

DESERT HORNED LIZARD (*PHRYNOSOMA PLATYRHINOS*)  
LOCOMOTOR PERFORMANCE: THE INFLUENCE OF CHEATGRASS  
(*BROMUS TECTORUM*)

T. A. SCOTT NEWBOLD\*

*Department of Biology and the Ecology Center, Utah State University, Logan, UT 84322*

*\*Correspondent: scott@biology.usu.edu*

**ABSTRACT**—Vegetation plays a critical role in lizard activities such as thermoregulation. Less understood is the influence of vegetation structure on lizard mobility. This study examined the influence of cheatgrass (*Bromus tectorum*) patches on: 1) distribution patterns of the desert horned lizard (*Phrynosoma platyrhinos*) using transect surveys along an elevational gradient, and 2) sprint performance of adult and juvenile *P. platyrhinos* using raceways established under field conditions. There was a significant negative association between cheatgrass cover and lizard scat abundance across the study gradient, suggesting horned lizards might avoid areas with higher cheatgrass cover. Adult and juvenile sprint performance were reduced on grass raceways by 50 to 70% of their bare-substrate speeds; adult speeds decreased from 0.93 m/s on bare substrate to 0.26 m/s on grass, and juvenile speeds decreased from 0.41 to 0.11 m/s. The findings were consistent based on 2 independent measures of velocity (burst and sustained). These results demonstrate the negative effect of cheatgrass on horned lizard mobility and highlight the potential consequences of cheatgrass invasion on patterns of local *Phrynosoma* distribution in western North America.

**RESUMEN**—La vegetación juega un papel importante en las actividades de los lagartos, tales como en la termorregulación. Menos entendido es el efecto que tiene la estructura de la vegetación sobre la movilidad del lagarto. Este estudio examina la influencia de parches del pasto *Bromus tectorum* en: 1) patrones de distribución del camaleón del desierto (*Phrynosoma platyrhinos*) usando observaciones de transectos a lo largo de una pendiente, y 2) la capacidad de correr de adultos y de juveniles de *P. platyrhinos*, utilizando pistas de carrera establecidas bajo condiciones de campo. Hubo una relación significativa inversa entre la cubierta del pasto y la abundancia de heces de lagartos sobre la pendiente estudiada, sugiriendo que los camaleones del desierto evaden áreas de más pasto. La capacidad de correr de adultos y de juveniles se redujo sobre las pistas de pasto entre un 50 y 70% al compararse con las velocidades sobre el substrato sin pasto; la velocidad de los adultos bajó de 0.93 m/s sobre el substrato sin pasto hasta 0.26 m/s sobre el substrato con pasto, y la velocidad de los juveniles se redujo de 0.41 hasta 0.11 m/s. Los resultados fueron consistentes basados en dos medidas independientes de velocidad (la velocidad en una distancia corta y la velocidad sostenida). Estos resultados demuestran el efecto negativo del pasto *B. tectorum* sobre la capacidad locomotora del camaleón del desierto, y subraya las consecuencias posibles de la invasión del tal pasto en patrones de distribución local de *Phrynosoma* en el oeste de Norteamérica.

Lizard fitness is determined by numerous interacting factors and processes, of which mobility is likely a critical component (Arnold, 1983; Garland and Losos, 1994; Irschick and Garland, 2001). Foraging, thermoregulation, and predator avoidance require that lizards move through their environment efficiently and, in the case of avoiding predators, rapidly. Impediments to locomotor performance might influence the efficiency of some or all

of these behaviors, with consequences for survival, growth, and reproduction. Linking factors that alter individual performance (e.g., vegetation cover) with their broader consequences (e.g., presence-absence of lizards), might improve our understanding of critical habitat requirements and patterns of local distribution (Dunham et al., 1989; Murphy and Weiss, 1992).

The effects of morphology (Garland, 1985;

Bonine and Garland, 1999), physiology (Martin, 1996), and behavior (Robson and Miles, 2000) on lizard locomotor performance are well documented. Although the role of environmental conditions on performance has received attention (Bennett, 1980; Huey and Hertz, 1982; Miles, 1994; Bonine and Garland, 1999), few studies addressed the influence of habitat structure on performance (Jayne and Irschick, 2000), and most examined arboreal species and plant stem diameter (Pounds, 1988; Losos and Sinervo, 1989). Though Jayne and Irschick (2000) observed slower lizard movement associated with terrestrial vegetation cover, they suggested that the pattern might be explained by behavioral thermoregulation activities (e.g., shade-seeking beneath cover objects), rather than the impediment of vegetation. Thus, the effects of plant structure on lizard mobility remain relatively unknown.

