TURNER, R. M., AND D. E. BROWN. 1982. Sonoran Desertscrub. Desert Plants 4:181–222.

UNITED STATES FISH AND WILDLIFE SERVICE. 1994. Desert tortoise (Mojave population) recovery plan. United States Fish and Wildlife Service, Portland, Oregon.

VAN DEVENDER, T. R., R. S. FELGER, AND A. BÚRQUEZ M. 1997. Exotic plants in the Sonoran Desert region, Arizona and Sonora. In: Kelly, M., and E. Wagner, editors. Proceedings California Exotic Pest Plant Council Symposium 3:10–15.

VAUGHAN, S. L. 1984. Home range and habitat use of the desert tortoise (*Gopherus agassizii*) in the Picacho Mountains, Pinal County, Arizona. Unpublished M.S. thesis. Arizona State University, Tempe.

VIEIRA, E. M. 1999. Small mammal communities and fire in the Brazilian Cerrado. Journal of Zoology 249:75–81.

WHELAN, R. J. 1995. The ecology of fire. Cambridge Studies in Ecology, Cambridge University Press, New York.

WHYSONG, G. L., AND M. H. HEISLER. 1978. Nitrogen levels of soil and vegetation in the Upper Sonoran Desert as affected by fire. Proceedings of the First International Rangeland Congress, Society of Range Management, Denver, Colorado. Pp. 697–699.

WOODBURY, A. M., AND R. HARDY. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecological Monographs 18:145–200.

WRIGHT, H. A., AND A. W. BAILEY. 1982. Fire ecology: United States and Canada. John Wiley and Sons, New York.

ZIMMERMAN, L. C., M. P. O'CONNOR, S. J. BULOVA, J. R. SPOTILA, S. J. KEMP, AND C. J. SALICE. 1994. Thermal ecology of desert tortoises in the eastern Mojave Desert: seasonal patterns of operative and body temperatures, and microhabitat utilization. Herpetological Monograph 7:45–59.

Submitted 17 August 2001. Accepted 13 March 2002. Associate Editor was Geoffrey C. Carpenter.

NATURAL HISTORY OF THE TEXAS HORNED LIZARD, *PHRYNOSOMA CORNUTUM* (PHRYNOSOMATIDAE), IN SOUTHEASTERN COLORADO

CHAD E. MONTGOMERY* AND STEPHEN P. MACKESSY

Department of Biological Sciences, University of Northern Colorado, Greeley, CO 80639-0017 (CEM, SPM)
Present address of CEM: Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701
**Correspondent: cemontg@uark.edu*

ABSTRACT—Colorado Division of Wildlife currently considers the Texas horned lizard a species of special concern. From May 1995 to October 1997, Texas horned lizards were captured or collected during the active season from 6 counties in Colorado to document abundance and distribution of the species. We captured or collected 290 Texas horned lizards (170 alive and 120 dead on road). In Colorado, average snout-vent length (SVL) for adult males was not significantly different from females; the largest male and female lizards measured 84.9 mm SVL and 90.4 mm SVL, respectively. The sex ratio of adult males to adult females is 1M:1.4F. Results of distribution and habitat analysis indicated that the Texas horned lizard in Colorado is locally common in arid shortgrass and sandsage prairie lacking ground litter. Activity of the Texas horned lizard in Colorado is diurnal in spring and fall and bimodal (almost crepuscular) in the summer. Texas horned lizards in Colorado apparently breed in May and June, and hatchlings emerge in late August to mid-September. Mortality due to vehicle traffic seems high, but because the Texas horned lizard occurs in remote areas, the Colorado population in general seems to be relatively stable.

