

Dog attacks on wild desert tortoises: A risk model

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Abstract

We retrospectively compiled a database of 6,727 live, wild Agassiz's desert tortoises (*Gopherus agassizii*) and evaluated them for clinical signs of trauma to shell and limbs at 50 sites in the Mojave and Colorado (western Sonoran) deserts of California, USA, spanning the years 1977–2006. Our objectives were to 1) identify tortoises with severe trauma to shell, limbs, and gular horns typically seen in attacks from dogs (*Canis familiaris*); 2) identify locations where severe injuries occurred; and 3) develop a risk model based on distances of tortoises from settlements, towns, or cities. Our models identified multiple variables of importance for tortoises with severe damage to shells, limbs, and gular horns: relative age and sex of tortoises, decades of occurrence, and location. Females and very old tortoises were more vulnerable to attacks than other tortoises. In the decades between the 1970s and 2000s, the risk of severe overall trauma to shell and limbs increased 4 times and to gular horns 16.5 times. Compared to previous decades, by the early 2000s the percent of tortoises with severe trauma increased exponentially the closer a tortoise site was to a settlement; the exponential increase began at approximately 12 km from a settlement. We suggest that the risks may be higher now because of the growth of human populations within the geographic range of the tortoise. The

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threats to tortoises from dogs are based on whether dogs are off-leash in the Mojave and Colorado deserts.

KEYWORDS

Canis familiaris, Colorado Desert, *Gopherus agassizii*, gular horn, Mojave Desert, shell, trauma

Populations of Agassiz's desert tortoise (*Gopherus agassizii*; hereafter tortoise or desert tortoise) have diminished from multiple causes, resulting in listings as a threatened species by the California Department of Fish and Wildlife in 1989 (California Natural Diversity Database 2025) and the United States Fish and Wildlife Service (USFWS) in 1990 (USFWS 1990). Population declines continued after the initial listings (Allison and McLuckie 2018), and the International Union for the Conservation of Nature placed the species on the Red List as critically endangered in 2021 (Berry et al. 2021). In 2025, the California Fish and Game Commission uplisted the tortoise to endangered status (California Natural Diversity Database 2025).

One threat identified in the first Recovery Plan for the species was attacks by dogs (*Canis familiaris*) at the urban-desert interface (USFWS 1994). The Recovery Plan recommended a prohibition on uncontrolled dogs out of vehicles in Desert Wildlife Management Areas, generally the equivalent of designated critical habitat units for the tortoise. Additional recommendations included 1) emergency measures to control unleashed dogs and dog packs in 2 critical habitat units, both of which were in the western Mojave Desert; and 2) fencing or signing or both at the boundary of settlements and communities adjacent to a critical habitat unit. The revised Recovery Plan (2011) stated that the threat of dogs is rising with increasing growth of settlements, towns, and cities, and will be difficult to control (USFWS 2011). In addition to the previous measures, live-trapping and development of a dog management plan were listed. None of the measures were implemented except in the Red Cliffs Desert Reserve (Reserve) in Washington County, Utah, USA, where ordinances requiring protective fencing or walls at boundaries of the urban interface and a leash requirement for dogs in the Reserve were first passed in 1997.

The threat of dogs to chelonians is a global concern. Veterinarians wrote of dogs as predators on captive tortoises and other species of chelonians: "...dogs are fond of chewing on chelonians' shells and appendages and can wreak havoc in a short time...Small chelonians are devoured without a trace" (Boyer and Boyer 2006:87). Barten (2006) described fractures caused by dog attacks and gnawing, subsequent infections, risks of anesthesia, and potentially lengthy treatments. Jacobson (1994) noted that gopher tortoises (*G. polyphemus*) attacked by dogs were frequently seen at the Veterinary Teaching Hospital at the University of Florida. Sack et al. (2017) summarized dog attacks on wildlife over 10 years at the College of Veterinary Medicine at North Carolina State University. Dogs attacked 5 species of wild and captive turtles; 8.6% (8/93) were dead or euthanized on arrival at the veterinary hospital (Sack et al. 2017). Wilson (2019) reviewed >31,000 records of rehabilitation centers across the United States and described dog attacks resulting in trauma to 3 critically endangered bog turtles (*Glyptemys muhlenbergii*), one endangered spotted turtle (*Clemmys guttata*), and frequent attacks on vulnerable species such as the eastern box turtle (*Terrapene carolina*) and gopher tortoise. Although no data were presented on final status of individuals, the author reported that most attacks resulted in death (Wilson 2019). Dogs destroyed nests of sea turtles (Fowler 1979), attacked healthy sea turtles, stranded or nesting, and caused severe injury or death (Margaritoulis et al. 2019, Rojas-Cañizales et al. 2022, Campos de Almeida et al. 2024). The dogs involved in these attacks were domestic pets off-leash or semi-feral. In a summary article in *Science* about attacks of dogs on sea turtle species worldwide, Pallardy (2024) described failed rescue and treatment efforts because of severe injuries and dozens of deaths at numerous locations, raising the question of whether endangered sea turtles could sustain such losses from dogs. In response to the threat of feral dogs, which operated in packs, to Galápagos tortoises (*Geochelone* [*Chelonoidis*] *niger*) and other rare and endemic wildlife on the Galápagos Islands, a control program for dogs was instituted using shooting, baits with compound 1080 (sodium monofluoroacetate), and capture and chemical vasectomy of males (Barnett and Rudd 1983, Barnett 1986).

We conducted many studies and research projects on desert tortoises in the Mojave and Colorado deserts of California (Berry and Medica 1995; Berry et al. 2006, 2014, 2020). The severity of trauma from dog attacks differed markedly in appearance from several other causes of trauma, where the tortoise remained alive. Our observations were comparable to those of Boyer and Boyer (2006), Barten (2006), and the Arizona Exotic Animal Hospital (2025). In a case with an immature tortoise with a radio-transmitter, we obtained assistance from law enforcement personnel to retrieve the tortoise from a house with dogs (Berry and Mack 2008, Berry et al. 2009). The tortoise was freshly injured with extensive damage to and chewing of limbs, removal of limb scales with bloody wounds, punctures of scutes and underlying bones of the anterior and posterior openings of the shell, the gular horn chewed away, and damage to and loss of humeral scutes and underlying bone of the plastron (ventral shell). Although severely damaged, the tortoise was left alive. Such exposure left the tortoise more vulnerable to additional attacks and death from predators (Berry 1974, Harding 1985). Other sources of trauma with definitive characteristics to the tortoise include gunshot (Berry 1986); collision with highway, off-highway, and military vehicles (Homer et al. 1998; Berry et al. 2006, 2024); kills by common ravens (*Corvus corax*; Boarman 1993, Boarman and Berry 1995); remains in pellets of red-tailed hawks (*Buteo jamaicensis*; Anderson and Berry 2019); and tortoise shells with evidence of predation by cougars (*Puma concolor*; Medica and Greger 2009).

