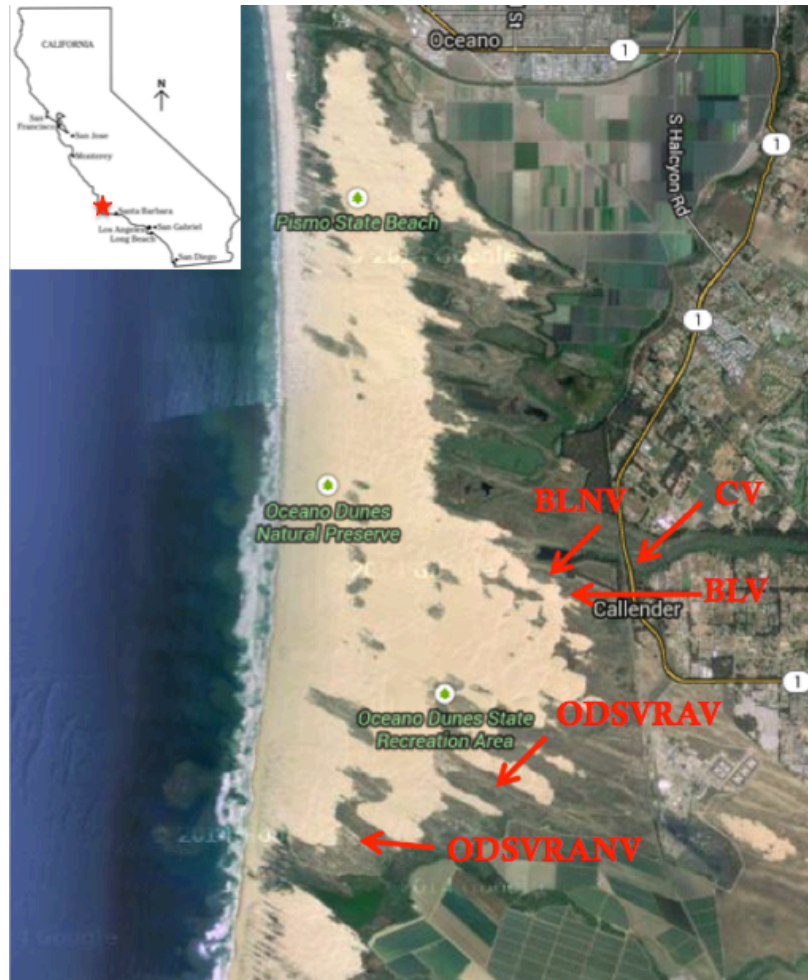


Figure 1: Field sites used for field running trials and collection of animals for captive trials. Field sites were located just east of the Oceano Dunes in San Luis Obispo County, and were chosen for their evidence of kangaroo rat activity and presence or absence of Veldt grass. Black Lake Non-Veldt (BLNV), Black Lake Veldt (BLV) and Callender Veldt (CV) belong to San Luis Obispo Land Conservancy. Oceano Dunes State Vehicular Recreation Area Veldt (ODSVRAY) and Oceano Dunes State Vehicular Recreation Area Non-Veldt (ODSVRANV) belong to California State Parks.



Figure 2: A runway used for running trials in the field. Runways were 3 m × 60 cm and spray painted matte tan on the interior. Wooden holding and receiving boxes included wire mesh backing to simulate an escape route. Three runways were built side by side in an area cleared of all vegetation and templates were used for replicate placement of Veldt grass tussocks across runways. The plastic bristled brush used to scare the animals is also shown. Density shown is medium (20%).



Figure 3: Housing conditions of kangaroo rats in the lab.