RESUMEN—La división de vida silvestre del estado de Colorado denomina el lagarto *Phrynosoma cornutum* como una de las especies en riesgo en el estado. De mayo de 1995 a octubre de 1997, se documentaron capturas y colectas del lagarto *P. cornutum* durante la época de actividad para determinar su abundancia y distribución en seis condados del estado de Colorado. Capturamos o colectamos 290 lagartos (170 vivos y 120 muertos en la carretera). En Colorado, el promedio longitudinal hocico-cloaca (LHC) para adultos macho no fue significativamente diferente que el de las hembras; el macho y la hembra más largos midieron 84.9 mm LHC y 90.4 mm LHC,

respectivamente. La proporción de machos y hembras adultos fue de 1M:1.4H. Los resultados de la distribución y el análisis de hábitat indican que el lagarto *P. cornutum* en Colorado habita praderas áridas de grama corta y de mata *Artemisia* que carecen de hojarasca. En Colorado, la actividad del lagarto *P. cornutum* es diurna durante la primavera y el otoño y bimodal (casi crepuscular) durante el verano. El lagarto aparentemente se aparea en mayo y en junio y sus crías emergen desde fines de agosto hasta mediados de septiembre. La mortandad debido al tráfico vehicular parece alta, pero dada la abundancia del lagarto en áreas remotas, la población de lagartos *P. cornutum* en Colorado parece ser relativamente estable.

The Texas horned lizard (*Phrynosoma cornutum*) is listed as a species of special concern by the Colorado Division of Wildlife. This designation means the status of the Texas horned lizard is unknown, but populations might be declining due to habitat modification and destruction. Previous studies of the Texas horned lizard have focused on morphology (Reeve, 1952; Montanucci, 1987, 1996), distribution (Reeve, 1952; Munger, 1984*a*; Whiting et al., 1993), status in Texas (Donaldson et al., 1994), ecology (Milne and Milne, 1950; Pianka and Parker, 1975), foraging behavior (Munger, 1984*b*; Schmidt and Schmidt, 1989), movement and home range (Munger, 1984*a*; Fair and Henke, 1999), reproduction (Howard, 1974), and predation and escape behavior (Munger, 1986; Sherbrooke, 1990). However, none of these studies included horned lizards from the northwestern limit of their range, which occurs in southeastern Colorado. Information about the natural history and ecology of the Texas horned lizard in Colorado can provide a habitat quality indicator and will aid in future management of the species.

The range of the Texas horned lizard includes Arkansas west through Kansas, Oklahoma, and Texas, into southeastern Colorado, eastern and southern New Mexico and southeastern Arizona, south into Mexico (Sherbrooke, 1981; Price, 1990). The historic range of the Texas horned lizard in Colorado includes Prowers and Baca Counties west through Bent County and Otero County and east-central Las Animas County (Hammerson, 1986). The objective of this research was to examine the natural history of the Texas horned lizard in southeastern Colorado, focusing on body size parameters, distribution, habitat preference, activity patterns, reproduction, and predation.

A 6-county area of southeastern Colorado, roughly consisting of the area south of the Arkansas River and east of Interstate Highway 25 (Baca, Bent, Las Animas, Otero, Prowers, and Pueblo counties), was surveyed for the Texas horned lizard. The region contains large expanses of private agricultural and ranching lands as well as military reservations, state wildlife areas, and the Comanche National Grassland. Survey efforts were concentrated within and immediately outside the known Colorado distribution of the Texas horned lizard (Hammerson, 1986). All *P. cornutum* captured or collected during this study were classified as recent localities, and previously published localities (Hammerson, 1986) are referred to as historic localities (Fig. 1). The recent localities were reported in Hammerson (1999), so they are not discussed here. All maps used during this analysis were adapted from Hammerson (1986) or United States Department of Agriculture (1965).

