Desert Massasauga Rattlesnake (*Sistrurus catenatus edwardsii*): A Technical Conservation Assessment

Prepared for the USDA Forest Service, Rocky Mountain Region, Species Conservation Project

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AUTHOR'S BIOGRAPHY

Stephen Mackessy is Professor of Biology at the University of Northern Colorado and PI of the Venom Research Lab. His research broadly encompasses the biology of venomous snakes and the biochemistry of snake venoms. He has conducted intensive herpetological surveys of the eastern plains of Colorado over the last ten years, focusing on several Species of Special Concern, and his group has worked with many aspects of the biology of the desert massasauga rattlesnake, both in the field and in the lab. He has recently completed work on the venom of the brown treesnake, an invasive species on Guam, and continues to work toward understanding the composition and biological roles of venoms from colubroid snakes. Other projects of his students have included ecotoxicology of herbicides toward anuran larvae, effects of introduced predatory species on vertebrates in Colorado, and natural history of the Texas horned lizard in Colorado. Dr. Mackessy also teaches numerous courses in vertebrate biology (Herpetology, Comparative Anatomy, Mammalogy) at UNC. He earned a B.A. (1979) and an M.A. (1985) in Biology, Ecology and Evolution section, at the University of California at Santa Barbara, and his Ph.D. was received from Washington State University, Department of Zoology (1989). He was a postdoctoral Research Associate at Colorado State University, Department of Biochemistry and Molecular Biology (1989-1991) before joining the Department of Biological Sciences at UNC in 1994.

COVER PHOTO CREDIT

Desert massasauga (*Sistrurus catenatus edwardsii*). This snake was from Lincoln County, and it is the largest desert massasauga (total length ~529 mm) found in Colorado in the last ten years. Photograph by the author.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE DESERT MASSASAUGA

Status

The massasauga rattlesnake (*Sistrurus catenatus*) is locally threatened or endangered throughout most of its range. The status of the desert massasauga (*S. c. edwardsii*) is as follows: Arizona, protected; Colorado, Species of Special Concern; Kansas, unknown; New Mexico, no special status; Oklahoma, unknown; Texas, unknown; Mexico, unknown. The desert massasauga is listed as a Species of Special Concern by the Colorado Division of Wildlife primarily because of the limited distribution of well-documented, stable populations. It is listed as a sensitive species by the USDA Forest Service (USFS), Rocky Mountain Region (Region 2), where populations are stable but uncommon in southeastern Colorado and southwestern Kansas.

Primary Threats

Long-lived, low fecundity animals such as the massasauga are inherently vulnerable to population losses because of limited replacement potential. In Region 2, the primary threat to massasauga populations is habitat loss and degradation due to urbanization, farming, heavy livestock grazing, and water table drawdown due to diversion and well water use. Like other xeric habitats, shortgrass prairie is severely affected by soil disruption (e.g., tilling, overgrazing, urbanization), and the arid nature of this habitat makes recovery following release from disturbance very lengthy and perhaps incomplete, particularly given the growing threat of invasive weeds. Massasauga populations in Colorado have benefited passively from geographic isolation in terms of distance from urban centers, but pressures from Front Range human populations could eliminate this isolation. Like all rattlesnakes, the common result of human encounters is death, and the effects of direct persecution in remote areas are nearly impossible to evaluate. Highway/road mortality is another anthropogenic threat to massasauga population stability and persistence. Conservation easements and public lands (e.g., State Trust lands, National Forest System lands) provide some protection, but presently these do not include areas in the state with the largest desert massasauga populations.

Primary Conservation Elements, Management Implications and Considerations

Protection and conservation of large, contiguous tracts of native shortgrass prairie habitat will be necessary for the long-term survival of the desert massasauga. Acquisition and management of lands by public agencies (e.g., USFS, Bureau of Land Management) and other groups will help to conserve this fragile habitat. However, much of Colorado is privately owned, often as large ranches (10,000 to 100,000 acres or more), so pursuit of conservation easement agreements with private property owners is likely a more productive means of providing broader protection. It is further suggested that desert massasaugas rangewide receive protected, no-take status. Direct intervention (e.g., captive breeding, reintroduction) for preservation of Region 2 populations is not indicated or recommended at this time; however, these types of programs are being undertaken in other parts of the species' range.

Populations of desert massasaugas in Colorado should be monitored at several levels. Sensitive and robust populations identified by the lead author of this assessment should be surveyed on a regular basis (i.e., 5 to 10 year interval, depending on funding availability) to ensure that new threats to the populations have not arisen. State and federal agencies should monitor land use changes, and if significant changes (e.g., urbanization, till farming, overgrazing) occur in areas occupied by massasaugas, impacts should be evaluated. Massasauga populations on National Forest System lands, in particular in the vicinity of the Baca County locality records, should be surveyed again in the near future with a concerted effort placed on the regions immediately adjacent to and within the Comanche National Grasslands. The Cimarron National Grasslands in southwestern Kansas should be surveyed extensively in late spring and early fall, when the likelihood of encounters is greatest, to determine unequivocally whether or not the desert massasauga occurs there (we expect it to occur there).

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Introduction

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). The desert massasauga rattlesnake (*Sistrurus catenatus edwardsii*) is the focus of an assessment because it is listed as a sensitive species in Region 2. A sensitive species may require special management, so knowledge of its biology and ecology is critical. This assessment addresses the biology, ecology, conservation, and management of massasauga rattlesnakes throughout their range in Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

The goal of this report is to summarize the existing primary literature and "gray" literature relevant to the status of the desert massasauga, a diminutive rattlesnake found in shortgrass/sand sage prairie habitat in the extreme southeastern portions of Region 2, including some lands within the National Forest System. With this summary, sensitive areas of habitat are identified, current and impending threats to the species are documented and/or proposed, and management recommendations are presented. The massasauga rattlesnake (*Sistrurus catenatus*) is threatened or endangered over much of its remaining distribution in the United States, but populations of desert massasaugas in Colorado (Region 2) are still reasonably secure. Therefore, it is likely that these populations will become of increasing importance to conservation of the species in general.

Scope

The primary focus of this assessment is on the biology, ecology, status, and conservation of the massasauga rattlesnake in Region 2, with emphasis on those areas within and adjacent to National Forest System lands (i.e., Comanche and Cimarron national grasslands). While most of the range of the species and subspecies is *not* within Region 2, and relatively little data are available for the species within Region 2, this assessment will focus on the desert massasauga, with an emphasis on data obtained from Colorado populations. Information that is relevant to the species rangewide will be included where appropriate, and specific reference will be made to information obtained on the other two subspecies, the eastern massasauga (*Sistrurus catenatus catenatus*) and the western massasauga (*S. c. tergeminus*).

Extensive work with the desert massasauga has only occurred with populations in Arizona and Colorado; elsewhere in its range, the status of desert massasauga populations is unknown. Based on human population growth trends in the southwestern United States and subsequent degradation of habitat quality, it is likely that most populations are in decline, some precipitously, others much more slowly. Therefore, the status of the desert massasauga rangewide is uncertain at this time and will only become clearer if extensive fieldwork is conducted. Inferences made about the desert massasauga in Region 2 are based on published information and on extensive fieldwork conducted by the author's lab, primarily from 1994-2005. From 1999-2004, we conducted less formal surveys of only some of the known populations in Colorado and have only monitored one population regularly (Lincoln County). In 2005, we reinitiated telemetry work with the Lincoln County population and have conducted several surveys throughout southeastern Colorado. Our knowledge of the current status of Region 2 populations is somewhat limited, but we believe that the information contained within this report is accurate and relevant to the current status. Road-based surveys and review of available remote monitoring data suggest that urban and agricultural land uses in the Region 2 areas have not significantly changed since 1997 (except for urban water utilization of Arkansas River water), so the importance of these threats to population stability have not likely changed. The years 1999-2003 were characterized by low rainfall/drought conditions, and we would expect these conditions to negatively impact massasaugas, particularly in marginal habitat. Upstream changes in Arkansas River drainage water use, specifically diversion, are expected to increase stress on these populations as a result of the effects of xerification.

Uncertainty

The lead author has worked extensively with the desert massasauga in Colorado and Arizona for over 12 years, and this work has provided a large amount of first-hand information on many different aspects of the biology of the massasauga. In this respect, the information contained in this monograph is considered scientifically robust and valid, recognizing that there are many factors which can change rapidly and which may not have been predicted as major effectors on the conservation status of the species. Land use practices appear relatively stable in many parts of the species' range in Colorado, but this is not the case in Arizona (San Bernardino Valley, Cochise County and Sulfur

Springs Valley, Graham County), where habitat conversion could occur at unpredictably rapid rates. Effects of xerification due to groundwater overuse and global warming are likely to become significant threats, but the rate of these changes is difficult to estimate. In short, though the recommendations suggested should be sufficient for the present and immediate future conservation and management of the massasauga, rapid changes in these and other factors could lead to rapid detrimental effects on massasauga populations.

Web Publication and Peer Review

To facilitate their use, species conservation assessments are being published on the USFS Region 2 World Wide Web site. Placing the documents on the Web makes them available to USFS personnel, other agencies, and the public more rapidly than publishing them as reports. More important, it facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the Web. Under the editorial guidance of Gary Patton (USFS Region 2), this report was reviewed through a process administered by the Society for Conservation Biology, employing two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Federal Endangered Species Act

Review of the taxonomic status of the massasauga rattlesnake is currently underway, and it appears that the eastern and western subspecies may represent clinal variants of a single species while the desert massasauga may warrant species-level recognition (Milne and Mackessy unpublished data). However, for the purposes of this assessment, the massasauga will be considered as a single species with three subspecies. Primarily because of habitat loss and persecution, the eastern massasauga is the most threatened of the three subspecies. It was added to the candidate list for consideration for listing as a threatened or endangered species by the U.S. Fish and Wildlife Service in October 1999 (Johnson et al. 2000), and as of October 2005, the U.S. Fish and Wildlife Service listing status was C (Candidate Taxon, Ready for Proposal). Therefore, most conservation efforts have been directed toward this subspecies. Populations of the desert massasauga in Colorado and Arizona currently receive limited protection status (no take) under state statutes, but there is no current effort to obtain federal protected status for this subspecies.

USDA Forest Service

The USFS currently recognizes the massasauga as a sensitive species in Region 2. Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance and/or in habitat capability that would reduce its distribution [FSM 2670.5 (19)]. The massasauga was added to the Regional Forester's sensitive species list in Region 2 during its list revision, effective December 2003.

Bureau of Land Management

Although the desert massasauga does not occur on any lands within Region 2 that are managed by the Bureau of Land Management, the massasauga is included on the sensitive species list of the Colorado State Office (http://www.co.blm.gov/botany/sens_species.htm), indicating that it is considered to be at risk of becoming endangered or extinct within the area managed.

State Wildlife Agencies

The Colorado Division of Wildlife considers the desert massasauga to be a Species of Special Concern and affords it a no take/no kill status (see http://wildlife.state.co.us/species_cons/list.asp). There are several large and apparently stable metapopulations of the desert massasauga in southeastern Colorado, particularly in southeastern Lincoln County, and additional protection does not appear to be necessary at this time. Kansas does not afford any special protection to the massasauga rattlesnake at this time.

Natural Heritage Ranks

The Colorado Natural Heritage Program (1999) considers the massasauga a species whose status needs to be monitored (positive tracking status). At the state level, it is ranked S2, indicating that it is considered imperiled because of rarity or because other factors make it vulnerable to extinction throughout its range. Globally, it is ranked G3G4, indicating that some populations are likely stable, but that it is rare, vulnerable, and/or geographically restricted in other parts of its range. Based on 12 years of fieldwork in Colorado and elsewhere, we disagree with these rankings. Several populations in Colorado are moderately large to very large, and the massasauga occurs in much of the southeastern part of the state in very rural areas. Accordingly, the massasauga is reasonably secure in the state, which would argue for a slightly higher rank, such as S3.

In Kansas, the massasauga (primarily the western massasauga) is considered rare, but the desert massasauga, with unknown distribution in the state, is not accorded any particular status. The Oklahoma Natural Heritage Inventory lists the desert massasauga as vulnerable/restricted to apparently secure globally (G3G4) and unranked (S?) at the state level. State status is given as imperiled (S2).

Mexico

The highly localized and apparently disjunct populations of desert massasauga have been accorded Subject to Special Protection status in Mexico (Secretaria de Medio Ambiente 2000).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The Natural Heritage Programs of Colorado and Arizona conduct monitoring programs of the desert massasauga in those states. The Colorado Division of Wildlife has provided partial protection for the desert massasauga through no-take regulations and is actively working with various conservation groups and directly with landowners to create conservation easements. The lead author continues to monitor the Lincoln County population, and this year is likely to be an appropriate time to discuss the possibility of a conservation easement with those landowners where much of this population resides. The Arizona Game and Fish Department also regulates take of massasaugas, and scientific permits are required to take or possess massasaugas originating in Arizona.

In Colorado, the desert massasauga occurs in areas where the possibility for active protection (from take or wanton destruction) by wildlife managers or law enforcement personnel is quite unlikely; personnel are too few and the area is too large. It is probable that most people kill massasaugas and other rattlesnakes on sight, and little can be done to cost-effectively counter this attitude, other than a public education/awareness program. Fortunately, because the desert massasauga is very cryptic and occurs in sparsely populated regions, human encounters are uncommon and probably very localized (e.g., ranch houses). Existing laws in Region 2 are probably sufficient from a legal perspective for protection as long as habitat loss does not accelerate.

Biology and Ecology

Systematics and description

Within the massasauga (*Sistrurus catenatus*) complex, three subspecies have been distinguished by morphometric data: the eastern massasauga (*S. c. catenatus*), the western massasauga (*S. c. tergeminus*), and the desert massasauga (*S. c. edwardsii*) (Klauber 1936, Gloyd 1940, Gloyd 1955, Klauber 1956, Conant and Collins 1991). Klauber (1936) described only the eastern and western subspecies; the latter included snakes from extreme southeastern Colorado, the plains of central and southern New Mexico, and extreme southeastern Arizona. Gloyd (1955) reviewed the massasaugas of the southwestern United States and included the only known specimen from Colorado (an unknown specific locality) as desert massasauga. This specimen is now known to have been collected in 1882 by Mr. A. E. Beardsley in Baca County, Colorado, and it is listed as voucher #96-265 in the Colorado State Normal College (now University of Northern Colorado) museum register (Mackessy et al. 1996). Wright and Wright (1957) then described specimens from western Missouri and southeastern Nebraska to southeastern Arizona and extreme northern Mexico as the western subspecies. Massasaugas in Colorado were considered western massasaugas until Maslin (1965) described them as an intergrade between western and desert subspecies. While Maslin's classification of massasaugas in Colorado has been considered valid since that time (Conant and Collins 1991), Maslin himself indicated that a more thorough investigation was needed and emphasized the need for more material. Maslin (1965) further noted that "scale characters of the Colorado population may be so distinctive that nomenclatural recognition of this biological entity might be justified". Based on results of a morphological study done at University of Northern Colorado (Hobert 1997, Hobert et al., in prep) in which 345 massasaugas from Colorado, Arizona, New Mexico, and Kansas were analyzed, the massasauga rattlesnakes in Colorado should be considered desert massasaugas.

The systematic status of the massasauga rangewide is currently the subject of a collaborative investigation involving several researchers from the University of Northern Colorado (S.P. Mackessy), Colorado State University (M. Douglas), Arizona State University (A. Holycross), and McMaster University (H.L. Gibbs). These studies are utilizing mitochondrial DNA sequences and may be able to unravel relationships between the currently accepted three subspecies. Based on venom studies in Mackessy's lab, desert massasaugas from Colorado and Arizona form a distinct clade separate from western and eastern subspecies, and western and eastern subspecies are essentially indistinguishable from one another. We believe that the desert massasauga may represent a lineage warranting species recognition status while the eastern and western subspecies may be clinal variants of a single separate species; this conclusion is also borne out by a morphological comparison of the three subspecies (Hobert 1997). However, several systematic studies are in progress, and preliminary DNA molecular data do not fully support this split.

The massasauga rattlesnake (*Sistrurus catenatus*) is one of only two or three species in the genus *Sistrurus*. Currently the taxonomic status of the Mexican pygmy rattlesnake, *S. ravus*, is being revised, and it has been included in the genus *Crotalus* (Murphy et al. 2002). The other species in the genus, *S. miliarius* (pygmy rattlesnake), is found in the southeastern United States (Conant and Collins, 1991). Snakes of the genus *Sistrurus* are characterized by the presence of nine enlarged scales on the top of the head, a meristic character that distinguishes them unequivocally from all other rattlesnakes in the United States.

The desert massasauga (**Figure 1a**) is the smallest subspecies of the massasauga rattlesnake, with adults reaching a maximum total length of 588 mm (Holycross 2001). In Colorado, the average adult total length is <400 mm, and the maximum recorded total length is 529 mm (Mackessy 1998a). Comparative data for 240 adult male and female desert massasaugas from Colorado are provided in **Table 1**.

The ground color of desert massasaugas in Region 2 (southeastern Colorado) is typically gray to light brown, with 37 to 40 darker brown saddles or semicircular blotches, outlined in black, forming a regular pattern on the dorsal surface. On the tail, there are alternating bands of gray and brown/dark gray. Laterally, there is a series of smaller and paler circular blotches in two alternating rows. A prominent dark brown to black stripe extends from the eye to the angle of the jaw, and a lyre-shaped or paired irregular set of stripes extends from the dorsal surface of the head to the first body blotch. The ventral surface is often light tan to white with no markings, but the ventral scales may be marked with partial or complete darker pigmentation on the posterior free margin. In adults, the tip of the tail (at the base of the rattle) is typically black, but in neonates, the tip is yellow and is likely used for caudal luring of prey (Reiserer 2002). The anal plate is undivided, and the keeled dorsal scales form 23 rows at midbody (**Figure 2**); the western and eastern subspecies show 25 scale rows (typically) at midbody (Hobert 1997).

Like all rattlesnakes, the desert massasauga is venomous, and the venom is notably toxic (intravenous LD_{50} ~1.4 µg/g mouse; Mackessy unpublished data). However, due to its small adult size, venom yields are low (20-40 µl, 4-8 mg), and human envenomations, though potentially serious, are not likely to be life-threatening. Ongoing studies in the lead author's lab are characterizing desert massasauga venom and isolated components, but at present, the venom appears to be similar in composition to that of many other species of rattlesnakes.

Distribution and abundance

Historically, the massasauga (*S. catenatus*) is known from fragmented populations in southern Ontario, Canada across parts of the Midwest and Great Plains south to several isolated (disjunct) populations in Chihuahua, northern Mexico (**Figure 3**). Both the eastern and the western massasaugas occupy a variety of mesic habitats, commonly marsh areas bordering open water. The desert massasauga, on the other hand, occurs most commonly in arid grasslands and occasionally sand dune habitat.

The desert massasauga is broadly distributed across the ecoregion, occurring over much of the shortgrass prairie habitat in southeastern Colorado, adjacent southwestern Kansas, and perhaps northwestern Oklahoma. The distribution in Kansas is unknown but was likely historically contiguous with populations in Colorado, based on continuity of appropriate shortgrass prairie habitat in western Kansas. However, widespread habitat loss due to farming in eastern Colorado may now pose a barrier to further gene flow.

Desert massasaugas also occur in parts of Arizona, New Mexico, Texas, and Mexico. Populations are highly localized in southeastern Arizona and likely threatened (Lowe et al. 1986, Holycross and Douglas 1996). They appear to be broadly distributed in south-central and southeastern New Mexico (Degenhardt et al. 1996), but the status of these populations is unknown

Figure 1a. Desert massasauga from Lincoln County, Colorado.

Figure 1b. Desert massasauga in typical resting coil at base of sand sage (*Artemesia filifolia*), Lincoln County, Colorado. Snake is at center of photograph.

Table 1. Comparative body measurements of adult male and female desert massasaugas from Colorado. Mean and SD are shown above the range and sample number (N). Data from Hobert (1997). Differing values for N result from use of road-killed animals; not all measures were obtainable for all specimens.

Sex	Snout-vent length (mm)	Tail length (mm)	Relative tail length	Tail bands	Body weight (g)
Male	355.1±49.1	43.5±7.1	0.123±0.01	7.7±1.3	42.1±18.6
	259-485	27-62	0.095-0.158	5-11	16-116
	N=127	N=128	N=125	N=130	N=68
Female	352.6±32.5	32.4±3.3	0.092±0.009	6.3±1.1	32.8±8.1
	270-453	24-44	0.075-0.127	4-9	15-60
	N=87	N=87	N=87	N=88	N=67

and in need of systematic survey work. Similarly, desert massasaugas are broadly distributed in western and southern Texas (Werler and Dixon 2000), but these populations are also of uncertain status, both in terms of population stability and taxonomic affinity. Isolated populations also occur in Coahuila and Nuevo León, Mexico (Campbell and Lamar 1989).

Within lands specifically administered by USFS Region 2, the desert massasauga is known to occur only in the northern and southern sections of the Comanche National Grassland in Colorado (**Figure 4**). We consider it probable but as yet undocumented on the Cimarron National Grassland in Kansas (**Figure 5**), which appears to have habitat appropriate for desert massasaugas (Collins and Collins 1992). Prior to extensive fieldwork in southeastern Colorado, the status of the massasauga in Colorado was poorly known. Because of a paucity of collection records, it was being considered for listing as a state-protected species. We have since identified several apparently robust populations in Colorado, and our surveys have expanded the known distribution as well (**Figure 6**; Mackessy 1998a). Most notable were collections of four specimens from northwestern Baca County, just north of the southern section of the Comanche National Grassland (Montgomery et al. 1998); the last recorded occurrence of the massasauga in Baca County was in 1882, and the original specimen was lost. In 2005, we obtained four more records from this same area of Baca County, suggesting that massasaugas are relatively common at this location.

Within Colorado, the range of the desert massasauga is confined to 11 southeastern counties (Hammerson 1999), but recent survey efforts resulted in verified occurrence in only 10 counties (none were found in Las Animas County). Massasaugas appear to be locally abundant at several localities within this range, with much smaller populations occurring in the six most southeastern counties. It is most abundant in southeastern Lincoln County. Based on 10 years of field work and the documentation of over 500 specimens in Lincoln County, desert massasauga populations there are reasonably robust and stable (Hobert 1997, Mackessy 1998a).

In National Forest System lands, it occurs uncommonly in parts of three counties: Otero, Las Animas, and Baca (**Figure 5**). Their rarity here perhaps makes them more susceptible to local extirpation. Since 1995, we have recorded over 800 specimens of desert massasaugas in Colorado, but only 14 of these were found on or near the Comanche National Grassland. Sampling bias alone cannot explain this lack of specimens because both sections of the national grassland were subject to extensive survey work. The reason for abundance differences in various parts of the state are unclear but may be due in part to available surface water and soil moisture differences. In some areas, habitat loss due to agricultural practices has led to localized extirpations (Mackessy 1998a).