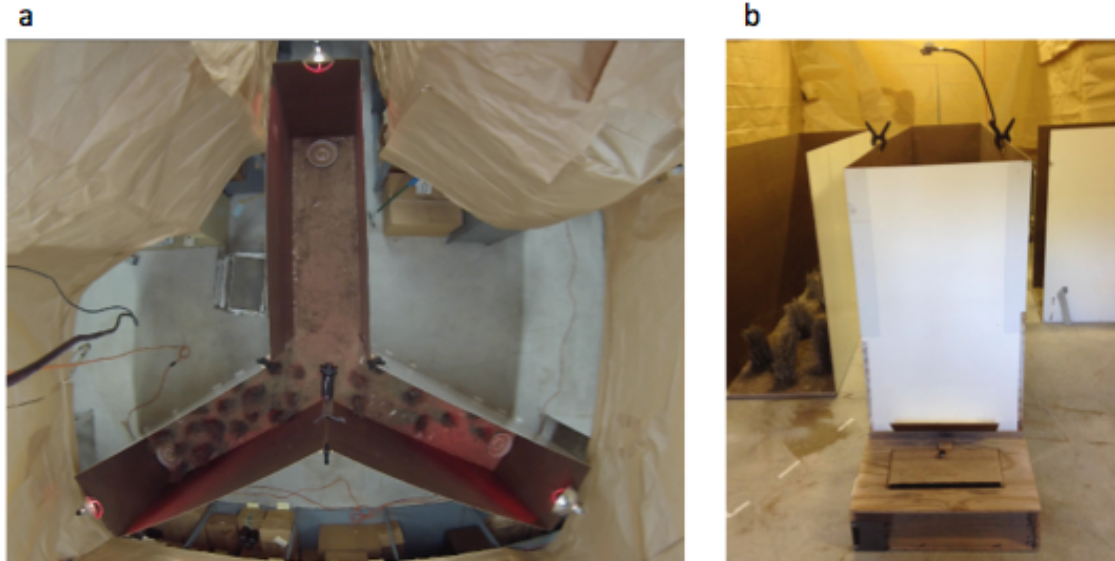
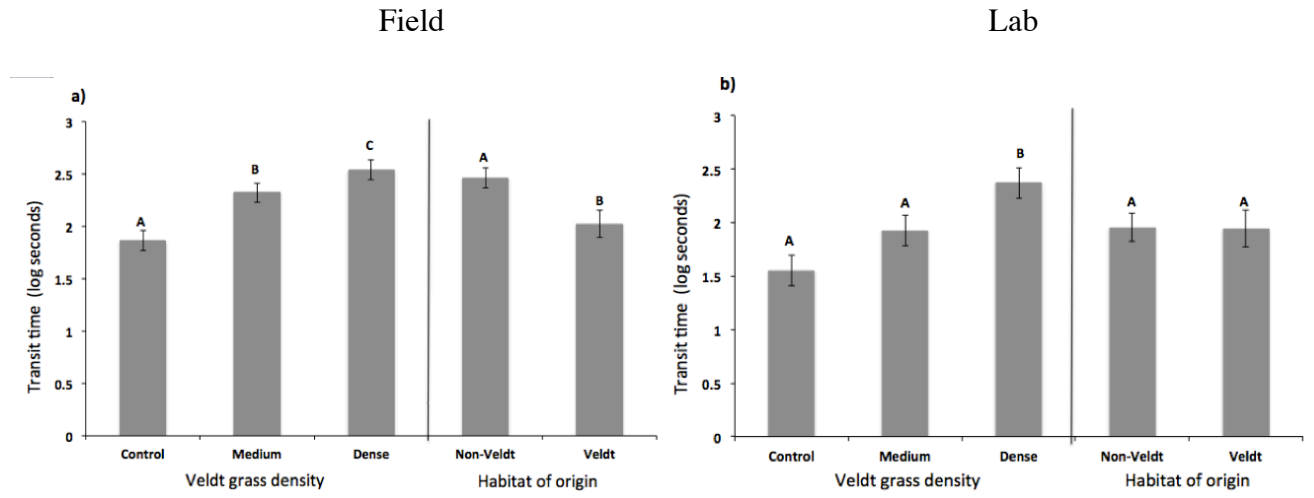
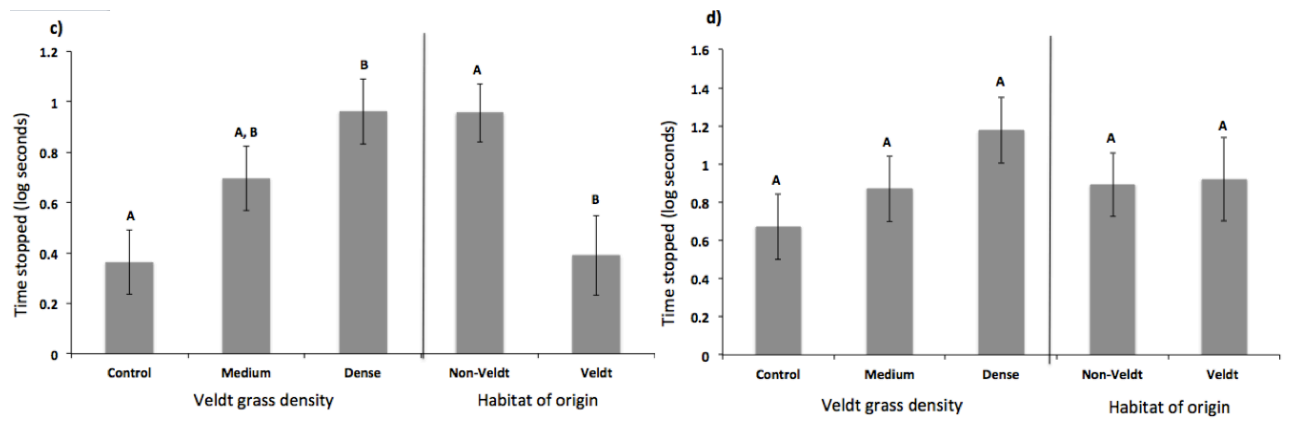