Specimens were located from vehicles while traveling about 24 to 40 kph and by visual searching of suitable habitat on foot. Surveys were conducted during the active season from 10 May 1995 to 15 October 1997. Road surveys comprised an estimated total of 200,000 km traveled in Baca (ca. 30%), Bent (ca. 10%), Las Animas (ca. 10%), Otero (ca. 25%), Prowers (ca. 20%), and Pueblo (ca. 5%) counties. Relative survey effort was randomly divided by county throughout the active season. Data collected for all live individuals included location, habitat type (including a survey of flora), time, air temperature (30 cm above ground), sex, snout–vent length (SVL), tail length (TL), morphological characters (as discussed below), age, and any behavior observed (e.g., feeding, copulation). Length measurements were made using a metric ruler and vernier calipers to the nearest millimeter. Adult males were identified by the presence of hemipenal bulges and enlarged femoral pores, and juvenile males were identified by manually everting the hemipenes; some dead specimens were dissected to determine sex. Snout–vent length was measured

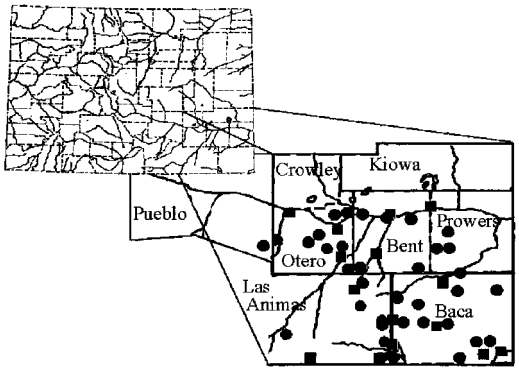

FIG. 1—Current distribution of *Phrynosoma cornutum* in Colorado. Squares represent historic localities, circles represent recent localities. County names are indicated.

from the tip of the snout to the posterior edge of the cloacal scale. Tail length was measured from the posterior edge of the cloacal scale to the tip of the tail. Specimens that were severely damaged were not used in the morphological analysis. Age class was recorded as hatchling when SVL was less than 35 mm (encountered in late August, September, and October). Age class was recorded as juvenile when SVL was between 35 mm and 60 mm. Based on our observations, neonates hatch in the fall at approximately 25 to 35 mm; juveniles reach 35 to 60 mm by the end of their second year but are not reproductive until their third year (second spring). Therefore, SVL greater than 60 mm is a good indicator that the animal is at least in its third year and sexually mature. Data collected for specimens found dead on the road (DOR) included location, habitat (including a survey of flora), sex (M = male, F = female), SVL, TL, and age class. All road-killed lizards were entered into the UNC-MNH Herpetology Collection. Location of individuals was recorded during the 1995 and 1996 field seasons using vehicle odometer distance (to one-tenth mile) from the nearest fixed landmark (e.g., junction of 2 roads, highway mile marker). A Trimble GeoExplorer II or Garmin 45L GPS unit (±100-m error) was used to determine latitude and longitude coordinates in 1997.

After measurements were taken, live specimens were PIT-tagged (passive integrated transponder; BioSonics, Inc., Seattle, Washington, and AVID, Inc., Norco, California) by injecting the small (11 mm × 2.1 mm) polymer-encased microchip subcutaneously in the left ventral region of the horned lizard (Camper and Dixon, 1986). The small wound was sealed with cyanoacrylate glue, and lizards were released at the site of capture.

Floral composition was determined using a variation of the line-intercept method (Cox, 1996). We used 30-meter transects, with data taken every 0.30 m at representative locations where lizards had been previously found. Vegetation at each point was classified as forb, grass, shrub, or cactus. If no vegetation was present, the point was classified as bare ground or litter. Frequency of vegetation type and percent aerial cover were determined for each transect. If the capture site was on a road, sampling was started just inside the fence (approximately 3 m from the edge of the road). We conducted 31 vegetation surveys for all localities in July and August 1997. Although the vegetation survey was conducted in 1997, there was no reason to suspect that 1997 was not a typical year based on climatological data (National Oceanic and Atmospheric Administration, 1995, 1996, 1997). Therefore, the floral survey conducted in 1997 was assumed to be representative of the vegetation present in the habitats surveyed for the entire study. Plant names used throughout this study are from Weber (1976).