Based on scats, prints, and remains of prey, we observed that the principal mesocarnivore attacking and killing wild tortoises within the Mojave and Colorado deserts was the coyote (*Canis latrans*), a close relative of the dog (Berry 1974, Esque et al. 2010, Cypher et al. 2018, Berry et al. 2023, Mack and Berry 2023). When coyotes killed and ate juvenile and immature tortoises, they often left tracks, scattered pieces of bone and scutes on the surface and in scats, and occasionally parts of shells (Nagy et al. 2015, Berry et al. 2023). For the larger immature tortoises, parts of crushed, fractured, and punctured shells remained, with soft tissues missing but no or little evidence of chewing. Pieces of bones and scutes were often present nearby or in coyote scats (Nagy et al. 2015, Berry et al. 2023). The evidence for coyote attacks on adults differed from the smaller tortoises. One of us (KHB) interrupted attacks in 3 cases and retrieved tortoises under attack in another (Berry 1974). An attack on a large adult tortoise with a radio-transmitter was interrupted; the tortoise was severely injured (front leg torn off, interior of body exposed) and removed from the field for treatment; the shell was undamaged (Mack and Berry 2023). Coyotes usually killed the tortoises, removed limbs and internal organs of adults with minor, if any, damage to the shell; often only a few scratches, gnaw marks, or punctures were evident (Berry et al. 2023, Mack and Berry 2023). Coyotes are versatile predators, and severe damage may occur to live adult tortoises such as seen with dogs (Arizona Exotic Animal Hospital 2025), but we did not observe such cases or find published descriptions. Other wildlife biologists may have observed different patterns of attack on tortoises remaining alive after the attack.

In the current study, our overall objective was to determine the risk to tortoises from dogs in and adjacent to critical habitat units and protected areas and to provide supporting evidence for managers and recovery actions. First, we developed a protocol for rating clinical signs of trauma on live desert tortoises from attacks by mammalian predators. We then applied our protocol to evaluate data retrospectively from live tortoises at multiple research sites in the deserts of California, USA. We used the database to develop risk models for tortoises based on size, sex, location, and decade. We evaluated whether the severity of attack differed by location and decade, specifically the role of distance from the source of the dog (settlement, town, and city) to the location of the tortoise. We noted management actions taken to curb dog attacks and benefit tortoises.

STUDY AREA

We revisited previously collected data sets from 50 research sites in the Mojave and Colorado (western Sonoran) deserts of Kern, Riverside, and San Bernardino counties, California, USA: 10 long-term demographic plots (Berry and Medica 1995, Berry et al. 2020), 5 plots at the National Training Center, Fort Irwin, and 7 sites in Goldstone (Berry et al. 2006), 11 sites on the Marine Corps Air Ground Combat Center (MCAGCC) at Twentynine Palms, and 17 other research sites used for sampling health, diseases, and other tortoise-related topics (Appendices 1 and 2; Figure 1). All sites were readily accessible to the public for recreation, including camping, by dirt or paved roads and trails, except for the

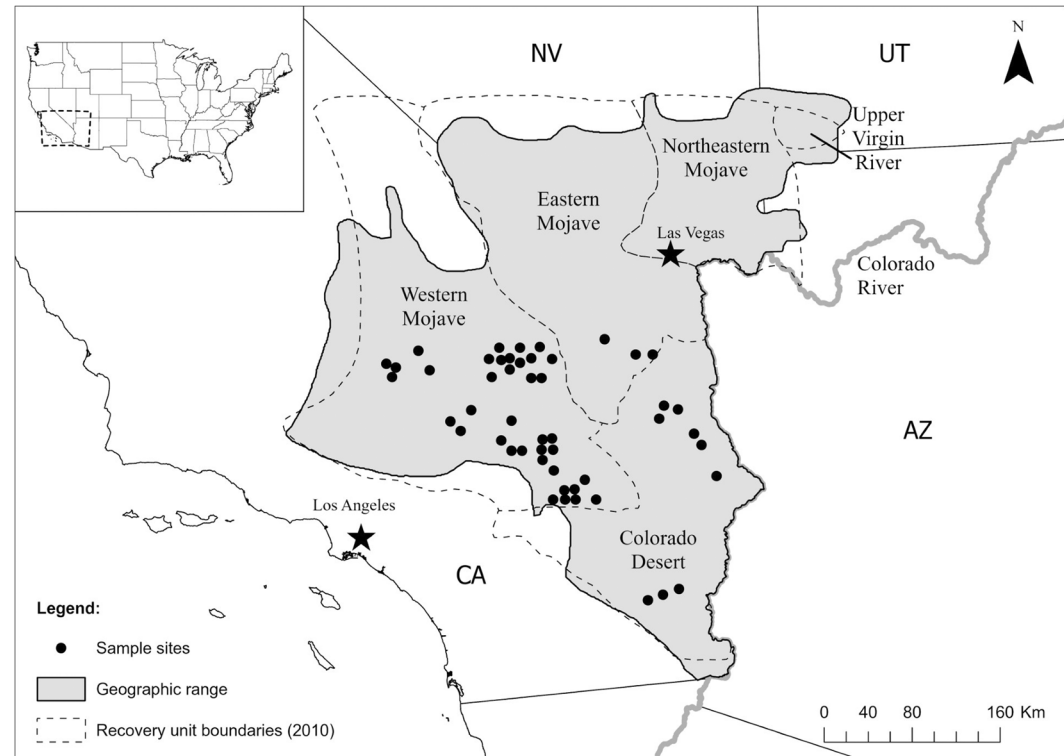


FIGURE 1 Location of 50 study sites for evaluation of individual Agassiz's desert tortoise (*Gopherus agassizii*) for trauma by domestic dogs (*Canis familiaris*) in the Mojave and Colorado deserts of California, USA, between 1977 and 2006. The boundaries of recovery units for the desert tortoise are shown for the geographic range and were taken from USFWS (2011).

Desert Tortoise Research Natural Area (accessible on foot), and military bases. Access to military bases is restricted except by permit. The western Mojave Desert, where most study sites occurred, was highly accessible and recreation use was very high (U.S. Bureau of Land Management 2019). Sites in the Mojave Desert were in Mojave mixed scrub and steppe, and a few sites contained yucca (*Yucca* spp). Sites in the Colorado Desert were in Sonoran Desert mixed woody scrub and succulents (Natural Diversity Database and Holland types in Sawyer and Keeler-Wolf 1995).

Mammalian predators of tortoises potentially occurring on study areas included coyote, and, rarely observed, kit fox (*Vulpes macrotis*), bobcat (*Lynx rufus*), and American badger (*Taxidea taxus*). Known and potential avian predators associated with study areas were the common raven, golden eagle (*Aquila chrysaetos*), red-tailed hawk, greater roadrunner (*Geococcyx californianus*), and loggerhead shrike (*Lanius ludovicianus*).

METHODS

Data collection from tortoises

For each of the 50 previously established research plots, we revisited existing data for 6,727 live tortoises and compiled a database. The database consisted of tortoises from capture-mark-release processing and included details of date of capture; unique identification number of tortoise; size, based on carapace length at the midline (mm) where adults were ≥ 180 mm and juveniles and immatures < 180 mm; sex (female, male, and unknown [juvenile or immature]); and clinical signs of health, trauma, and disease (Berry and Christopher 2001; updated form in Jacobson 2014). Photographs of carapace,

plastron, and presence of lesions or trauma were recorded for each tortoise on 35-mm slides or digital images. We used data sheets and images to assign shell wear and aging classes 1 to 7 of the carapace (Berry and Woodman 1984). The tortoise shell is composed of an epidermal layer (scutes) covering the bony skeleton. Classes were based on appearance of scutes on the carapace. Class 1 was a recently hatched tortoise with aerola (hatchling scutes) and no growth rings; classes 2 and 3 were typical of young juvenile and immature tortoises with several growth rings and most aerola still visible. Classes 3 and 4 occurred in large immature and young adult tortoises, with the bony shell becoming more substantial with growth and size; class 5 represented middle-aged adults with early growth rings worn away, and, in general, maximum shell thickness; classes 6 and 7 were characteristic of old and very old adults with few remaining growth laminae on scutes and sunken or concave scutes on thinning, porous bones.