Figure 4: Laboratory trials set-up. a) Lab arena for monitoring habitat use as seen from the video camera mounted above the arena. A nest jar was positioned in the center area of the Y, fitted with a PVC pipe triple-pronged exit that allowed a kangaroo rat to see all arms simultaneously from inside the exit portal. Seed pans with equal amount of seed and lettuce were positioned at the end of each arm. b) After two nights, arms were disassembled into the control, medium and dense Veldt density runways for lab based (post habitat use/familiarization) running trials.

Transit Time



Time Stopped



Average Velocity

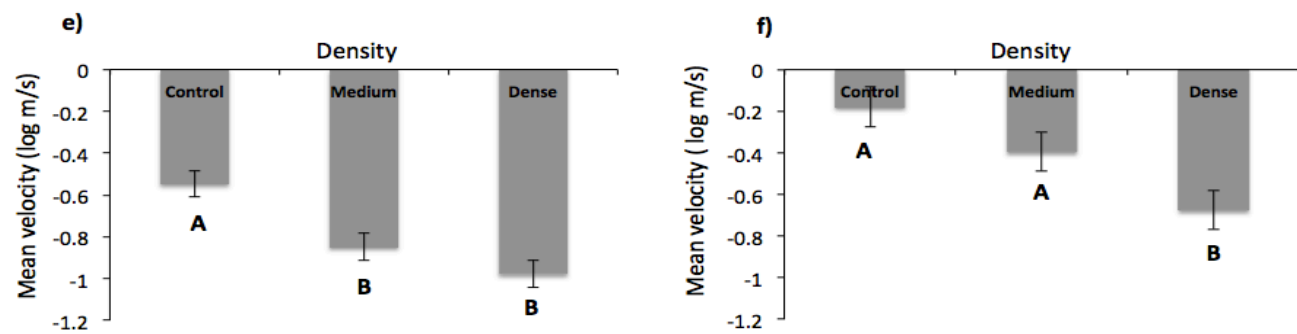


Figure 5: Running performance response variables of *D. h. arenae* as a function of habitat of origin and grass density for main effects that were significant in field and lab running trials. (a) Transit time was significantly affected by both grass density and habitat of origin in the field. (b) Transit time was significantly affected by grass density (only the dense treatment), but not habitat of origin, in the lab. (c) Time spent stopped was significantly affected by both grass density and habitat of origin in the field. (d) Time spent stopped was no longer affected by grass density or habitat of origin in the lab. (e) Average velocity was significantly lower in the medium and dense treatments than the control in the field. (f) Average velocity was significantly lower only in the dense treatment in lab. One can note the general correlation of decreasing performance with increasing grass density, as well as amelioration of the decreased performance in lab trials compared to field, or in a familiar habitat patch compared to a novel one. Log transformed data are shown because they satisfy normality and therefore confidence intervals are graphically meaningful. Average velocities are negative because they are log transformed and all values were originally less than one. Means not sharing the same letter are significantly different from each other (Tukey's HSD, $P < 0.05$).