We captured or collected 290 Texas horned lizards from 1995 through 1997, and of these, 170 were alive and 120 were dead. There was no significant difference between the number of individuals of each sex in each age class sex of live and dead lizards (*t*-test, $P = 0.197$) so

data for live and dead lizards were combined for all analyses. The largest female lizard was 90.4 mm SVL, and the largest male was 84.9 mm SVL. The smaller maximum size of individuals in our study area compared to lizards in southern portions of the range was an additional reason for assuming SVL of 60 mm at sexual maturity for both males and females in this study. The average SVL for adult males (67.9 ± 0.6 mm) was significantly smaller than the SVL of females (73.9 ± 0.8 mm) (*t*-test, $P < 0.001$). In addition, analysis of covariance on the regression of LogTL on LogSVL showed significant sexual dimorphism in the relationship of TL to SVL between males and females ($P < 0.001$), with males having a greater tail length at a given body size. The average SVL of hatchlings was 30.3 mm (26.0 to 32.5 mm). We captured or collected 198 adult lizards (77M:106F:15U), 74 juvenile (39M:35F), and 17 hatchling (6M:11F) lizards during this study. The sex ratio of adult males to adult females was 1M:1.4F. For juveniles the sex ratio was 1M:1F, and for hatchlings the sex ratio was 1M:1.8F. Caution should be taken when interpreting data for juveniles and hatchlings due to the low sample size and possible collecting bias of this study. In addition, because all but 4 lizards were collected on the road, sex ratios might be skewed due to differential activity of males and females (Sherbrooke, 2002).

Of 290 lizards captured or collected, most were found in Otero County (104), followed by Baca (89), Prowers (63), Bent (21), Las Animas (11), and Pueblo (1) counties (Fig. 1). The areas of greatest abundance of lizards were public lands with native habitats and limited grazing by cattle, including the 2 sections of Comanche National Grassland (central and southern Otero County and southeastern Baca County) and Two Buttes State Wildlife Area (on the Baca County/Prowers County line). We captured or collected 85 lizards within an area of approximately 5.2 km^2 in Two Buttes State Wildlife Area. Results of 15 floral transects within Two Buttes State Wildlife Area indicated that grasses were the dominant floral type (60%). Bare ground (31%), litter (6%), forbs (2%), and shrubs (1%) comprised the remainder of the transected cover types. Ten lizards were found in the southern unit of the Comanche National Grassland (southeastern Baca County), which is an area of publicly owned, grazed shortgrass and sandsage prairie contiguous with privately owned shortgrass prairie. This area is primarily dominated by blue grama (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), and sandsage (*Artemesia filifolia*). Three floral transects in this area indicated that bare ground was the dominant cover type (48%). Forbs (including sandsage) constituted 27% of the cover, with grass (14%) and litter (11%) comprising the remainder of the transected cover types. We captured or collected 47 *P. cornutum* in the northern portion of the Comanche National Grassland, located in Otero County. The area was primarily shortgrass prairie interspersed with canyon areas dominated by piñon (*Pinus*) and juniper (*Juniperus*). Lizards did not occur within the piñon-juniper, but were found at the boundary between the shortgrass prairie and piñon-juniper. Four floral transects in the central portion of this area indicated that bare ground (63%) was the dominant cover type; grasses (25%), litter (7%), forbs (3%), and shrubs (2%) comprised the remaining cover types. The northern portion of this area, where 9 floral transects were sampled, was comprised primarily of bare ground (54%) and grasses (44%), with litter, forbs, and shrubs making up less than 2% of the habitat cover type. The most common grasses in these 2 areas were blue grama and buffalo grass.

