

COLORADO PIKEMINNOW (*PTYCHOCHEILUS LUCIUS*) UPSTREAM OF CRITICAL HABITAT IN THE YAMPA RIVER, COLORADO

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ABSTRACT—The Colorado pikeminnow (*Ptychocheilus lucius*) is a federally endangered fish, which was once abundant and widespread in the Colorado River basin. During exotic fish removal sampling in the spring of 2003, 2004, and 2005, 2 Colorado pikeminnow were collected upstream of critical habitat in the Yampa River, Colorado. Collection of these specimens might be an artifact of low historical sampling effort, but they do serve to document potential habitat use of Colorado pikeminnow outside of critical habitat.

RESUMEN—El charalito del Colorado (*Ptychocheilus lucius*) es un pez catalogado en peligro de extinción por el gobierno federal, que anteriormente fue abundante y con una distribución amplia en la cuenca del río de Colorado. Durante el proceso de remover el pez exótico en la primavera de 2003, 2004 y 2005, se colectaron 2 charalitos río arriba del hábitat crítico en el río Yampa en Colorado. La colecta de estos especímenes puede ser un artefacto del bajo esfuerzo histórico del muestreo, pero sirve para documentar el uso potencial del hábitat del charalito del Colorado fuera del hábitat crítico.

The Colorado pikeminnow (*Ptychocheilus lucius*) is a federally endangered fish (Federal Register 32 [43]:4001), which was once abundant and widespread in the Colorado River basin (Tyus, 1991). Known subpopulations occur in the Upper Colorado River basin in the White, Green, Colorado, and Yampa rivers. Colorado pikeminnow in the Upper Colorado River basin, apart from the Colorado mainstem, exhibit seasonal potamodromy, moving considerable distances to find suitable spawning grounds (Tyus, 1990).

Critical habitat is defined as the area essential for the conservation of a species (i.e., recovery) to the point that the species no longer requires the protection of the Endangered Species Act. Despite this definition, the boundaries of critical habitat can be set more by geopolitical considerations than biological needs of a species (R. Muth, U.S. Fish and Wildlife Service, pers. comm.). In the Yampa River, critical habitat for the Colorado pikeminnow extends from river kilometer (Rk) 215.7 (Colorado Highway 13 bridge) downstream to its confluence with the Green River in Dinosaur National Monument (Federal Register 59 [54]:13374). My study site encompassed the portion of the Yampa River from the upstream extent

of Colorado pikeminnow critical habitat upstream to Rk 276.5.

While conducting removal sampling of introduced northern pike (*Esox lucius*), sampling crews collected a Colorado pikeminnow at Rk 232.9 (3 June 2004) and one at Rk 220.8 (9 May 2005), 17.2 and 5.1 km upstream, respectively, of critical habitat. The fish were 51.5 cm and 51.6 cm in total length, respectively. The fish were examined for the presence of internal and external marks; neither was previously tagged. Both were subsequently tagged with internal passive integrated transponder tags and released alive. Both were adults and were collected during 16 electrofishing passes across the width of the study site conducted from 2003 to 2005. Total electrofishing time for the 16 sampling passes exceeded 442 hours. Both fish were collected in swift moving water in the main channel over cobble substrate.

Historical capture of Colorado pikeminnow in the area upstream of critical habitat in the Yampa River has been sporadic. Reasons for this sporadic capture history outside of critical habitat might be that the area is sampled infrequently or that Colorado pikeminnow rarely occur outside of critical habitat. Areas within my study site were sampled in the 1990s by the

Colorado Division of Wildlife, who did not catch nor locate radio-tagged Colorado pikeminnow upstream of critical habitat (T. Nesler, Colorado Division of Wildlife, pers. comm.). However, an angler in the late 1980s caught a Colorado pikeminnow near Rk 260 (Recovery Program for Endangered Fishes of the Upper Colorado River Basin, unpublished data). Year 2004 sampling upstream (Rk 274.6 to 319.9) of the study site yielded no Colorado pikeminnow in 57.5 sampling hours (S. Finney, unpubl. data). However, year 2002 sampling below the study site (Rk 215.7 to 82.1) yielded 33 unique Colorado pikeminnow, and year 2003 yielded 31 unique Colorado pikeminnow (K. Bestgen, Colorado State University, pers. comm.). This evidence suggests that Colorado pikeminnow are rare within the study site, whereas they are more common downstream and absent upstream.

Despite the almost nonexistent historical captures of Colorado pikeminnow upstream from critical habitat in the Yampa River, my capture of 2 Colorado pikeminnow outside of critical habitat provides evidence for limited habitat use in the area. Their presence might be isolated or random behavior. Or, perhaps, Colorado pikeminnow might be trying to escape environmental perturbations, such as drought. Further, they might be attempting to find and establish a home range.

Marsh et al. (1991) reported the discovery of a Colorado pikeminnow in the Little Snake River, Wyoming, a Yampa River tributary. It was speculated to be a possible migrant from the

Yampa River. Other investigators have captured or located radio-tagged Colorado pikeminnow in areas outside of critical habitat in the Duchesne and Green rivers (Recovery Program for Endangered Fishes of the Upper Colorado River Basin, unpublished data). Sampling for, and the study of, Colorado pikeminnow in areas outside of critical habitat can lend further insight into the life history of this species.

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USE OF PLASTICINE REPLICAS OF LARGE AND SMALL SNAKES TO ELICIT ANTIPREDATOR BEHAVIOR IN THE CALIFORNIA GROUND SQUIRREL (*SPERMOPHILUS BEECHEYI*)

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ABSTRACT—We placed 72 plasticine replicas of large and small snakes near a California ground squirrel (*Spermophilus beecheyi*) colony in San Diego County, California. Ground squirrels aggres-

sively confronted both large and small replica snakes. Ground squirrels were more aggressive when attacking small replicas relative to large. Ground squirrels bit the smaller replicas a greater number of times, concentrating their attacks near the head of the replica. Large replicas were attacked more frequently near the tail. From the results we conclude: 1) California ground squirrels recognize increased risk of attacking larger versus smaller snakes, and 2) use of plasticine replicas is an effective method to investigate antipredator behavior of prey.

RESUMEN—Colocamos 72 replicas de culebras hechas de plasticina, algunas grandes y otras pequeñas, cerca de una colonia de ardillones de California (*Spermophilus beecheyi*) en el condado de San Diego en California. Los ardillones agresivamente confrontaron a ambas culebras de plasticina, las chicas y las grandes. Atacaron más agresivamente a las replicas de culebras pequeñas que a las grandes. Los ardillones mordieron las replicas pequeñas más, concentrando sus ataques cerca de la cabeza de las replicas. Las replicas grandes fueron atacadas con más frecuencia en el área de la cola. De los resultados concluimos que: 1) los ardillones de California reconocen que hay mayor riesgo al atacar a las culebras grandes que a las más pequeñas; y 2) el uso de replicas de plasticina es un método efectivo para investigar el comportamiento anti-depredador de una presa.

The use of plasticine (a plastic-based modeling compound) replicas in field studies of predator-prey interactions is becoming increasingly common. Plasticine replicas have been used in studies of color-pattern evolution in salamanders (Kuchta, 2001), lizards (Castilla et al., 1999), and snakes (Madsen, 1987; Brodie, 1993), and nest predation of birds (Keyser et al., 1998; Roos, 2002; Boulet et al., 2003). The use of plasticine replicas is a powerful method to study infrequent predatory events under natural conditions. Given the low cost and ease of making replicas, large samples can be quickly deployed with this method. Furthermore, imprints left on the surface of soft replicas record disturbances and allow for identification of attacking species (Madsen, 1987; Brodie, 1993).

Although widely successful when employed, use of plasticine replicas has been mostly limited to studies of the behavior of predators. To expand use of plasticine replicas in studies of predator-prey interactions, we used replicas of predators to investigate antipredator behaviors of prey.

We used plasticine replicas of snakes to elicit antipredator behaviors in California ground squirrels (*Spermophilus beecheyi*). Ground squirrels have an adversarial relationship with snakes, especially rattlesnakes (Viperidae, Crotalinae). Rattlesnakes are a common and persistent predator of California ground squirrels throughout their range (Fitch, 1949; Stebbins, 2003). Adult ground squirrels, partially immune to rattlesnake venom (Poran et al., 1987), are known to aggressively defend them-

selves and their young against rattlesnakes (Swaigood et al., 1999a), often confronting, harassing, and attacking the snakes when encountered (Owings and Coss, 1977; Coss and Owings, 1985).