Desert horned lizards (*Phrynosoma platyrhinos*) occur in valley and lower slope shadscale (*Atriplex confertifolia*) and sagebrush-steppe (*Artemisia tridentata*) communities from southeastern Oregon and southwestern Idaho to northern Mexico (Stebbins, 2003). Horned lizards are diurnal sit-and-wait predators that feed primarily on ants and burrow to escape extreme thermal conditions (Heath, 1965; Pianka and Parker, 1975). Horned lizards are dorsoventrally flattened and rely primarily on crypsis and spines to avoid predators, but also use rapid flight as an escape tactic when predators approach too closely (Manaster, 1997).

Cheatgrass (*Bromus tectorum*) is an introduced annual grass that invaded and currently dominates many shrub-steppe ecosystems in the western United States (Mack, 1981; Novak and Mack, 2001). Cheatgrass often occurs in large, dense, continuous patches and occupies both intershrub and below-shrub spaces (Kerrick, 1991). While the effects of this invasion on native vegetation are relatively well understood (Melgoza et al., 1990; Knapp, 1996; Evans et al., 2001), little is known about its influence on small vertebrates.

In my study system, *P. platyrhinos* seemed to avoid areas occupied by dense cheatgrass. Other researchers reported similar observations and suggested that dense vegetation might restrict lizard mobility (Pianka and Parker, 1975; Whiting et al., 1993; Burrow et al., 2001). Here, I attempt to substantiate these observa-

tions by quantifying the association between lizards and cheatgrass across an elevational transect. I then examine whether grass avoidance might be attributed to reduced sprint ability using raceways established under field conditions. Specifically, I compared lizard sprint performance under 2 conditions: presence and absence of cheatgrass.

**METHODS—Lizard and Cheatgrass Surveys**—This study was conducted in the eastern region of the Great Basin desert at the southern end of the Grouse Creek Mountains in Box Elder County, Utah (T9N, R16W, Sec. 25). In 2001, in conjunction with a larger study assessing habitat associations of horned lizards, 80 circular study plots (315 m<sup>2</sup>) were established along an elevational gradient (1,270 to 1,550 m), which spans the endpoints of the local distribution of *P. platyrhinos*. Plots were distributed across 4 soil types at 200-m intervals along an 11-km transect. All plots were systematically searched for horned lizard fecal pellets (hereafter referred to as "scat") during 2 surveys in May and July 2001. Scat counts were combined for the surveys and used as an index of overall lizard use on plots. Percent grass cover on each plot was determined using the average grass cover visually estimated at 10 randomly chosen points using a 50 cm by 20 cm frame (Daubenmire, 1959). To account for the possibility that scats were more difficult to see in cheatgrass, 3 independent scat surveys were conducted and 10 plots were rechecked for missed scats as a quality control measure; no scats were found during recheck surveys.

**Locomotor Performance**—Twenty-one adult (mass = 19.5 ± 2.9 g, 15.5 to 27.0 g; snout-vent length (SVL) = 77.6 ± 2.9 mm, 74 to 84 mm; all measurements are means ± 1 SD, and range) and 5 juvenile (mass = 10.5 ± 4.2 g, 7.5 to 12 g; SVL = 62.6 ± 1.8 mm, 56 to 67 mm) *P. platyrhinos* were collected on 4 and 5 June 2002 in a shadscale-sagebrush mixed shrub community approximately 10 km northeast of Lucin, Box Elder County, Utah. Lizards <13.0 g were considered juveniles after Rissing (1981). Lizards were maintained in 5-gallon buckets filled approximately 10 cm deep with sand for no more than 12 h during sprint performance trials. On the day of capture, the sex of each individual was determined and body mass, SVL, and tail length were measured.