Overall, we sampled 31 transects at 4 areas of known lizard occurrence during July and August 1997. The dominant cover types were grasses and bare ground. Grasses constituted a total of 46.3% ($SD = 0.13$) of the cover (range 30.5 to 63.0%), followed by bare ground (43.1%, $SD = 0.20$; range 14.0 to 54.0%). Litter and forbs constituted 5.1% ($SD = 0.04$; range 0.7 to 11.0%) and 4.5% ($SD = 0.12$; range 1.1 to 3.0%) of the cover, respectively, with shrubs accounting for approximately 1% ($SD = 0.01$; range 0.6 to 2.0%) of the cover. Buffalo grass and blue grama were the dominant grasses at every site; sandsage, yucca (*Yucca*), and cactus (*Opuntia*) were the dominant shrubs.

The Texas horned lizard seemed to be active in Colorado from mid April to late September. We found 6 lizards (3 alive and 3 DOR) in Otero County on 19 April 1997, which was the starting day for the 1997 study period, indicating that emergence occurred prior to that

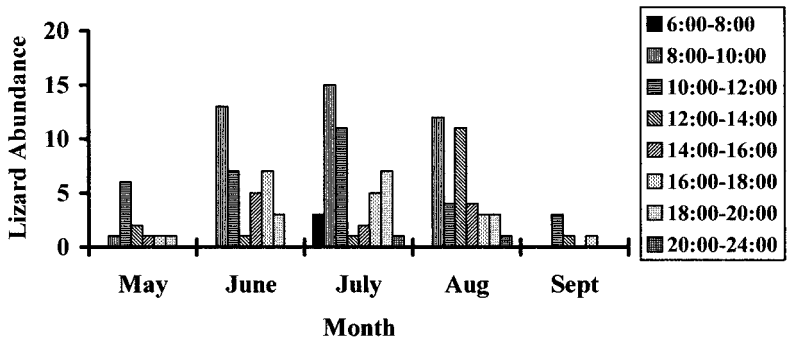

FIG. 2—Frequency of captures of *Phrynosoma cornutum* during daily time intervals per month for entire study. Lizards most frequently encountered in June and July, when activity was primarily crepuscular.

date. The last lizard of the year found during the study period was a juvenile located on 30 September 1997 in the northern portion of Comanche National Grassland. Based on 140 lizards for which temperature data were collected, lizards were active at air temperatures of 21 to 42°C, with the greatest number of lizards (41 of 140) captured between 29 and 31°C. The average air temperature for active lizards was 30.5 ± 3.7°C. The daily activity patterns of lizards changed throughout the season. During the cooler months of April, May, and September, when the average monthly temperatures are 11.1, 15.9, and 18.8°C, respectively, lizards were active throughout the day (Fig. 2). In the warmer months of June and July, when average 24-hour temperatures are 21.4 and 24.2°C, respectively, apparent daily activity became bimodal, with greater activity during the morning and evening hours (Fig. 2).

Two associating pairs (1M:1F) of small adult lizards were found on 21 June 1996. Neither pair of lizards was observed copulating, but no other pairs of lizards were found in such proximity during the study. A DOR adult female lizard found on 23 May 1997 contained 6 shelled eggs. A live female adult lizard captured on 24 May 1997 apparently was recently post-parturient. Hatchlings were found from 13 August to 17 September, with the majority of hatchlings (12 of 17) appearing around 30 August. The range of hatching dates suggests that eggs hatch at various times over the course of at least 35 days.

All 120 dead lizards except 1 were found on a road, killed by vehicular traffic. The other dead lizard was found hung on a barbed-wire fence, apparently killed by a shrike (*Lanius*). A Swainson's hawk (*Buteo swainsoni*) was seen carrying a *P. cornutum* in its talons, but this lizard was not recovered, so it was not included as a capture. An adult male lizard had a scarred, clubbed hind foot and broken occipital horn, possibly the result of a predatory attack. Also, a few lizards were found that were missing part or all of the tail. Live specimens lifted their bodies off of the substrate, ran to the side of the road and stopped as they were approached. These lizards were encountered on hard-packed dirt or paved roads and could not burrow under the surface. When pursued lizards ran a few meters and stopped; only 2 juvenile lizards did not run when approached. Captured lizards often used their occipital horns to jab and gaped to bite. Only 1 lizard out of 170 live captures used blood-squirting as a means of defense (Middendorf and Sherbrooke, 1992; Sherbrooke and Middendorf, 2001).