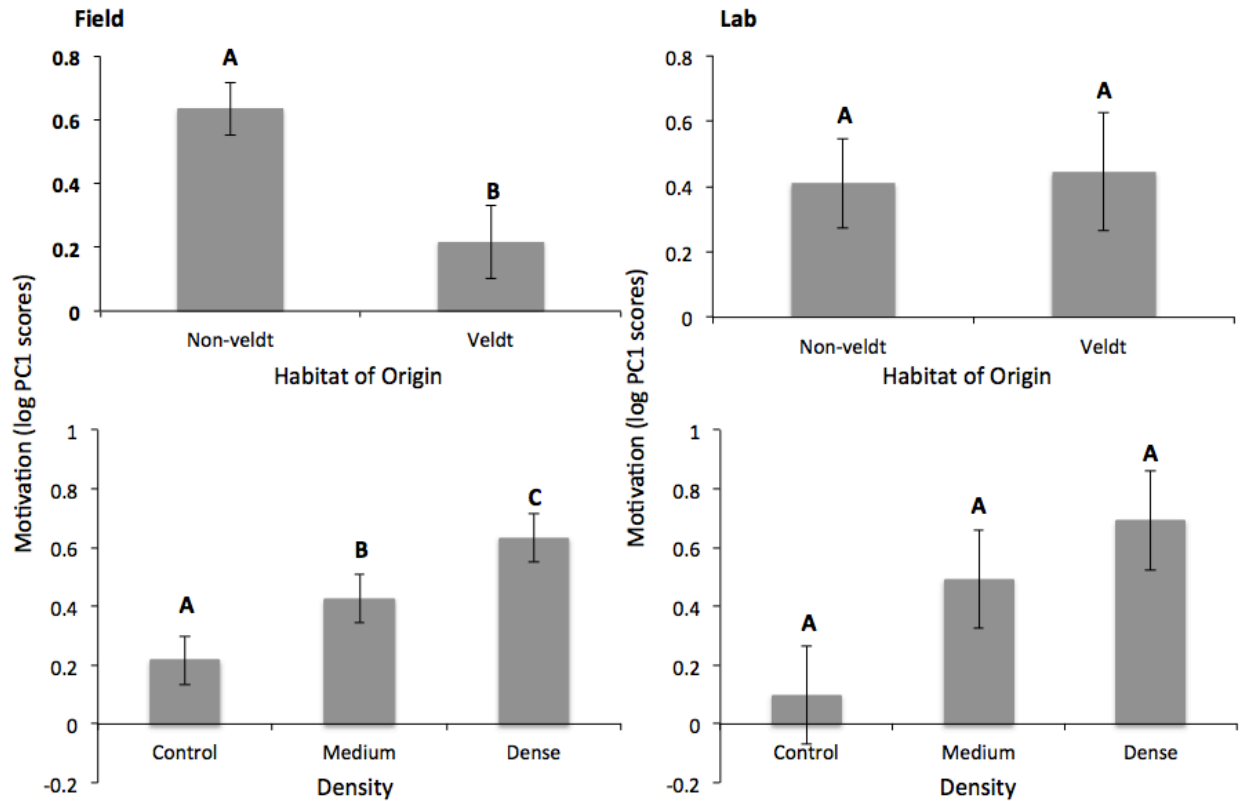