Larger snakes are more dangerous to ground squirrels than smaller snakes. Larger rattlesnakes release more venom, hold on to prey longer (Rowe and Owings, 1990), and, because snakes are gape-limited predators, are able to swallow larger prey items (Shine, 1991; Arnold, 1993; King, 2002). Swaigood et al. (1999b) showed in experimental trials that ground squirrels recognize the greater threat presented by larger rattlesnakes and take fewer risks when confronting larger rather than smaller snakes.

To assess the effectiveness of using plasticine replicas to elicit aggressive responses from California ground squirrels and learn whether differences in the antipredator response of ground squirrels exist when confronting more or less dangerous snakes under natural conditions, we exposed free-ranging ground squirrels to plasticine replicas of large and small snakes. Imprints left by the ground squirrels allowed us to measure the presence, intensity, and location of aggressive confrontations and test whether ground squirrels recognize the increased risk of attacking larger snakes.

Snake replicas were constructed from precolored nontoxic plasticine (Sculpy-III modeling compound). Replicas were cylindrical and light brown in coloration. On one end of each replica, we shaped a distinctive head region and added a pair of eyes with black clay. Rep-

licas were constructed as either large (50 cm long and 2 cm diameter) or small (30 cm long and 1.5 cm diameter). Replicas were threaded onto an S-shaped wire. Replicas were anchored to the ground with a 5-cm length of wire protruding from either end of the replica.

To assess antipredator behavior of ground squirrels under natural conditions, we placed snake replicas near a California ground squirrel colony at the Tijuana River National Estuarine Research Reserve in San Diego County, California (32°34'N, 117°07'W). Vegetation at the study site consisted mostly of annual grasses and disturbed coastal sage scrub. A set of replicas consisted of a large and small replica placed in the open and separated from each other by 2 to 5 m. Squirrels encountered the replicas independently because the space between replicas was filled with dense grasses and shrubs, concealing the location of one replica from the other. We placed 3 sets of replicas at 50-m intervals along 4, 100-m transects. Transects were equally distant and radiated out from the center of the ground squirrel colony. By placing the replicas in sets of small and large replicas at each 50-m interval, we assured the size classes experienced the same density of ground squirrel activity because squirrel densities were higher near the center of colonies. Replicas were left in the field for 96 hours. Replicas were then picked up, scored for bite-marks, reshaped, and returned to the field. This procedure was repeated 3 times during April and May 2004.

To identify the California ground squirrel bite-mark and confirm that ground squirrels were attacking replicas, we matched tooth-marks left on the replicas with the dentition patterns of a museum specimen *S. beecheyi* skull at the San Diego State University Vertebrate Collections. As a secondary confirmation source, we set up a motion sensitive camera (Non-Typical Deer Cam DC-200 Scouting Camera, Deer Cam, Park Falls, Wisconsin) next to a pair of snake replicas at the reserve during a sampling session and captured multiple photographs of California ground squirrels interacting with the replicas.

We scored each replica by first counting the total number of ground squirrel bite-marks, and second, by dividing the replicas into 6 sections of equal length and recording which body sections were attacked by ground squir-

rels. We considered a body section attacked if one or more bite-marks were present.

Analysis of the number of replicas attacked by size and the number of replicas attacked in sets versus singularly was performed using Pearson chi-square tests. Analysis of the number of bite-marks per replica by size was performed using a Mann-Whitney test because normality assumptions of *t*-tests were violated by the data. Analysis of differences in the ordered distribution of attacks across sections by replica size was performed using a single ordered Kruskal-Wallis R×C table test (StatXact, 2001) because we scored bites along consecutive, non-independent, segments of the replicas.

We used 72 snake replicas during the study. California ground squirrels attacked 29 (40.3%) of the 72 replicas. We found no evidence that squirrels attacked large and small snake replicas at different rates: 14 of 36 large replicas (38.9%) and 15 of 36 small replicas (41.7%) were attacked ($\chi^2 = 0.058$, $P = 0.810$, $df = 1$). Also, we found no evidence that squirrels attacked replicas in sets more frequently than they attacked replicas singularly: 16 replicas (8 large and 8 small) were attacked in sets, while 13 (6 large and 7 small) replicas were attacked singularly ($\chi^2 = 0.31$, $P = 0.577$, $df = 1$).

Despite similar overall rates of attack, the intensity of the attacks on the snake replicas differed by size class. The number of bite-marks on replicas ranged from 1 to 63 (mean = 8.8, $SE = 2.2$, $n = 29$). Although the mean numbers of bite marks were similar between replica sizes (large: mean = 8.6, $SE = 4.3$, $n = 14$, small: mean = 9.0, $SE = 1.63$, $n = 15$), small replicas had significantly more bite-marks than large replicas ($U = 55.5$, $P = 0.029$, $n = 29$). If we exclude the replica with 63 bite-marks (a large replica, with more than 3 times the total number of bite-marks than the next most frequently bitten replica) from calculations of the sample mean and standard error, large replicas had on average 50% fewer bite-marks (mean = 4.4, $SE = 1.04$, $n = 13$) than small replicas.

The distribution of ground squirrel attacks across sections of the snake replicas differed by replica size ($\chi^2 = 4.016$, $P = 0.045$, $df = 1$). Small replicas were attacked most frequently in the head region, with the number of attacks in this region averaging twice as many as any oth-

TABLE 1—Number of California ground squirrel (*Spermophilus beecheyi*) attacks on replica body sections for large and small snake replicas. Attacks by body section are summed across all replicas within each size category. The head of the snake replica is located in section 1 and the tail end of the replica is located in section 6.

Replica size	Section						Total attacks
	1	2	3	4	5	6	
Large	6	4	7	8	10	11	46
Small	11	4	6	6	6	5	38

er body section (Table 1). Large replicas were attacked most frequently near the tail end of the replica (Table 1).

Our results indicate that plasticine replicas of snakes, when encountered under natural conditions, elicit aggressive confrontations by free-ranging California ground squirrels, which apparently treat plasticine replica snakes as a significant threat. Thus, plasticine replicas can be useful in investigations of antipredator behaviors of prey. In this study, ground squirrels attacked approximately 40% of the large and small snake replicas left in the field during the 4-day sample periods. Because the 2 types of replicas were attacked at a similar rate, this result suggests the presence of a snake replica, regardless of size, near a California ground squirrel colony is enough to elicit an attack.

When attacking plasticine replicas, ground squirrels responded differently to large and small snake replicas. Ground squirrels attacked small replicas more aggressively than they did large, biting small replicas a greater number of times and concentrating attacks near the head of the replica. Ground squirrels seemed to attack the large snake replicas more cautiously, biting the replicas a fewer number of times and concentrating the attacks away from the head and closer to the tail end of the replica.

Differences in the intensity and location of the bite-marks between the 2 types of replicas suggests California ground squirrels recognize differences in the risks associated with aggressively confronting larger versus smaller snakes. Attacking ground squirrels seem to consider small snake replicas less of a threat than large replicas. This interpretation of the results is consistent with the greater lethality of larger snakes and the well-documented ability of California ground squirrels to assess risk when confronting predators (Swaigood et al., 2003).

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RANGE EXPANSION OF THE LEAST SHREW (*CRYPTOTIS PARVA*) IN COLORADO

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ABSTRACT—We report the collection of 4 specimens that extend the range of the least shrew (*Cryptotis parva*) in Colorado. The 2 collection locations are approximately 240 km and 290 km from previously collected specimens documented from the Cimarron River watershed in southeastern Colorado and approximately 300 km from those documented from the Arkansas River watershed in Kansas. These 4 specimens are the first individuals reported from the Arkansas River watershed in Colorado.

RESUMEN—Registramos la colección de 4 especímenes que extiende la distribución de la musaraña chica (*Cryptotis parva*) en Colorado. Las 2 áreas de colección están a aproximadamente 240 km y 290 km de los especímenes previamente colectados y documentados en la cuenca del río Cimarron en el sureste de Colorado y aproximadamente 300 km de los que fueron documentados de la cuenca del río Arkansas en Kansas. Estos 4 especímenes son los primeros que se han coleccionado en la cuenca del río Arkansas en Colorado.

The least shrew (*Cryptotis parva*) is distributed throughout the eastern United States, eastern Mexico, and portions of Central America (Whitaker, 1974; Hall, 1981). In northern

Colorado, *C. parva* has been found in marshy areas (Beidleman and Remington, 1955; Lechleitner, 1964; Williams and McArthur, 1972), in tall, dry grasses (Williams and McArthur, 1972), and in owl pellets near shortgrass prairie (Marti, 1972). In southeastern Colorado, Choate and Reed (1988) collected this species from riparian communities along the Cimarron River.