The influence of cheatgrass on running speed was assessed using 2 raceways (200 cm long × 20 cm wide × 25 cm high) established within 1 m of each other in a sandy, cheatgrass-dominated area. To provide sideboards for each raceway, Masonite wood strips (200 cm long × 30 cm high) were buried to a depth of 5 cm and held in place with 30-cm nails. The raceways were arranged in a north-south ori-

entation so that the substrate within the raceways received full sun at midday. All cheatgrass stems and roots were removed within one of the raceways (absence of cheatgrass condition = “no-grass”) by hand pulling. An effort was made to disturb the surface soil as little as possible. The second raceway was unaltered, serving as the presence of cheatgrass condition (“grass”). After 10 trials, the grass raceway was moved and re-established 1 m east to minimize effects of trampling due to repeated lizard use of the raceway. When sequential trials were analyzed for both grass raceways, there were no effects of trampling on performance with increased use.

Two measures of sprint performance were recorded on each raceway: 1) burst velocity (“burst”) and 2) velocity over the length of the 2-m raceway (“sustained”). Burst velocity was calculated using the distance and time recorded from the time the animal left the starting line to the first time it stopped, regardless of how far it traveled. Sustained velocity was the time required for the lizard to move the entire distance of the raceway while being prodded from behind using a meter-stick (Bennett, 1980). All times were recorded by the same observer using a stopwatch while standing approximately 1 m away from the raceways. A second observer released and captured lizards during each trial. I used a paired sample design so that each animal was tested on each raceway and its performance between grass and no-grass raceways compared. Each lizard was randomly assigned to a raceway, burst speed data were collected, and then the lizard was tested for burst speed on the other raceway. This procedure was repeated for sustained velocity immediately after the burst velocity trials were completed. These 2 measures of velocity are commonly used in sprint performance studies (e.g., Bennett, 1980; Downes and Shine, 2001) and might provide more robust results when combined than either measure alone. All trials took place between 1200 h and 1430 h on 4 and 5 June 2002 and air temperature was recorded at the beginning of each trial 15 cm above a denuded soil area between the raceways. I tested 21 adults and 5 juveniles; each individual was tested only once on 1 of the 2 trial days (4 June:  $n = 10$  adults and 2 juveniles; 5 June:  $n = 11$  adults and 3 juveniles).

**Statistical Analyses**—Significant association between lizard scat abundance and cheatgrass cover along the 11-km transect was determined using the Pearson correlation coefficient. Differences in locomotor performance, comparing grass and no-grass trials, were evaluated with a 2-tailed, paired sample  $t$  test for each sprint measure (burst and sustained). Because the trials were conducted on 2 subsequent days, I compared mean sprint velocity on the no-grass raceway between the 2 dates to determine whether there was an effect on velocity due to trial date. Finally, I examined the influence of body size

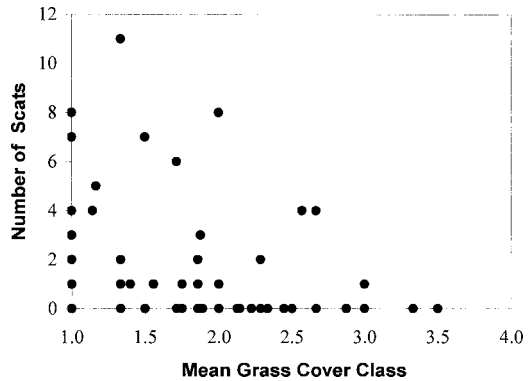


FIG. 1—Number of desert horned lizard (*Phrynosoma platyrhinos*) scats collected versus mean grass-cover class on 80 study plots in Utah. Grass-cover class scale: 1 = 1 to 5%, 2 = 5 to 25%, 3 = 25 to 50%, 4 = 50 to 75%. Data points represent the mean of 10 samples per plot for grass cover and the total number of scats from 2 systematic scat surveys per plot.

(SVL and mass) on velocity using simple linear regression.

**RESULTS**—There was a significant negative association between cheatgrass cover and lizard scat abundance across the study area ( $r = -0.28$ ,  $P = 0.01$ ,  $n = 80$ ) (Fig. 1). For the performance trials, the differences in sprint velocity for both adults and juveniles were normally distributed. Though mean air temperature did vary between the 2 trial days (day 1, mean = 42°C; day 2, mean = 34°C), this temperature difference did not significantly affect mean adult locomotor performance on bare substrate (burst,  $P = 0.85$ ; sustained,  $P = 0.25$ ), and therefore the sprint trial data from the 2 dates were pooled ( $n = 21$  adults;  $n = 5$  juveniles). Furthermore, although variation in body temperature can influence horned lizard sprint performance (Bonine and Garland, 1999), the paired performance results for each individual were likely unaffected by this temperature difference due to the paired sample design.