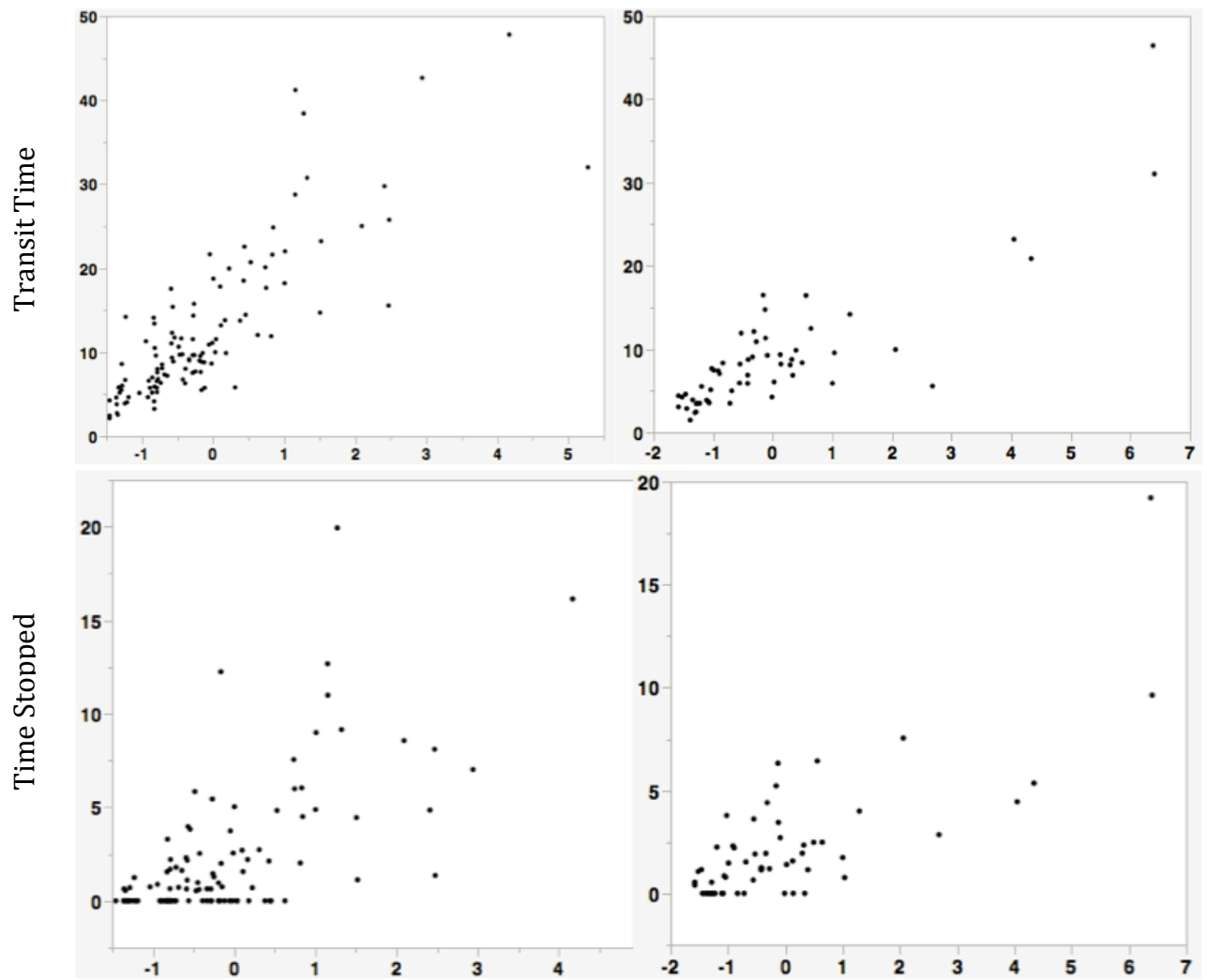