We report 3 specimens of *C. parva* collected in pitfall traps at 2 locations in Colorado. Two individuals (DMNS 9689 and 10173) were captured in terrestrial invertebrate pitfall traps (8-cm-diameter plastic cups) in the fall of 1999 on the Pueblo Chemical Depot, Pueblo County, Colorado (T20S, R62W, Sec. 14 and 22) at an elevation of 1,426 m. Surrounding habitat consisted primarily of greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus nauseosus*), alkali sacaton grass (*Sporobolus airoides*), and blue grama (*Chondrosium gracile*). Other small mammals live-trapped in the immediate vicinity during an associated small mammal study included *Dipodomys ordii*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, *Perognathus*, *Neotoma*, and *Onychomys leucogaster*. An additional male *C. parva* (DMNS 10884) was captured on 1 October 2002 in a pitfall trap (16-cm-diameter plastic bucket) in El Paso County, Colorado (T16S, R65W, Sec. 33) at an elevation of 1,640 m. The pitfall was placed in a trailside ditch in a riparian shrub and grassland community. Other small mammals captured along the trail were *Peromyscus boylii* and *Reithrodontomys megalotis*. No other soricids were captured from either location.

In 1993, a *C. parva* specimen (University of Colorado Museum 17739 collected by E. Lapioli) was collected from El Paso County (T16S, R65W, Sec. 29), but was unreported. The location from which this specimen was taken is <3 km from our collection location along the same creek.

The range of the least shrew has expanded westward (Hafner and Shuster, 1996). Choate and Reed (1988) documented its westward expansion in Kansas and into southern Colorado (Baca County), where it was locally common. These 4 specimens from Pueblo and El Paso counties represent range expansions to the northwest by approximately 240 km and 290 km, respectively, from the individuals recorded from Baca County. In addition, these are the

first specimens recorded from either county or from the Arkansas River watershed in Colorado. The closest locality from the Arkansas River drainage is in Finney or Scott counties, Kansas (Bee et al., 1981) and is approximately 300 km to the east.

Other studies have noted westward range extensions of *C. parva* in Nebraska (Benedict et al., 2000), New Mexico (Hoditschek et al., 1985), and Texas (Owen and Hamilton, 1986). Armstrong (1972) suggested extensive irrigation as a mechanism that facilitated the expansion of *C. parva* along the South Platte River in northern Colorado. This species could have expanded in a similar fashion from Kansas along the Arkansas River in southeastern Colorado. It is possible that these specimens represent expansions of *C. parva* from populations in the South Platte watershed, because the El Paso County collection locations are approximately 140 km the south-southeast from a collection location (DMNS 6972) in Jefferson County. However, it is more likely that the localities in Pueblo and El Paso counties represent a westward expansion in the Arkansas River watershed from Kansas or from the Cimarron River watershed in southeastern Colorado due to the suitable habitat found along these river systems.

Pueblo County specimens were caught during an invertebrate monitoring project on the Pueblo Chemical Depot funded by the United States Department of the Army. The El Paso County specimen was caught during a small mammal distribution study funded by the Colorado Division of Wildlife. Voucher specimens were deposited at the Denver Museum of Nature and Science.

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DISTRIBUTIONAL RECORDS FOR MAMMALS FROM CHIAPAS, MEXICO

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ABSTRACT—New distributional mammal records are reported for Yaxchilán, Chiapas, Mexico, and Belize. Nicéforo’s large-eared bat *Trinycteris nicefori* (Chiroptera, Phyllostomidae) is documented for the first time for Mexico, providing the northwesternmost locality for the species. A new Belizean locality also is reported and constitutes the northernmost record. The dark Mexican shrew *Cryptotis griseoventris* (Soricomorpha, Soricidae) has been reported previously from the highlands from Chiapas, in coniferous forest at elevations above 2,100 m; its presence in the lowland Selva Lacandona (below 90 m) is surprising and raises questions about its specific identity. Further studies are warranted.

RESUMEN—Nuevos registros de distribución de mamíferos se reportan para Yaxchilán, Chiapas, México y Belice. El murciélago orejón de Nicéforo *Trinycteris nicefori* (Chiroptera, Phyllostomidae) se documenta por primera vez en México, proveyendo el registro más al noroeste para la especie. También se registra una nueva localidad para Belice, representando el registro más norteño. La musaraña oscura mexicana *Cryptotis griseoventris* (Soricomorpha, Soricidae) ha sido previamente registrada de las tierras altas de Chiapas, en bosque de coníferas arriba de los 2,100 m; su presencia en las tierras bajas de la Selva Lacandona (abajo de 90 m) es sorprendente y plantea el cuestionamiento acerca de su identidad específica. Se planean futuros estudios.

From December 1997 to February 1999, we conducted an inventory of the mammal fauna of the Reserva Biológica Yaxchilán, municipality of Ocosingo, Chiapas, as part of a larger

project “The Biological Characterization of the Yaxchilán Natural Monument” and the first phase in developing a management plan for the area. The Reserva Biológica covers

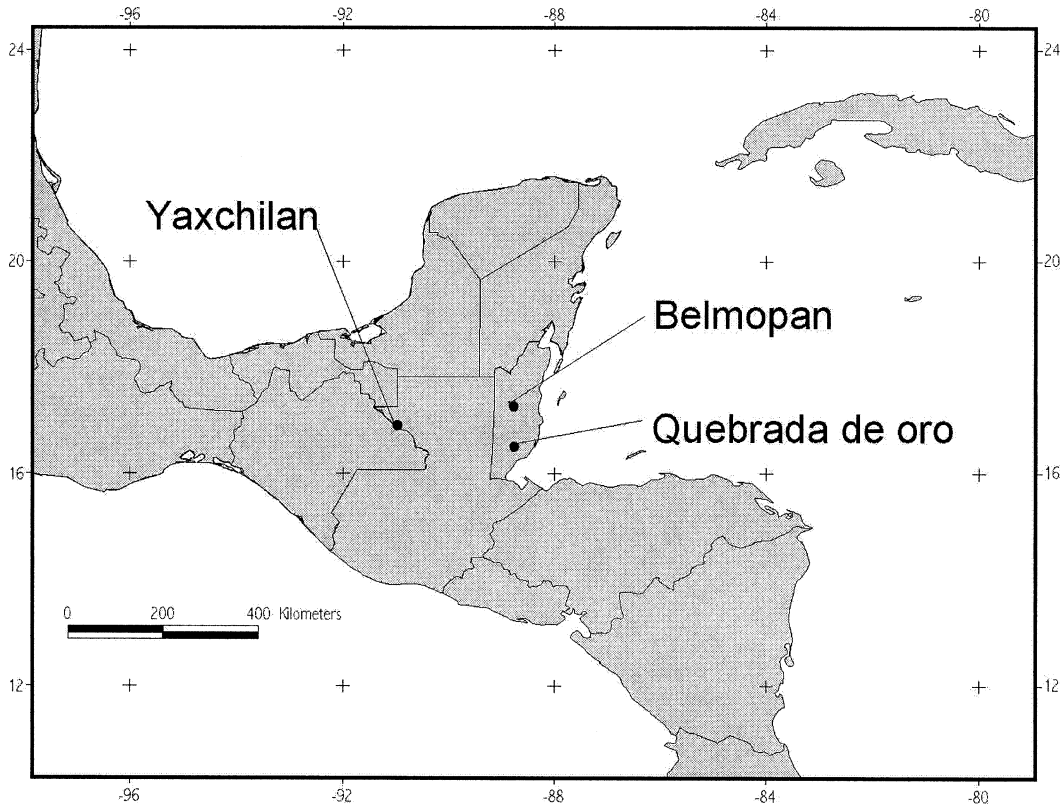


FIG. 1—Map showing the location of Yaxchilán, Chiapas, México, and the northernmost localities for *Trinycteris nicefori* in Belize.

2,621 ha (16°50'29" to 16°54'05"N, 90°56'48" to 91°00'30"W) and is located on the Río Usumacinta in the Selva Lacandona on the border with Guatemala. The vegetation is tall evergreen forest.