To evaluate tortoises for clinical signs of trauma, we used 35-mm slides, digital images, and original data sheets. Among plots with multiple years of surveys, each tortoise was included in the database once per sample year. The trauma database comprised fields for each of 37 scutes on the carapace, 16 scutes on the plastron (including the 2 scutes covering the gular horn), and condition of the 4 limbs. We categorized each scute as 1 of 6 classes for damage or injury: 1) none = no sign of damage or injury; 2) minimal = chips on marginal or other scutes, small (a few mm) compared to the size of each scute, and the process of replacing bone and scute may be underway; 3) minor = more than minimal but $\leq 10\%$ of scute damaged, small areas of bone may be exposed; 4) moderate = 11–40% of scute damaged, some underlying bone exposed, damaged or lost; 5) severe = 41–70% of scute damaged, some underlying bone exposed, damaged or lost; and 6) very severe = $> 70\%$ of scute damaged; significant underlying bone exposed, damaged, or lost. The classes of damage or injury to limbs were similarly defined with the proportion of scales and toenails damaged serving as a basis for the classes: 1) none; 2) minor = limb damage but loss of $< 10\%$ of scales or damage (broken or discolored) or loss of 2 toenails; 3) moderate = loss of 10–40% of scales or loss of > 2 toenails; 4) severe = loss of $> 40\%$ of scales; and 5) very severe = loss of $> 10\%$ of the limb.

For each entry of a tortoise into the database, we added 2 additional trauma ratings when a tortoise showed clinical signs of trauma: 1) the overall severity of trauma to the shell and limbs, and 2) the overall severity of injuries to the gular horn, or none. In the summary rating system for trauma to shell and limbs combined, the definitions of moderate damage were 11% to $\leq 40\%$ damage to ≤ 11 scutes with individual ratings of 4, or $< 10\%$ damage to ≥ 6 scutes with individual ratings of 4, or 11% to $\leq 40\%$ scale loss to one limb. The moderate rating also applied to cases where damage to anterior or posterior marginal scutes resulted in additional exposure to a limb and soft tissues. Severe damage was defined as $\geq 40\%$ damage to each of > 11 scutes, or $\geq 40\%$ damage to each of ≥ 1 scute, or loss of part or all of a limb, or loss of $> 40\%$ of scales on > 1 limb. Severe damage included enlargement of anterior or posterior openings of the shell by $\geq 40\%$ of marginal scutes chewed away, exposing limbs and soft tissues. For the final summary rating of overall trauma, we combined results of overall moderate, severe, and very severe trauma and assigned the term, overall severe trauma, because the trauma incurred at these levels was of sufficient magnitude when exposure of soft tissue from trauma to marginal scutes and bones was included.

Damage to gular horn and underlying bone was defined as moderate when 11% to $< 40\%$ of gular scutes and underlying bones were chewed away, whereas the severe rating applied when $\geq 40\%$ of scutes and underlying bone were damaged or entirely lost. For the overall rating of trauma to the gular horn, we combined moderate and severe trauma because of the overall loss of protection and negative effects on behavior.

The number of possible attacks were classed as 1) none, 2) 1 attack, and 3) possibly > 1 attack. For consistency, all data sheets, 35-mm slides and digital images were evaluated by the same person (AC). Tortoises were excluded if key information was missing.

Distance of a tortoise from settlements, towns, and cities

To evaluate the risk to a tortoise from a potential attack by a dog, we calculated the distance between the tortoise and the nearby settlement, town, or city. For most sites, we calculated distances from the edge of tortoise study

sites to the nearest settlement using Google Earth software 4.2 (Google LLC, Mountain View, CA, USA). For sites on 2 large areas, the Marine Corps Air Ground Combat Center (MCAGCC) and Daggett, the distance from each tortoise to the nearest settlement was determined using ArcMap GIS 9.2 software (Esri, Redlands, CA, USA). For MCAGCC, the urban-desert interface consisted of scattered homes extending roughly 24 km along the southwestern and southern boundary of the base. For Daggett, a single residence (with dogs) was an outlier on the desert edge from the Daggett community. To evaluate the effects of human population changes abutting critical habitat units, we sought census data for human populations living close to tortoise sites at the urban-desert interface from the United States Census Bureau (<https://census.gov>), specifically cities and towns. We also gathered human population data from the state of California.

Analysis of data

We used generalized linear models (GLMs) with a logit link for binary outcomes to identify explanatory variables that predicted the likelihood that a tortoise experienced 1) overall severe trauma to shell and limbs, and 2) overall severe trauma to the gular horn. We created a set of models for main effects ($n = 32$) with every combination of 5 variables: sex of tortoise (female, male, and juvenile or immature), carapace length at the midline (MCL), shell wear and aging class (1–7), decade of observation (1970, 1980, 1990, and 2000), and distance (km) to nearest settlement. One set of models was for overall severe trauma to carapace and limbs, and the second set of models was for overall severity of trauma to the gular horn. We used second-order Akaike's Information Criterion (AIC_c ; corrected for sample size) to assess model fit and reported the best fit model (i.e., lowest AIC_c) and those within 2 AIC_c values of the best fit model (Burnham and Anderson 2002). Additional model fit parameters are reported including Akaike weights and evidence ratios. We further evaluated the influence of distance from a settlement on trauma by fitting linear and non-linear models to values of percent of tortoises experiencing overall severe trauma to shell and limbs and overall severe trauma to the gular horn (at sites described in Appendices 1 and 2). For these models, we removed sites where <10 tortoises were evaluated and focused on sites with more robust numbers of samples. We conducted statistical analyses in R (version 4.3.1; R Core Team 2023).

RESULTS

The database consisted of 6,727 tortoise evaluations, of which 28.59% (1,923) were juvenile and immature tortoises (sex unknown), 34.76% (2,338) were adult females, and 36.66% (2,466) were adult males. We observed overall severe trauma to shell and limbs in 15.12% (1,017) of tortoises in the database and severe damage to the gular horns in 4.47% (301). A small portion of previously attacked tortoises was attacked a second time, 6.49% (66/1,017); evidence of limited healing had occurred prior to the second attack (Figure 2). Those tortoises experiencing overall severe trauma to shell and limbs and gular horn were observed with severe chewing, gnawing, and gnashing of the shell and gular horn, and chewing off of limb scales, while leaving the tortoise alive. The characteristics observed in the field from dog attacks on tortoises were comparable with our observations on 35-mm slides, digital images, and data sheets.

Models of tortoises with severe trauma

Models for both measurements of severe trauma (overall trauma to shell and limbs, and overall trauma to gular horn) performed similarly. The best fit model included all 5 predictor variables, but a similarly performing model (within 2 AIC_c) contained only 4 variables, with MCL dropping out (Table 1). Females were 22% more likely to have overall severe trauma to shell and limbs than males, and 27% more likely than immatures and juveniles (Figure 3A;