Figure 6: The effects of grass density and habitat of origin on composite motivation variable. Principle component 1 (PC1) scores represent the magnitude of composite scare tactic the animals were given to start and/or continue running, and come from a principle component analysis of the five scare tactics used to scare the animal. The first principle component fit most of the variance across the five tactics included in the analysis, combined. Scores along this component's axis were tested for significant differences across grass density treatments, and habitat of origins. The amount of composite scare tactic (PC1 score) was found to be significantly affected by both habitat of origin and grass density in the field, but not in lab. Grass density still shows a considerable trend, however it loses significance in post hoc corrections for multiple tests. Log transformed PC1 scores are shown so as to provide graphically meaningful confidence intervals. Means not sharing the same letter are significantly different (Tukey's HSD, $P < 0.05$).

Field

Lab



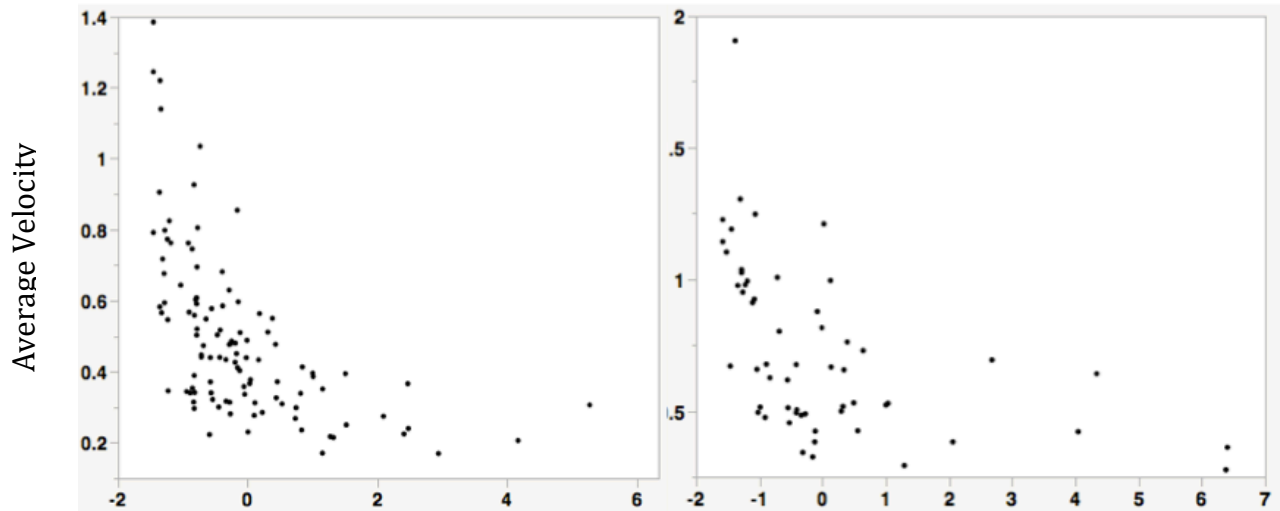


Figure 7: Correlations between running performance response variables and amount of combined motivation tactics employed. Principal component 1 (PC1) scores represent the magnitude of composite scare tactic the kangaroo rats needed to start and/or continue running, and come from a principle component analysis of the five scare tactics we used to scare the animal. The first principle component fit most of the variance across the five tactics included in the analysis, combined. Correlations confirm that the longer a kangaroo rat took to cross the runway (Field: $Rsq=0.686$, $p<.0001$; Lab: $Rsq=0.739$, $p<.0001$), the more time it spent stopped (Field: $Rsq=0.418$, $p<.0001$; Lab: $Rsq=0.599$, $p<.0001$), and the slower its average velocity (Field: $Rsq=0.313$, $p<.0001$; Lab: $Rsq=0.239$, $p<.0001$), the more we had to scare it. Therefore, kangaroo rat performance was not a function of the amount of motivation given, but the amount of motivation given was a function of its performance.

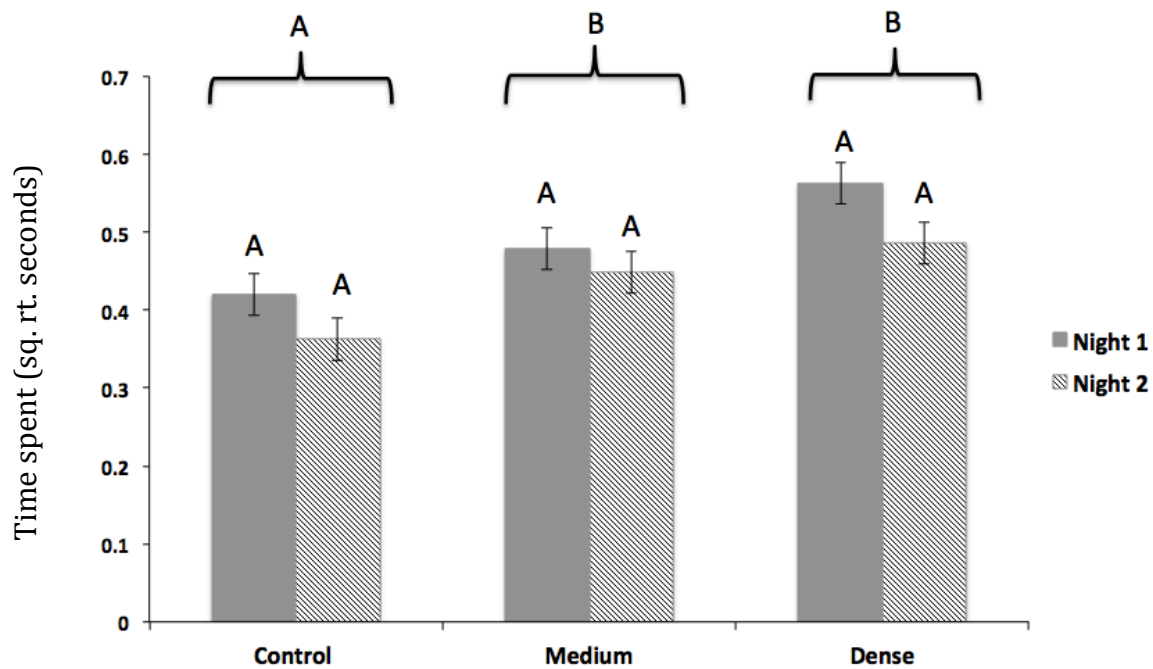


Figure 8: Time spent in grass density treatments during the two-night familiarization period in the lab. Kangaroo rats spent significantly more time in medium and dense treatments than the control. Though not significantly different within each density between night 1 and night 2, when all three densities are pooled they spent more time out of their nest jar during night 1 than night 2 (not shown). Square root transformed data are shown so as to include graphically meaningful confidence intervals. Means not sharing the same letter are significantly different (Tukey HSD, $p < 0.05$).