Trinycteris nicefori (Niccéforo's large-eared bat; Chiroptera, Phyllostomidae) is known from Belize, Nicaragua, Costa Rica, and Panama, south to Bolivia, and east to the Island of Trinidad and northeastern Brazil, but has not been recorded west of the Andes (Koopman, 1994). The species is uncommon to rare in the northern portion of its distribution (Central America), but more common in South America, where it is found in both evergreen and deciduous lowland forest (Reid, 1997). We mist-netted a male (testes enlarged) *T. nicefori* over an artificial pond surrounded by vegetation and near the archaeological area. This is the first record for Mexico and the northwesternmost for the species. Although Ceballos et al. (2002) listed the species from Mexico, this is the first

documented record, and it increases the number of bat species in Mexico to 139. The closest previous documented records are from Aguacate and Quebrada de Oro, Toledo, Belize (McCarthy, 1987; McCarthy and Blake, 1987). We also know of 2 male specimens [BM(NH)2003.111–112] collected at a cave entrance at Pond, Las Cuevas Research Station, Belize (17.25°N, 88.77°W) by R. Harbord and F. Greenaway that are on deposit at the Natural History Museum (London), and which constitute the northernmost record for the species. Pond is located straight from Yaxchilán approximately 237.5 km slightly to the east-northeast, but just 42 km north from the Mexican record (Fig. 1).

Trinycteris nicefori is a small bat (forearm, 35 to 41 mm), and the only species in the genus *Trinycteris* (sensu Simmons and Voss, 1998). Its dorsal pelage has 4 color bands; the basal band is pale, narrow, and inconspicuous. This is followed by a darker band, then a broad pale

band, and the darker hair tip; most descriptions describe the dorsal pelage as tricolored. The ventral pelage has 3 bands: a narrow pale basal band, a broad darker middle band, and a relatively long terminal pale band. The most common color pattern is brown above and paler below, with the ventral pelage tipped pale gray to white. Less common is the reddish color pattern, in which the banding pattern is obscured. This species has characteristic long, dark, and stiff hairs interspersed in the fur on the throat and conspicuous in both color phases. Most specimens have a faint, pale mid-dorsal stripe that is most evident on the lower back. The ventral margin of the nasal leaf is fused to the upper lip and lacks any demarcation between the horseshoe and the lip itself. The metacarpal of digit IV is shorter than the metacarpal of digits III and V, the third is longest; the second phalanges for digits III and IV are longer than first phalanx of the same digit. The calcar is markedly shorter than the foot (Sanborn, 1949; Simmons, 1996). The ear is pointed, with a concavity in the upper margin near the tip; an interauricular band is lacking. The dental formula and trifold the lower incisor are the same as in bats of the genera *Glyphonycteris*, *Lampronnycteris*, and *Neonycteris* (Sanborn, 1949; as subgenera of *Micronnycteris*).

The external and cranial measurements (in mm) for the specimen are: total length, 53; tail, 9; foot, 11.7; ear, 14; tragus, 6; forearm, 35.25; tibia, 14.7; condyloincisive length, 21.0; condylobasal length, 18.2; zygomatic breadth, 10.0; mastoid breadth, 9.9; postpalatal length, 9.7; postorbital constriction, 4.8; braincase breadth, 9.2; interorbital breadth, 4.9; maxillary tooththrow length, 7.7; maximum width across molars, 6.5; mass, 7.5 g. *Sturnira lilium* and *Myotis keaysi* were also collected in the same net.

On August 1998 and February 1999, 2 dark Mexican shrews *Cryptotis griseoventris* (Soricomorpha, Soricidae) were collected in pitfall traps, a female in August 1998 and an individual of unknown sex in February 1999. Neither specimen showed any sign of reproductive activity. The pitfall array was located in an area having numerous seedlings and a thick layer of fallen leaves.

The known distribution for *C. griseoventris* includes the highlands of Guatemala and Chiapas, Mexico (Woodman and Timm, 1999) at

elevations as high as 2,100 m in pine (*Pinus*) and fir (*Abies*) forests, as well as in oak (*Quercus*) forests. Some of these areas receive frost and occasional snow in the winter (Goldman, 1951). It is remarkable that these 2 specimens from Yaxchilán were collected as low as 90 m; the species had not been recorded previously in the Selva Lacandona.

Some of the diagnostic characters for the species *C. griseoventris* include darker and grayer (less reddish) pelage than that in *C. m. mexicana*. The venter is plumbeous, and they have a larger skull (Jackson, 1933).

External measurements (in mm) for the female and the specimen of unknown sex, respectively, are: total length, 116.0, 111.2; head-body, 81.0, 78.2; tail, 35, 33; hind foot, 12, 12; mass, 8, 6 g. Cranial and mandibular measurements were taken following Woodman and Timm (1993): condylbasal length (not including upper incisors), 20.6, 19.7; cranial breadth, 9.8, 9.7; breadth of zygomatic plate, 2.4, 2.6; interorbital breadth, 5.7, 5.9; breadth across first unicuspid, 2.7, 2.4; breadth across third unicuspid, 2.9, 3.1; breadth across second molars, 5.7, 5.7; palatal length, 8.4, 8.7; upper tooththrow length, U1 to M3, parallel to the long axis of the skull, 8.0, 7.6; unicuspid tooththrow length, parallel to the unicuspid tooththrow, 2.8, 2.3; length of molariform tooththrow length, P4 to M3, parallel to the long axis of the skull, 5.3, 5.5; posterior width of M1, across hypcone and metastyle, 1.6, 1.5; mandibular length (from inferior sigmoid notch to posterior edge of mental foramen), 6.8, 7.0; height of coronoid process, 5.3, 5.2; depth of coronoid valley, 3.0, 3.0; height of articular condyle, 4.2, 4.1; breadth of articular condyle, 4.0, 4.1; articular condyle to posterior edge of m3, 4.7, 4.5; lower tooththrow length, p3 to m3, 6.4, 5.9; and length of lower first molar, 1.9, 1.9.

A. L. Gardner kindly verified the Mexican bat species identification and reviewed an earlier manuscript draft, providing many changes that improved the text. L. Carraway studied the shrew specimens and agreed on their identification. P. Jenkins kindly allowed the use and provided the data for the Quebrada de Oro specimens housed at The Natural History Museum (London). Two anonymous reviewers provided helpful comments for improving the manuscript.

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DEJECTION AND EXPULSION RATES OF COYOTES (*CANIS LATRANS*) IN CAPTIVITY

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ABSTRACT—We obtained dejection and expulsion rates for use as correction factors in studies of diet and relative abundance of coyotes (*Canis latrans*). Feeding tests were performed at the Zacango Zoo, Calimaya, Mexico. We tested 3 treatments with different categories of biomass (10 to 80 g, 100 to 700 g, and 1,000 to 4,500 g). Dejection rates averaged 0.79 ± 0.22 SD excrementos/g of biomass, with no significant difference among treatments. Expulsion rates significantly differed, with 1.33 scats produced/g of biomass for the first category (10 to 80 g), 4.69 scats/g of biomass for the second category, and 6.91 scats/g of biomass for the third. We compared these values with those from other studies performed with wolf (*Canis lupus*) and lynx (*Lynx pardinus*).

RESUMEN—Obtuvimos tasas de deyección y expulsión para utilizarlas como factores de corrección en estudios de dieta y abundancia relativa de coyotes (*Canis latrans*). Se realizaron pruebas alimentarias en el zoológico de Zacango, Calimaya, México. Probamos 3 tratamientos con diferentes cantidades de biomasa (10 a 80 g, 100 a 700 g, y 1,000 a 4,500 g). La tasa de deyección fue de 0.79 ± 0.22 DE excrementos/g de biomasa, sin diferencia significativa entre tratamientos. Las tasas de expulsión difirieron significativamente, con 1.33 excrementos producidos/g de biomasa para la primera categoría (10 a 80 g), 4.69 excrementos/g de biomasa para la segunda categoría,

y de 6.91 excrementos/g de biomasa para la tercera. Comparamos estos valores con los de otros estudios realizados con en lobo gris (*Canis lupus*) y el lince pardo (*Lynx pardinus*).

Insufficient economic resources and time have reduced our ability to collect meaningful information about the relative abundance of carnivores in the wild. Several methods have been proposed to estimate abundance of terrestrial carnivores (Wilson and Delahay, 2001). One reliable and relatively economical method is based on counting the deposition of scats (Guitian and Bermejo, 1989). However, to apply this method, it is necessary to have reliable indexes, such as defecation rates, which, in spite of their use, have not been sufficiently defined experimentally (Sutherland, 1996). The usefulness of obtaining these rates for partially free-ranging individuals (Rogers, 1988) for subsequent application in the field has been demonstrated with white-tailed deer (*Odocoileus virginianus*) (Galindo-Leal et al., 1993). In the present study, we planned to obtain defecation rates for coyotes (*Canis latrans*) and to examine possible variations due to the amounts of biomass ingested. Such data then could provide references for studies of relative abundance in the field with similar sampling effort.