Of 156 PIT-tagged lizards, only 3 were recaptured (1.9%), therefore no representative movement or growth data were collected for Colorado lizards. Low recapture rates for *P. cornutum* (6.2%) have been reported previously (Henke and Montemayor, 1998).

The significant difference in the relationship of TL to SVL between males and females, with females having shorter TL relative to SVL, has been shown previously in *P. cornutum* (Sherbrooke, 1981). The adult sex ratio of 1M:1.4F shown in the Colorado population of Texas horned lizards agrees with Whiting et al. (1993), who reported a male-biased sex ratio of 1.5M:1F, which was not significantly different from 1:1 due to small sample size ($n = 35$),

in a 160,000-m^2 area in Concho County, Texas. The juvenile and hatchling sex ratios are probably an artifact of small sample size in these age classes.

Currently the distribution of the Texas horned lizard in southeastern Colorado is limited to an area south of the Arkansas River and roughly east of an imaginary line between La Junta and Trinidad. Within this area, the distribution can be characterized as scattered, with several areas of local abundance. Southwestern Las Animas County and eastern Prowers County represent the western and eastern limits of the Texas horned lizard in Colorado.

The Texas horned lizard is a species of the semi-arid grassland in southeastern Colorado, as in the rest of its range (Sherbrooke, 1981; Munger, 1984*a*; Whiting et al., 1993). The abundance of shortgrass prairie with large patches of bare ground at each capture site examined suggested that the presence of *P. cornutum* was dependent upon the presence of bare ground. Considering the broad body form and sit-and-wait predatory strategy of this lizard, it is logical that this lizard would prefer open ground; dense vegetation and litter would not allow the lizard to move efficiently. Our data agree with those of Whiting et al. (1993), who also showed that Texas horned lizards select open areas that are partially vegetated for foraging, basking, and movement. Pianka (1966) stated that *Phrynosoma* prefer foraging in open areas between plants, and Fair and Henke (1997) showed that *P. cornutum* preferred burned areas, which have little ground cover, to areas where ground cover is high. However, they also showed that *P. cornutum* did not select for or against grazed land, which had lower amounts of ground litter. In our study, Texas horned lizards were found on roads between pasture and agricultural fields, but no lizards were found in agricultural fields or on roads between adjacent agricultural fields. The lack of horned lizards in these areas suggests that agriculture has a negative effect on Texas horned lizard distribution. The plowing of fields can directly kill hibernating lizards or destroy egg clutches (Donaldson et al., 1994; Fair and Henke, 1997), which will quickly extirpate the lizard from an agricultural area. However, Fair and Henke (1997) indicated that horned lizards do not select for or against plowed agricultural fields. Timing and duration of plowing in their study might have allowed *P. cornutum* to utilize the fields, and it is probably not a long-term representative result of the effects of agriculture.

The Texas horned lizard was observed to be active primarily between mid April and late September, and earlier activity occurred when local climate conditions were suitable. This is consistent with Hammerson (1986), who reported activity beginning prior to May and ending in September. Most *P. cornutum* in Colorado were active at air temperatures between 29 and 31°C, although the range of activity was between 21 and 42°C. Our results differ from those of Prieto and Whitford (1971), who reported that Texas horned lizards prefer 38.5°C. The temperature range of activity of the Texas horned lizard in Colorado also influenced the daily activity of this lizard. When average daily temperatures were relatively low during April, May, and September, lizards were diurnal. As average daily temperatures increased in June and July, lizards became crepuscular. During August, lizards were active during the morning and afternoon hours, with reduced activity during the evening. Bimodal activity allows these lizards to be active at times when air temperature approximates the preferred air temperature of activity. A similar pattern of bimodal activity might be expected during August (when the average 24-hour temperature was 22.3°C); however, this expectation was not supported by the data. This change in activity pattern might be due to activity of neonates, which have just hatched, as well as juveniles and adults that need to forage heavily to gain the necessary fat stores to overwinter. However, because of small sample size of neonates and hatchings, this question was unresolved. Henke and Montemayor (1998) showed a similar pattern of activity in southern Texas; however, the peak months of activity were shifted later in the year by 1 month in our study, probably due to temperature differences associated with latitude. Bimodal daily activity during warmer months was also reported in *P. platyrhinos* (Pianka and Parker, 1975).