Massasaugas in Colorado inhabit a variety of habitats in the Arkansas River drainage, ranging from arid open sagebrush prairie to shortgrass prairie below 1500 m (5500 ft.) (Hammerson 1986, 1999). However, there appear to be macrohabitat differences between areas with apparently lower abundance and areas of relatively high abundance. The areas of greatest abundance have more native habitats with limited grazing and farming (**Figure 7**). These areas are becoming increasingly fragmented, which may result in the isolation of small populations of desert massasaugas into areas of intact habitat.

It is likely that desert massasauga populations were once continuous over much of their historic range from northern Mexico to eastern Colorado. Presently, populations of the desert massasauga, like those of the western and eastern massasaugas, are fragmented and

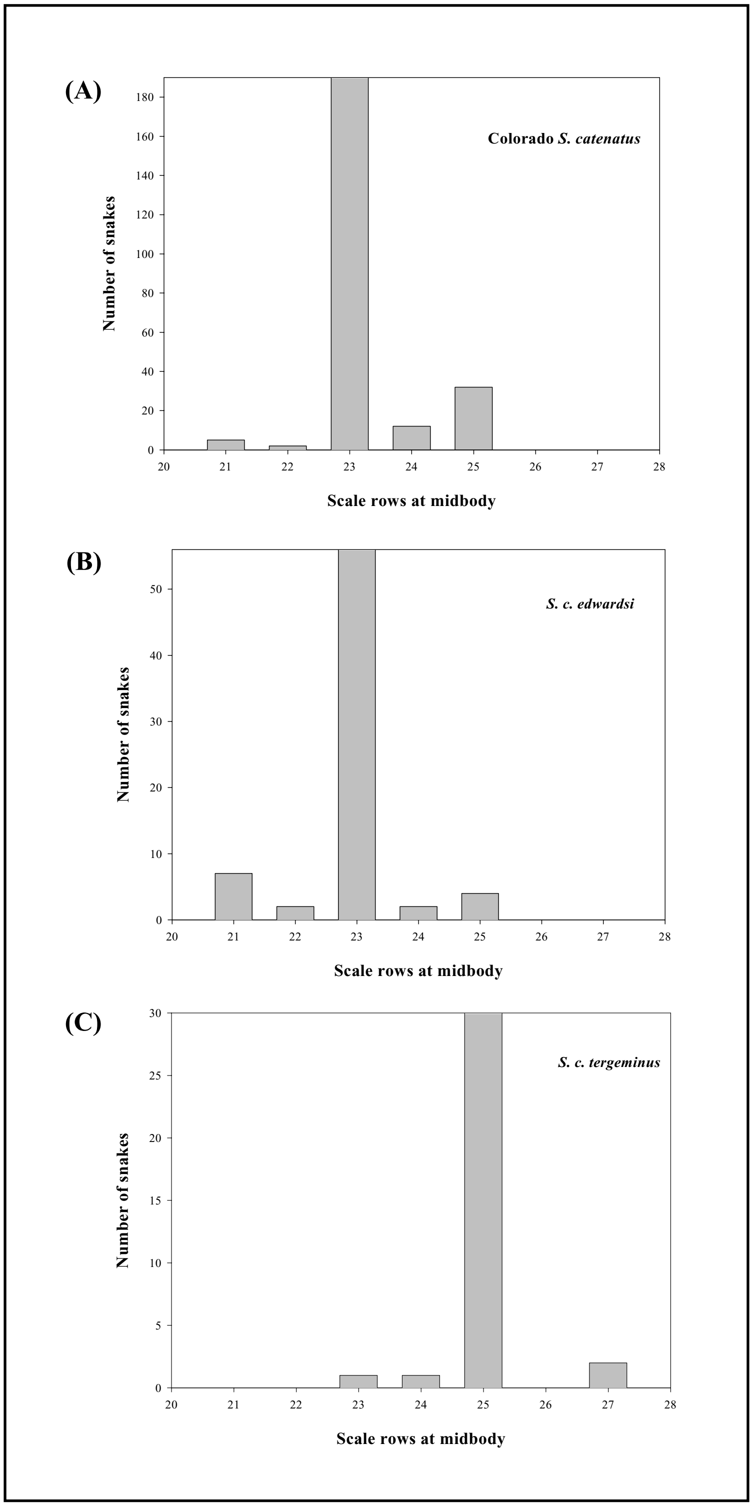

Figure 2. Scale counts at midbody for desert massasaugas in Colorado **(A)**, desert massasaugas in Arizona **(B)**, and western massasaugas from Kansas **(C)**. This character, along with general habitat requirements, adult size and venom characteristics, were the basis for considering massasaugas in Colorado to be desert massasaugas (Hobert 1997, Hobert et al. 2005).

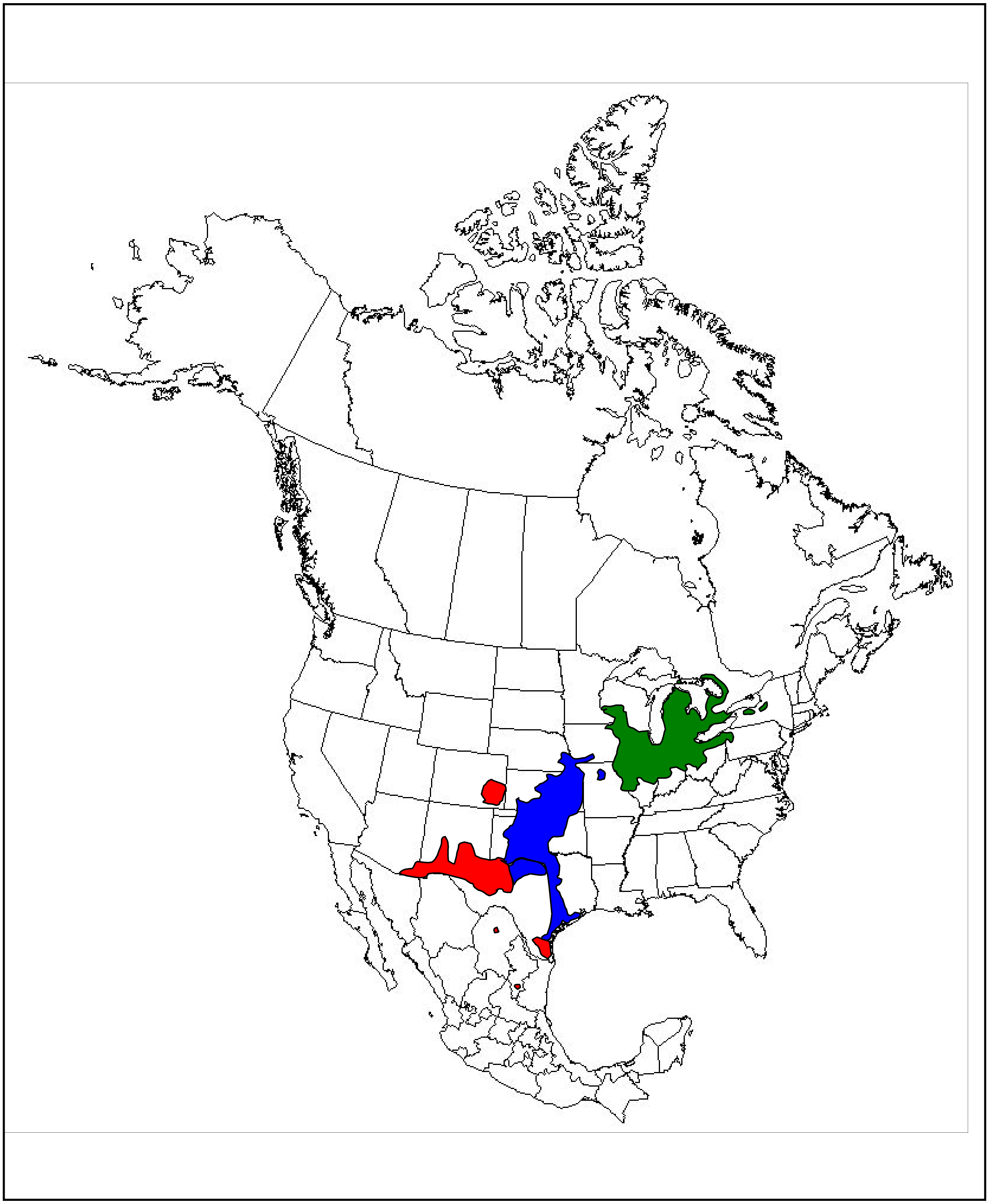

Figure 3. Approximate distribution of the massasauga (*Sistrurus catenatus*) in North America. The desert massasauga (*S. c. edwardsii*) is shown in **red**; the western massasauga (*S. c. tergeminus*) is shown in **blue**; and the eastern massasauga (*S. c. catenatus*) is shown in **green**. Redrawn largely from Conant and Collins (1991). Note that for most ranges, particularly for the eastern massasauga, populations are not continuous, nor do they occupy the entire area shaded.

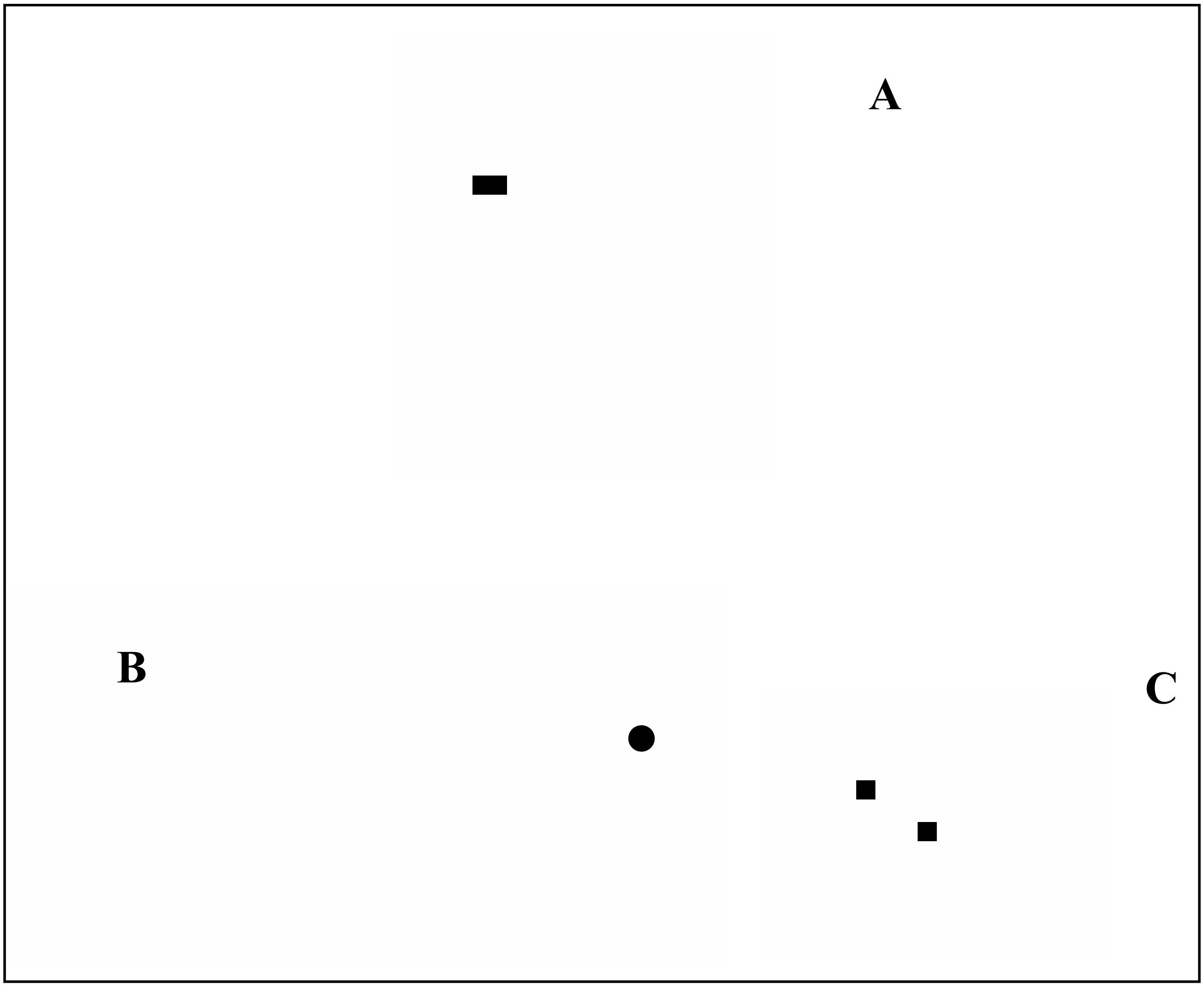

Figure 4. Distribution of the desert massasauga in Otero (A), Las Animas (B), and Baca (C) counties, Colorado. The Comanche National Grassland of Region 2 occurs in these three counties. Specific localities are indicated by solid circles (historic) or squares (resulting from the 1995-1997 survey). Most localities indicate a single specimen.

discontinuous. The timing and causes of population discontinuity are difficult to determine unequivocally, but they include long-term climatic changes that have resulted in natural changes in the shortgrass prairie habitat of the Great Plains (e.g., Madole 1995) and anthropogenic changes that have exacerbated xerification and have resulted in large expanses of habitat loss (Hammerson 1999). Currently, Colorado populations (including those in National Forest System lands) of desert massasaugas are discontinuous with all other populations except (perhaps) those in western Kansas (i.e., Cimarron National Grasslands, if they exist) and in western Oklahoma. This lack of connectivity between the various populations may gradually lead to genetic divergence, as there appears to be a high level of genetic structure and differentiation even among continuous populations (based on the eastern massasauga; Gibbs et al. 1997). The effects of a restriction of gene flow in fragmented populations on overall viability are unknown for massasaugas, but they may be negative (Couvet 2002).

Population trend

There are insufficient data to document abundance trends of desert massasaugas in Region 2, but it is most likely that desert massasaugas on the national grasslands were historically more abundant and have declined over the last 50 to 100 years (H.M. Smith personal communication, 1996). However, there are populations just north in Kiowa County that appear to be moderately robust, and there may be one or more small populations in Baca County (north of the southern section of the Comanche National Grassland), where massasaugas are moderately abundant. In at least one locale, in Lincoln County, desert massasaugas are quite

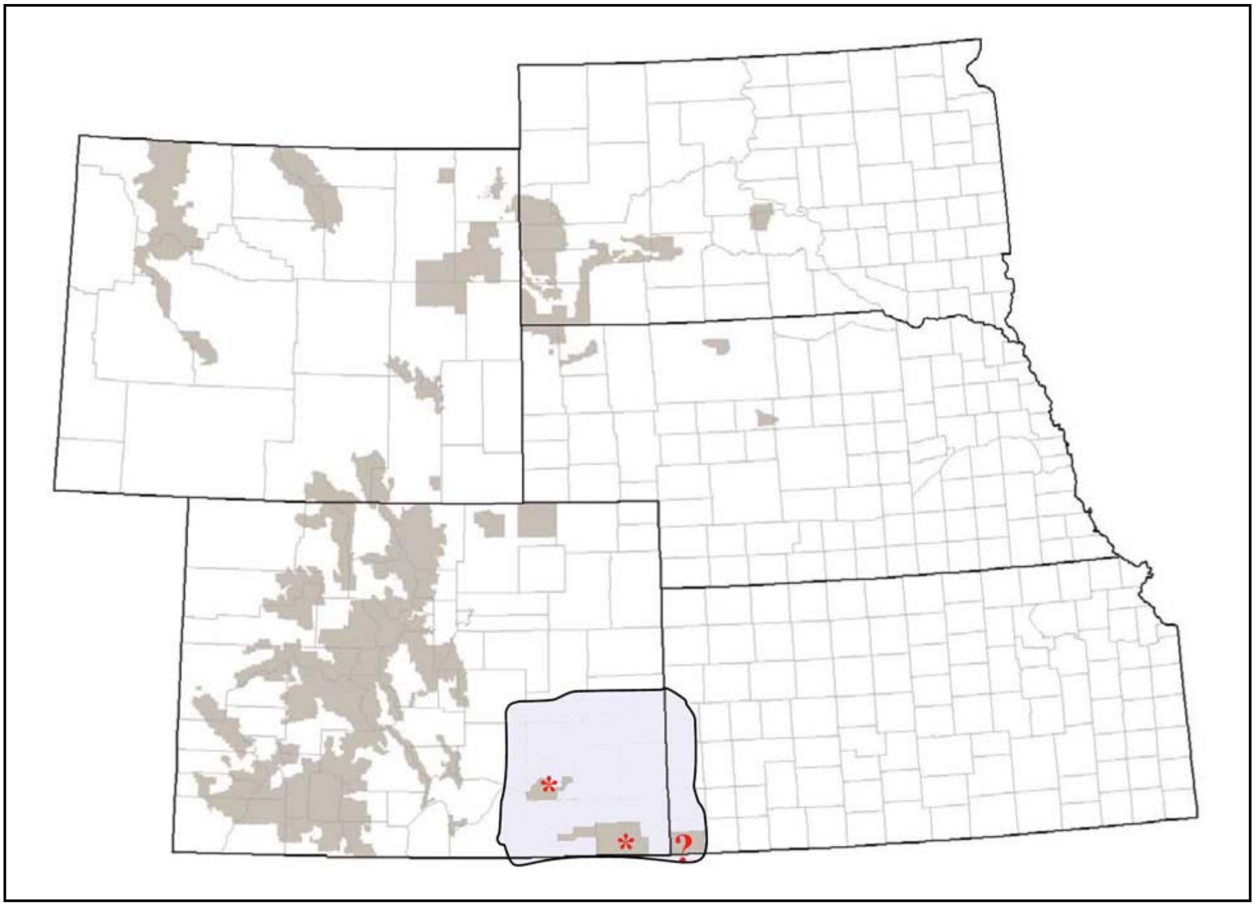

Figure 5. Distribution of the desert massasauga in USDA Forest Service Region 2. Although the desert massasauga is known to occur only on the northern and southern sections of the Comanche National Grasslands (*) in appropriate shortgrass prairie habitat within National Forest System lands (light grey shading), it is broadly distributed in southeastern Colorado and likely also occurs in southwestern Kansas and northeastern New Mexico (light purple shading). Occurrence in appropriate habitat on the Cimarron National Grassland (?) is likely but has not been documented, despite survey work conducted there (Collins and Collins 1991).

common, and abundance trends in this population likely have been stable for some time (we have documented abundance in this population only since 1995).

Desert massasauga populations in Colorado are the largest known (Mackessy 1998a) and appear to be stable in some areas. As such, they are of particular conservation value and concern. With a bit of foresight and some proactive protective measures, Colorado populations may remain the most stable of all desert massasauga populations (see below).

Activity and movement patterns

Massasauga rattlesnakes are active in Colorado from approximately mid-April until late October. The earliest date a snake was found was 13 April, when two dead-on-road adult snakes were located within 100 m of each other. Since these snakes were discovered some distance from probable hibernation sites, an earlier date of emergence from hibernacula is probable. The latest date a snake was seen active (crossing a road) was 15 October in 1995. A radio-tagged snake (see below) was found above ground next to a rodent burrow, which it used as a hibernaculum, on 12 November, so it is probable that snakes remain locally active if surface temperatures are sufficiently high. Snakes were found most commonly in September, October, and April and were least commonly encountered from May through August (**Figure 8**). The increased capture success at the beginning and end of the activity season is due to the seasonal migration of these snakes to and from hibernation areas in several localities. Also, because most snakes were found on roads, there could be a bias in the perceived seasonal activity cycle of these snakes.

Based on observations of radio-tagged snakes, desert massasaugas in Lincoln County appear to

Figure 6. Distribution of the desert massasauga in Colorado (Hobert 1997, Hobert et al. 2004). New localities (■) are those recorded since Hammerson (1986) and are largely a result of survey work conducted in southeastern Colorado from 1995 through 1997 (Mackessy 1998a).

hibernate individually; snakes were never observed together. This is in strong contrast to the synoptic prairie rattlesnake (*Crotalus viridis viridis*). A communal den of more than 20 prairie rattlesnakes, also utilizing a rodent burrow, was found within 100 m of the rodent burrow utilized by desert massasauga A-8 as a hibernaculum (Mackessy 1998a). However, in 2005 we obtained evidence that massasaugas may be sharing a larger nearby prairie rattlesnake hibernaculum; several massasaugas were found basking at the entrance to this den site (Wastell and Mackessy unpublished data).

Although habitat utilization studies have been conducted on the eastern massasauga (Reinert and Kodrich 1982, Weatherhead and Prior 1992, Johnson 2000), there was no information available for the desert massasauga. All populations of the desert subspecies are very different in habitat requirements from the western and eastern subspecies, so results from previous studies may be only partially relevant at best for the desert massasauga. In light of the status of the Colorado populations of the desert massasauga as a state Species of Special Concern (Colorado Division of Wildlife designation), the apparent isolation of this population from others in Kansas and New Mexico, and the paucity of information available on the life history of the desert massasauga, the lead author conducted a radiotelemetric study of massasaugas in south Lincoln County of Colorado (Manzer and Mackessy unpublished results). Radiotelemetry studies provide an efficient method for obtaining information on activity patterns, habitat utilization, and movement of otherwise cryptic and secretive species like the massasauga, data that are essentially unattainable by any other methods (Reinert 1992). Results of this study (conducted on a private ranch in 1997 and 1998) have provided information

Figure 7a. Typical shortgrass prairie habitat of the massasauga rattlesnake in Lincoln County, Colorado. Dominant vegetation includes grama grasses, buffalograss, and sand sage. Photograph taken in fall.

Figure 7b. The same general habitat in late spring. Note that ranching of cattle with rotation of herds in pastures is compatible with massasauga abundance, and mild grazing is likely beneficial to maintenance of native shortgrass prairie.