Including the frequency of indigestible residues in scats in dietary analyses of carnivores can lead to imprecise conclusions regarding the importance of certain foods (Delibes, 1980; Gamberg and Atkinson, 1988; Weaver, 1993). To determine the importance of various food items more precisely, various researchers have examined the dry weight of indigestible residues (Johnson and Hansen, 1978) and considered the probability of detection in scats, realizing that one might underestimate or overestimate different types of food (Floyd et al., 1978; Weaver and Hoffman, 1979). Few studies have shown that the frequency of appearance of food in scats is proportional to the amount consumed. One possible solution to this dilemma is to calculate the number of scats required to expel indigestible residues (expulsion rate). Expulsion rates then also might allow us to predict more precisely the impact of predators on prey populations.

We performed tests on 3 female and 2 male coyotes, including 4 adults >1.5 years old of approximately the same weight (12 kg) and 1 female <1 year (8 kg) at the Zacango Zoo, Cal-

imaya, Mexico. One of the coyotes was transferred out of the zoo during our study. The tests were conducted individually in a cage of 4 m × 2 m.

Major dietary items of *C. latrans* include Mexican voles (*Microtus mexicanus*), pocket gophers (*Cratogeomys*), and cottontail rabbits (*Sylvilagus floridanus*) (Salas, 1987; Aranda et al., 1995; Servín, 2000). These items can be divided into 3 categories of biomass: 10 to 80 g for *M. mexicanus*, 100 to 700 g for *Cratogeomys*, and 1,000 to 4,500 g for *S. floridanus* (Ceballos and Galindo, 1984; Ceballos and Miranda, 1986). We offered our subjects similar categories of biomass in the form of mice (*Mus musculus*), rats (*Rattus norvegicus albinus*), and laboratory rabbits (*Oryctolagus cuniculus*). The experimental design consisted of 3 repetitions for each category of biomass for each coyote. Results from our pilot tests indicated that appropriate offering periods were 3, 6, and 10 days for biomass placed in the small, medium, and large categories, respectively. In both pilot and experimental tests, prey items were weighed before being offered and were left in the cage for one day. Indigestible residues were weighed to determine the actual biomass consumed. During the periods between treatments, each coyote was provided 2,000 g of hair-free donkey meat daily, except Wednesdays and Sundays; water was provided ad libitum.

Scats were collected daily, and we recorded the date, number of scats, and wet weight of each dropping. To determine the number of scats in which the consumed biomass was expelled, scats were washed and the hairs and bones of the ingested prey were identified. Once the total number of scats of each individual was obtained, we determined the average number of scats deposited per day (daily defecation rate). The data were classified by treatment, and the variation between them and among individuals was measured using a Kruskal-Wallis test. Variations among sex were analyzed through a Mann-Whitney *U*-test. We compared these data for all treatments with individual defecation rates using correlation analysis (Sokal and Rohlf, 1995; Zar, 1999).

The scats deposited per biomass (expulsion

TABLE 1—Number of scats expelled per coyote (*Canis latrans*) per treatment, with consumed biomass (g) in parenthesis. Each treatment was presented 3 times to each individual. Coyote number 2 was transferred out of the zoo during the course of our study.

Coyote	Treatments		
	10–80 g	100–700 g	1,000–4,500 g
1	1 (38)	5 (483)	8 (1,794)
	1 (38)	5 (306)	10 (1,500)
	2 (51)	4 (400)	6 (3,971)
2	1 (39)	—	—
	1 (55)	—	—
	1 (20)	—	—
3	2 (78)	4 (511)	5 (1,350)
	1 (30)	4 (487)	6 (1,350)
	1 (40)	7 (420)	10 (2,300)
4	1 (28)	3 (123)	5 (1,865)
	1 (34)	5 (220)	10 (1,800)
	2 (29)	5 (350)	7 (2,308)
5	2 (40)	6 (600)	5 (2,000)
	2 (23)	6 (143)	5 (2,963)
	1 (60)	3 (137)	6 (1,500)

rate), were classified according to treatments (3 categories of ingested biomass) and a Kruskal-Wallis test was applied to these values for evaluating variation between treatments. The relationship between the ingested biomass and the number of deposited scats was subjected to correlation analyses to determine the best-fitting model and to infer the number of scats that a coyote might deposit depending on the biomass ingested (Sokal and Rohlf, 1995; Zar, 1999).

We processed 159 scats, averaging 32 scats for each individual. Although the greatest amount of biomass offered was 4,500 g, the largest amount of consumed biomass weighed 3,971 g. The general average dejection rate (number of scats per day) was 0.79 ± 0.22 scats/coyote (mean \pm SD). Dejecting rates ranged from 0.70 scats/coyote for the smallest category of biomass (10 to 80 g) to 0.88 scats/coyote for the intermediate category (100 to 700 g). The differences between dejection rates in each treatment were not statistically significant ($H = 3.94$; $df = 2$; $P > 0.13$).

A slight linear relationship ($r = 0.104$; $r^2 = 1.086$; $P > 0.52$) between the dejection rate and the consumed biomass resulted, suggesting that the average number of deposited

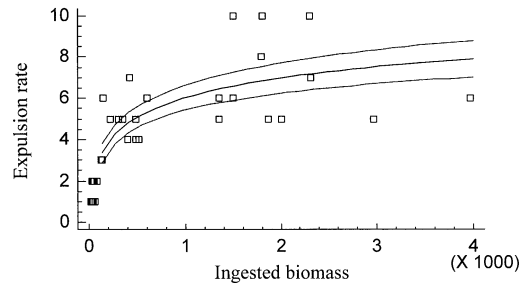


FIG. 1—The relationship between ingested biomass and the number of scats deposited per coyote (*Canis latrans*) as described by the equation $Y = 0.321082 \times X^{(0.414961)}$.

scats/coyote/day was independent of the consumed biomass. When increasing the ingested biomass and keeping the number of deposited scats per day constant, the weight of the scats increased, presenting a non-linear, positive, and significant relationship between the amount of ingested biomass and the weight of scats ($r = 0.88$; $r^2 = 78.85$; $P < 0.0001$).

The expulsion rate (number of scats produced per ingested biomass) differed significantly among treatments ($H = 30.57$; $df = 2$; $P < 0.0001$). Average rates ranged from (mean \pm SD) 1.33 ± 0.48 scats/g of biomass/day ($n = 15$) for 10 to 80 g of biomass, up to 6.91 ± 2.06 scats/g of biomass/day ($n = 12$) for 1,000 to 4,500 g of biomass. When presented food in the smallest category of biomass (10 to 80 g), coyotes ingested from 23 g to 78 g of meat and produced 1 to 2 scats/g/day. For the second treatment (100 to 700 g), they ate 123 to 600 g and produced 3 to 7 scats/g/day. In the case of the third treatment (1,000 to 4,500 g), the consumed biomass ranged between 1,350 g and 3,971 g, and 5 to 10 scats/g/day were expelled (Table 1).

There was a non-linear, positive, and significant relationship between the ingested biomass and the number of scats expelled (expulsion rate; $r = 0.887$; $P < 0.00001$), which can be expressed by the equation $Y = 0.321082 \times X^{(0.414961)}$ (Fig. 1). In this relationship, one of the variables (expulsion rate) is adjusted to an exponential scale. This relationship suggests that when increasing the amount of ingested biomass, the number of scats expelled per coyote increases exponentially, demonstrating that analyzing the importance of the prey in

the coyotes diet through the frequency or percentage of appearance is not entirely reliable.

The average defecation rate was 0.79 ± 0.22 scats/coyote/day (mean \pm SD) for vertebrate prey; defecation rates might increase when the main foods are fruits (Andelt and Andelt, 1984; Servín, 2000). Our average is smaller than that reported for wolves (2.6 ± 0.6 scats/individual/day; Weaver, 1993). This difference suggests that the ability to digest prey between the 2 species might differ or might reflect different study designs; biomass was offered ad libitum to the wolves, after 72 hours of fasting, and the data were obtained from a group rather than from individuals. However, similar results were obtained elsewhere for wolves (Weaver, 1993), where the average defecation rate did not vary with respect to the ingested biomass; results indicated a linear relationship ($r = 0.09$; $P > 0.81$) and there was a non-linear, positive relationship between the amount of consumed biomass and the weight of the scats ($r = 0.84$; $P < 0.004$) similar to that in our study. One can deduce something similar with respect to the non-linear relationship of these last variables ($r = 0.91$; $P < 0.0005$) from the data from Floyd et al. (1978).