Adult burst and sustained velocities were reduced in the grass raceway (Fig. 2a), and the difference in velocity between raceways was significant (burst,  $P < 0.0001$ ; sustained,  $P < 0.0001$ ) (Fig. 3a). Cheatgrass also reduced sprint performance in juvenile trials (Fig. 2b), but because of higher variance associated with

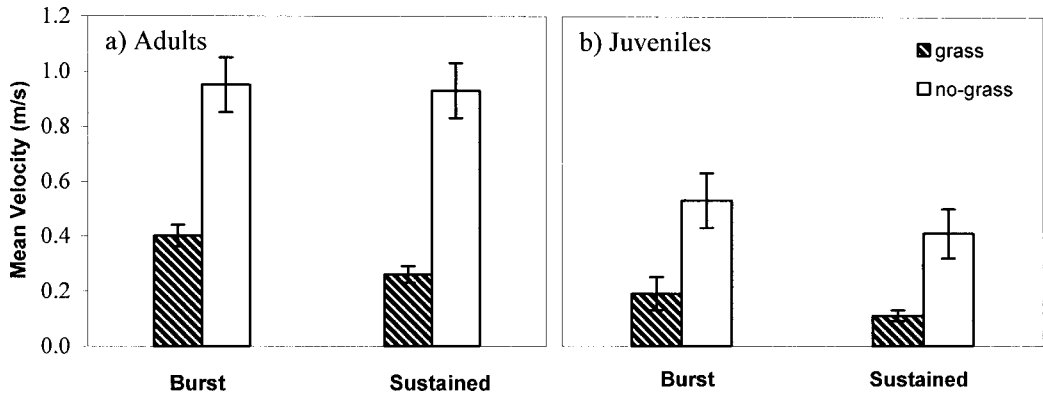


FIG. 2—Mean burst and sustained sprint speeds (m/s  $\pm$  SE) for (a) 21 adult and (b) 5 juvenile desert horned lizards (*Phrynosoma platyrhinos*) in grass (striped bars) and no-grass (light bars) raceways in Utah.

the small sample size in juvenile trials, the difference between raceways was not as pronounced (burst,  $P = 0.04$ ; sustained,  $P = 0.02$ ) (Fig. 3b). When compared to adult performance, juveniles sprinted at approximately half the rate of adults for all mean velocity comparisons (raceway and sprint measure) (Fig. 2). The 2 sprint measures (burst and sustained) revealed similar patterns for both adult and juvenile performance, though mean burst velocities were slightly higher than sustained velocities (Fig. 2). Finally, there was a significant negative relationship between adult male SVL and sustained velocity on the no-grass raceway ( $R^2 = 0.53$ ,  $P = 0.005$ ,  $n = 13$ ); however, this relationship did not affect performance results because morphological and

sprint differences between individuals were accounted for using the paired sample design. There were no significant associations between body size (SVL or mass) and sprint velocity for any other comparison (raceway, sprint measure, sex, or age class).

**DISCUSSION**—Desert horned lizards were less likely to occur in areas dominated by cheatgrass at the study site, suggesting that lizards might actively avoid areas with high cheatgrass cover. Cheatgrass reduced adult and juvenile horned lizard sprint performance by more than half of their bare substrate speeds. In the case of sustained velocity measurements, adults were as much as 70% slower on the cheatgrass raceway, with a decline in average velocity from