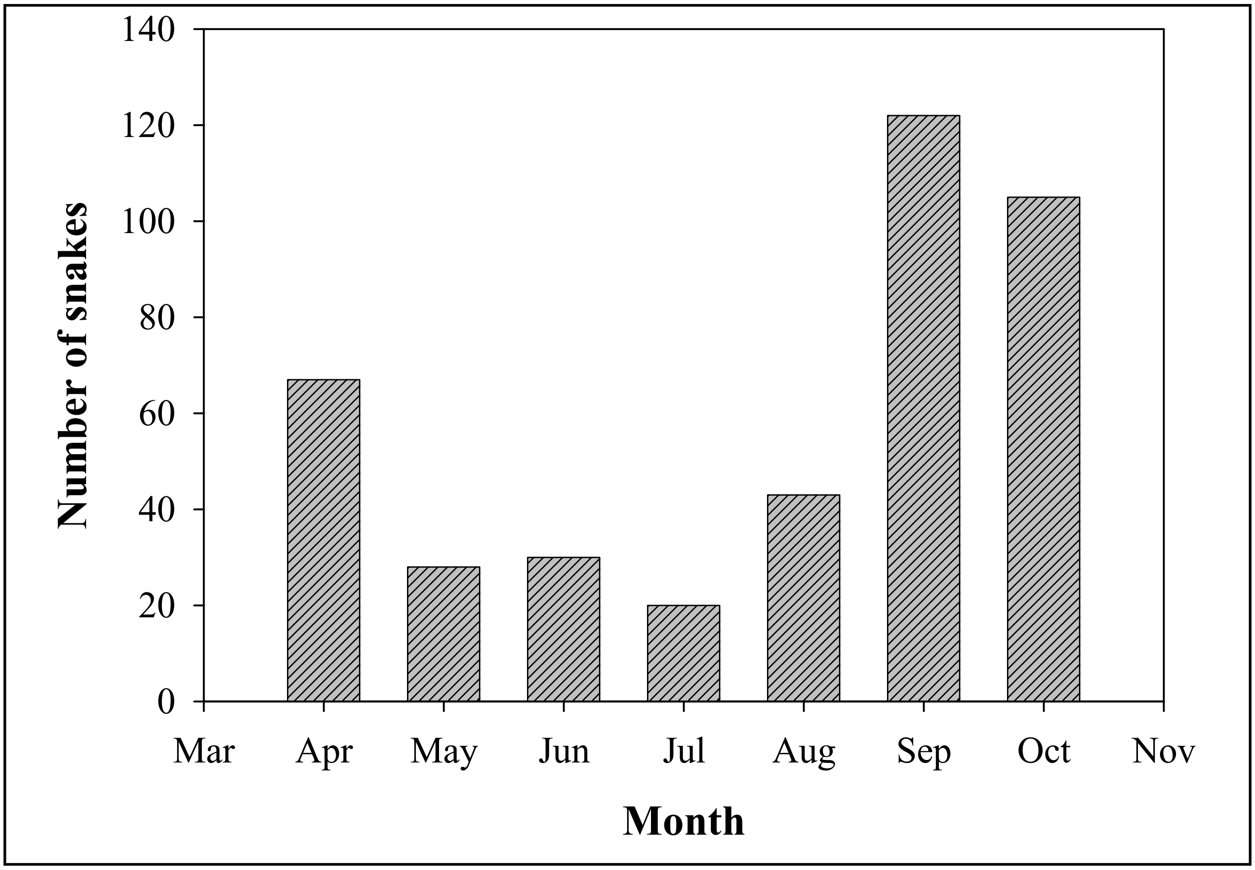

Figure 8. Desert massasauga encounters per month in southeastern Colorado from 1995 through 1997. Data include both live and road-killed encounters; approximately 35 percent of all encounters were road-killed snakes

on habitat preference and utilization, activity patterns, and effect of ambient temperature on behavior and hibernation sites.

The study area ranges in elevation from approximately 1,380 to 1,470 m (4,527 to 4,823 ft.) and is divided along the north/south axis by a dirt road. East of the road, the area is characterized by gently sloping, grass-stabilized sandhills and loose sandy soils. The dominant vegetation of the area consists of grama grasses (*Bouteloua* spp.), buffalograss (*Buchloe* spp.), sand sage (*Artemisia filifolia*), scattered yucca (*Yucca* spp.), and dense stands of bluestem grasses (*Andropogon* spp.), a typical mixed-grass prairie association. West of the road, the area slopes gradually downward and contains the lowest elevation of the site (approximately 1380 m [4,527 ft.]); it is thus the drainage basin for the area.

Snakes were tracked for a minimum of 23 days (**Table 2**). Daily movements ranged from 1 to 350 m (3.3 to 1,148 ft.) and were correlated with time of year. A fairly typical movement pattern is shown by snake A8 (**Figure 9**). Snakes were collected on and released just east of the county road, and they promptly moved toward the summer foraging habitat. Line transect surveys and small mammal trapping (>500 trap-nights) demonstrated that this area had a much more abundant prey base than the area west of the county road. Potential prey observed or trapped included lizards (*Cnemidophorus sexlineatus*, *Holbrookia maculata*, *Sceloporus undulatus garmani*), small rodents (*Dipodomys ordii*, *Onychomys leucogaster*, *Perognathus flavescens* and *P. flavus*, *Reithrodontomys megalotis*), and centipedes (*Scolopendra* spp.).

Linear regression analyses of movements during migration movements (spring and fall) and foraging movements (summer) were possible for two snakes that were tracked the entire season (see also **Figure 9**). When traveling from and to the hibernacula, snakes made essentially straight-line movements (r^2 = 0.82-0.93), differing from movements made in the sandhills during summer (r^2 = 0.1-0.14). All snakes spent the summer months (June-mid-August) in the sandhills, and snakes were commonly found in a resting coil at the base of a sand sage plant (**Figure 1b**). Snakes were typically encountered above ground when ambient temperatures

Table 2. Prey consumed by desert massasaugas (from Holycross and Mackessy 2002).

Prey taxon	***f***	**(%)**
ARTHROPODA	**15**	**(9.1)**
Scolopendra spp.	15	(9.1)
ANURA	**1**	**(0.6)**
Spea bombifrons	1	(0.6)
MAMMALIA	**51**	**(30.9)**
Baiomys taylori	1	(0.6)
Notiosorex crawfordi	3	(1.8)
Onychomys leucogaster	1	(0.6)
Perognathus spp.	1	(0.6)
Perognathus flavescens	8	(4.9)
Peromyscus spp.	1	(0.6)
Reithrodontomys megalotis	8	(4.9)
Unidentified mammal	28	(17.0)
SQUAMATA	**98**	**(59.4)**
Tantilla nigriceps	1	
Cnemidophorus spp.	6	
Cnemidophorus sexlineatus	3	
Cnemidophorus sexlineatus	25	
Holbrookia maculata	20	
Eumeces obsoletus	2	
Sceloporus spp.	4	
Sceloporus undulatus	29	
Urosaurus ornatus	1	
Uta stansburiana	2	
Unidentified lizard	5	
Total	**165**	**(100)**

(taken in shade at 1 m elevation) were 17 to 32 °C (63 to 90 °F) (**Figure 10**), but microhabitat temperature conditions were likely considerably narrower.

Over the course of the active season, massasaugas moved a considerable distance. Although our telemetry studies were hampered by radio failures, data from three snakes indicated that total distance movements may be 2 to 4 km (1.2 to 2.5 miles), an impressive feat for a snake with an adult body size of <400 mm. Estimations of home range were similarly compromised by hardware failures, but estimates for five snakes that were tracked for a minimum of 50 days each were 45 to 413 hectares (111 to 1,021 acres; 95% isopleth harmonic means; Dixon and Chapman 1980) and 35 to 109 hectares (86 to 269 acres; 100% minimum convex polygon; Jennrich and Turner 1969) (Manzer and Mackessy unpublished data). Regardless, these data indicate that desert massasaugas in this population move a considerable distance from the hibernaculum (up to 2 km) and that home ranges are relatively large. These data are comparable to values obtained for eastern massasaugas by Johnson (2000) but are greater than those obtained for eastern massasaugas by Reinert and Kodrich (1982) and Seigel (1986).

Desert massasaugas also show seasonally-dependent changes in daily activity patterns. During the spring and fall, when evening temperatures fall rapidly after sunset, massasaugas were observed crossing roads in morning and late afternoon (essentially crepuscular). In the summer, when daytime temperatures become prohibitive to long diurnal movements in the open, massasaugas adopt a nocturnal pattern of movement and are primarily active between 1900-2100 hrs (Mackessy 1998a). Before we initiated telemetry studies, we believed that this partitioning of activity was near absolute, as massasaugas were never observed in the

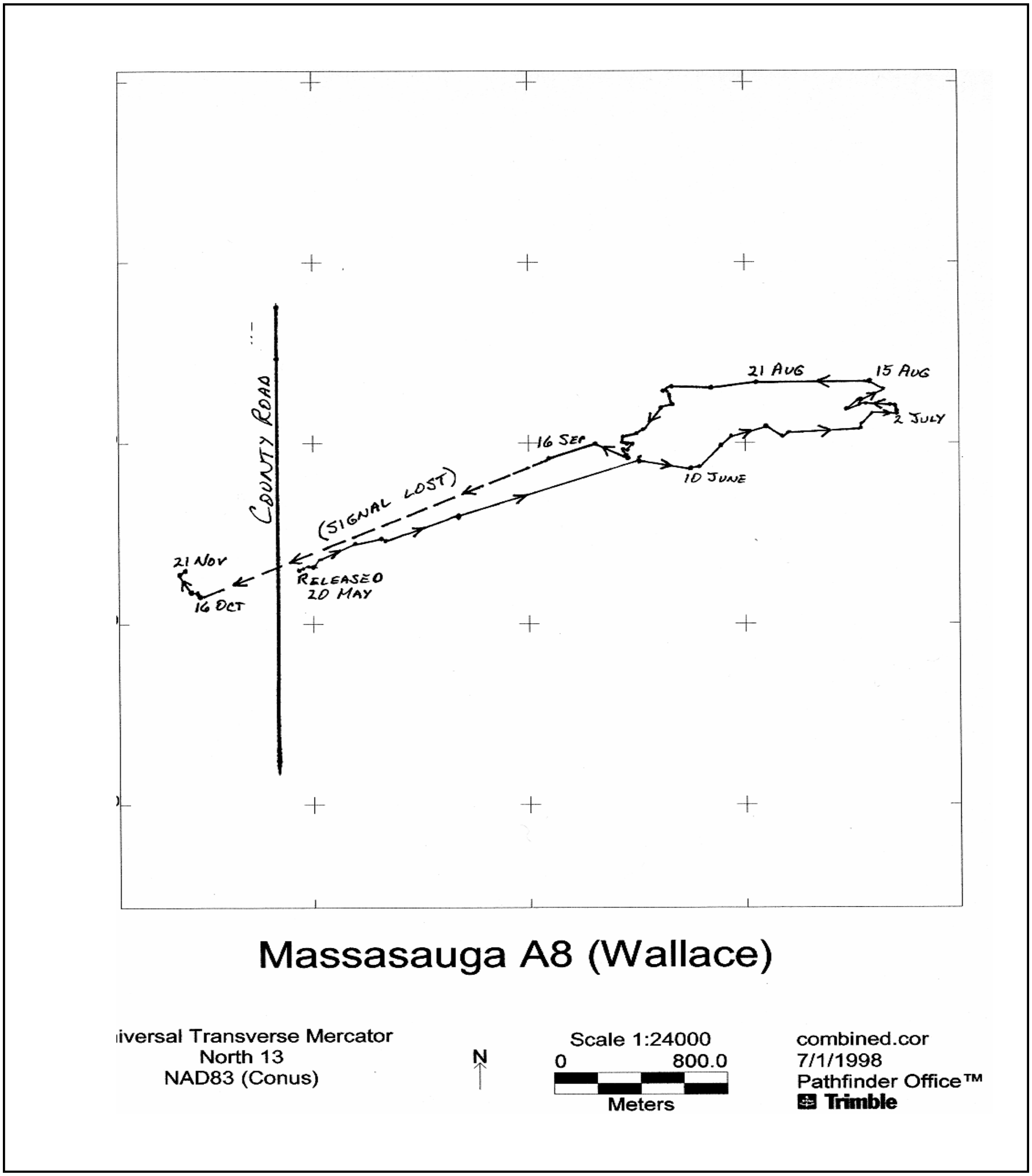

Figure 9. Movement plot for radio-tagged desert massasauga A8; this snake was followed for the entire season (1998) and the general pattern shown is believed to be representative for this population. Hibernacula are on hardpan on the west side of the road, and sand hills are to the east.

day in summer. However, observations of radio-tagged snakes firmly established that desert massasaugas spend a considerable amount of time during the day above ground (**Figure 11**), but they are typically observed in resting coils at the base of sand sage, which provides cover for thermoregulation and predator avoidance (and perhaps avoidance of excess water loss). They are highly cryptic in this microenvironment (**Figure 1b**), and non-radio-tagged snakes were very rarely seen in the field when not crossing roads.

Figure 10. Snout-vent lengths (SVL) of desert massasaugas in Colorado (n=240). Bars above histograms indicate approximate age classes (in years). Data from Hobert (1997) and Hobert et al (2004).

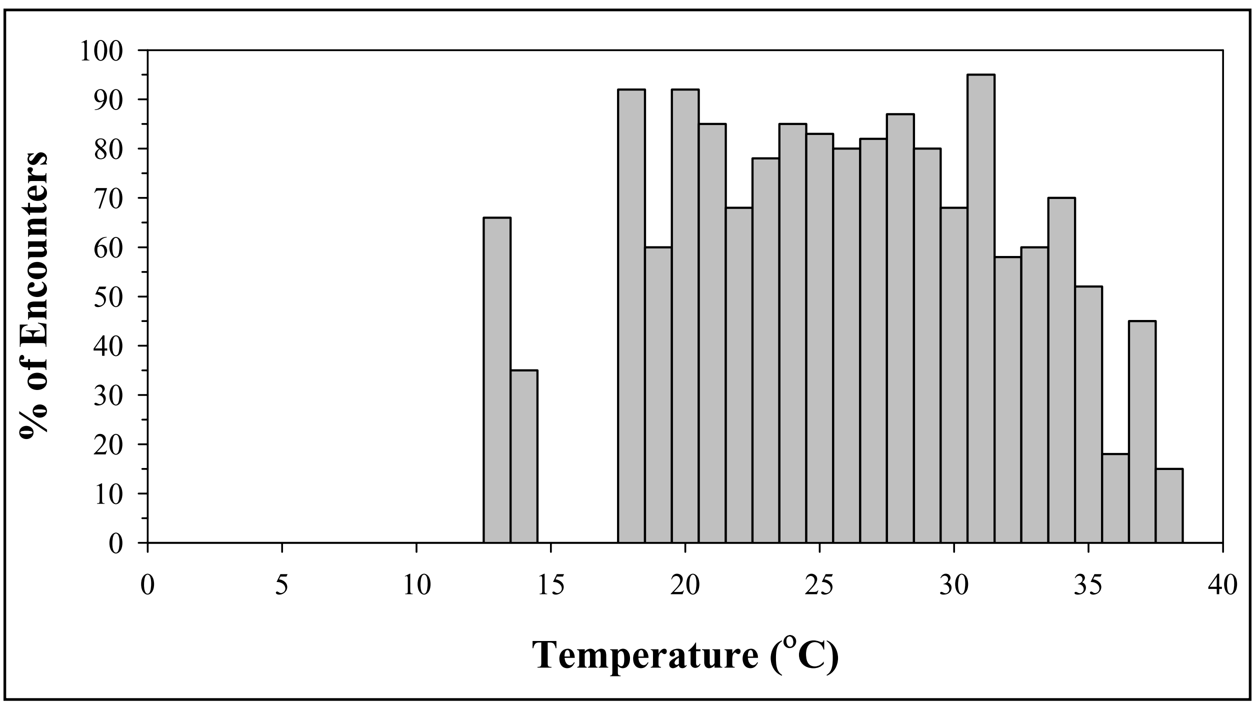

Figure 11. Effect of ambient temperature on aboveground activity of desert massasaugas. For each surface temperature reading, above or below ground occurrence of radio-tagged snakes was recorded. Note that most aboveground sighting occurred between 17 and 34 °C, and below 13 and above 38 °C, all observations were belowground.

Habitat

General requirements

In Colorado, the desert massasauga is most commonly associated with shortgrass prairie habitat with abundant sand sage (*Artemesia filifolia*), buffalograss (*Buchloe dactyloides*), and blue grama (*Bouteloua gracilis*) on aridisols. Specific habitat requirements appear to vary both seasonally and geographically, but in general shortgrass prairie habitat dominated by buffalograss and grama grasses and below approximately 1,500 m (5,500 ft.) elevation is an absolute requirement. Mixed shortgrass-tallgrass habitat, including bluestem grasses, sand sage, and yucca with loose sandy soils, is associated with the largest populations of desert massasaugas observed in Colorado, but snakes frequenting this habitat in summer move to adjacent hardpan shortgrass habitat in the fall to hibernate.

Although desert massasaugas are adapted to more xeric conditions than the western and eastern massasaugas, they are most abundant in areas of shortgrass prairie that are more mesic, specifically in Lincoln County, Colorado. Encounters in more arid portions of the prairie tend to be less frequent, but apparent abundance may be affected by sampling bias because massasaugas are typically active in summer near a refuge (e.g., rodent burrow, sand sage plant) and the snakes are exceptionally cryptic (**Figure 1b**). Radio-tagged snakes were often extremely difficult to see even when the observer was within 1 m of the snake. However, the hypothesis that desert massasaugas in Colorado are more abundant in more mesic regions is supported by linear north-south transect surveys extending from southeastern Lincoln County through Kiowa County. In Lincoln County, where massasaugas are abundant, rainfall is more frequent and the vegetation in general is more lush and denser than in areas to the south. As one approaches the northern edge of Kiowa County, the vegetation becomes sparser and is dominated by buffalograss and grama grasses, sand sage is infrequent, and the habitat is much drier. Massasaugas occur in this area but are much less frequently encountered. This north-south transect has been driven several hundred times in the last 10 years, during both drought and high rainfall years, and the pattern of relative abundance has held.

In general, within National Forest System lands, desert massasaugas are mostly found on intact prairie habitat that has not been tilled or overgrazed by livestock. The desert massasauga appears to be very sensitive to till farming and heavy overgrazing, but is common in several grazed areas where less-intensive pasture rotation of herds is practiced (Mackessy 1998a, Hobert et al. 2004). Where native shortgrass prairie is adjacent to fallow-tilled fields, snakes appear to be able to utilize the modified habitat if it has at least partially recovered (indicated by the presence of both native grasses and shrubs and introduced crop or weed species). A gravid female was found in a rodent burrow in a previously cultivated field that had lain fallow for several to many years and that was characterized by both weedy species and native shortgrass prairie species. Because rodent burrow refugia and hibernacula are destroyed by tilling, the presence of this snake suggests recolonization. Large areas of tilled ground, particularly if repeatedly farmed and with signs of soil loss, are typically devoid of massasaugas and most prey species (e.g., lizards, centipedes, and rodents) upon which they depend. Both of these conclusions are supported by extensive survey data from 1995-1998 (Mackessy 1998a) and by approximately 300 additional locality records obtained between 1999 and 2005 (Mackessy unpublished observations).

Seasonal and life history shifts

Based on telemetry data obtained for snakes in Lincoln County, desert massasaugas remain fairly localized in areas of higher prey densities (better potential foraging success) during summer months (**Figure 9**), and movements during these months are typically short-range (daily movements <1-10 m). Longer, potentially migratory (Dingle 1996) movements of up to 350 m per day have been recorded by snakes moving from and to hibernacula in spring (mid-April to early June) and fall (late August to early October). It is not known whether desert massasaugas rangewide utilize different habitats seasonally, but the areas utilized by radio-tagged snakes during the active period and for hibernation were very different. Soils in the vicinity of hibernacula were dense, moist and loamy (hardpan), with typical shortgrass prairie plant associations, perhaps providing better insulation and more stable soil structure for over-wintering. Fewer species and lower densities of both lizard and small rodent prey were available in this area. In contrast, the area occupied in summer was sandy soil with a mixed-grass (tall and short) species association, and lizard and rodent prey were much more abundant. Additionally, because of the orientation of the sand hills, abundance of rodent burrows, and frequency of sand sage, more precise thermoregulation may be possible in this area.

Desert massasaugas show no apparent life stage-dependent changes in habitat usage, but there are very little data on this, other than the observation of both neonates and adults in the same microhabitat. It is likely that gravid female massasaugas have microhabitat preferences that favor an ability to maintain elevated body temperatures. In 2005 we radio-tagged three gravid female snakes, all of which spent most of the summer in the vicinity of SE to SW-facing rodent burrows, frequently sunning themselves just within the mouth of burrows.

Landscape context

Appropriate habitat for the desert massasauga occurs over a broad area of southeastern Colorado and southwestern Kansas (e.g., northern section of Comanche National Grassland). However, in many areas, including much of the eastern portions of Kit Carson, Cheyenne, and Kiowa counties and large parts of the southern section of the Comanche National Grassland in Baca County, habitat alteration (primarily farming) has created large tracts of unusable habitat, leaving a discontinuous mosaic of appropriate native shortgrass prairie habitat. Although cattle grazing *per se* is compatible with conservation of the desert massasaugas, and ranching is highly preferable to other extractive land uses, some regions of formerly usable habitat are severely degraded due to overgrazing. Partial recovery of this habitat could occur with the removal of cattle, but the time frame for recovery sufficient for recolonization from adjacent intact habitat is likely lengthy. Similarly, recovery of at least part of the native shortgrass flora appears to be sufficient for recolonization of farmed lands by desert massasaugas (based on observations in southern Lincoln County), but again, the time necessary for sufficient recovery is unknown and is probably lengthy.

Absolute home ranges are unknown, but based on our preliminary telemetry data, the home range of a desert massasauga may encompass 100 to 1000 acres. It is highly unlikely that home ranges are utilized exclusively, and the very high densities of massasaugas found in the Lincoln County population suggest extensive home range overlap. From a management perspective this has both good and bad points. One the one hand, it suggests that high density populations could be maintained on relatively small total continuous habitat (perhaps 500 to 1000 acre preserves). On the other hand, the fact that snakes make long-distance movements indicates that the shape and spatial orientation of preserves must be considered. If the habitat occupied by the southeastern Lincoln County population is indicative of optimum habitat requirements, then areas with both shortgrass and mixed-grass habitat will be required to support highest densities on the smallest continuous plots possible. Furthermore, provision for interconnected summer and over-wintering habitats are essential.

Food habits

Food habits of the desert massasauga specifically and the species in general were recently described (Holycross and Mackessy 2002), and the following is derived from this paper. In Arizona and New Mexico we recorded 155 field encounters (captures + recaptures + dead-on-road: 132 Arizona, 23 New Mexico) with 146 individual desert massasaugas (124 Arizona, 22 New Mexico). Seventy-one (63 Arizona, 8 New Mexico) of these encounters yielded 84 identifiable prey (75 Arizona, 9 New Mexico). In Colorado, 32 of 80 snakes encountered dead-on-road (1995-1998) contained remains of 33 identifiable prey, and feces collected from 21 live specimens (1995-1996) yielded 23 prey. Twenty-three of 64 museum specimens (36 percent) examined, exclusive of those from field work, yielded 25 identifiable prey (9 Arizona, 2 Colorado, 14 New Mexico).