The increase in expulsion rates following a rise in ingested biomass observed by us has been reported for other carnivores, such as wolf (*C. lupus*) and lynx (*Lynx pardinus*) by Floyd et al. (1978), Delibes (1980), and Weaver (1991). The number of expelled scats per biomass might vary due to different digestion rates for different prey (Floyd et al., 1978; Weaver and Hoffman, 1979; Gamberg and Atkinson, 1988) or to different energetic needs. Therefore, when analyzing the importance of prey in the diet of coyotes through the frequency of appearance, small prey (<100 g) are underestimated in numerical terms in relation to large prey (>100 g). A nonlinear relationship also has been reported in other studies, as in the case of lynx ($r = 0.81$; $P < 0.03$) (Delibes, 1980) and wolf ($r = 0.86$; $P < 0.003$; Weaver, 1993). Expulsion rates can be used to assign correction factors to estimate impacts on prey populations more precisely. This could be done by dividing the frequency of appearance for each kind of food by the correction factors recommended here. If working with prey of larger mass than those in this study, the correction factor can be calculated using the

equation $Y = 0.321082 \times X^{(0.414961)}$ or by taking the value of 3,971 g as the largest amount of biomass ingested by coyotes in a day, where Y = the number of scats deposited (expulsion rate) and X = weight or average biomass of the prey.

Our indexes can be important tools for conducting studies on relative abundances and diets in the field. We recommend that indexes be obtained with partially free-ranging animals to decrease the possible bias generated by captive conditions, as was done with cervids (Rogers, 1988).

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IS THERE A GENETIC BASIS FOR ANTLER AND PEDICLE MALFORMATIONS IN REINTRODUCED ELK IN NORTHERN ARIZONA?

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ABSTRACT—Morphological abnormalities can be associated with inbreeding depression or heritability in natural populations. We explored a genetic basis for antler and pedicle deformities documented in a population of reintroduced elk (*Cervus elaphus*) on the Hualapai Indian Reservation in northwestern Arizona. We used 12 microsatellite loci to compare individual multi-locus heterozygosity (IH) and internal relatedness (IR) between bull elk with antler malformations ($n = 23$) and individuals with normal antler conformation ($n = 17$). Additionally, we used 3 pairwise relatedness coefficients to determine whether males with deformed antlers were more closely related than males with normal antlers. Mean IH and mean IR were not significantly higher for the group with deformed antlers. Similarly, the relationship between antler malformations and pairwise relatedness also was not significant, suggesting that deformed males did not share the antler trait because of a closer genetic relationship. Other factors, such as nutritional or environmental characteristics, might be associated with the deformities. Further research is necessary to determine the underlying causes of the antler and pedicle malformations documented in the introduced elk herd in northern Arizona.

RESUMEN—En poblaciones naturales las anomalías morfológicas se pueden asociar con la depresión por cruzamiento consanguíneo o la heredabilidad. Exploramos una base genética para las deformidades de cuerno y de pedúnculo (base del cuerno) documentadas en una población reintroducida del alce (*Cervus elaphus*) en la Hualapai Indian Reservation en el noroeste de Ari-

zona. Usamos 12 loci de microsatélites para comparar la heterocigosidad individual de múltiples loci (IH) y parentesco interno (IR) entre alces adultos machos con malformaciones ($n = 23$) e individuos que presentaron formación normal de cuerno ($n = 17$). Adicionalmente, utilizamos 3 coeficientes de parentesco pareados para determinar si los machos con cuernos deformados estuvieron más estrechamente relacionados entre sí que los machos con cuernos normales. La media de IH y la media de IR no fueron significativamente más altas para el grupo de cuernos deformados. Asimismo, la relación entre las malformaciones de cuerno y los coeficientes de parentesco pareados tampoco fue significativa, lo que sugiere que los machos deformados no comparten esta característica entre sí debido a una relación genética más cercana. Otras causas, como factores nutricionales o ambientales, podrán estar asociadas con estas deformidades. Se necesita investigación adicional para determinar las causas fundamentales de las malformaciones de cuerno y de pedúnculo documentadas en el grupo de alces introducidos en el norte de Arizona.

Inbreeding can reduce fitness in natural populations as a result of an increased frequency of deleterious alleles and a decreased frequency or loss of beneficial alleles (Charlesworth and Charlesworth, 1987; Ralls et al., 1988; Crnokrak and Roff, 1999). Increases in homozygosity through inbreeding also have been correlated with reduced heterosis, or hybrid vigor, where individuals that are heterozygous exhibit greater fitness (Rossiter et al., 2001; Keller and Waller, 2002). Consequently, inbreeding can negatively impact a variety of life history traits (e.g., neo-natal survival and fecundity), as well as morphological traits (Coulson et al., 1998; Coltman et al., 1999; Reed and Frankham, 2003). For example, morphological abnormalities in wildlife populations, including malformation of sperm in the Florida panthers (*Puma concolor coryi*; Hedrick, 1995) and failure of testicular development in koala bears (*Phascolarctos cinereus*; Seymour et al., 2001), have been linked to inbreeding and low genetic diversity. Horn or antler size and growth in bighorn rams (*Ovis canadensis*) and white-tailed deer (*Odocoileus virginianus*) also seem to be influenced by genetic variability (Scribner and Smith, 1990; Smith et al., 1991; Fitzsimmons et al., 1995).

Heritability of quantitative traits in the wild has been challenging to quantify because of the difficulty in reconstructing pedigrees for individuals outside of captivity. However, the advent of marker-based estimators of heritability has allowed for determination of relatedness between individuals of unknown pedigrees (Ritland, 2000a, 2000b). In addition, merging estimates of relatedness and phenotypic similarity has provided a method for estimation of heritability in wild populations (Ritland, 2000a, 2000b). Studies of various cer-

vids, including captive elk (*Cervus elaphus*) and natural populations of red deer, have documented a significant heritability of antler size (Williams et al., 1994; Wang et al., 1999; Kruuk et al., 2002). Antler size is of particular importance in polygynous ungulates in the wild because males with smaller horns or antlers might mate less often and, thus, might exhibit reduced fitness (Van Ballenberghe and Miquelle, 1993; Kruuk et al., 2002; Coltman et al., 2003).

Rocky Mountain elk (*C. e. nelsoni*) were re-established on the Hualapai Indian Reservation in northwestern Arizona in the 1960s with individuals translocated from Yellowstone National Park. Deformities in antlers and pedicles were initially documented in small numbers of elk on the Hualapai Indian Reservation in the early 1990s (Rachlow et al., 2003). Severity of the antler malformation varied, but size of the deformed antlers was smaller than antlers exhibiting normal conformation. Furthermore, in each case, the malformed antlers were associated with abnormal and asymmetrical pedicles, and in most cases, only one antler per male was deformed (Rachlow et al., 2003). In 1993, only 3 deformed bulls were recorded on the Hualapai Indian Reservation, but during annual aerial surveys in 1996, 47 bulls with abnormal antlers were observed. Although the deformities might have been present in the population prior to the 1990s, the frequency of bulls with abnormal antlers and pedicles in the population seemed to increase throughout that decade (Rachlow et al., 2003). Additional individuals with similar antler and pedicle deformities have been observed on adjacent lands. Interestingly, one of the original males from Yellowstone National Park was harvested following translocation, and asymmetry of the

pedicles was visible in the taxonomic mount of that animal (Rachlow et al., 2003). This suggests that a heritable gene or gene complex might be responsible for the deformities.

Several factors might contribute to the observed antler and pedicle malformations, including nutritional deficiencies, environmental contaminants, and hormonal irregularities (Fennessy and Suttie, 1985; Gogan et al., 1988; Colburn et al., 1996; Carrasco et al., 1997). Additionally, the Hualapai elk herd exhibits a relatively high bull-to-cow ratio, which might result in more aggressive interactions among males and ensuing damage to pedicles and antlers (Rachlow et al., 2003). Our goal was to evaluate a potential genetic basis, either inbreeding or inheritance, for the observed deformities by comparing bull elk in northern Arizona that displayed malformed antlers and pedicles with those that exhibited normal antler-pedicle conformations. Specific objectives were to determine whether abnormal bulls had lower levels of genomic diversity than non-deformed bulls and to evaluate whether there was increased relatedness among bull elk sharing deformed antlers and pedicles, which would support the possibility that the trait was heritable. Our analyses help narrow the search for the underlying cause of antler-pedicle deformities in this reintroduced population of Rocky Mountain elk.