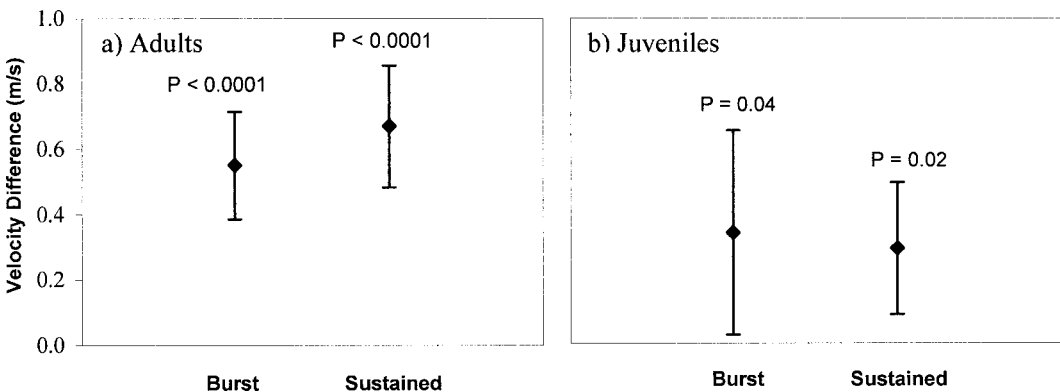


FIG. 3—Mean differences between grass and no-grass raceways in burst and sustained sprint speeds (m/s  $\pm$  95% confidence intervals) for (a) 21 adult and (b) 5 juvenile desert horned lizards (*Phrynosoma platyrhinos*) in Utah.  $P$ -values illustrate the results of paired  $t$ -tests comparing the mean sprint speed difference between raceways to zero.

0.93 m/s in the no-grass raceway to 0.26 m/s in grass. The reduction in sprint performance due to cheatgrass was greater for adults than juveniles, perhaps indicating a more adverse effect on adult mobility because of their wider bodies. The wider body of horned lizards might be more restricted by cheatgrass than lizards that are more cylindrical in cross section (e.g., western whiptail, *Cnemidophorus tigris*). Horned lizards observed fleeing from approaching humans in areas of dense cheatgrass at the study site moved with increased lateral movements as they “weaved” through grass stems, often resulting in a non-linear path. This weaving pattern seemed more erratic and less linear than typical horned lizard locomotion and often resulted in slower movement, especially when lizards crawled over matted or tangled cheatgrass stems (pers. obser.).

Reduced sprint ability has been associated with increased vulnerability to predation (Wassersug and Sperry, 1977; Downes and Shine, 2001; but see Schwarzkopf and Shine, 1992). Although horned lizards rely primarily on crypsis to avoid predator detection, they resort to rapid flight when they perceive immediate danger. Reduced mobility during this critical moment of escape might affect the outcome of predation attempts. Other studies provide support for the link between impaired locomotor performance and increased predation risk for cryptic species, especially those that flee from an approaching predator at the last moment (Martin, 1996). Predation on horned lizards is reasonably well documented (Pianka and Parker, 1975; Duncan et al., 1994; Turner and Rorabaugh, 1998). In a study of predation rates on *P. cornutum* and *P. modestum*, Munger (1986) found that both species suffered significant predation by avian and mammalian predators. While only 2 of the approximately 300 lizards encountered had missing limbs during 3 summers of research at my study site, predation pressure might provide a stress on horned lizards that is compounded in areas of high cheatgrass density.

Reduced mobility also might have direct consequences on foraging success (e.g., number of ant mounds visited per foraging time), though performance in this study was only evaluated for stressed or high-speed movements, and it is unknown whether lizard movement at slower speeds would be affected simi-

larly. *Phrynosoma platyrhinos* move long distances, as much as 230 m/day (Tanner and Krogh, 1973; Pianka and Parker, 1975), but their foraging range might be more restricted or limited when occupying high-density cheatgrass areas. Lizards also might be affected indirectly via changes in prey availability if cheatgrass-dominated areas support different ant assemblages.

Animals occupy habitat based on a set of interrelated requirements (e.g., reproductive sites, forage availability, optimal thermal conditions). If individual requirements or combinations of requirements are not met in certain habitat types, animals will be less likely or unable to persist in such habitats. Most studies of the influence of vegetation structure on distribution patterns of ectotherms have employed a biophysical approach (Porter and Gates, 1969; Tracy, 1976; Dunham et al., 1989; Porter et al., 2002), evaluating changes in the thermal environment of animals due to changes in the physical architecture of vegetation (Miles, 1994). But the physical structure itself also has non-thermal effects on animals (Hatley and MacMahon, 1980; Parmenter and MacMahon, 1983), as shown in this study. Shrub and grass densities alter the amount and patterns of bare substrate available to horned lizards and might impose limits on where lizards occur.