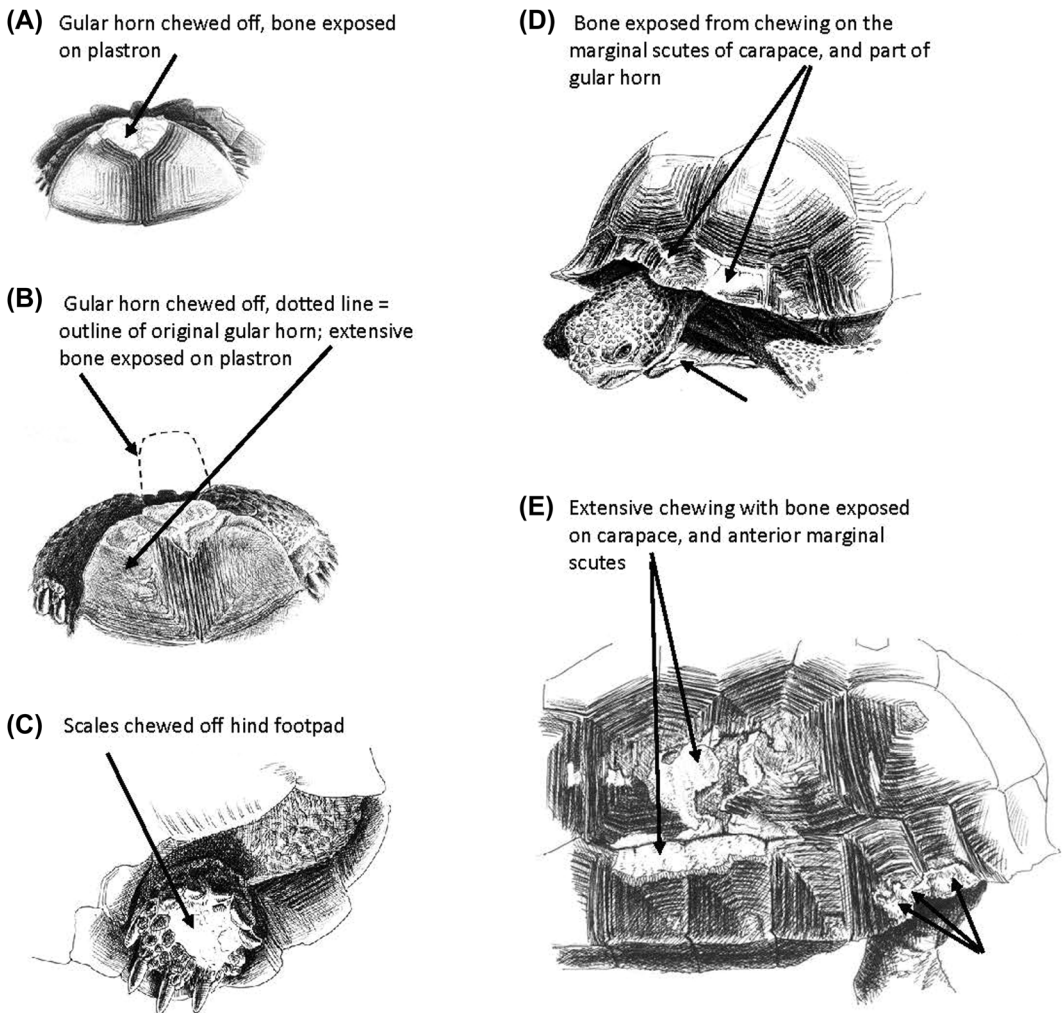


FIGURE 2 Examples of severe damage to shells, limbs, and gular horns of Agassiz's desert tortoises (*Gopherus agassizii*) attacked by dogs (*Canis familiaris*) in the Mojave and Colorado deserts of California, USA, between 1977 and 2006. Illustrations by Tim Shields from study animals.

Tables 1 and 2). Compared to the oldest or more worn tortoises (shell wear and aging class = 7), tortoises with other shell wear and aging classes (1–6) were on average 49% (range = 17–92%) less likely to have severe overall trauma to their shells and limbs, and most shell wear and aging classes (1, 2, 5, and 6) were on average 52% (range = 6–100%) less likely to have severe trauma to their gular horns (Figure 3B; Tables 1 and 2). The beta coefficient for distance to settlement in the best-fit model was negative for both measurements of trauma, suggesting the likelihood of severe trauma to a tortoise decreased as the distance from a settlement increased (Figure 4; Tables 1 and 2). The likelihood of tortoises having severe trauma to shell and limbs increased 4-fold with each decade, from 6.7% in the 1970s to 28.7% in the 2000s (Figure 4; Tables 1 and 2). Severe trauma to the gular horn also increased with each passing decade, from 0.7% in the 1970s to 11.67% of tortoises in the 2000s, a 16.5-fold increase. Most sites with tortoises experiencing severe trauma overall and to the gular horn were 1.5–44.5 km from a settlement. Compared to all other decades, by the early 2000s, the percentage of tortoises with trauma increased exponentially the closer a tortoise was to a settlement (Figure 4A, B). This exponential increase began approximately 12 km from a settlement. Sites in ascending order of increasing distance from a settlement to 12 km

TABLE 1 Best fit model and models within 2 corrected Akaike's Information Criterion (AIC_c) for evaluating variables associated with overall severe trauma to the shell and limbs and the overall severe trauma to Agassiz's desert tortoises (*Gopherus agassizii*) from dog (*Canis familiaris*) attacks in the Mojave and Colorado deserts of California, USA, from 1977 through 2006. We measured performance of generalized linear models ranked according to AIC_c , difference in AIC_c relative to the best model (ΔAIC_c), Akaike weight, cumulative weight, and evidence ratios. Variables included 1 of 7 shell wear and aging classes (swc), sex of tortoise, decade of evaluation, distance to nearest settlement, and carapace length at the midline of tortoise (mcl).

Severe trauma	Model	AIC_c	ΔAIC_c	Akaike weight	Cumulative weight	Evidence ratio
Gular horn	swc, sex, decade, settlement, mcl	2,017.12	0.00	0.47	0.47	1.00
	swc, sex, decade, settlement	2,017.20	0.08	0.45	0.92	1.04
Shell and limbs	swc, sex, decade, settlement, mcl	5,236.16	0.00	0.56	0.56	1.00
	swc, sex, decade, settlement	5,236.67	0.51	0.43	0.99	1.29

were: Daggett, Lucerne Valley, MCAGCC-Sandhill, Hinkley, Kramer Hills, 3 sites on the MCAGCC, Fremont Valley, Desert Tortoise Research Natural Area (interior and Honda experimental site), and Fort Irwin (Alvord; Appendices 1 and 2). Most tortoises with severe overall trauma and severe trauma to the gular horn were living on these sites. In addition, most observations (88.70%, 268/301) of severe trauma overall and severe trauma to the gular horns occurred in tortoises living in the western, southern, and central regions of the Mojave Desert or West Mojave Recovery Unit (USFWS 2011). The remaining sites (11.30%, 34/301) were in the Colorado Desert.

DISCUSSION

We identified 4 factors contributing to the risk of overall severe trauma to shell and limbs and to gular horn from attacks by dogs on tortoises: sex, shell wear and aging class, decade of occurrence, and distance of the tortoise from nearest settlement, city, or town. Carapace length was also important as a fifth factor. We developed a database retrospectively from existing data for the evaluation of effects of dog attacks on wild tortoises but did not design a field study specifically to address the topic. Thus, our study has limitations. Some examples of weaknesses are 1) the single sites were relatively small and not interconnected; 2) no site encompassed distances of 40–50 km from the potential source of dogs (home or settlement), thereby introducing potential bias to results; 3) although data on detection of tortoises were available for some sites, no data on detection were collected beyond study site boundaries or in unsampled areas between sites; and 4) we cannot be assured that all tortoises with overall severe trauma and severe trauma to the gular horn were attacked by dogs and not coyotes. Use of DNA to swab for hairs and saliva would be of benefit in addressing this subject. Future designs for projects on the topic face challenges in locating appropriate sites with settlements coupled with continuous quality habitat, unbroken by unsuitable soils, topography, or severely degraded areas. The continuing decline of tortoise populations, low tortoise densities, and increasing human populations (USFWS 2011, Allison and McLuckie 2018) are additional challenges.