From our three populations of desert massasauga, we identified remains of 97 lizards (58.8 percent), 51 mammals (30.9 percent), 15 centipedes (9.1 percent), one toad (0.6 percent, *Spea bombifrons*, Colorado), and one snake (0.6 percent, *Tantilla nigriceps*, central New Mexico). Identifications of lizards and mammals are provided in **Table 2**. All 15 centipedes were identified as *Scolopendra* spp., which, like lizards, were typically swallowed headfirst. Seventeen snakes contained two or more prey, and one snake contained remains of three genera of lizards. Of the 165 prey identified, 60 were identified from remains in the stomach and 105 from the colon or feces.

Predator snout-ventral length (SVL) significantly differed among prey categories (Kruskal-Wallis test, $H_{(2)} = 7.90$, $P = 0.01$; **Figure 12a**). Snakes that ate mammals were longest (mean SVL = 362 ± 7 mm, $n = 51$), followed in turn by those that fed on centipedes (349 ± 12 mm, $n = 15$) and lizards (329 ± 8 mm, $n = 95$). Snakes that fed on *Cnemidophorus* spp. ($n = 34$), *Sceloporus* spp. ($n = 33$), and *Holbrookia maculata* ($n = 19$) did not significantly differ in SVL (Kruskal-Wallis test, $H_{(2)} = 2.13$, $P = 0.34$). Juveniles and adults contained similar proportions of centipedes, but juveniles contained significantly more lizards and fewer mammals ($G_{\text{Williams}} = 10.8$, $df = 2$, $P < 0.01$). Diet was

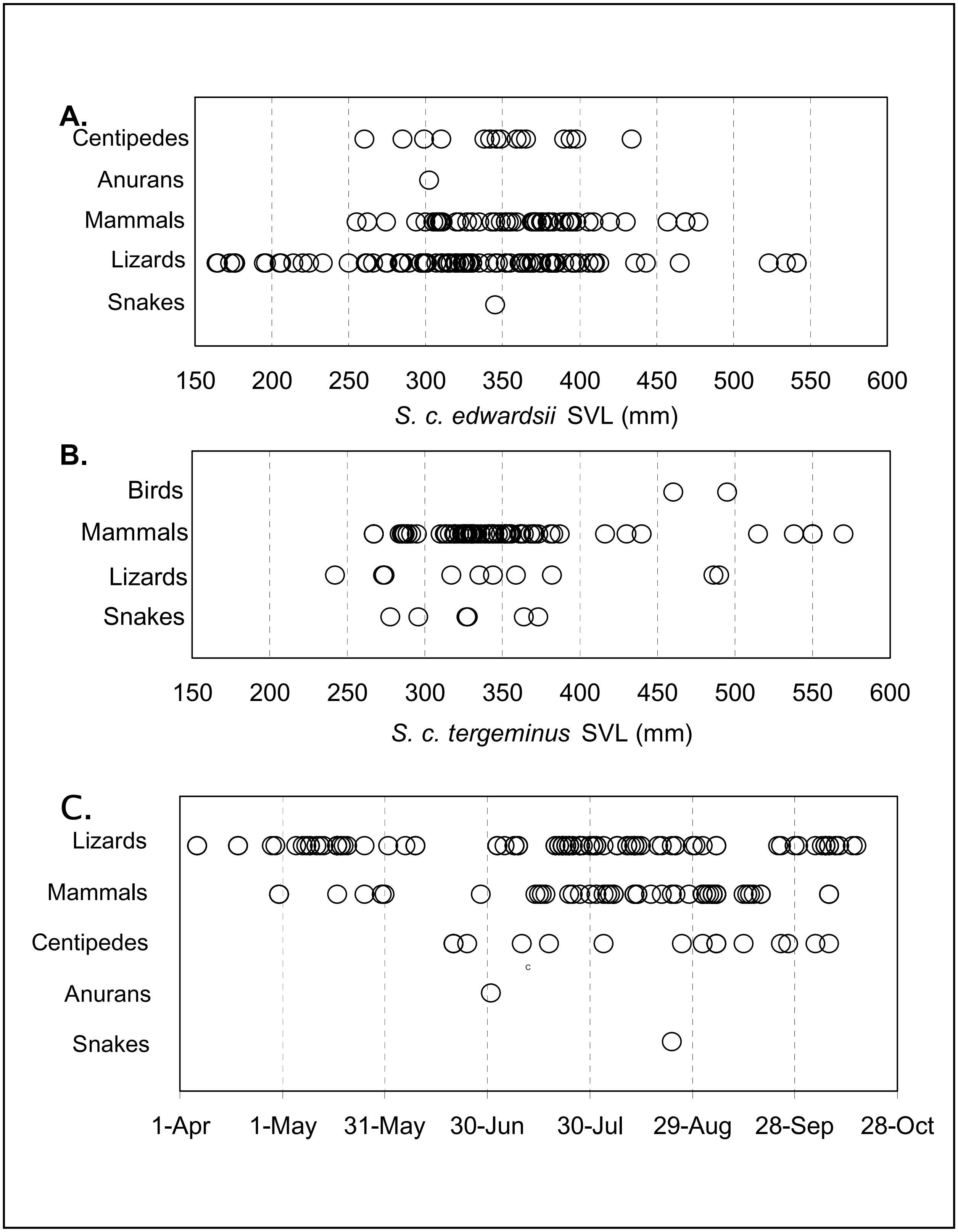

Figure 12. Prey class consumed by desert massasaugas (A) or western massasaugas (B) as a function of size. Note the strong dependence of all size classes of desert massasaugas on lizards. (C). Prey preference of desert massasaugas as a function of time of year. All figures from Holycross and Mackessy (2002).

independent of sex (G_{Williams} = 0.7, *df* = 2, *P* = 0.70) and source (stomach vs. colon/feces) of sample (G_{Williams} = 5.8, *df* = 2, *P* = 0.06). Centipedes and mammals appear to be taken more frequently later in the foraging season (**Figure 12c**). Proportion of prey classes consumed by desert massasaugas differed among populations (G_{Williams} = 14.0, *df* = 4, *P* = 0.007; **Table 3**). However, all pair-wise comparisons (AZ-CO, AZ-NM, CO-NM) between populations comprised non-significant subsets (*G* = 1.7, 10.3, 11.7 respectively) of this analysis. The small New Mexico sample contained proportionately more centipedes and fewer mammals than the other two samples.

From the Texas western massasaugas that we examined, we identified remains of 70 mammals (79.5 percent), 10 lizards (11.4 percent), six snakes (6.8 percent), and two birds (2.3 percent). Mammals consisted of 39 soricids (four identified as *Cryptotis parva*), 13 cricetids, two heteromyids (*Perognathus* spp.), one geomyid, and 15 unidentified further. Lizards consisted of five *Cnemidophorus* spp. and five unidentified skinks. One snake was identified as *Tropidoclonion lineatum*. We detected remains of two prey species in five snakes: mammal + mammal (*n* = 2), snake + mammal (*n* = 2), and lizard + mammal (*n* = 1). Orientation of prey remains in the stomach suggested that 18 mammals, three *Cnemidophorus* spp., three skinks (identified from tails in the stomach), two snakes, and one bird were consumed headfirst whereas one mammal was consumed rump first. Proportions of prey classes for this population are provided in **Figure 12b**.

In comparisons among subspecies, we found that proportion of mammals vs. squamates depended on source population (G_{Williams} = 120.8, *df* = 6, $P \approx 0$). The Michigan, Missouri, and Wisconsin samples comprised a non-significant subset of this analysis (*G* = 4.3), as did the Arizona, Colorado, and New Mexico samples (*G* = 3.3). Interestingly, the Michigan, Missouri, and Texas populations also comprised a non-significant subset (*G* = 1.9). Snake SVL did not significantly differ between desert massasaugas (pooled) and western massasaugas (our sample from Texas) that ate squamates (ANOVA, $F_{(1,110)}$ = 0.35, P = 0.56) or mammals (ANOVA, $F_{(1,119)}$ = 0.89, *P* = 0.35). Nevertheless, proportion of squamates vs. mammals consumed by 300 to 400 mm SVL desert massasaugas and 300 to 400 mm SVL western massasaugas from Texas was dependent on subspecies (G_{Williams} = 31.9, *df* = 1, *P* <0.01; **Figure 12**).

Lizards comprise a surprisingly large proportion of the adult diet of desert massasaugas relative to the diet of conspecifics and to the prevalence of mammals in the diet of many northern pit vipers (Mushinsky 1987, Ernst 1992). Ontogenetic shifts in diet account for prevalence of lizards in the diet of some rattlesnakes (Mackessy 1988, Holycross et al. 2002, Mackessy et al. 2003), but only partially explain their prevalence in the diet of desert massasaugas. Clearly, desert massasaugas <250 mm SVL feed exclusively on lizards, probably because these snakes are physically incapable of ingesting even small rodents. However, squamates (lizards) are consumed 1.5 times more often than mammals even after these gape-limited predators exceed 300 mm SVL and begin to consume a variety of small mammals (**Figure 12a**).

The high number of solitary centipede records suggests directed foraging on live centipedes rather than secondary ingestion or scavenging. Large centipedes are not uncommon in the diets of other rattlesnakes, including *Sistrurus miliarius* (Hamilton and Pollack 1955), *Crotalus enyo* (Taylor 2001), *C. willardi* obscurus (Holycross et al. 2002), and *C. lepidus klauberi* (A.T. Holycross, unpublished data). Although foraging behaviors associated with mammalian prey

Table 3. Movement parameters of radio-implanted desert massasaugas in Lincoln County, Colorado. Data from Manzer and Mackessy, in prep.

Snake ID	Sex	Days tracked	Dates tracked (m/d)	Straight line distance moved (m)	Home range (95% harm. mean; ha)	Home range (convex polygon; ha)
A-1	M	41	5/20-7/10	994	2.04	6.13
A-3	M	56	9/15-10/30	1,600	44.9	35.1
A-4	F	94	5/20-9/28	2,350	117.7	94.2
A-8	M	100	5/20-10/30	3,442	413.0	108.8
B-2	M	63	5/28-10/4	1,665	50.7	88
B-3	M	36	5/28-7/2	778	31.2	76.7
B-4	M	28	5/28-7/8	2,758	80.5	50.7

A-x = snakes tracked in 1997; B-x = snakes tracked in 1998.

have been studied extensively, very little is known of how rattlesnakes forage on centipedes. Nevertheless, it is likely that centipede-eaters have evolved specific adaptations for foraging on this fractious and venomous prey. For example, Rubio (1998) wondered if centipede-eaters are resistant to centipede venom. Several observations suggest centipede-specific prey-handling behaviors in *C. lepidus*, *C. willardi*, and desert massasaugas (Rubio 1998). Regardless of how centipedes are envenomated and handled, our observations indicate that desert massasaugas usually ingest them headfirst.

The diets of the three desert massasauga populations are essentially homogeneous in both intra- and inter-subspecific comparisons. Not only do individuals from these populations consume similar proportions of broadly defined taxa, but they also consume many of the same prey genera and species (e.g., *Holbrookia maculata*, S*celoporus undulatus*, *Cnemidophorus* spp.). Likewise, Wisconsin and Michigan eastern massasauga and Missouri western massasauga populations all consume similar proportions of mammals vs. squamates and consume similar prey genera. Thus, similarities within and differences among the diet of these eastern and western groups are not limited to proportion of mammals vs. squamates consumed but extend to the taxa of mammals and squamates consumed. Populations in Arizona, Colorado, and New Mexico appear to rely primarily on harvest mice (*Reithrodontomys* spp.) and pocket mice (*Perognathus* spp.) while Michigan, Wisconsin, and Missouri populations rely chiefly on voles (*Microtus* spp.) and shrews (*Blarina* spp. and *Sorex* spp.) and occasionally jumping mice (*Zapus* spp.). Correspondingly, Arizona, Colorado, and New Mexico populations rely heavily on lizards and rarely eat snakes, whereas snakes are the only squamates documented in the diet of Michigan, Wisconsin, and Missouri populations and were usually consumed by juveniles (Keenlyne and Beer 1973, Seigel 1986, Hallock 1991). The Texas population of western massasaugas did not significantly differ from the Michigan and Missouri populations in proportion of mammals vs. squamates consumed, and they likewise consumed a high proportion of shrews. Infrequent consumption of ranid frogs and the absence of centipedes also suggest primary dietary affiliations with eastern populations. The Texas sample of squamates consisted of similar proportions of snakes and lizards. Hence, the Texas population appears intermediate between the divergent diets of eastern and western groups, but it appears to have more diet commonality with eastern groups.

Breeding biology

Breeding phenology

Reproduction in the desert massasauga was described recently by Goldberg and Holycross (1999), and the following discussion is largely from this paper. Snakes examined were from Arizona and Colorado. For Arizona, females (n = 39) measured 380 mm mean SVL (± 36.5 mm SD, range = 329 to 523 mm), males (n = 20) measured 368 mm (± 60.1 SD, range = 298 to 541 mm), and neonates (n = 4) measured 168 mm (± 5.9 SD, range = 162 to 176). From Colorado, females (n = 7) measured 358 mm (± 26.0 SD, range = 330 to 398 mm), males (n = 17) measured 374 mm (± 55.2 SD, range = 280 to 473 mm), and neonates (n = 3) measured 198 mm (± 9.6 SD, range = 188 to 207).

Testicular histology was similar to that reported in the viperid snake, *Agkistrodon piscivorous* by Johnson et al. (1982) and the colubrids, *Masticophis taeniatus* and *Pituophis catenifer* (= *melanoleucus*) by Goldberg and Parker (1975). In the regressed testes, seminiferous tubules contained spermatogonia and Sertoli cells. In recrudescence, there was renewal of spermatogenic cells characterized by spermatogonial divisions; primary and secondary spermatocytes and spermatids were sometimes present. In spermatogenesis, metamorphosing spermatids and mature sperm were present. Monthly distribution of stages in the testicular cycle of Arizona and Colorado samples were combined, as no obvious phenological differences between them were noted. The smallest reproductively active male (spermiogenesis in progress) measured 280 mm SVL. Males measuring less than 280 mm SVL were excluded from the study (Goldberg and Holycross 1999) to avoid bias from including sub-adults in the analysis. This size is smaller than the minimal size for female reproductive activity (329 mm SVL) found in this study and suggests that males mature at an earlier age than females. When considered with size class/frequency distributions (**Figure 10**), these data indicate that male desert massasaugas become sexually mature in the end of their second year or the start of their third year while females become sexually mature during their third year of life.

Small sample size prevented a complete description of reproductive phenology; however males were found undergoing spermiogenesis in June through October. Histological examination of vasa deferentia revealed sperm present in males (# present/# examined) in the following proportions: April 7/7, May 3/3, June 7/7, August 2/2, September 4/4, and October 1/1;

examination of the epididymes revealed sperm present in the following proportions: April 3/3, May 1/1, July 0/1, August 1/2, and October 1/1. The testicular cycle of desert massasaugas appears to fit the aestival spermatogenesis category of Saint Girons, in which spermiogenesis ends in September or October; a variety of New and Old World snakes have testicular cycles fitting this pattern (Saint Girons 1982, Seigel and Ford 1987). Male kidney sexual segments were enlarged and contained secretory granules as follows: April 7/7, May 1/1, June 1/1, August 3/3, September 4/4, and October 3/3. Mating is known to coincide with hypertrophy of the kidney sexual segment (Saint Girons 1982).

Ernst (1992) suggested that the breeding period for massasaugas extended from March to November. Based on observations of captive snakes, Lowe et al. (1986) reported that desert massasaugas in Arizona mate in both spring and fall. Findings of sperm in the vasa deferentia of desert massasaugas from April through October suggest that males are capable of inseminating females throughout this period. In the lab, desert massasaugas were observed exhibiting courtship behavior in late June (Chiszar et al. 1976). In Colorado, a male was found in the field lying on top of a female on 3 September, and a male and a female were observed on the side of a prairie dog mound within 10 cm of each other on 24 April. In 2005 we observed two incidences of copulation in the field in late September. These observations indicate that desert massasaugas in Colorado breed in the fall, but the possibility of copulation in the spring cannot yet be ruled out.

To avoid the possibility of including sub-adult females in the analysis of the ovarian cycle, females below the minimum size of the smallest gravid female (329 mm SVL) found during the study were excluded. Only 15 percent (7/46) of the females were reproductively active (vitellogenic follicles or gravid; 3/7 Colorado, 4/39 Arizona). Proportions of reproductively active females from Arizona (combining data from museum specimens and captured and released females) were: May 0/2, June 2/2, July 1/2, August 1/18, and September 0/8. For Colorado females, using data from museum specimens, the ratios were: April 1/2, May 2/2, and August 0/3. These observations indicate that only part of the desert massasauga female population reproduces each year, as previously suggested for eastern massasaugas by Reinert (1981), who found 15/26 (58 percent) gravid adult females in Pennsylvania. In Missouri, the percentage of reproductive females varied from 33 to 71 percent over three years (Seigel 1986). Seigel et al. (1998) reported a significantly lower percentage (23 percent) of gravid female massasaugas from Missouri during 1993-94, after a severe flood in 1993, as opposed to 50 percent gravid between 1979 and 1983. The data, gathered in Arizona (four seasons) and Colorado (two seasons), may suggest that females from these populations reproduce less frequently than other populations studied. In view of the findings of Seigel et al. (1998), however, one must consider that percentages of gravid females may vary markedly in different years.

Phenology of parturition was inferred from first appearance of neonates and cessation of the appearance of gravid females during continuous mark-recapture collecting efforts over four years (1993 to 1996), in addition to radio-telemetric observation. A gravid Arizona female collected 2 August 1995 was implanted with a radio transmitter and located daily until she gave birth on ca. 11 September 1995, when she was observed with a single, moist neonate (#3 below). During the course of field studies in Arizona, four neonates were captured and released: (#1) 166 mm SVL, 5.1 g, 6 September; (#2) 162 mm SVL, 3.9 g, 10 September; (#3) neonate with fresh umbilicus, 167 mm SVL, 4.9 g, 11 September; (#4) 176 mm SVL, 3.4 g, 28 September. Three Colorado desert massasauga neonates were collected in early October: (#1) 188 mm SVL, 5 October; (#2) 207 mm SVL, 5 October; (#3) 200 mm SVL, 10 October. Based on the captive-born Colorado litter (see below), these wild-caught snakes had grown over 20 percent in the month following parturition. We have also found road-killed neonates in Lincoln County, Colorado as early as 1 September.

According to our observations, desert massasaugas in Arizona and Colorado give birth from late August through September, generally later in the year when compared with species-wide reports of parturition from late July to late September (Ernst 1992). All of the Arizona and Colorado neonates weighed less than the range of neonatal weights reported for the species as a whole (8 to 10 g) by Ernst (1992).

Breeding behavior

Breeding behavior of desert massasaugas have not been observed in the field, but courtship behaviors were observed for captive desert massasaugas from Colorado (Chiszar et al. 1976). The male snake rubs his chin on the female's head and neck, and his tail is looped over the female's tail, perhaps as a precopulatory behavior. Copulation involves insertion of one of the hemipenes in the female's vent, and snakes may remain coupled for several hours.

Parental behaviors have been observed for several viperids (Greene et al. 2002), and these are best documented for northern blacktailed rattlesnakes (*Crotalus molossus molossus*) and dusky pygmy rattlesnakes (*Sistrurus miliarius barbouri*). Neonate blacktailed rattlesnakes remain associated with the mother for approximately 10 days after birth, about the same time as their first shed. Presumably, remaining with the much larger adult during the first week or so of life may increase initial survivorship due to decreased predation. Adult female and neonate pygmy rattlesnakes also associate for at least a short period after birth. Laboratory trials with females and their neonates demonstrated that female pygmy rattlesnakes positively associated with their young. A female western massasauga was found with 11 neonates in pre-shed condition, and several occurrences of a female attending neonates have been recorded for the eastern massasauga (Swanson 1930, Reinert and Kodrich 1982, Johnson 2000). A phylogenetic analysis of parental care in viperids suggests that it is a shared, derived character of the Crotalinae (Greene et al. 2002), and as such, it would be expected to occur in desert massasaugas as well.

In August 2005, two radio-tagged snakes gave birth to four and five offspring on 24 August and 25 August, respectively (Wastell and Mackessy unpublished data). Neither the females nor the offspring were collected or disturbed, and they remained associated (in same burrow, sunning together) for approximately five days post-parturition. These observations suggest that female attendance occurs in desert massasaugas.

Fecundity and survivorship

On 24 July 1998, the lead author collected a gravid female in Lincoln County, Colorado. This female was held in captivity until parturition specifically to determine when birth occurred, what litter size was for this population, and how large neonate snakes were. The female was allowed to thermoregulate via a HotRock heated stone and was fed twice during the month before birth (one 4-5 g mouse pup each time); birth lengths and masses of neonates should therefore have been affected minimally. At the time of capture, the female weighed 54.0 g; after the birth of seven offspring she weighed 39.9 g (difference of 14.1 g). Length, mass, and first venom yield data for neonate snakes are presented in **Table 4**. Average SVL for neonates was 148 mm, tail length was 16 mm, and mass was 3.46 g. Interestingly, the date of birth (24 August) is identical to that observed in the field in 2005.

Litter sizes from the Arizona sample were determined by palpating live females found in the field. Colorado litter sizes were determined through counting enlarged follicles of preserved specimens and from the one female found gravid who was held until parturition. Mean litter size for Arizona females was 5.8 ± 1.7 SD (n = 4, range = 4 to 8), and for Colorado females it was 5.3 ± 1.4 SD (n = 3, range = 4 to 7). Mean litter size of both populations pooled was 5.6 ± 1.5 SD (n = 7, range = 4 to 8). Note that these data differ from those presented by Goldberg and Holycross (1999) because the data presented here include information from the Colorado litter born in captivity.

There is considerable variation in massasauga brood sizes in different parts of its range. Fitch (1970) summarized data on 54 massasauga litters (from Klauber 1956) ranging from 2 to 19, and calculated an average litter size of 8.16 ± 0.44 SE. Using different data, Fitch (1985) later reported a range of 3 to 13 for 115 massasauga litters from much of its range in the United States. In this study, litter sizes appeared to increase from east to west and from south to north. Seigel (1986) reported a mean litter size of 6.4 ± 1.9 (range = 4 to

Table 4. Data on desert massasauga litter born 24 August 1998. Female was from Lincoln County, Colorado.