Predation on *P. cornutum* by a hawk and a shrike was observed. Other reported predators of horned lizards were observed in the area, including several species of hawks (*Buteo*), greater roadrunners (*Geococcyx*), grasshopper mice (*Onychomys*), canids, and several species

of snakes (Munger, 1986; Sherbrooke, 1990). Vehicle traffic resulted in high mortality of Texas horned lizards in southeastern Colorado, and this was further exacerbated by their habit of using roadsides for basking. In this study, auto traffic was the greatest source of observed mortality, but this might be misleading because most non-anthropogenic sources of mortality go unnoticed and most sampling was conducted on roads. The low frequency of blood-squirting (<1%) by *P. cornutum* is consistent with previous reports of the frequency of blood-squirting at humans by Texas horned lizards (Lambert and Ferguson, 1985; Middendorf and Sherbrooke, 1992; Sherbrooke and Middendorf, 2001). The escape behaviors exhibited by *P. cornutum* in southeastern Colorado also have been reported previously in *Phrynosoma* (Lambert and Ferguson, 1985; Wone and Beauchamp, 1995; Henke and Montemayor, 1998).

Texas horned lizard populations in Colorado seem to be stable in areas that are not plowed, though no historical population data exist. The high density of lizards in state wildlife areas and the national grassland suggests that large sections of native grassland habitat are necessary for the continued success of this lizard, and because of the limited use of these areas, some protection is provided. However, in most other parts of its range, the Texas horned lizard is being extirpated, primarily by a variety of anthropogenic causes (Donaldson et al., 1994), and the population in Colorado, therefore, might provide valuable data for the conservation of the species and be important for the overall survival of the species.

This research was supported by a grant from the Great Outdoors Colorado Project and the Colorado Division of Wildlife to S. P. Mackessy. Field work was conducted under Colorado Division of Wildlife scientific collecting permits (#95-0456, 96-0456, 97-0456). We are grateful to E. Bergmann, S. Boback, T. Childers, R. Donoho, J. Hobert, R. Manzer, J. Sifert, and K. Waldron for assistance in the field collecting Colorado specimens; J. Sigala-Rodríguez and V. Carmona for translating the summary; S. Beaupre for his invaluable suggestions on data analysis and draft revisions; and 3 anonymous reviewers and W. C. Sherbrooke for helpful criticism of and comments on the manuscript.

Literature Cited

Camper, J. D., and J. R. Dixon. 1986. Evaluation of a microchip marking system for amphibians and reptiles. Texas Parks and Wildlife Department, Austin.

Cox, G. W. 1996. Laboratory manual of general ecology, seventh edition. Wm. C. Brown Publishers, Dubuque, Iowa.

Dondaldson, W., A. H. Price, and J. Mosre. 1994. The current status and future prospects of the Texas horned lizard (*Phrynosoma cornutum*) in Texas. Texas Journal of Science 46:97–113.

Fair, W. S., and S. E. Henke. 1997. Effects of habitat manipulations on Texas horned lizards and their prey. Journal of Wildlife Management 61:1366–1370.

Hammerson, G. A. 1986. Amphibians and reptiles in Colorado. Colorado Division of Wildlife Publication Number DOW-M-I-3-86.

Hammerson, G. A. 1999. Amphibians and reptiles in Colorado, second edition. University Press of Colorado, Niwot.

Henke, S. E., and M. Montemayor. 1998. Diel and monthly variations in capture success of *Phrynosoma cornutum* via road cruising in southern Texas. Herpetological Review 29:148–150.