Effects of trauma on the tortoise

The effects on tortoises from dog attacks, even if not injured or immediately killed, may influence survival in both short- and long-term intervals. During the attack, the tortoise may be dragged or tossed and is likely to use

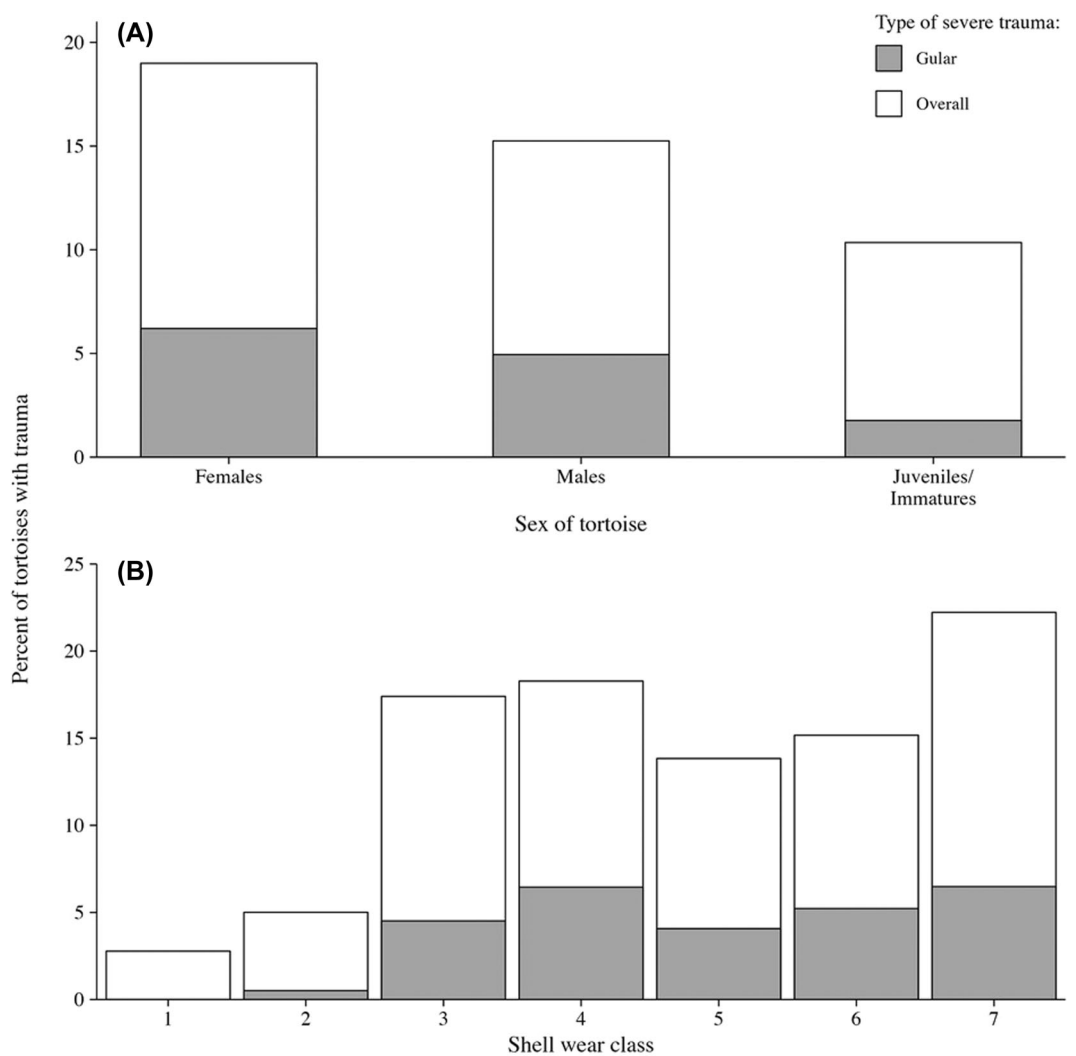


FIGURE 3 Sex (A) and shell wear and aging classes (B) were contributing factors in the models of risk to Agassiz's desert tortoises (*Gopherus agassizii*) for overall severe trauma to shell and limbs and severe trauma to the gular horn characteristic of attacks by dogs (*Canis familiaris*) in the Mojave and Colorado deserts of California, USA, between 1977 and 2006.

defensive measures: voiding the bladder and defecating. Loss of bladder fluid can be a serious threat, reducing survival, because tortoises store water in the bladder and can resorb it during dry seasons or drought years (Nagy and Medica 1986, Peterson 1996). Water is a limiting resource in desert environments, and tortoises drink copiously during rain events, rehydrating and filling the bladder to use for maintenance, growth, reproduction, and survival (Peterson 1996, Henen 1997, Henen et al. 1998, Berry et al. 2023). Loss of bladder fluid can limit above-ground activity and compromise survival during droughts (Berry et al. 2002).

Puncture wounds to the shell and limbs and loss of limbs may result in death within hours or weeks. If wounds become maggot-infested or infected, the long-term result may be septicemia and death (J. Roberts and E. R. Jacobson, unpublished report, Necropsy 95-1, U.S. Geological Survey files). If tortoises survive the loss of a limb, long-term survival rates may be lowered. For example, wood turtles (*Clemmys [Glyptemys] insculpta*) with mutilated

TABLE 2 Best fit model results (beta [β] coefficients, standardized [std.] β coefficients, and percent change) for predictor variables associated with severe trauma to Agassiz's desert tortoises (*Gopherus agassizii*) from attacks by dogs (*Canis familiaris*) in the Mojave and Colorado deserts of California, USA, from 1977 through 2006. Total model set (main effects only) included 32 models. Variables included the effect of decade of evaluation (decade), distance to nearest settlement (settlement, km), shell wear and aging class (SWC), sex, and carapace length (mm) at the midline of the tortoise (MCL).

Variable ^a	Level	Type of severe overall trauma					
		Gular horn			Shell and limbs		
		β (std. β)	SE	% Change	β (std. β)	SE	% Change
Decade	1980s	1.41 (0.70)	0.43	311.56	0.74 (0.36)	0.15	108.75
	1990s	2.25 (1.02)	0.43	847.17	1.18 (0.54)	0.15	225.69
	2000s	2.71 (1.00)	0.42	1409.19	1.72 (0.63)	0.15	457.00
Settlement		-0.09 (-1.26)	0.01	-8.50	-0.03 (-0.48)	0.00	-3.30
SWC	1	-13.56 (-2.39)	252.11	-100.00	-2.53 (-0.45)	0.51	-92.01
	2	-1.17 (-0.37)	0.67	-68.94	-1.61 (-0.52)	0.30	-80.08
	3	0.37 (0.17)	0.31	45.33	-0.19 (-0.09)	0.18	-16.90
	4	0.17 (0.07)	0.27	18.25	-0.25 (-0.11)	0.16	-22.46
	5	-0.37 (-0.13)	0.29	-31.11	-0.60 (-0.21)	0.17	-45.27
	6	-0.07 (-0.02)	0.29	-6.33	-0.50 (-0.16)	0.17	-39.45
Sex	Males	-0.40 (-0.19)	0.15	-33.03	-0.25 (-0.12)	0.09	-22.07
	Juveniles or immatures	-0.39 (-0.17)	0.27	-31.97	-0.32 (-0.14)	0.15	-27.30
MCL		0.004 (0.26)	0.003	0.41	-0.003 (-0.16)	0.00	-0.26

^aReference categories were 1970 (decades), 7 (SWC), and females (sex).

or amputated limbs from predator attacks had significantly lower recapture rates than intact turtles (Harding 1985). The quality of health, overall, can also be reduced. Wild tortoises with lesions from trauma were, in general, more likely to have anemia (Christopher et al. 2003). Tortoises left upside down after an attack or injury may be unable to right themselves and may die of exposure (Woodbury and Hardy 1948).