Snake #	S/V length (mm)	Tail length (mm)	Total length (mm)	Mass (g)	Venom (µl)
1	156	17	173	3.7	3.0
2	145	15	160	3.4	5.0
3	150	17	167	3.8	4.0
4	144	18	162	3.5	4.0
5	150	14	164	3.5	5.0
6	156	18	174	3.6	3.0
7	136	13	149	2.7	3.0
Average	**148**	**16**	**164**	**3.46**	**3.9**

Gravid female (field #098-078) was collected 24 July 1998, held in captivity, and allowed to thermoregulate until birth occurred 24 August 1998. Female was 385 mm S/V, 31 mm tail; pre-parturition mass was 54.0 g, post-parturition was 39.9 g.

10) for 17 massasaugas from Missouri and summarized variation in litter size in different parts of the species' range (range = 3 to 19). Keenlyne (1978) reported 11.1 young per female massasauga in Wisconsin (n = 58). Schuett et al. (1984) mentioned two litters of eastern massasaugas from Michigan with 15 young each. Lowe et al. (1986) reported litters of five and seven young born to two captive females from Arizona. While litter sizes of desert massasaugas in Arizona and Colorado from this study (range = 4 to 8; Goldberg and Holycross 1999) are within the ranges previously reported for this species, litter sizes tended towards the lower end of the published ranges for the species.

The size class frequency distribution of 240 desert massasaugas collected in Colorado allowed us to estimate age classes and indicates that the average snake encountered was approximately 3 years old (**Figure 10**). Four-year-old snakes were also commonly encountered, but we found only three snakes that we would consider to be five years of age or older. The relationship of size class and age is uncertain beyond the fourth year, and there may be some unknown factor that biases sampling of older animals. The paucity of snakes of a size unequivocally greater than the fourth year size class suggests that survival past four years of age is unusual for desert massasaugas in Colorado. However, the lead author has held captive animals from the same population for over 14 years, demonstrating the potential for longer lifespans. Predation, persecution by humans (killing), and/or disease may be important factors greatly limiting the survivorship potential for these small rattlesnakes in the wild.

Based on the reproduction study of desert massasaugas by Goldberg and Holycross (1999) and on post-parturition condition of females found in the field in Colorado, reproduction for female desert massasaugas is typically biennial. Females found in the field that had recently given birth typically had poor body muscle tone (discernable upon palpation of post-parturient versus non-reproductive females of equivalent length), and from the few recapture records we obtained for females, body mass was greatly diminished (**Table 5**). For the female that was held until parturition (see above), nearly 26 percent of her body mass was lost.

If the size/age distribution data obtained for the Colorado snakes is accurate (we believe that it is) and if reproduction for females is biennial, then the average adult female desert massasauga in Colorado can be expected to reproduce only once during her lifetime. This indicates that under optimal conditions, the total reproductive output of a female over her entire lifetime would be seven offspring (maximum litter size observed for desert massasaugas from Colorado). Actual reproductive output might be lower (average litter size = 5.6). These comments should be taken into consideration when evaluating the life history model detailed below, because it is probable that the model greatly overestimates reproductive potential, which in turn will greatly affect population recovery potential following local disturbance or extirpation.

Population demography

Life history parameters

Based on size/age distributions (**Table 5**) and the observation that of over 150 snakes marked, we have not recaptured a PIT-tagged snake more than two years post-tagging, survivorship of adults in the Lincoln County, Colorado population appears to be low, most likely not exceeding 4 years total age. The small neonates (total length ~164 mm) would be expected to be vulnerable to heavy predation pressures, and neonate survival is therefore also likely low. Additionally, the low number of second year snakes captured (**Figure 10**) suggests low survivorship. Furthermore, as noted above, the lifetime reproductive output of females is likely quiet low. In spite of these limitations, this population is robust and may be the largest metapopulation of desert massasaugas in the entire range. Conditions for this population appear to be ideal, in terms of habitat and microhabitat availability and condition, abundance of appropriate prey, and lack of significant anthropogenic disturbance. Recruitment to the population via reproduction is likely significant, regardless of relatively low neonate survivorship and female fecundity, because the population is large and total annual reproductive output is therefore high. However, these conclusions also suggest that the desert massasauga may be very sensitive to disruptive changes (see below), as its capacity to rebound from severe population decreases is probably very poor.

Very little is known about social systems in desert massasaugas. Unlike the (often) massive aggregations of snakes at den sites seen among prairie rattlesnakes (Klauber 1956), desert massasaugas appear to hibernate individually (Mackessy 1998a). No records of male-male combat, as occurs among several of the larger rattlesnake species, are known for desert massasaugas, and no intraspecific interactions in the wild have been reported. Therefore, at present, it is not possible to

Table 5. Recapture data for desert massasaugas from the Lincoln County, Colorado population (Mackessy 1998a).

	A-1258 PIT Tag: 22423F2808	A-1261 PIT Tag: 2242286729	A-1352 PIT Tag: 414557374B	A-1354 PIT Tag: 4145490766	A-1361 PIT Tag: 22421B1B79	A-1366 PIT Tag: 2242127528	A-1369 PIT Tag: 414539754C	C-126 PIT Tag: 2242127528
Gender	Male	Female	Male	Male	Male[M]	Female	Female	Male
Capture date	26-Sep-95	26-Sep-95	26-Apr-96	24-Apr-96	24-Apr-96	24-Apr-96	24-Apr-96	10-Sep-96
Initial length (mm)	395/47	365/32	373/47	336/44	320/14	365/31	378/35	375/45
Initial weight (g)	61.8	42.2	47.4	29.0	24.2	36.8	42.2	37.9
Initial rattle#	3I	4C	2I	2I	●	3I	3C	5C
Recapture date	26-Apr-96	4-Sep-96*	4-Sep-96	5-Sep-96	21-Sep-96	5-Oct-96*	5-Sep-96	21-Sep-96
Recapture length	404/47	383/32	390/49	375/45	376/16	385/36	400/37	375/45
Recapture weight	53.6	40.6	51.7	41.4	51.2	36.0	53.2	37.9
Recapture rattle#	4I	3I	3I	4I	●	4I	4C	5C
Recapture interval	211	343	132	133	149	163	133	11
Difference in length	9/1	18/0	17/2	39/1	55/2	20/5	22/2	●
Difference in weight	-8.2	-1.6	+4.3	+12.4	+27.0	-0.8	+11.0	●
Difference in rattle#	+1	-1	+1	+2	●	+2	+1	●

Rattle# - I=incomplete; C=complete. M denotes snake with posterior 2/3 of tail missing. * denotes snake at post-parturition.

comment on potential social systems by extrapolating from interactions known for other rattlesnakes because of actual or potential differences known.

Similarly, patterns of dispersal are unknown for desert massasaugas. Based on the limited movement data we obtained (2 to 4 km annually), hibernaculum egression movements could lead to dispersion from natal habitat, leading to expansion of range and/or recolonization of disturbed habitat that has subsequently recovered (e.g., farmed or overgrazed shortgrass prairie).

Historical factors limiting population growth are likely those processes associated with xerification, including the effects of episodic, prolonged drought that was widespread in the Great Plains during the Holocene (Madole 1994). As mentioned above (see also Holycross and Mackessy 2002), although the desert massasauga is much more adapted to xeric conditions than the other two massasauga subspecies, it still may favor more mesic conditions *within* a generally drier macrohabitat and is more abundant in Colorado in areas showing such characteristics. Lack of tolerance of highly xeric conditions (i.e., desert), coupled with increasing xerification, both natural and anthropogenic, likely limit the expansion of current populations of desert massasaugas.

However, the main factors limiting desert massasauga populations at present are associated with habitat fragmentation and loss. Desert massasaugas are not tolerant of habitat disturbance resulting from tilling or overgrazing, and even in rural areas, roads and the limited developments present serve to disrupt habitat continuity. The effects of dirt and paved roads may be more disruptive than previously believed because as snakes cross these open areas, they are highly vulnerable to predation, and automobile traffic exacts a very heavy toll. For example, of 214 desert massasaugas encountered in the 1997 field season in southeastern Colorado, 82 (39 percent) were found dead on roads (Mackessy 1998a). These conditions are exacerbated if road(s) bisect historical movement pathways (as in the Lincoln County population) since snakes must cross roads at least twice each active season. As habitat fragmentation and loss increase, a critical threshold of minimum habitat size required may be crossed, and populations would be expected to decrease precipitously.

Spatial characteristics

Metapopulation genetic structure, and to a large extent even occurrence, has not been evaluated for the desert massasauga (see also Distribution and abundance section above). Although populations in southeastern Colorado were likely continuous historically, land use practices have resulted in fragmentation into metapopulations of varying size, the structure and dynamics of which are poorly investigated. We identified several apparently viable metapopulations in southeastern Colorado (Mackessy 1998a), but the extent of isolation (or lack thereof) from adjacent metapopulations is not known. Natural drainage features (e.g., Arkansas River) and habitat fragmentation have certainly created discontinuity between the largest known population (Lincoln County) and those found in the two sections of the Comanche National Grassland, and habitat changes due to till farming have likely further isolated the northern and southern section metapopulations. Morphometric and venom biochemistry analyses have not indicated any structuring within or between metapopulations of desert massasaugas in Colorado, but it is unlikely that these tools are sensitive enough to evaluate such relationships. Blood samples obtained from more than 200 live individuals throughout Colorado and stored at –80 °C awaiting time and resource allocation for analysis, and microsatellite or RAPD DNA analysis might address this question (cf. Lougheed et al. 2000).

Genetic concerns

Prior to work in the lead author's lab (Hobert 1997), the massasauga in Colorado was considered to be an intergrade between the western and desert subspecies (Maslin 1965, based on six specimens). However, we have clearly demonstrated that massasaugas throughout Colorado show much greater affinities with the desert massasauga than with the western massasauga (based on morphometrics, diet and habitat, venom biochemistry, and very limited DNA sequencing data), and the Colorado populations are to be considered desert massasaugas. The larger question of whether or not desert massasaugas intergrade/hybridize with western massasaugas in *any* of the supposed contact zones (**Figure 3**) still needs to be addressed.

As indicated above, genetic studies with a focus on population structure have not been conducted on desert massasaugas, but such studies have been conducted on five populations of the eastern massasauga including the most northeastern extent of the species (Gibbs et al. 1997). This study used data from six microsatellite DNA loci to evaluate levels of inbreeding within populations and of genetic differentiation between populations in Ontario, New York, and Ohio. These populations, like many populations of massasaugas rangewide, exist as remnant fragmented populations that are disjunct, and the potential for gene flow between them has essentially been permanently eliminated. All populations sampled differed significantly in allele frequency, and on average, 23 percent of alleles sampled were population specific. Within-population analyses demonstrated a high level of genetic structure, indicating low levels of gene flow and genetic isolation, which the authors believe are naturally occurring, rather than resulting from anthropogenic changes that have resulted in the present discontinuity of populations (Gibbs et al. 1997). Each of these populations is genetically distinct and perhaps locally adapted, making them particularly important from a conservation perspective. However, based on modeling of effects of population fragmentation leading to gene flow restriction, the observed genetic isolation could be deleterious to these populations via the accumulation of deleterious mutations and decreased individual viability (Couvet 2002).

In Colorado and several other parts of the desert massasauga's range, habitat fragmentation has not been as extensive as has occurred for the eastern massasauga. It would be interesting to see if populations of desert massasaugas show similar high levels of genetic structure. I would predict that within Colorado, where distances between populations of desert massasaugas are greater than the populations of eastern massasaugas evaluated by Gibbs et al. (1997), populations would *not* show a high level of structure and genetic distinctiveness. However, comparisons between desert massasaugas from Colorado and from Arizona, southern New Mexico, and Texas likely would indicate genetically distinct populations.

Life history model

The life history described by Ernst (1992) provided the basis for a life cycle graph (**Figure 13**) and a matrix population analysis with a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2000) for the massasauga rattlesnake. The model has three kinds of input terms: P_i describing survival rates, m_i describing fertilities, and B_i describing probability of reproduction (**Table 6**). **Figure 14a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure 14b** gives the corresponding numeric values. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female. The population growth rate (λ was 1.000 based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value is subject to the many assumptions used to derive the transitions and should not be interpreted as an indication of the general well-being and stability of the population. Other parts of the analysis provide a better guide for assessment.

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. Sensitivity is the effect on λ of an **absolute** change in the vital rates (a_{ij}, the arcs in the life cycle graph [**Figure 13**] and the cells in the matrix, **A** [**Figure 15**]).

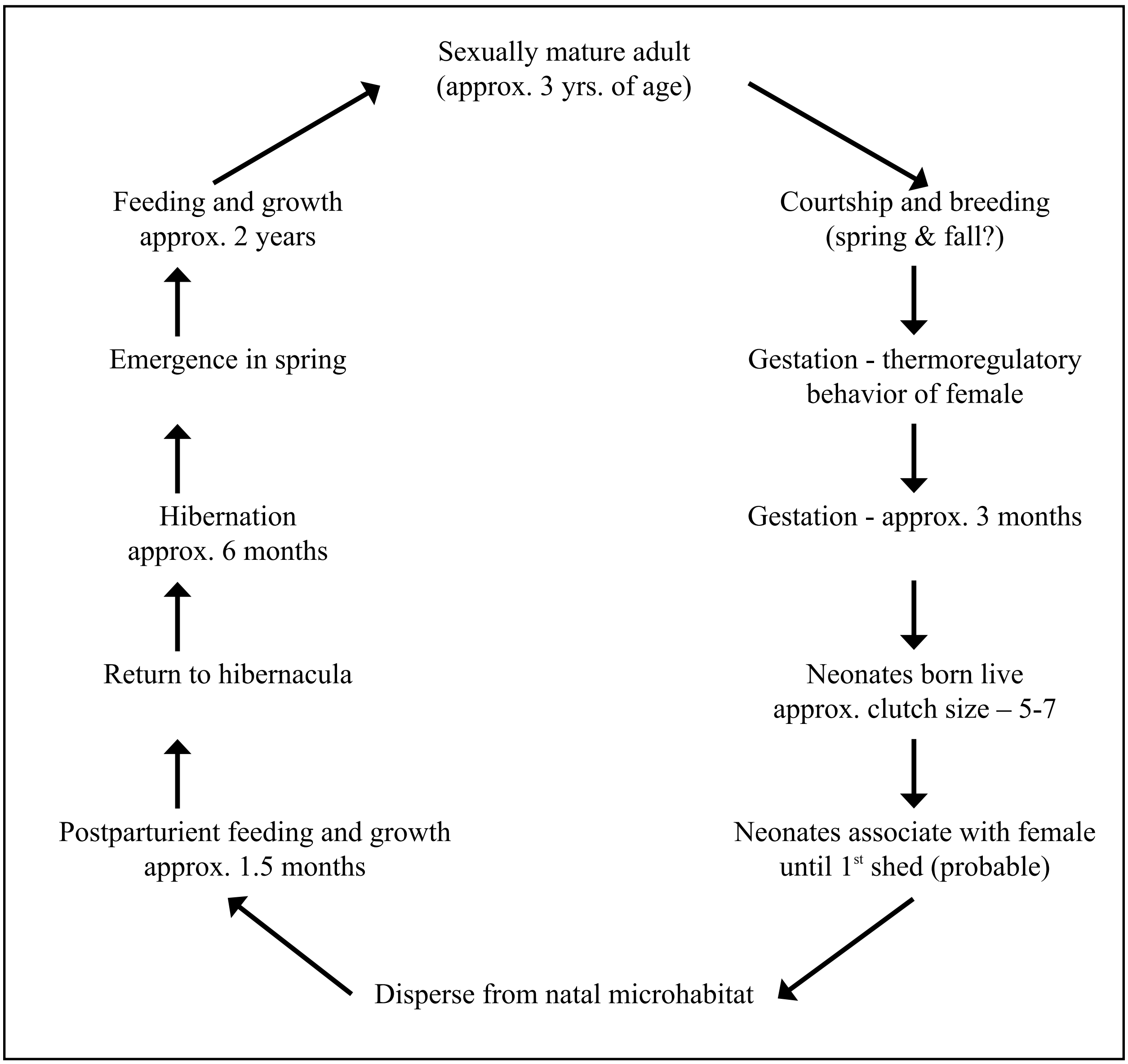

Figure 13. Life cycle of the desert massasauga.

Table 6. Parameter values for the component terms (P_i, m_i, and B_i) that make up the vital rates in the projection matrix for massasaugas.

Parameter	Numeric value	Interpretation
m_3	3	Number of female offspring produced by a female of Age-class 3
m_4	4	Number of female offspring produced by a female of Age-class 4
m_a	5	Number of female offspring produced by a fully developed female
B	0.5	Probability of reproduction
P_1	0.245	First-year survival rate (Age-class 1)
P_j	0.5	Annual survival rate of pre-reproductives (Age-class 2)
P_a	0.8	Annual survival rate of reproductives

Sensitivity analysis provides several kinds of useful information (see Caswell 1989, pp.118-119). First, sensitivities show "how important" a given vital rate is to λ or fitness. For example, one can use sensitivities to assess the relative importance of survival (P_i) and reproductive (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but it could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing λ of endangered species or the "weak links" in the life cycle of a pest. **Figure 15** shows the "possible" sensitivities only matrix for this analysis; one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible – for example, the sensitivity of λ to moving from Age-class 3 to Age-class 2.

In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. For example, any factor that changes the annual survival rate of Age-class 3 females is very likely to cause similar changes in the survival rates of other "adult" reproductive females (i.e., those in Age-classes 4 through 14). Therefore, it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is that the summed sensitivities of l to changes in first-year, pre-reproductive, and reproductive survival are relatively evenly distributed. First-year survival sensitivity is 0.629 (37 percent of total). The summed "pre-reproductive" survival sensitivity is 0.308 (18 percent of total), and the summed "reproductive" survival sensitivity is 0.672 (40 percent of total). Massasaugas show less sensitivity (0.089, 5 percent of total) to changes in fertility rates (the first row of the matrix in **Figure 15**). The major conclusion from the sensitivity analysis is that the survival of all age classes is important to population viability.

Elasticity analyses are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivity analyses. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, a change of 0.5 in survival may be a major alteration (e.g., a change from a survival rate of 90 to 40 percent). On the other hand, a change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and thus largely avoid the problem of differences in units of measurement. The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species.

Elasticities for massasaugas are shown in **Figure 16**. The λ of massasaugas is most elastic to changes in first-year survival (Age-class 1) and the survival of "pre-reproductive" females (Age-class 2), followed by the survival of females at age of

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1			P_aBm_3	P_aBm_4	P_aBm_a	P_aBm_a	P_aBm_a	P_aBm_a	P_aBm_a	P_aBm_a	P_aBm_a	P_aBm_a	P_aBm_a	P_aBm_a	
2	P_{21}														
3		P_j													
4			P_a												
5				P_a											
6					P_a										
7						P_a									
8							P_a								
9								P_a							
10									P_a						
11										P_a					
12											P_a				
13												P_a			
14													P_a		
15														P_a	

Figure 14a. Demographic matrix with symbolic values.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1			1.2	1.6	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	
2	0.245														
3		0.5													
4			0.8												
5				0.8											
6					0.8										
7						0.8									
8							0.8								
9								0.8							
10									0.8						
11										0.8					
12											0.8				
13												0.8			
14													0.8		
15														0.8	

Figure 14b. Demographic matrix with numeric values.

first reproduction (Age-class 3). The sensitivities and elasticities for massasaugas correspond in the rank magnitude of the three most important transitions, a phenomenon that is not always the case in other life histories (*cf*. Technical Conservation Assessments for Townsend's big-eared bat, plains killifish). The early survival rates are therefore the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Partial sensitivity and elasticity analyses assesses the impact on λ of changes in "lower-level terms" (Caswell 2000, pp. 218 and 232). Some transitions (e.g., the F_i) include lower-level component terms (P_i, m_i, and B_i) related to the different kinds of transitions in the life cycle (e.g., survival, fertility, breeding probability terms). Partial sensitivity results indicate that changes in the P_i (survival rates) will have by far the greatest impact on λ (83.8 percent of the total partial sensitivity). Changes in fertility (m_i) will have far less of an impact on λ (1.7 percent of the total partial sensitivity). Changes in probability of reproduction (B_i) will also have less impact on λ (14.6 percent of the total partial sensitivity). Similarly, P_i terms account for 76.2 percent

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1			0.019	0.015	0.012	0.010	0.008	0.006	0.005	0.004	0.003	0.003	0.002	0.002	
2	**0.629**														
3		**0.308**													
4			**0.164**												
5				0.134											
6					0.104										
7						0.080									
8							0.061								
9								0.045							
10									0.033						
11										0.023					
12											0.015				
13												0.009			
14													0.004		
15														0.000	

Figure 15. "Possible" sensitivities only matrix, $\mathbf{S_p}$ (remainder of matrix consists of zeros). The three transitions to which the population growth rate (λ) of massasaugas is most sensitive are highlighted: first-year survival (S_{21} = 0.629), survival of pre-reproductives (S_{32} = 0.308), and survival of females at the first age of reproduction (S_{43} = 0.164).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1			0.023	0.024	0.024	0.019	0.015	0.012	0.010	0.008	0.006	0.005	0.004	0.003	
2	**0.154**														
3		**0.154**													
4			**0.131**												
5				0.107											
6					0.083										
7						0.064									
8							0.049								
9								0.036							
10									0.026						
11										0.019					
12											0.012				
13												0.007			
14													0.003		
15														0.000	

Figure 16. Elasticity matrix, **E** (remainder of matrix consists of zeros). The population growth rate (λ) of massasaugas is most elastic to the three highlighted values – changes in the first-year survival of newborns and pre-reproductive survival ($e_{21} = e_{32}$ = 0.1539) followed by the survival of females at the first age of first reproduction (e_{43} = 0.1313).

of the total partial elasticity, with 11.9 percent accounted for by mi terms and other 11.9 percent accounted for by B_i terms. Again, every aspect of the analysis suggests that massasaugas are most susceptible to environmental change and habitat degradation that affects survival.

The stable (st)age distribution (SAD; **Table 7**) describes the proportion of each stage or age class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary, or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For massasaugas at the time of the post-breeding annual census (just after the end of the breeding season), newborns represent 55 percent of the population, juvenile stages represent 13 percent, and the adult stages represent the remaining 32 percent.