Howard, C. W. 1974. Comparative reproductive ecology of horned lizards (genus *Phrynosoma*) in southwestern United States and northern Mexico. Journal of the Arizona Academy of Sciences 9:108–116.

Lambert, S., and G. M. Ferguson. 1985. Blood ejection frequency by *Phrynosoma cornutum* (Iguanidae). Southwestern Naturalist 30:616–617.

Middendorf, G. A., III, and W. C. Sherbrooke. 1992. Canid elicitation of blood-squirting in a horned lizard (*Phrynosoma cornutum*). Copeia 1992:519–527.

Milne, L. J., and M. J. Milne. 1950. Notes on the behavior of horned toads. American Midland Naturalist 44:720–741.

Montanucci, R. R. 1987. A phylogenetic study of the horned lizards, genus *Phrynosoma,* based on skeletal and external morphology. Contributions in Science at the Natural History Museum Los Angeles County 390:1–36.

Montanucci, R. R. 1996. Morphological variation in the gular fold in the horned lizard genus, *Phrynosoma* (Iguania: Phrynosomatidae). Herpetologica 52:46–55.

Munger, J. C. 1984*a*. Home ranges of horned lizards (*Phrynosoma*): circumscribed and exclusive? Oecologia 62:351–360.

Munger, J. C. 1984*b*. Optimal foraging? Patch use by horned lizards (Iguanidae: *Phrynosoma*). American Naturalist 123:654–680.

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.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1995–1997. Climatological Data: Colorado. Volumes 99–101.

PIANKA, E. R. 1966. Convesity, desert lizards, and spatial heterogeneity. Ecology 47:1055–1059.

PIANKA, E. R., AND W. S. PARKER. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. Copeia 1975:141–162.

PRICE, A. H. 1990. *Phrynosoma cornutum*. Catalogue of American Amphibians and Reptiles 469:1–7.

PRIETO, A. A., AND W. G. WHITFORD. 1971. Physiological responses to temperature in the horned lizard *Phrynosoma cornutum* and *Phrynosoma douglassii*. Copeia 1971:498–504.

REEVE, W. L. 1952. Taxonomy and distribution of the horned lizards genus *Phrynosoma*. University of Kansas Scientific Bulletin 34, Part 2, Number 14.

SCHMIDT, P. J., AND J. O. SCHMIDT. 1989. Harvester ants and horned lizards predator-prey interactions. In: Schmidt, J. O., editor. Special biotic relationships in the arid southwest. University of New Mexico Press, Albuquerque. Pp. 24–51.

SHERBROOKE, W. C. 1981. Horned lizards: unique reptiles of western North America. Southwestern Parks and Monuments Association, Globe, Arizona.

SHERBROOKE, W. C. 1990. Predatory behaviour of captive greater roadrunners feeding on horned lizards. Wilson Bulletin 102:171–174.

SHERBROOKE, W. C. 2002. Seasonally skewed sex-ratios of road-collected Texas horned lizards (*Phrynosoma cornutum*). Herpetological Review 33:21–24.

SHERBROOKE, W. C., AND G. A. MIDDENDORF, III. 2001. Blood-squirting variability in horned lizards (*Phrynosoma*). Copeia 2001:1114–1122.

UNITED STATES DEPARTMENT OF AGRICULTURE. 1965. Colorado: Soil Conservation Service Administrative Offices and Watershed Projects M-4497-ABC, Soil Conservation Districts. USDA-SDS, Portland, Oregon.

WEBER, W. A. 1976. Rocky Mountain flora. University Press of Colorado, Niwot.

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.

WONE, B., AND B. BEAUCHAMP. 1995. Observations on the escape behaviour of the horned lizard *Phrynosoma mcalli*. Herpetological Review 26:132.

Submitted 8 May 2001. Accepted 15 January 2002.
Associate Editor was Geoffrey C. Carpenter.