Females in our study were more likely to be severely damaged than males or immature tortoises. Potentially, this vulnerability is associated with the smaller mass of females than males (Woodbury and Hardy 1948, Berry and Murphy 2019). Another possibility is the condition (strength) of shell and limb bones during the lengthy reproductive process of vitellogenesis, which begins in fall and culminates when shelled eggs are deposited in nests during spring and early summer (Rostal et al. 1994). During vitellogenesis, calcium circulates in maternal blood, supporting the embryo and eggshell. The source of calcium may be from resorption of bone (Wink and Elsey 1986) and osteoderms in the bony shell (Klein et al. 2009). Another source may be calcium at mineral licks (Marlow and Tollestrup 1982). Reproductively active females engaged in geophagy during the nesting season. During life, the bones of tortoises are constantly in a state of remodeling (Botha 2017). Shells may become weakened during drought when both herbaceous forage and water are lacking, especially in the smaller, growing tortoises and females (Henen 2002, Loehr et al. 2007).

The age class of tortoises was another factor in dog attacks. Very old tortoises (class 7) were the most vulnerable: scutes on the carapace were thin and concave, and underlying bone was also concave, porous, and typical of osteoporosis (Berry and Woodman 1984). Comparable to reproducing females, this could leave older tortoises more vulnerable to shell damage during an attack. In contrast, tortoises in classes 3 and 4 were rapidly

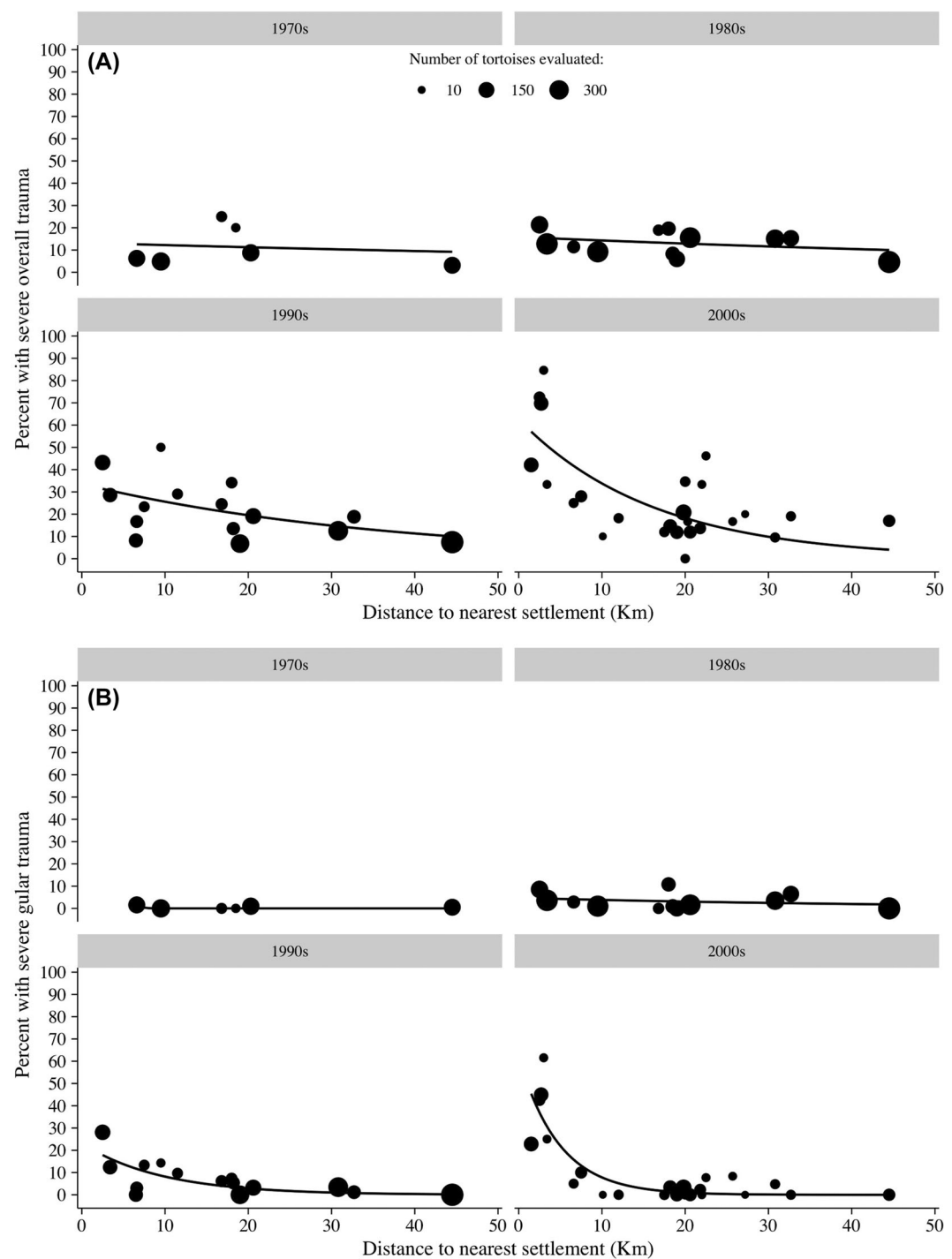


FIGURE 4 The passage of time (decades) and the distance to settlements, towns, or cities influenced the percent of Agassiz's desert tortoises (*Gopherus agassizii*) with overall severe trauma to shell and limbs and overall severe trauma to the gular horn in the Mojave and Colorado deserts of California, USA, between 1977 and 2006. We analyzed severe trauma to shell and limbs (A) and severe trauma to the gular horn (B) separately.

growing and developing the bony shell, whereas bones were well developed in tortoises with class 5 or 6 and growth had slowed. In addition to shell vulnerability, older tortoises may be more likely to show scars of attacks from decades of living.

Damage to the shell can require years to heal (Woodbury and Hardy 1948, Barten 2006). Tortoises cannot regenerate limbs, a lost or severely damaged gular horn, or replace the marginal scutes of the carapace to former sizes, shapes, or layers of laminae. The protective function of the shell can be compromised by missing parts, even if healed and eventually covered with new bone and scute. The loss of bone and scute limits the ability of the tortoise to withdraw tightly into the shell with minimal exposure and withstand future attacks from predators. In addition, we suspect that energy directed to healing is unavailable or less available for growth, reproduction, and other critical activities, such as foraging.

Damage to or loss of the gular horn in males may have profound effects on social behavior. The gular horn, a secondary sexual trait, is more developed in males than females (Woodbury and Hardy 1948). As the adult male ages, the gular horn becomes increasingly enlarged and upturned, in some cases forming a hook in older individuals. Males use the gular horn in male-to-male combat, first pulling in the head and then pushing and ramming the shell of the opponent, ramming face to face, and using the gular horn to flip the opponent. Males also ram females repeatedly during courtship (Woodbury and Hardy 1948, Ruby and Niblick 1994). Importantly, the gular horn protects the head during aggressive encounters, such as ramming and hooking. Burge (1977) reported male-to-male encounters beginning at a burrow and ending 60 m away. The encounters can be lengthy; we observed an encounter lasting almost 3 hours. Generally, the loser retreats, often aggressively pursued by the winner of combat. In experiments with semi-wild male adults, success in combat was dependent on size, past encounters, and residence in home pens with size being most important (Niblick et al. 1994). During first courtship encounters in experiments, Niblick et al. (1994) reported that females preferred larger males. The presence and size of a gular horn appear essential to combat and courtship. If the gular horn is reduced in size or completely chewed off by a dog, the male is less likely to be successful in male-to-male and male-female interactions.