The Hualapai Indian Reservation encompasses >3,800 km² of semidesert grasslands and woodlands in northwestern Arizona. In the 1960s, Rocky Mountain elk were introduced to the area when approximately 35 individuals were translocated from the northern range herd in Yellowstone National Park. Demographic information was not documented during the initial years following the reintroduction of elk to the Hualapai Indian Reservation, and therefore, population growth rates are unknown. However, the biologists in the Hualapai Wildlife, Fisheries and Parks Program estimated the population size to be approximately 1,900 in 1999 based on aerial counts (R. K. Riley, unpubl. data). Although portions of the reservation are fenced, elk move readily between the reservation and the adjacent lands.

We used samples of skin and muscle tissue from bull elk on the Hualapai Indian Reservation and adjacent areas for genetic analyses.

We collected samples of dry skin from the skulls of 29 males with abnormal antlers that were harvested on the reservation during 1997 through 1999. Muscle samples from individuals with normal antler conformation were collected during 1999 and 2000 from 9 males harvested on the reservation and 8 males harvested in Arizona game management units 10, 15, and 18B that border the reservation. We defined normal antlers and pedicles as those exhibiting the usual conformation observed for this species (Hudson and Haigh, 2002).

We isolated DNA from all tissue samples using standard protocols for the Qiagen tissue kit (Qiagen Company, Valencia, California). Dry skin samples from the skulls of malformed elk were extracted using a modified Qiagen tissue protocol. Buffer ATL was replaced with 1X Nucleic Acid Purified Lysis Buffer (Applied Biosystems, Foster City, California), which assists in the saturation and lysis of desiccated skin samples (Qiagen Company). Polymerase chain reaction (PCR) was used to amplify extracted DNA at the following 12 dinucleotide (CA/GT) microsatellite loci: BL42, BM203, BM415, BM4107, BM4208, BM5004, BM6506, BM848, BM888, FCB193, MAF109, and RM006 (Buchanan and Crawford, 1992; Swarbrick and Crawford, 1992; Kossarek et al., 1993; Bishop et al., 1994). Protocols for microsatellite amplification followed Williams et al. (2002). We used 3 multiplex PCRs (BM4107/BM5004, BM4208/BM888, RM006/MAF109) to maximize efficiency; all other loci were amplified individually. We ran negative controls with each set of reactions to detect PCR contamination and to identify bleed-through during allele scoring. PCR products were electrophoresed by using 6% acrylamide gels and an ABI 377 DNA automated sequencer (Applied Biosystems, Foster City, California). We used GENESCAN software to extract and track gel-lanes, and GENOTYPER 2.5 software (Applied Biosystems) was used to size alleles. Genotypes from 6 males with abnormal antlers were excluded from analyses due to inconsistent amplification.

We tested for deviations from linkage and Hardy-Weinberg equilibria with GENEPOP 3.4 using an exact test based on a Markov chain algorithm (Raymond and Rousset, 1995*a*, 1995*b*). Tests were adjusted for multiple comparisons using sequential Bonferroni correc-

tions (Rice, 1989). Observed heterozygosity (HO) and unbiased expected heterozygosity (HE) were calculated per locus using Cervus version 2.0 (Marshall et al., 1998). We quantified the amount of gene flow (FST) between the Hualapai Indian Reservation and neighboring Arizona game management units using Fstat version 2.9.3.2 (Weir and Cockerham, 1984; Goudet, 2002). Additionally, we investigated potential inbreeding in deformed bulls by determining individual multilocus heterozygosity (IH) and internal relatedness (IR) for each individual, both deformed and non-deformed. We calculated IH by scoring heterozygosity at each locus (0 = same alleles, 1 = different alleles), and then dividing the sum by the total number of loci at which an elk was scored. Individual heterozygosity values were arc-sine transformed, and per group (i.e., normal and deformed) means for IH were compared using one-tailed *t*-tests (null hypothesis: normal > deformed; StatView 5.0.1, SAS Institute Inc., Cary, North Carolina). For each individual elk, IR was calculated as:

$$\text{Internal relatedness (IR)} = \frac{2H - \sum f_i}{2N - \sum f_i}$$

where *H* is the number of loci that are homozygous, *N* is the total number of loci, and *f_i* is the frequency of the *i*th allele contained in the genotype (Amos et al., 2001). Mean group IR values also were compared using one-tailed *t*-tests (null hypothesis: deformed ≥ normal).

We explored potential heritability of deformed antlers using relatedness coefficients. We used SPAGED1 1.0 (Hardy and Vekemans, 2002) to calculate the pairwise estimators “r” (Queller and Goodnight, 1989), “R” (Lynch and Ritland, 1999), and “W” (Wang, 2002) between each pair of individuals within each antler group. We calculated mean relatedness estimates per group by using the pairwise estimates, and jackknife standard errors (across loci) were computed for each mean relatedness estimate by using SPAGED1 1.0 (Hardy and Vekemans, 2002). For each of the 3 relationship coefficients, we tested the hypothesis that pairwise relatedness values within antler groups did not differ from randomly selected relatedness values assorted between antler groups by using a non-parametric, 2-group randomization test with 5,000 permutations (So-

TABLE 1—Mean (\pm SE) multilocus individual heterozygosity (IH), mean internal relatedness (IR), and mean pairwise relatedness values (r, R, W) for male elk (*Cervus elaphus*) with normal ($n = 23$) and deformed ($n = 17$) antler conformations harvested in northern Arizona from 1997 through 2000. One-tailed *t*-tests (IH, IR) and 2-group randomization tests (r, R, W) were used to evaluate differences between normal and deformed antler groupings.

Measure	Normal	Deformed	<i>P</i>
IH	0.564 (0.026)	0.540 (0.025)	0.328
IR	0.032 (0.037)	0.057 (0.036)	0.361
r	-0.040 (0.016)	-0.017 (0.019)	0.287
R	-0.040 (0.006)	-0.028 (0.007)	0.414
W	0.139 (0.031)	0.168 (0.064)	0.140

kal and Rohlf, 1995; Onorato et al., 2004). Thus, we could determine whether males with malformed antlers were more related to one another than males with normal antler conformation.

DNA from 40 individuals ($n = 23$ deformed; $n = 17$ normal) was amplified at 12 microsatellite loci. Pooled observed and expected heterozygosities per locus ranged from 0.270 to 0.737 (mean = 0.547) and 0.478 to 0.723 (mean = 0.585), respectively, and the number of alleles per locus ranged from 2 to 6 (mean = 4). Significant linkage disequilibrium was not detected after adjusting for multiple comparisons ($P > 0.05$), but deviations from Hardy-Weinberg equilibrium were detected at 2 loci: BM4208 and BM888 ($P < 0.001$). However, our other research, which incorporated 4 other reintroduced elk populations, indicated that no other populations deviated significantly from Hardy-Weinberg proportions and that, globally, BM4208 and BM888 were not out of Hardy-Weinberg equilibrium (Hicks, 2004).

We did not find evidence of inbreeding in the deformed elk when compared to elk with normal antlers conformation. Mean IH and mean IR were not significantly higher in deformed bulls (Table 1). Additionally, we documented a high degree of gene flow (FST = 0.013, C.I. = -0.015 to 0.042) between the Hualapai elk and herds on adjacent game management units, which suggests that the Hualapai elk are not an isolated population. Inbreeding is most common in small, isolated populations (Ralls et al., 1986; Frankham et al.,

2002), which does not seem to be the scenario for the Hualapai elk herd. These results suggest that loss of diversity from inbreeding has not affected the Hualapai elk population.

Recent research indicated that life-history traits exhibited greater inbreeding depression than morphometric traits (Coltman and Slate, 2003); therefore, quantifying a link between antler deformities and reduced genetic diversity might be difficult, even if the 2 characteristics were related. Further, the power to identify inbreeding-fitness associations using microsatellite heterozygosity is low, and other approaches might provide a stronger test (Slate and Pemberton, 2002; Pemberton, 2004). Consequently, our ability to detect a correlation between antler deformities and inbreeding probably was limited. However, we found no evidence that deformed males exhibited lower levels of genetic diversity than males bearing normal antlers.