Reproductive values (**Table 8**) can be thought of as describing the "value" of a stage as a seed for population growth relative to that of the first (newborn or, in this case, egg) stage. The reproductive value of the first stage is always 1.0. A female individual in Age-class 2 is "worth" 4.1 female newborns, and so on (Caswell 2000). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The peak reproductive value (8.9 at Age-class 5) is considerably higher than that of

Table 7. Stable age distribution (right eigenvector) for female massasaugas. At the census, 55 percent of the individuals in the population should be newborns. Another 13 percent will be pre-reproductive. The remaining 32 percent of individuals will be reproductive adults.

Age Class	Description	Proportion
1	Newborns	0.549
2	Pre-reproductive	0.134
3	First reproduction (F_i = 1.2)	0.067
4	Reproductive (F_i = 1.6)	0.054
5	Reproductive (F_i = 2.0)	0.043
6	"	0.034
7	"	0.027
8	"	0.022
9	"	0.018
10	"	0.014
11	"	0.011
12	"	0.009
13	"	0.007
14	"	0.006
15	Maximum Age Class	0.005

Table 8. Reproductive values for female massasaugas. Reproductive values can be thought of as describing the "value" of an age class as a seed for population growth relative to that of the first (newborn) age class. The reproductive value of Age-class 1 is always 1.0. The peak reproductive value is highlighted.

Age Class	Description	Proportion
1	Newborns	1.00
2	Pre-reproductive	4.09
3	First reproduction (F_i = 1.2)	8.18
4	Reproductive (F_i = 1.6)	8.73
5	Reproductive (F_i = 2.0)	**8.92**
6	"	8.65
7	"	8.32
8	"	7.90
9	"	7.37
10	"	6.72
11	"	5.90
12	"	4.88
13	"	3.60
14	"	2.00
15	Maximum Age Class	0.00

the newborns (1.0; **Table 8**). That the peak reproductive value occurs several years after age of first reproduction is probably due to increases in both survival and fertility for older, larger females. In humans (Keyfitz 1985) and many species of mammals and birds, the peak is generally close to the age of first reproduction. We see that "adult" females are the most important stage in the life cycle of massasaugas. The cohort generation time for massasaugas is 6.5 years (SD = 2.9 years).

We conducted a stochastic matrix analysis for massasaugas. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (**Table 9**). Under Variant 1 we altered the fertilities (F_i). Under Variant 2 we varied only the survival of the female newborns, P_{21}. Under Variant 3 we varied the survival of all age classes, P_i. Variant 4 combined fluctuations in fertilities and first-year survival. Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the SAD under the deterministic model. Beginning at the SAD helps to avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We varied the amount of fluctuation by changing the standard deviation of the random normal distribution from which the stochastic vital rates were selected. The default value was a standard deviation of one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Variant 5 affected the same transition as Variant 3 (P_i) but was subjected to slightly larger variation (SD was 1 / 3.5 [= 0.286 compared to 0.25] of the mean). We calculated the stochastic growth rate, $log\lambda_S$, according to Eqn. 14.61 of Caswell (2000), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (**Table 9**) produced two major results. First, altering the survival rates had a much more dramatic effect on λ than did altering all of the fertilities. For example, the median ending size under the changed fertilities of Variant 1 (13,544) was actually slightly larger than the starting size of 10,000. In contrast, changing the survival of newborns under Variant 2 resulted in a median ending size of 2,604.0. Changing the survival rates of all age classes under Variant 3 resulted in an even more dramatic decline of median size (177.4). This difference in the effects of stochastic variation is predictable from the sensitivities and elasticities. λ was much more sensitive/elastic to changes in first-year survival, P_{21}, than it was to changes in the entire set of fertilities, F_i. Second, large-effect stochasticity on elastic transitions has a negative effect on population dynamics. This negative effect occurs despite the fact that the average vital rates remain the same as under the deterministic model – the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2000). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. For massasaugas under the

Table 9. Summary of five variants of stochastic projections for massasaugas.

Input/Output Factors	Variant 1	Variant 2	Variant 3	Variant 4	Variant 5
Input factors:					
Affected cells	F_i	P_{21}	P_i	$F_i + P_{21}$	P_i
S.D. of random normal distribution	1/4	1/4	1/4	1/4	1/3.5
Output values:					
Deterministic λ	1.00024	1.00024	1.00024	1.00024	1.00024
# Extinctions / 100 trials	0	0	34	0	51
Mean extinction time	—	—	1,558.4	—	1,377.1
# Declines / # surviving populations	30/100	73/100	58/66	72/100	45/49
Mean ending population size	15,735.6	10,340.9	21,388.1	17,295.3	3,799.2
Standard deviation	9,862.8	20,012.4	105,448.0	41,856.6	11,752.3
Median ending population size	13,543.67	2604.02	177.37	3,328.87	119.20
Log λ_s	0.000124	-0.000481	-0.00348	-0.000558	-0.00473
λ_s	1.0001	0.9995	0.9965	0.9994	0.9953
Percent reduction in λ	0.0118	0.0722	0.371	0.0799	0.496

survival Variant 3, 35 out of 100 trials of stochastic projection went to extinction vs. 0 under the fertilities Variant 1. Variant 5 also shows that the magnitude of fluctuation has a potentially large impact on the detrimental effects of stochasticity. Increasing the magnitude of fluctuation increased the severity of the negative impacts – the number of extinctions went from 35 in Variant 3 to 51 in Variant 5 when the magnitude of fluctuation was slightly amplified. These results suggest that populations of massasaugas are relatively tolerant to stochastic fluctuations in production of newborns (due, for example, to annual climatic change or to human disturbance), but they are extremely vulnerable to variations in survival. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously invariant vital rates (such as annual adult survival), with consequent detrimental effects on population dynamics. Further, in the case of massasaugas with their high sensitivity of λ to changes in first-year survival, selection may be relatively ineffective in reducing variability that surely results from a host of biotic and abiotic factors.

Clearly, the better the data on survival rates, the more accurate the resulting analyses. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variation in vital rates. Where we varied F_i and P_i values simultaneously, we assumed that the variation was uncorrelated, based on the assumption that factors affecting reproduction and, for example, overwinter survival would occur at different seasons or be due to different and likely uncorrelated factors (e.g., predation load vs. climatic severity or water levels). Using observed correlations would improve on this assumption by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Community ecology

Predators and competitors

Actual and potential predators of desert massasaugas include a wide array of raptorial birds, carnivorous mammals, and several species of snakes. Swainson's hawks (*Buteo swainsoni*) and northern harriers (*Circus cyaneus*) were observed carrying snakes in areas where massasaugas were abundant, but positive identification of the snake was not possible. Most hawks, eagles, and owls, both diurnal and nocturnal, are probable predators of desert massasaugas, and shrikes may also prey upon them. Badgers (*Taxidea taxus*), coyotes (*Canis latrans*), and foxes (*Vulpes* spp.) are common predators of snakes in the area, and longtail weasels (*Mustela frenata*), skunks (*Mephitis* spp.), and raccoons (*Procyon lotor*) may feed upon snakes, including massasaugas. Potential snake predators include racers (*Coluber constrictor*), coachwhips (*Masticophis flagellum*), milk snakes (*Lampropeltis triangulum*), and kingsnakes (*L. getula holbrookia/ splendida*); the latter are known from several counties south of the Arkansas River (Mackessy 1998a).

Potential competitors include almost any carnivore that utilizes lizards, centipedes, and/or small rodents as prey. Competition between snake species has not been observed, but it may be expected that prairie rattlesnakes, which utilize the same lizard and rodent prey and which are abundant and synoptic with massasaugas in Colorado, could be important competitors for limited prey resources. Many other species of colubrid snakes are common in intact shortgrass prairie (Mackessy 1998a), and most also utilize the same or similar prey.

Disease and parasites

Bacterial and viral diseases of rattlesnake in the wild are poorly known. Many rapidly fatal diseases, such as paramyxovirus, occur frequently among captive animals but are unknown in wild animals. However, the reintroduction of infected animals to native populations could be devastating, and this is a valid concern for captive propagation efforts or if animals are held temporarily and then returned to the wild. In addition, paramyxovirus is not uncommon in collections found among herpetoculturists and reptile dealers, and so a relatively large number of the lay public could serve as a focal point for disease introduction, via either intentional release or inadvertent escape of animals. The risk associated with infected captive animals being released to the wild is unknown but could potentially be high in some areas. In addition, there has been some discussion about trying to use paramyxovirus as a control agent for problem species, such as brown treesnakes (*Boiga irregularis*) on Guam. However, the virus has limited host specificity and containment would be impossible, so intentional establishment in the wild, even in highly modified environments such as Guam, could be disastrous.

As predators, snakes are subject to numerous parasitic diseases, but the occurrence of parasites in desert massasaugas is poorly documented. A recent note (Goldberg et al. 2001) described the presence of three species of nematodes (*Hexametra boddaertii*, *Physaloptera* and *Physocephalus*) in the gut and body cavity of desert massasaugas from Chaves County, New Mexico. A variety of other nematode, platyhelminth, and protist parasites are to be expected, but no other species are currently documented. An unusual pentastomid lung worm (*Porocephalus crotali*) is known from western diamondback rattlesnakes (*Crotalus atrox*) and other species of *Crotalus* (Roberts and Janovy 2000); it requires a rodent intermediate host, so it is possible that massasaugas could harbor this species as well.

Symbiotic and mutualistic interactions

As predators, desert massasaugas can influence prey populations, particularly where these snakes are common. Desert massasaugas utilize several mammals as prey, particularly *Perognathus* and *Reithrodontomys*, but because the feeding requirements for ectothermic snakes are quite low, it is unlikely that they have more than a small moderating effect on prey populations; bird and mammal predators likely take much greater numbers of these rodents. Their effects on lizard and centipede prey populations are unknown but likely are moderately important predatory influence on these animals. Massasaugas are also consumed by numerous predators, and they may contribute significantly to some raptor's diets in areas where snakes are abundant. Quantitative data are lacking for the importance of desert massasaugas as both predator and prey. No mutualistic interactions involving desert massasaugas have been identified.

Envirogram

Andrewartha and Birch (1984) outline a "Theory of Environment" that seeks to organize the ecology of a species into a coherent and logically connected web of factors that influence its ability to survive and reproduce. The heart of this endeavor is the envirogram, which orders these factors in a hierarchical dendrogram. The main stem of this dendrogram is comprised of a "centrum" of components that act directly on the species under consideration. From this centrum are branches that "trace pathways from distal causes in the web to proximate causes in the centrum." We have developed such an envirogram for the massasauga (**Figure 17**).

CONSERVATION OF THE DESERT MASSASAUGA IN REGION 2

Extrinsic Threats

Direct anthropogenic and natural threats

The most profound threat to desert massasaugas comes from anthropogenic alterations in habitat that render it unfit for persistence of this species (see below). As with most other rattlesnakes in most areas where they occur, desert massasaugas are killed on sight by humans, many of whom consider them a nuisance, at best. Because they are venomous, and occasional fatalities do still result from rattlesnake bites in the United States, more vigorous efforts are made by some to eliminate rattlesnakes whenever and wherever possible. These efforts include destruction of historical den sites and their occupants, as well as active searching for and destruction of snakes. Rattlesnake roundups occur in many states (perhaps all?) where rattlesnakes occur, often with the blessing of local community officials. These campaigns of destruction can be incredibly harmful to populations on a broad scale, as participants may travel long distances to collect snakes. Additionally, once one knows where to look most productively for rattlesnakes, one can efficiently remove significant numbers from a population. At one annual rattlesnake roundup in Sweetwater, Texas, upwards of 10,000 snakes are killed during the several days of "festivities". Since the inception of roundups in Sweetwater in 1958, over 123 tons of western diamondbacks (*Crotalus atrox*) have been killed (http://www.rattlesnakeroundup.com/home.html), yet the organizers still question whether or not this harvest has a deleterious effect on populations.

Mortality from automobiles on roadways, both paved and dirt, is of unknown absolute consequence but is likely a significant threat rangewide. As mentioned above, 39 percent of all desert massasaugas observed in 1997 were road-killed snakes ($n = 214$), and comparable percentages have been recorded for all years we have been monitoring massasaugas in Colorado (since 1994).

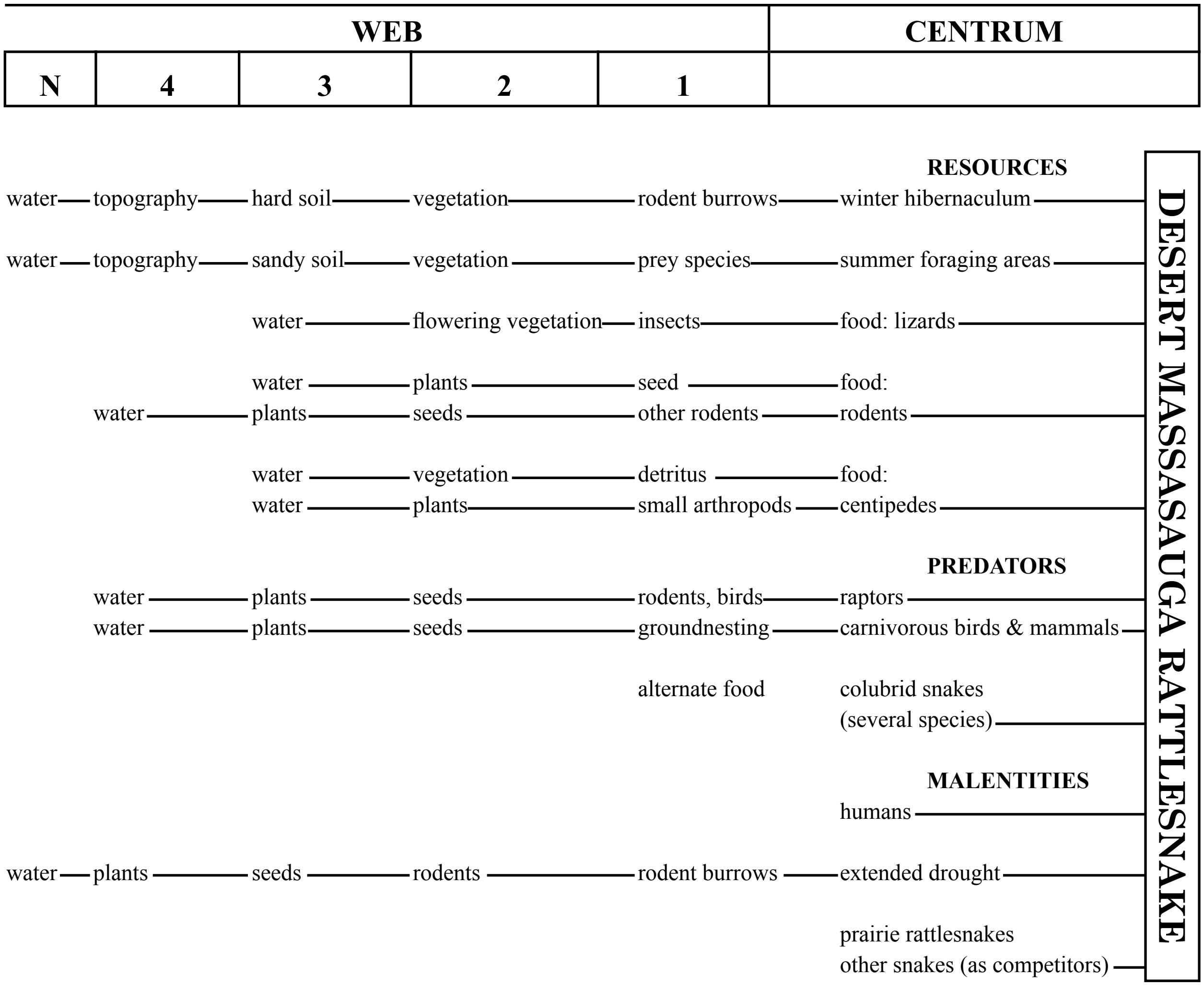

Figure 17. Envirogram for the desert massasauga.

Because these snakes may sit for extended periods on roads, particularly paved roads, the chance of a fatal encounter with an automobile is increased. Drivers in southeastern Colorado with a "kill on sight" mentality may intentionally aim for snakes on roads, and our field survey crews were "instructed" by local inhabitants on numerous occasions in the best methods for killing snakes with automobiles. This prevalent attitude of killing all snakes seen increases incidental road kills by an unknown but likely significant extent.

Commercial collection for the hobbyist trade may also represent a significant threat to desert massasaugas, as small rattlesnakes are popular among many hobbyists as pets or curios. Desert massasaugas are currently for sale at retail outlets such as Glades Herps, Inc. in Florida. The source of these snakes is unknown and may be legal, but at the current retail listing of $95.00, there may be an incentive for commercial collection, legal or illegal. Legal collection is permitted in New Mexico and Texas if a commercial collecting license is obtained. Some monitoring of interstate trafficking in these snakes is probably warranted. Small rattlesnakes have long attracted the attention of fanciers of snakes, and an overseas market also exists (extent unknown). Overseas trade in desert massasaugas may be important, as prices are often two to five times higher than in the United States, providing significant monetary incentive. However, there are no records available for trade in desert massasaugas, so this source of threat to populations is of unknown magnitude.

Anthropogenic and natural threats to habitat

Although humans represent a direct threat to massasaugas because they typically kill any rattlesnake encountered, this source of mortality is limited to those snakes that are encountered by humans. Because desert massasaugas are cryptically colored, small, and somewhat secretive, they are typically only encountered during seasonal movements from and to hibernacula. Their sensitivity to direct persecution is therefore somewhat limited.

Habitat loss, on the other hand, is a much more potent threat, and based on effects on eastern massasaugas, habitat modification and conversion will be the most significant threat to the persistence of desert massasaugas. Urbanization more or less permanently eliminates suitable habitat for massasaugas, but it often occurs after habitat has been negatively modified initially. For example, rural farming communities, which are widespread in eastern Colorado, have already exacted a heavy toll on native habitat via till farming and/or overgrazing by livestock. Urbanization has been most extensive and explosive along the Front Range, and much of the farmland-ranchland that is being converted into housing developments was previously severely disturbed. However, urbanization in these areas also eliminates "refugia", smaller regions within rural agricultural communities that were previously undisturbed, and recovery of native shortgrass prairie habitat from the effects of urbanization, if it ever occurs, will be exceptionally slow. On national grasslands, urbanization represents a minimal direct threat to the persistence of desert massasauga populations, but *indirect* effects of increased urbanization, even if at some distance from intact populations of these snakes, may present a serious threat.

Agriculture has had a tremendous effect on Great Plains grasslands in general, and the shortgrass prairie of eastern Colorado is no exception. Extensive modification of this environment resulting from till farming of arid lands is apparent from satellite photos of eastern Kiowa and Cheyenne counties in Colorado (Hammerson 1999). These disturbed areas presently define the eastern known distribution of the massasauga in Colorado and create an impenetrable barrier to massasauga dispersion, immigration, and/or emigration. Farming can also have a large effect beyond the actual point of surface disturbance through overuse of groundwater and underground aquifer sources for irrigation (Farrell et al. 1984). Together with upstream diversion and containment (dams), the net effect can be to lower the water table sufficiently in more mesic areas such that temporal ponds and streams become even more ephemeral, sometimes disappearing completely. There are indications that this has occurred over the last 30 or 40 years in the habitat immediately adjacent to the Lincoln County population of desert massasaugas, as long-term residents of the area commented on the disappearance of small local streams and ponds (Mackessy 1998a, J. Palmer personal communication 1996). If the grassland-adapted desert massasauga is presently at the limit of its tolerance for aridity, further xerification may result in loss of these populations.

Farming and overgrazing may also have long-term effects on habitat quality through disruption of soil-anchoring plant communities. Tilled and overgrazed shortgrass prairie is subject to severe soil erosion, and in a region characterized by near-constant and often strong winds, soil loss may be very extensive. Associated with the loss of appropriate habitat, and contributing to the long recovery time following such damage, is the loss of appropriate prey species and the food webs that ultimately support massasauga populations. A notable quality of the Lincoln County population is the abundance of appropriate prey, both lizard and rodent. This is due in large part to an intact shortgrass/mixed-grass habitat. Based on line transect surveys and small mammal trapping, abundance of lizard and rodent prey is much lower in adjacent areas that have been farmed.

Although the extent of global warming trends remains controversial, general climatic warming may accelerate xerification processes, both natural and anthropogenic, and extremes in weather conditions. Because habitat loss is largely of anthropogenic origin and global warming is probably at least accelerated and intensified as a result of industrialization, both are potentially, though arguably, reversible or capable of being mitigated. Certainly, reversal of these trends will require long-term commitments, especially in the case of global warming. In the foreseeable future, these two threats to population stability and persistence are likely to become more serious, and in the absence of other cataclysmic changes, one can expect massasauga populations to continue to decrease.

Biological Conservation Status

Abundance and abundance trends

Massasaugas were once abundant in regions of appropriate habitat rangewide, but all available data indicate that most populations have showed a downward trend in abundance, and many populations, particularly in the east, have been extirpated relatively recently (last 50 years). As discussed by Beltz (1993) the distribution of massasaugas rangewide was not as continuous as indicated by range maps (e.g., Conant and Collins 1991; **Figure 3**, this report), but current distributions have become extensively fragmented, and remaining populations are in decline (cf. references in Johnson and Leopold 1998, Seigel 1986).

On Region 2 national grasslands, desert massasaugas are uncommon to rare in the northern section of the Comanche National Grassland, and they are likely also rare in the southern section. There is insufficient data to document abundance trends, but it is most likely that desert massasaugas on the national grasslands were historically more abundant and have declined over the last 50 to 100 years (H.M. Smith personal communication 1996). However, there are populations just north in Kiowa County that appear to be moderately robust, and there may be one or more small populations in Baca County (north of the southern section of the Comanche National Grassland), where massasaugas are moderately abundant. In at least one locale, in Lincoln County, desert massasaugas are quite common, and abundance trends in this population likely have been stable for some time (we have documented abundance in this population only since 1995).

Distribution trends

Across its North American range, the massasauga rattlesnake has suffered tremendous loss of habitat, and present distribution rangewide has been reduced to pockets of fragmented populations (Seigel 1986, Gibbs et al. 1997, Johnson and Leopold 1998, Johnson et al. 2000). Because anthropogenic changes in habitat are the leading cause of declines in abundance and population extirpations, it is expected that the general trend for the species rangewide will be contraction of distribution, eventually culminating in remnant populations in a few reserves. If a sufficient area of high quality is maintained, isolated massasauga populations are expected to persist, but restricted gene flow resulting from fragmentation and isolation could become deleterious (Couvet 2002). Given current human population increase trends, coupled with increased demands on natural resources and effects of global climate change, it is unlikely that range expansions for these snakes will be observed. Consequently, maintenance of the species rangewide may require numerous reserves where massasaugas are accorded protected species status.