Growth of human populations

The relationships between increasing severity of trauma to tortoises over the decades and distance to settlements appear to be related to growth of human populations. Human populations in the Mojave and Colorado deserts have grown in cities, towns, and settlements since the 1970s and even earlier (Hughson 2009, U.S. Census Bureau). Boundaries of human population areas are close to or abut critical habitat units and other protected areas (e.g., the Desert Tortoise Research Natural Area and Joshua Tree National Park, CA; Red Cliffs Desert Reserve, UT). California City, which borders the Desert Tortoise Research Natural Area, increased more than 5-fold between 1980 and 2020 (Table 3). Cities and towns serving as suburbs to the Southern California megapolis, Adelanto and Victorville, showed exceptional growth between 1980 and 2020 of 17- and 9-fold, respectively. They are close to 3 long-term tortoise plots. Cities bordering Joshua Tree National Park and the MCAGCC (Joshua Tree, Yucca Valley, and Twentynine Palms) have increased more than 2 to 3-fold (Table 3). In Utah, the city of St. George abuts a critical habitat unit and the Red Cliffs Desert Reserve in the northeastern Mojave Desert; the human population increased 337.6% between 1980 and 2000 (U.S. Census Bureau). Las Vegas, another desert city in the northeastern Mojave Desert, Nevada, is within Clark County; both city and county have rapidly increasing populations and are close to or contain critical habitat units. Las Vegas grew 350.3% in the 20-year interval between 1980 and 2000 (U.S. Census Bureau). Throughout the listed portion of the geographic range of the tortoise, the pattern is one of rapid human population growth, increasing the urban and ex-urban interfaces with critical habitat units and thus the potential risk to tortoises from dog attacks. Even a single home with dogs at the desert edge, such as the Daggett study site, can have a substantial impact on the locality (Berry and Mack 2008, Berry et al. 2009; Appendix 2). In contrast, the urban-desert interface extends for kilometers along the southern boundary of the MCAGCC at Twentynine Palms

TABLE 3 Changes in human populations occurring in cities, towns, and settlements in the Mojave and Colorado deserts of California, USA, between 1980 and 2020 and close to study sites for Agassiz's desert tortoises (*Gopherus agassizii*). NA = not applicable; data were from the United States Census Bureau and the state of California.

County	City	Population change (%) by multi-decade in cities, towns, and settlements						Total change
		1980	1990	2000	1980–2000	2010	2020	
Kern	California City	2,743	5,955	8,385	305.69	14,120	14,971	545.6
	Johannesburg			176	NA		90	−195.6
	Randsburg			78	NA		78	0.00
	Ridgecrest	14,929	27,725	27,989	187.48	27,616	27,929	185.07
Riverside	Blythe	10,856	13,857	18,125	166.96	20,817	18,304	168.61
	Desert Center						288	NA
San Bernardino	Adelanto	2,184	6,791	18,130	830.13	31,765	38,042	1741.85
	Apple Valley		46,079	54,239	117.71	69,135	75,786	164.41 ^a
	Barstow	17,690	21,720	21,119	119.38	22,639	25,409	143.63
	Daggett			1000	NA	633		
	Helendale				NA	6,319	5,432	NA
	Joshua Tree	2,083	3,898	4,807	230.77	7,398	7,398	355.16
	Lucerne Valley			5,998	NA		5,998	0.0
	Needles	4,120	5,191	4,921	NA	4,844	4,929	119.64
	Twentynine Palms city		11,821	14,764	NA	25,048	28,067	237.43 ^a
	Victorville	14,220	40,674	64,029	450.27	115,903	134,804	947.99
	Yucca Valley	8,294	13,701	16,865	203.34	20,700	21,740	261.63

^a= total change was for 30 years.

(Appendix 2) and the density of homes is patchy, high in some areas and low in others; tortoises living on adjacent desert may be affected for distances of ≥ 1.5 km. Domestic dogs allowed to roam freely may form packs, returning to homes for food.

Not all tortoise-dog encounters occur in association with homes, settlements, towns, and cities. The Mojave and Colorado deserts are sites of high interest for several types of recreation, including hunting for upland game and deer, target shooting, hiking, wildlife viewing, and camping (U.S. Bureau of Land Management 2019). Individuals and families may include dogs on outings, and dogs may freely roam from campsites. Vehicle-oriented recreation has grown since the 1970s and is particularly high in the western, southern, and central Mojave Desert regions (U.S. Bureau of Land Management 1980, 2019). A high-density network of dirt roads, vehicle trails, and tracks exists from cross-country travel in this part of the Mojave Desert (U.S. Bureau of Land Management 1980, 2019). Unrestricted vehicle use and camping occur in 6 designated areas; all 6 occur in desert tortoise habitats and 4 of the 6 abut critical habitat units (U.S. Bureau of Land Management 2019). Unauthorized

cross-country travel and creation of new trails have continued as major issues (e.g., U.S. District Court, Northern District of California, Case No. 21-cv-07171-SI [2024](#)).

Existing challenges to protecting desert tortoises (and people) from dogs

Management of dogs off leash and in packs is a special challenge for wildlife biologists and law enforcement authorities. Three examples of pack behaviors illustrate types of issues encountered; all packs in these examples were thought to be composed of domestic dogs. In spring of 2001, a person surveying tortoises at a long-term plot deflected an attack from a pack of dogs by yelling and arm waving. Severely chewed tortoises occurred at the site, which was within a critical habitat unit in the western Mojave Desert. The pack was 6–8 km from the nearest settlement (Appendix 1). Also in the western Mojave Desert, a pack of German shepherd-appearing dogs threatened contractors and employees 6–8 km inside Edwards Air Force Base in June of 2004 (Skeen [2005](#)). The owner of the pack lived in a recreational vehicle about 1.6 km south of the southern boundary of the base. With the assistance of animal control, the size of the pack was reduced. The third example occurred in fall of 2018, when a pack of about 12 dogs in the central Mojave Desert charged a group of 4 adults 3 times within 15 minutes and were only repelled by yelling and throwing rocks (M. W. Tuma, U.S. Geological Survey, personal communication). The adults were processing a tortoise about 15 km from the nearest residence or settlement where the pack may have lived. When staff requested assistance from the Interagency Dispatcher, they were notified that Animal Control does not respond to dogs in the open desert and recommended carrying a gun when in the area (firearms were one method of managing dog packs in the Galápagos Islands; Barnett and Rudd [1983](#)).

More detailed information about control efforts was available from the Red Cliffs Desert Reserve in Washington County, Utah. The Reserve lies adjacent to the city of St. George and is the smallest and most vulnerable of the recovery units for tortoises (USFWS [1994](#)). To protect the Reserve, the Washington County Commission ([1996](#)) implemented an agreement for the Washington County Habitat Conservation Plan. Builders adjacent to the Reserve are required to construct a fence that is tortoise-human-pet proof prior to construction (St. George Municipal Code 9-12-1, Fencing Along Red Cliffs Desert Reserve; Washington County, Utah, Code of Ordinances 9-5-1 Fencing Plan Approval). Types of fences ranged from block walls to metal. Frequent monitoring was essential to identify and repair holes, breaks, or wash-outs after storms and to maintain the integrity of the barriers. In addition, a Washington County Ordinance (Code of Ordinances for the Red Cliffs Desert Reserve, Chapter 2, Pets 7-2-10) requires dogs (pets) to be on leash on trails when in the Reserve. Fences are effective when maintained, whereas the ordinance for dogs on leash is not entirely effective, according to Ann McLuckie at the Division of Wildlife Resources (personal communication, 2024). Several office records exist for dogs off-leash injuring tortoises, in some cases severely, in the Reserve (Ann McLuckie, personal communication). According to the amended Habitat Conservation Plan for Washington County Commission ([2020:47](#)), "...dogs (and ravens) likely play a role in the population dynamics of MDT [Mojave Desert Tortoise] within the Reserve...and the decline of MDT within the Permit Area."