The invasion and dominance of alien grasses is a major conservation concern. The problem might be compounded in western North America where fire and grazing are common and can promote the spread of exotics (D’Antonio and Vitousek, 1992; Fleischner, 1994). Altered soil properties (e.g., soil moisture and temperature, nutrient cycling) and exclusion of native plants are well known consequences of cheatgrass dominance (Walker and Smith, 1997). Change in habitat structure due to invasion and proliferation of grasses might be one pathway by which animals are likely to be affected by cheatgrass. Results from this study suggest that cheatgrass reduces desert horned lizard sprint performance and influences local patterns of abundance and distribution at this study site. These findings highlight the potential negative consequences that cheatgrass invasion in western North America might have on some small vertebrate populations.

Many people contributed to the development and synthesis of this project. Foremost, J. MacMahon and E. Brodie, Jr. were instrumental in the planning and design phases of this study. E. Evans, G. Belovsky, and J. Mendelson also contributed invaluable ideas that enhanced the study methods. I would especially like to thank B. Sessions for his help with the sprint performance trials, and J. Hunt for assistance with the vegetation survey data. J. Mendelson, J. Rieder, N. Welch, and especially J. MacMahon, along with 2 anonymous reviewers, provided thoughtful reviews that have improved this manuscript. S. Durham and N. Welch provided helpful suggestions regarding analyses. G. Simonds kindly permitted access to the land he manages, and the Utah Division of Wildlife Resources graciously provided use of a cabin during the study. U. Linkogli translated the abstract into Spanish. Financial support was provided by a Graduate Student Fellowship from the Utah State University Ecology Center, a Datus Hammond Scholarship from the Utah State University Biology Department, and the Theodore Roosevelt Memorial Fund of the American Museum of Natural History.

#### LITERATURE CITED

- ARNOLD, S. J. 1983. Morphology, performance and fitness. *American Zoologist* 23:347–361.
- BENNETT, A. F. 1980. The thermal dependence of lizard behaviour. *Animal Behavior* 28:752–762.
- BONINE, K. E., AND T. GARLAND, JR. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *Journal of the Zoological Society of London* 248:255–265.
- BURROW, A. L., R. T. KAZMAIER, E. C. HELLGREN, AND D. C. RUTHVEN, III. 2001. Microhabitat selection by Texas horned lizards in southern Texas. *Journal of Wildlife Management* 65:645–652.
- D'ANTONIO, C. M., AND P. M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- DAUBENMIRE, R. F. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43–64.
- DOWNES, S. J., AND R. SHINE. 2001. Why does tail loss increase a lizard's later vulnerability to snake predators? *Ecology* 82:1293–1303.
- DUNCAN, R. B., T. C. ESQUE, AND K. L. ECHOLS. 1994. *Phrynosoma mcallii* (flat-tailed horned lizard). Predation. *Herpetological Review* 25:68.
- DUNHAM, A. E., B. W. GRANT, AND K. L. OVERALL. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiological Zoology* 62:335–355.
- EVANS, R. D., R. RIMER, L. SPERRY, AND J. BELNAP. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* 11:1301–1310.
- FLEISCHNER, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8:629–644.
- GARLAND, T., JR. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *Journal of the Zoological Society of London* 207:425–439.
- GARLAND, T., JR., AND J. B. LOSOS. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: P. C. Wainwright and S. M. Reilly, editors. *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago, Illinois. Pp. 240–302.
- HATLEY, C. L., AND J. A. MACMAHON. 1980. Spider community organization: seasonal variation and the role of vegetation architecture. *Environmental Entomology* 9:632–639.
- HEATH, J. E. 1965. Temperature regulation and diurnal activity in horned lizards. University of California Publications in Zoology 64:97–136.
- HUEY, R. B., AND P. E. HERTZ. 1982. Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *Journal of Experimental Biology* 97:401–409.
- IRSCHICK, D. J., AND T. GARLAND, JR. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annual Review of Ecology and Systematics* 32:367–396.
- JAYNE, B. C., AND D. J. IRSCHICK. 2000. A field study of incline use and preferred speeds for the locomotion of lizards. *Ecology* 81:2969–2983.
- KELRICK, M. I. 1991. Factors affecting seeds in a sagebrush-steppe ecosystem and implications for the dispersion of an annual plant species, cheatgrass (*Bromus tectorum* L.). Unpublished Ph.D. dissertation, Utah State University, Logan.
- KNAPP, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert. *Global Environmental Change* 6:37–52.
- LOSOS, J. B., AND B. SINERVO. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *Journal of Experimental Biology* 145:23–30.
- MACK, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145–165.
- MANASTER, J. 1997. Horned lizards. University of Texas Press, Austin.
- MARTIN, J. 1996. Effects of recent feeding on locomotor performance of juvenile *Psammotromus al-girus* lizards. *Functional Ecology* 10:390–395.
- MELGOZA, G., R. S. NOWAK, AND R. J. TAUSCH. 1990. Soil water exploitation after fire: competition be-