Similarly, if current human population trends continue, then desert massasaugas in Region 2 will likely suffer further range contraction. However, there is the possibility of range expansion in parts of the Comanche National Grassland, because habitat restoration efforts may increase the area of appropriate habitat for massasaugas, which will encourage immigration from neighboring populations. In Baca County, large expanses of former farmland have been removed from tilling as the acreage has been converted to CRP revegetation or was incorporated into the southern section of the Comanche National Grasslands. In Otero County (northern section of Comanche National Grassland), once native prairie species are re-established in overgrazed areas, the rotation of cattle herds through shortgrass pastures to provide minimal grazing pressures may encourage stabilization of native prairie, likewise favoring expansion of range or increases in massasauga population densities.

Habitat trends

Eastern Colorado is largely rural, and much of the human population relies on farming and/or ranching. Extensive tilling associated with farming is highly disruptive to the native shortgrass prairie habitat, and recovery after abandonment, if it occurs, is exceptionally slow. Similarly, very dense cattle ranching without herd rotation off pastures can lead to (semi)permanent changes in vegetation and soils that render large areas unsuitable as massasauga habitat. Based on satellite images, the current limit of massasauga range in Colorado may be defined by disruptive agricultural practices, as the southern and eastern borders of the massasauga's range are characterized by extensive habitat modification (Hammerson 1999). Because these changes in habitat are extensive and produce a barrier of inhospitable habitat, massasaugas in Colorado are now effectively isolated from other populations that (may) occur to the south and east in New Mexico, Oklahoma, and Kansas. Increasing patterns of habitat fragmentation in Colorado could greatly accelerate rates of decline of these populations.

Changes in groundwater uses in the area may also be contributing to the loss of habitat for massasaugas in Colorado. Desert massasaugas are much more adapted to xeric grasslands conditions than are the eastern and western subspecies (Holycross and Mackessy 2002), but they still are most abundant in Colorado (including Region 2) in areas with somewhat greater surface water availability (Mackessy 1998a), suggesting that their tolerance of xeric conditions is restricted. Upstream water diversion projects on major drainages, particularly along the Arkansas River, are likely affecting groundwater recharge over a broad area in southeastern Colorado, and well water use for agriculture and human consumption further exacerbates this problem. As anthropogenic xerification of habitat increases, coupled with additional stress resulting from drought conditions, habitat appropriate for massasaugas may be lost in these rural areas even *without* direct habitat modification resulting from farming or overgrazing.

The remote location of the massasauga in Colorado relative to major urban centers has provided for passive protection of the species. However, as elsewhere, human encroachment into grassland habitat is increasing, particularly in Pueblo and El Paso counties, and massasauga populations will be expected to be impacted negatively from increases in human populations. The effects of the current drought could also increase the rate of habitat conversion. In many parts of the eastern plains, including Lincoln County, ranching is minimally profitable even in good rainfall years, and recent drought conditions have forced ranchers to sell their herds because winter feeding and the prospects of a dry spring make continued ranching unprofitable. If this trend continues, it can be expected that ranchers will begin to sell off property for other uses, which will lead to habitat loss for massasaugas. As development encroaches toward the western edge of the massasauga's habitat in eastern Colorado, land values will increase, creating greater incentive for landowners to sell part or all of their property for non-ranching purposes. Habitat loss and conversion from agriculture to urban land use is most intense in the vicinity of Colorado's Front Range communities, but even formerly rural towns, such as La Junta (just north of the northern section of the Comanche National Grassland), are not immune to the destabilizing effects of growth.

Intrinsic vulnerability

As mentioned above, the massasauga has the potential to live perhaps 20 years or more, but based on size/age class distributions, the more typical lifespan is four to five years. Desert massasaugas show relatively low fecundity (**Table 4**; Goldberg and Holycross 1999, Mackessy unpublished data), even when compared with other subspecies of massasaugas (Fitch 1970, Ernst 1992). Desert massasaugas in Region 2 appear to have a low tolerance of habitat disturbance, and they are much more abundant in shortgrass prairie habitat that has a relatively long history without disturbance, particularly till farming (Mackessy 1998a). Old fallow fields in sandy soils that are partially recovered may be utilized, and massasaugas were occasionally seen in disturbed areas with intact adjacent habitat. Movement through these more open, disturbed areas is expected to increase risk to predation. These factors combined suggest that recovery of populations of desert massasaugas following severe habitat disturbance will be very slow.

Because desert massasaugas require (prefer?) relatively undisturbed shortgrass prairie habitat, progressive till farming followed by slow regeneration of native habitat, as seen in parts of extreme eastern Colorado, may eliminate metapopulations of massasaugas stepwise before they can recover into fallow disturbed areas. From a historical landscape perspective, this ever-moving impact on native habitat may explain in part the present-day low density occurrence of massasaugas in parts of Region 2. Populations in the past may have been sufficiently impacted that at present they are barely sustaining, but there is insufficient data available on former abundance of massasaugas in this region to provide more than speculation.

Management of the Desert Massasauga in Region 2

The known range of the desert massasauga encompasses only a small portion of shortgrass prairie habitat on National Forest System lands within Region 2: the Comanche National Grassland in Colorado and possibly the Cimarron National Grassland in Kansas. Clearly, preservation of existing natural shortgrass prairie habitat within the national grasslands and encouragement of good land use practices in adjacent private property will be most effective in maintaining desert massasauga populations. Care must be exercised in grazing of cattle on the grasslands, particularly under drought conditions, as overgrazing is detrimental to both the prey of massasaugas (lizards and small rodents) and to massasaugas themselves.

Grasslands in North America have been modified or destroyed over most of the Great Plains, and only remnants remain. The shortgrass prairie looks essentially homogenous over much of eastern Colorado, but there are subtle differences in large sections between major drainages such that different species assemblages occur west to east and along a north-south gradient. The current range of the desert massasauga is largely defined by the Arkansas River drainage below about 1500 m (5,500 ft.) elevation (Hammerson 1999), and in this southeastern corner of Colorado, many other species of amphibians and reptiles (and other floral and faunal elements) reach the northern and/or eastern limit of their distributions. Since fall of 2000, the lead author has led a survey of the northeastern plains of Colorado. Compared to the southeastern quadrant, this herpetofauna is depauperate, and most species sharing distributions are less abundant in the northeastern plains. These preliminary data further indicate the unique nature of Region 2's southern national grasslands. In addition to the desert massasauga, the Comanche National Grassland may become a significant refuge for many species (Mackessy 1998b).

Most of the issues surrounding conservation of the desert massasauga in Region 2 are relevant to conservation of the species rangewide. Because the Comanche National Grasslands are managed by the USDA Forest Service and because very recent observations (September 2005) suggest that desert massasaugas may be more common there than was previously thought (e.g., Mackessy 1998a,b), the grasslands offer a logical focal point for initiating the conservation strategies outlined below. One obvious difficulty for conservation efforts with this taxon is the uncertain taxonomic status (unique species/subspecies vs. clinal variant of a widespread species), but it is anticipated that this uncertainty will be addressed soon (Hobert et al. *in review*, Douglas personal communication 2005).

Conservation elements

The single most important factor affecting long-term stability of this species is habitat loss. Other threats, as noted above under Extrinsic Threats, are difficult to prioritize because there is little direct evidence of the relative importance of factors after habitat preservation. We believe the three main elements necessary to conserve the desert massasauga in Region 2 are habitat preservation and restoration, protection from direct mortality, and monitoring. The rationale behind each of these is discussed in more detail below, and suggestions on how to implement these elements are discussed in the subsequent section on Tools and practices.

Habitat preservation and restoration

Our extensive surveys have demonstrated that in Region 2, desert massasaugas are most abundant in intact, shortgrass prairie habitat that is adjacent to sandy soils with mixed-grass species association and an abundance of lizard, centipede, and rodent prey (Wastell and Mackessy *in prep*.; see also Biology and Ecology above). Conversely, massasaugas are rare to non-existent in heavily degraded habitat. Therefore, in order to ensure that desert massasauga populations remain stable and viable, the most important consideration is preservation of high quality habitat, which can be measured by the abundance of native flora and fauna typical in areas of high massasauga density, the lack of major weedy species, and undisturbed soils. As mentioned below, preservation of high quality habitat *does not* preclude some human uses of this habitat. Practices that lead to habitat degradation (e.g., tilling, severe overgrazing, urbanization, other practices that result in xerification) *will* negatively affect populations (see Extrinsic Threats above) of massasaugas and other species, including some game species. It is possible that if landowners become aware of the effects of habitat degradation, they may be more amenable to considering ameliorative measures, such as conservation easements. Less intensive uses, including cattle ranching, are often well tolerated by massasaugas and associated shortgrass species.

Based on our studies, there are three key aspects of habitat preservation that must be addressed to assure this species' conservation: hibernacula, migration corridors, and summer foraging areas.

- ❖ Protection of hibernacula sites: Desert massasaugas do not appear to form large hibernacula like prairie rattlesnakes, so it is more difficult to describe absolute features of the hibernaculum. However, we have very recently discovered (12 November 2005) a specific region within the Lincoln County population that appears to be utilized by not only a large number of massasaugas but also by prairie rattlesnakes and at least several additional non-venomous colubrid snakes. These massasaugas are making long-distance movements from summer foraging areas to reach this hibernaculum. If, in general, desert massasaugas make such movements, then appropriate hibernacula may be limiting, and their protection is critical. An additional benefit of this recent discovery is that it may be possible to protect multiple species by focusing efforts on hibernaculum requirements for massasaugas.

- ❖ Protection of migration corridors: Occurrence of specific regions of high-density movement of ungulates is well known, and mediation of road mortality (for example) has included construction of barriers and safe passages. It is becoming increasingly apparent that similar needs occur for many smaller animals, including desert massasaugas. In remote areas, road mortality may be a major cause of mortality for these snakes, and if movements occur over a relatively small length of roads, then barriers and underpasses could be constructed cost-effectively and have a large effect on survivorship.

- Protection of summer foraging areas: Although individual home ranges of desert massasaugas appear to be fairly large, the high density of some populations suggests that there is considerable overlap in these home ranges. If this is the case generally, then the identification and preservation of key high density areas obviously is necessary for species persistence. These areas also must have robust populations of prey (e.g., small rodents, lizards, centipedes), and these requirements generally preclude development of any kind or till farming. Conservation easements with limited use by livestock are one way to protect relatively large areas of habitat while allowing for rural families to continue using their land.

Protection from direct mortality

No protection exists over much of the desert massasauga's actual or potential range. Management of this species rangewide and in Region 2 has largely been limited to protected or no-take status. In practice, however, protection is difficult to enforce as the desert massasauga occurs in large, remote areas with few conservation personnel. One case of illegal collection and subsequent prosecution occurred in Arizona in the mid-1990s, but illegal collection and outright killing of desert massasaugas occur rangewide.

Many small animals are subject to high mortality when crossing roads, and desert massasaugas are no exception. Mortality due to automobile traffic is increased by specific habits of some species, and the tendency for massasaugas to bask on roads increases the likelihood of fatal encounters with cars. Adding to this risk is the tendency of many individuals to aim for snakes intentionally. Two anecdotes illustrate the serious threat posed by roads and drivers. In May 2005 a landowner saved for us roadkilled massasaugas collected for one week over a one-mile stretch of road. Fifteen adult snakes were received, and this is a very remote, rarely traveled gravel county road. Later the same year, the same landowner helped a bus driver pull his vehicle out of a ditch after the driver swerved to hit a snake (another massasauga) on this same remote road. If one considers this attitude toward snakes and the many thousands of miles of roads within actual and potential massasauga habitat in Colorado, the importance of some form of mitigation or small animal exclusion from roadways becomes obvious.

As more roads are constructed, habitat becomes further fragmented and open habitat (i.e., the roadways and shoulders) becomes more abundant, likely increasing risk to aerial predators. Desert massasaugas are highly cryptic in native shortgrass prairie and sandsage (**Figure 1b**), but they are very exposed on open surfaces like roads. It is expected that predation by birds of prey during both diurnal (e.g., falcons, hawks, shrikes) and nocturnal (e.g., owls) movements will be greater on roads than in unaltered habitat.

There is a growing demand for many species of snakes in the pet and herpetoculture trades, and small rattlesnakes are particularly desirable, in spite of the fact that possession of venomous snakes is illegal in many cities. Because of the predictability of movement patterns, massasaugas are prone to overcollection, and we have encountered several instances of illegal collection in the vicinity of the Lincoln County population. As mentioned above, desert massasaugas are available through various reptile suppliers, many of which supply lists via the Internet. Because of the dollar value attached to these small rattlesnakes, it is expected that illegal collection of desert massasaugas will become an increasingly important concern for conservation.

Related to the collection of live snakes for the pet trade is collection of snakes for skins and/or flesh. Because of their small size, desert massasaugas are not particularly sought out, but they may be taken as "bycatch", and many people are not capable of distinguishing massasaugas from the more widespread prairie rattlesnake. While there are no known organized rattlesnake roundups in Colorado, as there are in many other states, it is likely that "unofficial" roundups occur in the state.

Inventory and monitoring

Also of critical importance in the conservation of desert massasaugas is a solid information base on their distribution, abundance and, especially, trends in population and habitat status. The status of the desert massasauga has been the subject of several extensive surveys in Colorado (Mackessy 1998a) and in Arizona (Holycross and Douglas 1996). Therefore, we have a reasonable idea of its baseline presence/absence, upon which we can base distribution monitoring efforts that are critical to documenting the effectiveness of conservation efforts.

As a result of our earlier extensive survey of massasauga populations in Colorado (Mackessy 1998a; see Distribution and abundance above), the known range within the state has increased somewhat and the known abundance has increased tremendously. Our work demonstrated the utility of long-distance road surveys for estimating relative abundance and distribution, and although this method has a potential for significant sampling bias, it is particularly cost-effective for obtaining presence-absence data over vast areas and on limited budgets. A variety of other methods, including telemetric and mark and recapture studies in limited areas, will provide more definitive estimates of population densities locally, but these will be at the expense of not obtaining broad distributional data or will be labor and cost-intensive. Extensive road surveys focused on National Forest System lands and occurring in both spring and fall would likely turn up numerous specimens, and this work could be conducted with minimal personnel and over about 1 1/2 months total time.

Specific movement and microhabitat use patterns are unknown for most desert massasauga populations. Based on ongoing radiotelemetric monitoring of the Lincoln County populations, desert massasaugas on National Forest System lands are likely to make large (1 to 4 km) seasonal movements, but this still needs to be confirmed or refuted by telemetric studies. Because of these apparent long-distance movement patterns, the likelihood of encountering snakes during road-based surveys is increased if they occur during these periods. An approach to this type of monitoring is given below.

Tools and practices

Habitat preservation and restoration

The inclusion of large tracts of public land in the Comanche National Grassland is a good start. If economically feasible, the southern section of the Comanche National Grassland should be increased to include lands to the north, in the immediate vicinity of County Road 12 (north/south) between County Roads JJ and RR. This area contains good habitat for massasaugas and was the source of four specimens collected and tagged in 1997 (Mackessy 1998a, Montgomery et al. 1998). Particularly in the southern section, resource management should begin to include reseeding of disturbed prairie with native, locally-obtained grasses; Conservation Reserve Program reclamation efforts may not be as effective at restoring required habitat components (Montgomery and Mackessy 2003).

In much of the range of the desert massasauga, large tracts of property are owned by private individuals or state and national entities. It has been the experience of the lead author that private landowners are often very willing to allow studies on their lands, provided they receive sufficiently sincere assurances that information found will not be turned against them. There is a potent disinformation campaign conducted by various reactionary "wise-use" groups, and landowners are often very hesitant initially to allow access to their property. An understanding of this and sensitivity to their values are necessary for productive cooperation to exist. For private holdings of good massasauga habitat (parts of Baca and Lincoln counties), establishment of conservation easements should be encouraged via permanent agreements with landowners and including monetary incentives. This approach is being used by several agencies in a number of areas in Colorado, including an in-progress agreement involving a large tract of land northeast of the southern section of the Comanche National Grassland (Colorado Natural Heritage Program and Nature Conservancy).

It has become obvious to the lead author that cattle ranching and maintenance of habitat for desert massasaugas are completely compatible, provided that herd rotation to simulate natural grazer effects is implemented. In the absence of native bison, rotational grazing at moderate herd densities may actually improve habitat by promoting growth of grasses and quality of forage (Walton et al. 1981). This type of information should be made known to landowners unfamiliar with the benefits of rotational grazing because with a modest change in their practices they can promote conservation *and* (importantly) likely increase their own productivity and profits (Ostrom and Jackson-Smith 2000). On the other hand, overgrazing can severely degrade habitat, so it is essential that easement agreements include herd rotation and density requirements, and occasional monitoring of habitat quality.

Protection from direct mortality

The desert massasauga is a venomous snake, and it is often difficult to generate empathy for the fate of potentially lethal animals among the general public. However, the risk to the general public from this small rattlesnake is small, and the public has a fascination for snakes in general and venomous snakes in particular. Education and information campaigns on the national grasslands should include information about the unique and important place of these animals in the healthy ecology of prairie ecosystems. Although amphibians and reptiles in these areas are often uncooperative in appearing upon command, nature walk programs that include discussions about these animals could be conducted. Visitor centers and poster boards in more remote areas should also include information about desert massasaugas. Although there may be valid concerns about unduly frightening visitors, it is our impression that most visitors would appreciate the information. As one increases the profile of desert massasaugas and snakes in general, one can generate an interest in these animals among the public, and the long-term effect on conservation efforts is likely to be positive. We generally care more for organisms we know about, and a positive information campaign would help to dispel the many myths about rattlesnakes held by the public.

The no take/no kill status of the desert massasauga in Colorado provides some protection and a legal basis for prosecution in the event of illegal collecting or killing of massasaugas. However, the passive protection afforded these snakes by their occurrence primarily in remote, low population regions makes it difficult to monitor illegal actions. For these reasons, education and outreach-based programs could have a greater effect; and visits to rural schools by USFS and other agency personnel would likely generate positive results. There are many misconceptions and myths concerning snakes that circulate as fact among the general public, and for this reason we also make presentations to school groups about snakes and other misunderstood animals.

Internet-based sites have the potential to inform and educate vast numbers of people, and a model site for eastern massasaugas, which could be emulated for the desert massasauga, is the web page (http://www.massasauga.ca/homepage.html) maintained by the Eastern Massasauga Recovery Team in Canada. Many other regional web sites are also available, such as that of the Michigan Department of Natural Resources (http://www.michigan.gov/dnr/0,1607,7-153-10370_12145_12201-32995--,00.html). An important consideration for any web-based information is that it not provide specific locality information, as commercial collection of desert massasaugas could greatly impact populations.

Where large populations of massasaugas (most likely in Baca County) are located, and where movement corridors are identified between hibernacula and summer foraging habitat, protection from road mortality should be considered. Such protection could be afforded by creating underpasses with exclusion fences on either side, creating a "safe passageway" for massasaugas and other small animals.

Captive propagation and reintroduction

At present, populations in Colorado and specifically Region 2 appear stable, and captive propagation for reintroduction is not suggested. However, if continuing habitat loss accelerates, a need for such intervention may arise. Relocation and reintroduction of snakes remains controversial (Seigel personal communication 1995), primarily because of concerns over lack of survival of relocated snakes; however, there is very limited information available on actual survival in the field (but see Reinert and Rupert 1999). For this reason, we would like to conduct relocation studies with radio-tagged snakes to evaluate whether or not snakes moved from a different location can orient and survive in a new location. Results of such studies have direct application not only to massasaugas rangewide, but also to other species of endangered or threatened snakes.

Inventory and monitoring

Monitoring of the desert massasauga in Region 2 should utilize a multifaceted approach. Because the desert massasauga occurs over a very large area and access is frequently limited, either by private exclusion (permission to trespass refused by landowner) or by physical access difficulties (few roads), a first approach should utilize remote sensing methods (satellite or airplane-based imagery) to assess changes to habitat. This can be done relatively efficiently and on a regular basis (at least biennially) at low cost and will provide a landscape-level analysis of habitat fragmentation or loss due to changes in land use. Land use practices over the last 100 years should be evaluated and compared with current habitat quality; this historical information was not available for this assessment but could be very important toward addressing unknowns such as length of time required for re-establishment of shortgrass prairie habitat occupied by desert massasaugas.

Ground verification of remote imagery and inventories of desert massasaugas via surveys should be conducted on a 5 to 10 year schedule, as has been recommended by several investigators (Seigel 1986, Mackessy 1998a). Standard survey protocols for massasaugas (Casper et al. 2001) and for herpetological surveys (Mackessy 1998a) are available and include collecting as much data as possible about snakes and the environment in which they are encountered. Collecting of blood samples, as recommended by Casper et al. (2001), can be done in the field by sufficiently trained personnel, and samples for genetic studies can be stored indefinitely in preservative or at -80 °C.

Field inventories and surveys are much more time- and labor-intensive than remote methods, but they are essential for establishing measures of occurrence and distribution, abundance, habitat use, and overall population stability. Limited experimentation with pitfall and drift fence sampling in southeastern Colorado indicates that these methods, even in the region of highest massasauga monitoring, are quite ineffective. One way to increase efficiency of field surveys is to conduct intensive field work at times that coincide with major movements (i.e., egression and ingression). In Region 2 this will be during the last two weeks of April, early May, most of September, and the first week or two in October (**Figure 8**). These dates will be influenced by particulars of climate for a given year, but they have remained productive times for inventories for massasaugas in Colorado for the last 10 years. Because massasaugas tend to make long-distance movements at these times, field work is further facilitated by the presence of dirt or paved road surveys, where a field worker drives at 20 to 30 mph. Much greater distances can be covered, but this method suffers from potential sampling biases.

Although we surveyed the Comanche National Grassland for massasaugas and other herpetofauna (Mackessy 1998b), both sections need to be examined more carefully at times of most likely encounter (see above). Major movements to and from hibernacula may occur over short periods (i.e., one or two weeks), so limited surveys are likely to miss the most productive times. The Cimarron National Grassland in Kansas should be surveyed again, focusing on the dates of likely movement given above, as it is likely that desert massasaugas will occur in this region. Extensive basic field work is also needed in many parts of the desert massasauga's range, and particular efforts should be concentrated in western Kansas and Oklahoma. The robust population in Lincoln County, Colorado is being monitored by my group at present, and given the fact that this small region includes the largest known population of desert massasaugas rangewide, it warrants even more intensive monitoring.

Greater interagency interaction will increase efficiency of monitoring and maintaining populations of desert massasaugas on public lands, as funding for monitoring programs likely will become more limited in the future, and by combining resources and coordinating efforts, redundant sampling of target species by different agencies will be minimized. This type of combined agency approach (e.g., USFS and Colorado Division of Wildlife) allowed Dr. Mackessey to survey massasauga populations, as well as other species of amphibians and reptiles, more effectively and economically than could have been done individually for either agency (Mackessy 1998a,b).