CONSERVATION IMPLICATIONS

Tortoises living within 12 km and possibly as distant as 44.5 km from a settlement, town, or city with dogs are potentially vulnerable to serious injury or death. This source of loss can occur within edges of protected areas, critical habitat units, and other areas where tortoises and dogs co-occur. Injury or death of tortoises from dog attacks has high potential for contributing to population declines locally, and ultimately within a region. We identified females and very old tortoises as being more susceptible to trauma from dog attacks. Survival of healthy, uninjured females, especially the larger and older females, is essential to recovering declining or inviable populations

because large, older females produce more eggs than young, small females (Mueller et al. 1998, Wallis et al. 1999, McLuckie and Fridell 2002). However, protection of all sizes and age classes is critical for rebuilding populations (Berry et al. 2020). Implementation of recovery actions to protect tortoises from dogs could provide measurable benefits (USFWS 1994, 2011). When implemented, especially in the West Mojave Recovery unit and locations we identified herein (Daggett, Lucerne Valley, MCAGCC-Sandhill and 3 sites, Hinkley, Kramer Hills, Fremont Valley, Desert Tortoise Research Natural Area [interior and Honda] and Fort Irwin [Alvord]), the USFWS recommendations could provide measurable benefits and reduce losses of tortoises (USFWS 1994, 2011). County ordinances associated with construction and development of homes and for control of pets, especially associated with boundaries of critical habitat units, also may benefit recovery of tortoises and improve management of dogs on wildlands. For protected areas comparable to the Reserve where leashed dogs are allowed on trails, an enforcement officer frequently walking or riding horseback on trails could provide benefits by educating visitors and warning or citing individuals with off-leash dogs. If compliance fails, closure of trails to dogs could assist recovery of the tortoise population. More protected areas with fencing designed to prevent entry by dogs and patrolled to ensure integrity of the fence could benefit recovery of tortoise populations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

For this retrospective analysis of existing data, no tortoises were handled, either captives or wild individuals. The earlier collection of data and handling of tortoises were covered under state and federal permits from the California Department of Fish and Game (Permit No. SC-003623) and USFWS (Permit No. TE-06556 and amendments), respectively, to KHB. For data collected prior to 1990, animal care procedures were approved by the California Department of Fish and Game. After 1993, animal care procedures were approved by the permitting agencies and Western Ecological Research Center, U.S. Geological Survey's Animal Care and Use Committee.

DATA AVAILABILITY STATEMENT

Data is available as a U.S. Geological Survey Data Release at <https://doi.org/10.5066/P13F8LEV>.

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APPENDIX 1

See Table A1.

TABLE A1 Data for Agassiz's desert tortoises (*Gopherus agassizii*) from 13 long-term sites and 3 other sites in the Mojave and Colorado deserts of California, USA, 1977–2006. *n* = sample size of data for tortoises available for examination.

Site	Year	<i>n</i>	Desert region	Distance (km) to nearest settlement
Chemehuevi	1978	38	Northern Colorado	20.3
	1979	168		
	2002	12		
Chuckwalla I	1982	253	Eastern Colorado	20.6
	1988	120		
	1992	106		
	1997	52		
	2004	67		
Chuckwalla Valley	1980	92	Eastern Colorado	32.7
	1987	79		
	1991	69		
	1995	16		
	2003	3		
Desert Tortoise Natural Area- Honda	2005	18	Western Mojave	7.5
	1998	30		
	2003	50		
Desert Tortoise Natural Area-interior	1978	57	Western Mojave	9.5
	1979	191		
	1982	231		
	1988	171		
	1996	14		
Fremont Peak	2002	8	Western Mojave	18.5
	1978	15		
	1980	43		
	1985	36		
	1989	30		
Fremont Valley	1993	8	Western Mojave	6.6
	1979	203		
	1987	70		
	1991	45		
	1995	21		
Fenner Valley	2001	20	Eastern Mojave	44.5
	1977–1978	171		

(Continues)

TABLE A1 (Continued)

Site	Year	<i>n</i>	Desert region	Distance (km) to nearest settlement
Ivanpah Valley	1980	202	Northeastern Mojave	19.0
	1986	255		
	1990	230		
	1994	242		
	2000	53		
	1986	168		
	1990	129		
	1994	137		
	2001	22		
	2002	54		
Johnson Valley	1980	83	Southern Mojave	18.0
	1986	19		
	1990	18		
	1994	23		
	2003	2		
Lucerne Valley	1980	115	Southern Mojave	2.5
	1986	96		
	1990	74		
	1994	66		
	2002	14		
Shadow Valley	2005	26	Northeastern Mojave	16.8
	1978	32		
	1988	35		
	1992	49		
Soda Mountains	2002	6	Central Mojave	19.8
	2001	25		
	2002	24		
	2003	44		
	2004	30		
	2005	24		
Stoddard Valley	2006	7	Southern Mojave	6.5
	1991	98		
Ward Valley	1980	142	Northern Colorado	30.8
	1987	117		
	1991	202		
	1995	118		
	2001	21		

APPENDIX 2

See Table A2.

TABLE A2 Locations where data were collected on Agassiz's desert tortoise (*Gopherus agassizii*) in the Mojave and Colorado deserts of California, USA, 1997–2006. MCAGCC= Marine Corps Air Ground Combat Center. *n* = sample size of tortoises evaluated for a site in a particular year.

Site	Year	<i>n</i>	Desert region	Distance (km) to nearest settlement
Chocolate Mountains Aerial Gunnery Range	2002	25	Eastern Colorado	17.5
Daggett	2003	27	Southern Mojave	1.5
	2004	42		
	2005	21		
	2006	24		
Fenner	2002	5	Eastern Mojave	67.0
Fort Irwin-Alvord 6	1997	32	Central Mojave	12.6
Fort Irwin-Eastgate 1	2000	2	Central Mojave	23.0
	2002	3		
Fort Irwin-Eastgate 2	2000	16	Central Mojave	26.5
	2002	12		
	2003	17		
Goldstone-2	1998	1	Central Mojave	21.8
Goldstone-4	1998	1	Central Mojave	22.5
Goldstone-6	1998	1	Central Mojave	16.3
Goldstone-7	1998	3	Central Mojave	18.1
Goldstone-9	1998	1	Central Mojave	16.1
Goldstone-12	1998	6	Central Mojave	11.5
Goldstone-15	1998	6	Central Mojave	6.0
Fort Irwin-Tiefert	1997	74	Central Mojave	18.2
	2002	24		
	2003	33		
	2004	30		
	2005	2		
Ft. Irwin-Hatchery	2002	3	Central Mojave	22.5
Fremont-Kramer	2002	13	West Mojave	2.4
Hinkley	2003	13	West Mojave	3.0
Ivanpah	2002	16	Northeastern Mojave	20.0
MCAGCC-1	2004	1	Southern Mojave	5.0
MCAGCC-2	2004	2	Southern Mojave	3.0

(Continues)

TABLE A2 (Continued)

Site	Year	<i>n</i>	Desert region	Distance (km) to nearest settlement
MCAGCC-3	2002	7	Southern Mojave	12.0
	2003	11		
	2006	4		
MCAGCC-4	2005	7	Southern Mojave	10.1
	2006	3		
MCAGCC-5	2003	9	Southern Mojave	6.5
MCAGCC-6	2003	3	Southern Mojave	21.8
MCAGCC-7	2002	10	Southern Mojave	27.2
MCAGCC-8	2006	1	Southern Mojave	0
MCAGCC-9	2006	1	Southern Mojave	0
MCAGCC-10	2005	7	Southern Mojave	20.5
MCAGCC-11	2001	17	Southern Mojave	2.7
	2002	24		
	2003	19		
	2004	19		
	2005	31		
MCAGCC-12	2005	12	Southern Mojave	25.7
MCAGCC-VSTOL	2004	1	Southern Mojave	4.5
Ord-Rodman	2001	12	Southern Mojave	20.0
	2002	14		
Superior-Cronese	2001	3	Central Mojave	22.0
	2002	9		