- tween *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7–13.
- MILES, D. B. 1994. Population differentiation in locomotor performance and the potential response of a terrestrial organism to global environmental change. *American Zoologist* 34:422–436.
- MUNGER, J. C. 1986. Rate of death due to predation for two species of horned lizard, *Phrynosoma cornutum* and *P. modestum*. *Copeia* 1986:820–824.
- MURPHY, D. D., AND S. B. WEISS. 1992. Effects of climate change on biological diversity in western North America: species losses and mechanisms. In: R. L. Peters and T. E. Lovejoy, editors. *Global warming and biological diversity*. Yale University Press, New Haven, Connecticut. Pp. 355–368.
- NOVAK, S. J., AND R. N. MACK. 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (cheatgrass). *BioScience* 51:114–122.
- PARMENTER, R. R., AND J. A. MACMAHON. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. *Oecologia* 59:145–156.
- PIANKA, E. R., AND W. S. PARKER. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. *Copeia* 1975:141–162.
- PORTER, W. P., AND D. M. GATES. 1969. Thermodynamic equilibria of animals with environment. *Ecological Monographs* 39:227–244.
- PORTER, W. P., J. L. SABO, C. R. TRACY, O. J. REICHMAN, AND N. RAMANKUTTY. 2002. Physiology on a landscape scale: plant-animal interactions. *Integrative and Comparative Biology* 42:431–453.
- POUNDS, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. *Ecological Monographs* 58:299–320.
- RISSING, S. W. 1981. Prey preferences in the desert horned lizard: influence of prey foraging method and aggressive behavior. *Ecology* 62:1031–1040.
- ROBSON, M. A., AND D. B. MILES. 2000. Locomotor performance and dominance in male tree lizards, *Urosaurus ornatus*. *Functional Ecology* 14:338–344.
- SCHWARZKOPF, L., AND R. SHINE. 1992. Costs of reproduction in lizards: escape tactics and susceptibility to predation. *Behavioral Ecology and Sociobiology* 31:17–25.
- STEBBINS, R. C. 2003. *A field guide to western reptiles and amphibians*, third edition. Houghton Mifflin, Boston, Massachusetts.
- TANNER, W. W., AND J. E. KROGH. 1973. Ecology of *Phrynosoma platyrhinos* at the Nevada Test Site, Nye County, Nevada. *Herpetologica* 29:327–342.
- TRACY, C. R. 1976. A model of the dynamic exchanges of water and energy between a terrestrial amphibian and its environment. *Ecological Monographs* 46:293–326.
- TURNER, D. S., AND J. RORABAUGH. 1998. *Phrynosoma platyrhinos* (desert horned lizard). Predation. *Herpetological Review* 29:101.
- WALKER, L. R., AND S. D. SMITH. 1997. Impacts of invasive plants on community and ecosystem properties. In: J. O. Luken and J. W. Thieret, editors. *Assessment and management of plant invasions*. Springer-Verlag, New York. Pp. 69–86.
- WASSERSUG, R. J., AND D. G. SPERRY. 1977. The relationship of locomotion to differential predation on *Pseudacris triseriata* (Anura: Hylidae). *Ecology* 58:830–839.
- WHITING, M. J., J. R. DIXON, AND R. C. MURRAY. 1993. Spatial distribution of a population of Texas horned lizards (*Phrynosoma cornutum*: Phrynosomatidae) relative to habitat and prey. *Southwestern Naturalist* 38:150–154.

Submitted 31 October 2003. Accepted 4 March 2004.  
Associate Editor was Geoffrey C. Carpenter.