Information Needs

As the reader of this assessment will appreciate, while the inferences made in several places above are based on high likelihood, there are large gaps in our understanding of many aspects of the biology of the desert massasauga. Basic presence/absence and relative abundance surveys are needed in many parts of the species' range, and a schedule of regular population monitoring (as suggested above) needs to be established. In Region 2, more extensive surveys need to be conducted to delineate unequivocally the occurrence of the desert massasauga on the Cimarron National Grassland and elsewhere. Hopefully, genetic studies in progress will establish affinities among the putative subspecies of massasaugas, but preliminary information suggests that genetically distinct populations within the desert massasauga's range will occur.

A variety of methods for monitoring population trends is available, but all require significant commitment in terms of resources and time. Although we know that the massasauga cannot tolerate disruption of native habitat, the specific level of tolerance is not known. More extensive surveys in areas of differing levels of disturbance could help address this uncertainty (e.g., define tolerance of level of grazing impacts). It is likely that desert massasaugas utilize specific microhabitat when gravid, but the nature of this microhabitat and its use is speculative. Radiotelemetry studies could be used to address this and many other aspects of the basic natural history which are still unknown for this species, such as when mating occurs. Similarly, though we have good information on seasonal movements from one population, the microhabitat structure existing at this site is not uniformly available to all desert massasauga populations, even within the state. Could the lack of sufficiently differentiated foraging and hibernating habitat limit population densities in other areas? Is minor disturbance of one or the other of greater importance?

Comments above suggest that desert massasaugas can repopulate disturbed areas once sufficient recovery has occurred, but we really do not know what "sufficient" constitutes. Also, the length of time required is unknown, but informative data may be available form cooperative extensions working on grassland habitats. We also lack well-defined data on population structure and longevity, and because this information is central to modeling of life history trends (above), the reliability of the model is uncertain. In the event that captive propagation and reintroduction become necessary for the management of this species, we will need to know what factors are important to successful re-establishment.

Research priorities in Region 2 should begin with renewed survey efforts on the Comanche and Cimarron national grasslands, as has been mentioned above. Once areas of occurrence or abundance are identified, then the conservation and management practices detailed above should be concentrated in those areas. It likely will not be possible to preserve the desert massasauga across all parts of its range, but the species' persistence in Region 2 can be secured by preserving and expanding appropriate habitat within these publicly owned lands.

References

Andrewartha, H.G. and L.C. Birch. 1984. The Ecological Web. University of Chicago Press, Chicago, IL.

Beltz, E. 1993. Distribution and status of the eastern massasauga rattlesnake Sistrurus catenatus catenatus (Rafinesque, 1818) in the United States and Canada. Pages 26-31 *in* B. Johnson and V. Menzies, editors, International Symposium and Workshop on the Conservation of the Eastern Massasauga Rattlesnake, 8-9 May, 1992, Toronto Zoo, Toronto, ON.

Campbell, J.A. and W.W. Lamar. 1989. The Venomous Reptiles of Latin America. Comstock Publishing Associates/ Cornell University Press, Ithaca, NY. 425 pp.

Casper, G.S., T.G. Anton, R.W. Hay, A.T. Holycross, R.S. King, B.A. Kingsbury, D. Mauger, C. Parent, C.A. Phillips, A. Resetar, R.A. Seigel, and T.P. Wilson. 2001. Recommended standard survey protocol for the eastern massasauga, *Sistrurus catenatus catenatus*. U.S. Fish and Wildlife Service, Fort Snelling, MN.

Caswell, H. 2000. Matrix Population Models: Construction, Analysis, and Interpretation. Second Edition. Sinauer Associates, Sunderland, MA.

Chiszar, D., K. Scudder, H.M. Smith, and C.W. Radcliffe. 1976. Observations of courtship behavior in the western massasauga (*Sistrurus catenatus tergeminus*). Herpetologica 32:337-338.

Cochran, M.E. and S. Ellner. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations, Ecololgical Monographs 62:345-364.

Collins, J.T. and S.L. Collins. 1991. Reptiles and amphibians of the Cimarron National Grasslands, Morton County, Kansas. University of Kansas Printing Service, Lawrence. 60 p.

Colorado Natural Heritage Program. 1999. Status of the massasauga rattlesnake. Internet site: http://www.cnhp.colostate.edu/tracking/amphibians_reptiles.html.

Conant, R. and J.T. Collins. 1991. A Field Guide to Reptiles and Amphibians. Eastern and Central North America. Houghton Mifflin Co., Boston, MA.

Couvet, D. 2002. Deleterious effects of restricted gene flow in fragmented populations. Conservation Biology 16: 369-376.

Degenhardt, W.G., C.W. Painter, and A.H. Price. 1996. The Amphibians and Reptiles of New Mexico. University of New Mexico Press, Albuquerque, NM. 431 pp.

Dingle, H. 1996. Migration - The biology of life on the move. Oxford University Press, New York, NY.

Dixon, K.R. and J.A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Douglas, M.E. 2005. Colorado State University, Department of Fishery and Wildlife Biology, Fort Collins. Personal communication.

Ernst, C.H. 1992. Venomous reptiles of North America. Smithsonian Institution Press, Washington, D.C. 236 pp.

Farrell, K.R., F.H. Sanderson, and T.T. Vo. 1984. U.S. food and fiber – abundance or austerity? Pages 2-20 *in* Resources for the Future. Resources No. 76 (spring). Washington, D.C.

Fitch, H.S. 1970. Reproductive cycles in lizards and snakes. University of Kansas Museum of Natural History Miscellaneous Publications 52:1-247.

Fitch, H.S. 1985. Variation in clutch and litter size in New World reptiles. University of Kansas Museum of Natural History Miscellaneous Publications 76:1-76.

Gloyd, H.K. 1940. The rattlesnakes, genera *Sistrurus* and *Crotalus*. Chicago Academy of Science, Special Publication No. 4.

Gloyd, H.K. 1955. A review of the massasauga, *Sistrurus catenatus*, of the southwestern United States. Bulletin of the Chicago Academy of Sciences. 10:83-98.

Gibbs, H.L., K.A. Prior, P.J. Weatherhead, and G. Johnson. 1997. Genetic structure of populations of the threatened eastern massasauga rattlesnake, *Sistrurus c. catenatus*: evidence from microsatellite DNA markers. Molecular Ecology 6:1123-1132.

Goldberg, S.R., C.R. Bursey, and A.T. Holycross. 2001. *Sistrurus catenatus edwardsii* (Desert Massasauga) endoparasites. Herpetological Review 32:265.

Goldberg, S.R. and A.T. Holycross. 1999. Reproduction in the desert massasauga, *Sistrurus catenatus edwardsii*, in Arizona and Colorado. Southwestern Naturalist 44:531-535.

Goldberg, S.R. and W.S. Parker. 1975. Seasonal testicular histology of the colubrid snakes, Masticophis taeniatus and Pituophis melanoleucus. Herpetologica 31:317-322.

Greene, H.W. and G.V. Oliver, Jr. 1965. Notes on the natural history of the western massasauga. Herpetologica 21: 225-228.

Greene, H.W. and J.A. Campbell. 1992. The future of pitvipers. Pages 421-427 *in* J.A. Campbell and E.D.Brodie, Jr., editors. Biology of the Pitvipers, Selva, Tyler, TX.

Greene, H.W., P.G. May, D.L. Hardy, Sr., J.M. Sciturro, and T.M. Farrell. 2002. Parental behavior by vipers. Pages 179-205 *in* G.W. Schuett, M. Höggren, M.E. Douglas, and H.W. Greene, editors. Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, UT. 578 pp.

Hallock, L.A. 1991. Habitat utilization, diet and behavior of the eastern massasauga (*Sistrurus catenatus catenatus*) in southern Michigan. M.S. Thesis. Michigan State University, Lansing, MI.

Hamilton, Jr., W.J. and J.A. Pollack. 1955. The food of some crotalid snakes from Fort Benning, Georgia. Natur. Hist. Misc. 140:1-4.

Hammerson, G.A. 1986. Amphibians and reptiles in Colorado. Colorado Division of Wildlife Publication No. DOW-M-I-3-86, Denver, CO. 131 pp.

Hammerson, G.A. 1999. Amphibians and reptiles in Colorado. Second edition. University Press of Colorado, Niwot, CO. 484 pp.

Hobert, J.P. 1997. The massasauga rattlesnake (*Sistrurus catenatus*) in Colorado. Unpublished M.S. Thesis, University of Northern Colorado, Greeley, CO.

Hobert, J.P., C.M. Montgomery, and S.P. Mackessy. 2004. Natural history of the desert massasauga rattlesnake (*Sistrurus catenatus edwardsii*) in Colorado. Southwestern Naturalist 49:321-326.

Hobert, J.P., C.M. Montgomery, and S.P. Mackessy. 2005. Morphological variation and taxonomic status of the massasauga rattlesnake (*Sistrurus catenatus*) in Colorado. Copeia (in review).

Holycross, A.T. 1999. Arizona State University, Department of Biology, Tempe. Personal communication.

Holycross, A.T. 2001. *Sistrurus catenatus edwardsii* (desert massasauga). Maximum length. Herpetology Review 33: 59.

Holycross, A.T. and M.E. Douglas. 1996. Distribution, abundance, and ecology of the desert massasauga rattlesnake, *Sistrurus catenatus edwardsi*. Unpublished report to the Arizona Game and Fish Department, IIPAM I93004, Phoenix, AZ.

Holycross, A.T. and S.P. Mackessy. 2002. Variation in the diet of *Sistrurus catenatus* (massasauga), with emphasis on *Sistrurus catenatus edwardsii* (desert massasauga). Journal of Herpetology 36:454-464.

Holycross, A.T., C.W. Painter, D.G. Barker, and M.E. Douglas. 2002. Foraging ecology of the threatened New Mexico ridge-nosed rattlesnake (*Crotalus willardi obscurus*). Pages 243-252 *in* G.W. Schuett, M. Höggren, M.E. Douglas, and H.W. Greene, editors. Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, UT.

Jennrich, R.I. and F.B. Turner. 1969. Measurement of non-circular home range. Journal Theoretical Biology 22:227-237.

Johnson, G. 2000. Spatial ecology of the eastern massasauga (*Sistrurus c. catenatus*) in a New York peatland. Journal of Herpetology 34:186-192.

Johnson, G. and D. J. Leopold. 1998. Habitat management for the eastern massasauga in a central New York peatland. Journal of Wildlife Management 62:84-97.

Johnson, G., B. Kingsbury, R. King, C. Parent, R. Seigel, and J. Szymanski. 2000. The Eastern Massasauga Rattlesnake: A Handbook for Land Managers. U.S. Fish and Wildlife Service, Fort Snelling, MN. 52 pp.

Johnson, L.F., J.S. Jacob and P. Torrance. 1982. Annual testicular and androgenic cycles of the cottonmouth (Agkistrodon piscivorous) in Alabama. Herpetologica 38:16-25.

Keenlyne, K.D. 1978. Reproductive cycles in two species of rattlesnakes. American Midland Naturalist 100:368-375.

Keenlyne, K.D. and J.D. Beer. 1973. Food habits of *Sistrurus catenatus catenatus*. Journal of Herpetology 4:381-382.

Keyfitz, N. 1985. Applied Mathematical Demography. Springer-Verlag, NY.

King, R., C. Berg, and B. Hay. 2004. A repatriation study of the eastern massasauga (*Sistrurus catenatus catenatus*) in Wisconsin. Herpetologica 60:429-437.

Klauber, L.M. 1936. A key to the rattlesnakes with summary of characteristics. Transactions of the San Diego Society of Natural History. 8:185-276.

Klauber, L.M. 1956. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. Volume I. University of California Press, Berkeley, CA.

Lougheed, S.C., H.L. Gibbs, K.A. Prior, and P.J. Weatherhead. 2000. A comparison of RAPD versus microsatellite DNA markers in population studies of the massasauga rattlesnake. Journal of Heredity 91:458-463.

Lowe, C.H., C.R. Schwalbe, and T.B. Johnson. 1986. The venomous reptiles of Arizona. Arizona Game and Fish Department, Phoenix, AZ.

Mackessy, S.P. 1988. Venom ontogeny in the Pacific rattlesnakes *Crotalus viridis helleri* and *Crotalus viridis oreganus*. Copeia 1988:92-101.

Mackessy, S.P. 1998a. A survey of the herpetofauna of southeastern Colorado with a focus on the current status of two candidates for Protected Species status: the massasauga rattlesnake and the Texas horned lizard. Final Report to the Colorado Division of Wildlife. 418 pp.

Mackessy, S.P. 1998b. A survey of the herpetofauna of the Comanche National Grasslands in southeastern Colorado. USDA/Forest Service. 61 pp.

Mackessy, S.P., J. Hobert, R. Donoho, C. Montgomery, and K. Waldron. 1996. Geographic distribution. *Sistrurus catenatus*. Herpetology Review 27:36.

Mackessy, S.P., K. Williams, and K.G. Ashton. 2003. Ontogenetic variation in venom composition and diet of *Crotalus oreganus concolor*: a case of venom paedomorphosis? Copeia 2003:769-782.

Madole, R.F. 1994. Stratigraphic evidence of desertification in the west-central Great Plains within the past 1000 yr. Geology 22:483-486.

Madole, R.F. 1995. Spatial and temporal patterns of late quaternary eolian deposition, eastern Colorado, U.S.A. Quaternary Science Review 14:155-177.

Maslin, T.P. 1965. The status of the rattlesnake *Sistrurus catenatus* (Crotalidae) in Colorado. Southwestern Naturalist 10:31-34.

McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 *in* D. Power, editor. Current Ornithology, Volume 10. Plenum Press, New York, NY.

Minton, S.A. 1983. *Sistrurus catenatus* (Rafinesque) Massasauga. Catalogue of American Amphibians and Reptiles 332.1-332.2.

Montgomery, C., T. Childers, E. Bergman, J.D. Manzer, J. Sifert, B. Hill, and S.P. Mackessy. 1998. Geographic distribution. *Sistrurus catenatus edwardsii*. Herpetology Review 29:116.

Montgomery, C.E. and S.P. Mackessy. 2003. Natural history of the Texas horned lizard, *Phrynosoma cornutum* (Phrynosomatidae), in southeastern Colorado. Southwest Naturalist 48(1):111-118.

Murphy, R.W., J. Fu, A. Lathrop, J.V. Feltham, and V. Kovac. 2002. Phylogeny of the rattlesnakes (*Crotalus* and *Sistrurus*) inferred from sequences of five mitochondrial DNA genes. Pages 69-92 *in* G.W. Schuett, M. Hoggren, M.E. Douglas, and H.W. Greene, editors. Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, UT. 578 pp.

Mushinsky, H.R. 1987. Foraging Ecology. Pages 302-334 *in* R.A. Seigel, J.T. Collins, and S.S. Novak. Snakes: Ecology and evolutionary biology. McGraw-Hill, New York, NY.

Ostrom, M.R. and D.B. Jackson-Smith. 2000. The Use and Performance of Management Intensive Rotational Grazing Among Wisconsin Dairy Farms in the 1990s. PATS Research Report No.8. Program on Agricultural Technology Studies, University of Wisconsin-Madison, Madison, WI.

Palmer, J.P. 1996. Rancher, Lincoln County, CO. Personal communication.

Pfister, C.A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proc. Nat. Acad. Sci. USA 95:213-218.

Reinert, H. 1992. Radiotelemetric field studies of pitvipers: data acquisition and analysis. Pages 185-198 *in* J.A. Campbell and E.D. Brodie, Jr., editors. Biology of the Pit Vipers, Selva Press, Tyler, TX.

Reinert, H.K. 1981. Reproduction by the massasauga (*Sistrurus catenatus catenatus*). American Midland Naturalist 105:393-395.

Reinert, H.K. and W.R. Kodrich. 1982. Movements and habitat utilization by the massasauga, *Sistrurus catenatus catenatus*. Journal of Herpetology 16:162-171.

Reinert, H.K. and R.R. Rupert, Jr. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. Journal of Herpetology 33:45-61.

Reiserer, R. 2002. Stimulus control of caudal luringand other feeding responses: a program for research on visual perception in vipers. Pages 361-383 *in* G.W. Schuett, M. Höggren, M.E. Douglas, and H.W. Greene, editors. Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, UT. 578 pp.

Roberts, L.S. and J. Janovy. 2000. Foundations of Parasitology. Sixth edition. McGraw-Hill, Boston, MA. 670 pp.

Rubio, M. 1998. Rattlesnake: Portrait of a Predator. Smithsonian Institution Press, Washington, D.C.

Saint Girons, H. 1982. Reproductive cycles of male snakes and their relationships with climate and female cycles. Herpetologica 38:5-16.

Secretaría de Medio Ambiente. 2000. Diario Oficial de la Federacion. Page 54.

Schuett, G., D.L. Clark, and F. Kraus. 1984. Feeding mimicry in the rattlesnake *Sistrurus catenatus*, with comments on the evolution of the rattle. Animal Behavior 32:625-626.

Secretaría de Medio Ambiente. 2000. Diario Oficial de la Federacion. Page 54.

Seigel, R.A. 1986. Ecology and conservation of an endangered rattlesnake, *Sistrurus catenatus*, in Missouri, USA. Biological Conservation 35:333-346.

Seigel, R. 1995. Towson University, Department of Biological Sciences, Maryland. Personal communication.

Seigel, R.A. and N.B. Ford. 1987. Reproductive ecology. Pages 210-252 *in* R.A. Seigel, J.T. Collins, and S.S. Novak, editors. Snakes: Ecology and Evolutionary Biology. Macmillan, New York, NY.

Seigel, R.A., C.A. Sheil, and J.S. Doody. 1998. Changes in a population of an endangered rattlesnake *Sistrurus catenatus* following a severe flood. Biological Conservation 83:127-131.

Smith, H.M. 1996. University of Colorado, Boulder, Department of EPO Biology. Personal communication.

Smith, H.M., T.P. Maslin, and R.L. Brown. 1965. Summary of the distribution of the herpetofauna of Colorado. University of Colorado Studies, Ser. Biol. 154:1-52.

Stebbins, R.C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Company, Boston, MA.

Swanson, P.L. 1930. Notes on the massasauga. Bull. Antivenin Inst. America 4:70-71.

Szymanski, J. 1998. Status assessment for the eastern massasauga (*Sistrurus c. catenatus*) 1998. Endangered Species Division, U.S. Fish and Wildlife Service, Fort Snelling, MN. 68 pp.

Taylor, E.N. 2001. Diet of the Baja Rattlesnake, *Crotalus enyo* (Viperidae). Copeia 2001:553-555.

Walton, P.D., R. Martinez, and A.W. Bailey. 1981. A comparison of continuous and rotational grazing. Journal of Range Management 34:19-21.

Wastell, A. and S.P. Mackessy. In prep. Ecology and habitat use by the desert massasauga in Colorado.

Weatherhead, P.J. and F.W. Anderka. 1984. An improved radiotransmitter and implantation technique for snakes. Journal of Herpetology 18:264-269.

Weatherhead, P.J. and K.A. Prior. 1992. Preliminary observations of habitat use and movements of the eastern massasauga rattlesnake (*Sistrurus catenatus catenatus*). Journal of Herpetology 26:447-452.

Werler, J.E. and J.R. Dixon. 2000. Texas Snakes. Identification, Distribution and Natural History. University of Texas Press, Austin, TX. 437 pp.

Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100: 687-690.

Wright, A.H. and A.A. Wright. 1957. Handbook of snakes of the U.S. and Canada, Vol. 2. Cornell University Press, Ithaca, NY.

Other References

Anton, T.G. 1999. Presence/absence surveys for two state-listed snake species at Goodenow Grove Forest Preserve, Crete Township, Will County, Illinois. Final report from The Ecological Consulting Services, Winnetka, IL.

Anton, T.G. 2000. Presence/absence surveys for two state-listed snake species and snake community structure analysis at Goodenow Grove Nature Preserve, Crete Township, Will County, Illinois. Final report from The Ecological Consulting Group, Winnetka, IL.

Anton, T.G. 2001. Surveys of rare and threatened amphibians and reptiles in the Plum Valley region, Crete Township, Will County, Illinois and eastern massasauga monitoring at Goodenow Grove Nature Preserve. Final report from The Ecological Consulting Group, Winnetka, IL. Email: TAnton2963@aol.com.

Arizona Game and Fish Department. 2001. Desert massasauga, *Sistrurus catenatus edwardsii*. Unpublished abstract compiled and edited by the Heritage Data Management System, Arizona Game and Fish Department, Phoenix, AZ. 6 pp.

Durbian, F.E. 2001. Eastern massasauga population demographics, habitat use, and the effects of alternative habitat management strategies on vegetative communities and survivorship of snakes on the Squaw Creek National Wildlife Refuge. Proposal submitted to the USDI and the USFWS. Email: Frank_Durbian@fws.gov.

Durbian, F.E. Potential effects of summer burning and pre-burn mowing on snakes at Squaw Creek National Wildlife Refuge. Report submitted to U.S. Fish and Wildlife Service.

Durbian, F.E. 2000/2001 eastern massasauga rattlesnake surveys on Squaw Creek National Wildlife Refuge and associated geographic information system database. Report submitted to the U.S. Fish and Wildlife Service.

Johnson, B. and V. Menzies. 1993. Proceedings of the international symposium and workshop on the conservation of the eastern massasauga rattlesnake, *Sistrurus catenatus catenatus*. Metro Toronto Zoo, West Hill, Ontario, Canada.

Kingsbury, B.A. 1996. Status of the eastern massasauga, *Sistrurus catenatus catenatus*, in Indiana, with management recommendations for recovery. Proc. Indiana Acad. Sci. 105:195-205.

Mauger, D. 1993. Habitat use of massasauga rattlesnake at Goodenow Grove Forest Preserve: an interim report. Forest Preserve District of Eill County, IL.

Mauger, D. 2000. 1999 massasauga monitoring report. Email: dmauger@fpdwc.org.

Mauger, D. and D. Stillwaugh, Jr. 1998. Additional survey for massasauga (*Sistrurus catenatus*) and Kirtland's snake (*Clonophis kirtlandi*) at Goodenow Grove Nature Preserve.

Parent, C.E. and P.J. Weatherhead. 2000. Behavioral and life history responses of the eastern massasauga (*Sistrurus catenatus catenatus*) to human disturbances. Oecologia 125:170-178.

Upton, D. 2000. Priority recovery actions for massasaugas (*Sistrurus catenatus*) in peatland and prairie ecosystems. ESRF Final Report.

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