We investigated potential heritability of deformed antlers using 3 pairwise relatedness coefficients. Mean relatedness estimates for all 3 coefficients did not differ significantly between bulls with normal and deformed antlers (Table 1). Thus, there was no evidence that deformed bulls were more closely related than normal bulls, suggesting that there might not be an inherited genetic basis for the occurrence of deformed antlers. However, inheritance could be further assessed by examining the distribution of mtDNA haplotypes between antler groups, which would provide information about matrilineal substructuring.

Neither inbreeding nor heritability seemed to be correlated with the presence of pedicle antler deformities in elk in northern Arizona. Therefore, it is possible that other, non-genetic factors are ultimately responsible for the observed malformations. The proximate cause of the deformities might be injury of the pedicles followed by abnormal antler regrowth in the next year (Rachlow et al., 2003). The elk population on the Hualapai Reservation and adjacent game management units has a relatively high bull-to-cow ratio (67 bulls per 100 cows in 2000), which might result in more sparring between bulls during rut and, consequently, a higher number of pedicle injuries. Alternatively, environmental contaminants and nutritional deficiencies also might influence pedicle and antler structure. For example, copper and

phosphorous deficiencies have been correlated with antler breakage and malformations in tule elk (*C. e. nannodes*) in California (Gogan et al., 1988). Future research should be aimed at investigating these and other potential factors to ascertain their role in antler and pedicle malformations in bull elk.

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HISTORICAL DISTRIBUTION OF DESERT BIGHORN SHEEP (*OVIS CANADENSIS MEXICANA*) IN COAHUILA, MEXICO

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ABSTRACT—Historically, desert bighorn sheep occurred throughout Coahuila, Mexico, as far south as latitude 25°43′02″N. The subspecies *Ovis canadensis mexicana* probably was extirpated in Coahuila by 1970. We determined the historical range of desert bighorn sheep through a review of the available literature, interviews with long-term local residents, and a subjective habitat assessment. We found historical documentation of bighorn sheep in 14 mountain ranges (Sierra Alamos, Sierra Maderas del Carmen, Sierra la Encantada, Sierra Hechiceros, Sierra del Pino, Sierra Mojada, Sierra el Rey, Sierra San Marcos y del Pino, Sierra Gavia, and Sierra la Paila), including 4 previously not recorded (Sierra el Fuste, Sierra el Almagre, Sierra de la Madera, and Sierra la Fragua). In addition, one archaeological site with remains of bighorn sheep was identified (La Candelaria Cave). The introduction of domestic livestock, particularly sheep and goats, and unregulated hunting probably were the major factors contributing to the extirpation of the subspecies in Coahuila. These factors persist in 7 areas, and we learned of the presence of aoudad (*Ammotragus lervia*) in 3 mountain ranges (Sierra Mojada, Sierra Hechiceros, and Sierra la Fragua).

RESUMEN—Históricamente, el borrego cimarrón presentó una distribución amplia en Coahuila, México, llegando al sur hasta la latitud 25°43'02"N. La subespecie *Ovis canadensis mexicana* probablemente fue extirpada en Coahuila para 1970. Determinamos la distribución histórica del borrego cimarrón mediante una revisión de literatura disponible, entrevistas con ancianos residentes del área, y un análisis subjetivo del hábitat. Encontramos registros históricos del borrego para 14 sierras, (Sierra Alamos, Sierra Maderas del Carmen, Sierra la Encantada, Sierra Hechiceros, Sierra del Pino, Sierra Mojada, Sierra el Rey, Sierra San Marcos y del Pino, Sierra Gavia y Sierra la Paila) incluyendo 4 que no habían sido registradas (Sierra el Fuste, Sierra el Almagre, Sierra de la Madera y Sierra la Fragua). Adicionalmente, un sitio con registros arqueológicos de la especie fue identificado (La Cueva de la Candelaria). La introducción de ganado doméstico, particularmente borregos y cabras, y la cacería sin regulación probablemente fueron los principales factores que contribuyeron a la extirpación de la subespecie en Coahuila. Estos factores persisten en 7 áreas, y nos enteramos de la presencia de aoudad (*Ammotragus lervia*) en 3 sierras (Sierra Mojada, Sierra Hechiceros, y Sierra la Fragua).

Desert bighorn sheep (*Ovis canadensis mexicana*) in Mexico were widely distributed throughout the northern states of Chihuahua, Coahuila, Nuevo Leon, Sonora, Baja California, and Baja California Sur (Baker, 1956; Leopold, 1959; Tinker, 1971; Cossio, 1975; Sandoval, 1985). However, the subspecies is extinct in Chihuahua, Coahuila, and Nuevo Leon (Krausman et al., 1999). Viable populations still persist in Sonora, Baja California, and Baja California Sur (DeForge et al., 1993; Lee and Lopez-Saavedra, 1993, 1994; Lopez et al., 1995; Lee and Mellink, 1996; Tarango and Krausman, 1997; Sandoval and Espinosa, 2001). Information on desert bighorn sheep in Mexico is lacking. During the past 85 years, only 39 articles on desert bighorn have been published (Tarango and Krausman, 1997). Little is known regarding the historical distribution of the subspecies in the states of Chihuahua, Coahuila, and Nuevo Leon (Eaton-Gonzalez and Martinez-Gallardo, 2001).

A program to reintroduce desert bighorn in Coahuila was initiated in 2000 with the establishment of a propagation facility in Sierra Pilares, in extreme northern Coahuila. The objective is to raise surplus numbers in captivity for restoring free-ranging populations in northeastern Mexico. The purposes of our study were to determine the historical range of the subspecies in Coahuila, to identify the probable factors responsible for the extirpation of the subspecies, and to determine whether these factors persisted.

The state of Coahuila is located in northeastern Mexico and is bounded on the east by Nuevo Leon, on the west by Chihuahua, and on the north by Texas in the United States.

The present study was focused on mountain ranges in those municipalities that historically supported desert bighorn sheep, i.e., Cuatro Ciénegas, Sierra Mojada, and Ocampo (Baker, 1956; Villa, 1959; Cossio, 1975; Monson, 1980; Sandoval, 1985).

This region is situated in the Sierra Madre Oriental Province. Basin and range landscapes prevail throughout. A vast expanse of rain-shadowed basins, outwash plains, low hills, and bajadas occupies the lower elevations. Most of the north-south trending mountains are large anticlines, some of which rise >2,000 m from the valley floor and are covered by chaparral, pines (*Pinus*), oak (*Quercus*), and firs (*Abies*). The climate throughout this region is characterized by hot summers and cold winters. Annual precipitation means range from a low of about 200 mm to >300 mm. Most of the precipitation falls as summer thunderstorms (Secretaría de Programación y Presupuestos, 1981).

Vegetation of the study area is typical of the Chihuahuan Desert. Lower elevations are characterized by a succulent-scrub community, which intergrades into a rich assemblage of succulent scrub (such as *Agave*) and stem succulents (such as *Yucca* and *Dasyliion*). A variety of large woody shrubs and cacti is associated with these succulent-scrub upland communities, including creosote (*Larrea*), ocotillo (*Fouquieria splendens*), *Opuntia*, and catclaw (*Acacia farnesiana*). These succulent-scrub communities grade into semidesert grassland at their upper limits. Grassland and herbaceous components are varied, and dominant grasses include *Muhlenbergia*, *Bouteloua*, and *Heteropogon* (Villa-real and Valdes, 1993).

The study was accomplished in 2 phases. During phase 1, a review of the available literature on desert bighorn sheep in Mexico was undertaken to delineate areas of known historical occurrence (Baker, 1956; Leopold, 1957; Monson, 1980; Hall, 1981; Desert Bighorn Council Transactions, 1959 through 2003). The archaeological report for Coahuila by Gilmore (1947) and a publication on hunting in Mexico by Imaz (1949) also were reviewed. Records of historical occurrence were then delineated by specific mountain ranges and plotted on topographic maps published by the Instituto Nacional de Estadística Geografía e Informática, with a scale of 1:250,000.

During phase 2, we visited communities near reported areas of historical occurrence to interview local residents. Interviewees were categorized according to age, length of residency, and occupation (e.g., ranchers, hunters, and livestock herders). The interview consisted of a series of general questions regarding existing species of wildlife in the area. These were followed by questions on wildlife that no longer occurred in the area, specifically desert bighorn sheep. To corroborate descriptions of bighorn sheep, interviewees had to identify correctly a desert bighorn sheep from a series of photographs, which also included images of aoudad (*Ammotragus lervia*) and mouflon sheep (*Ovis musimon*). The interviews were recorded on magnetic tape.

Historical bighorn habitat was evaluated subjectively based on known habitat requirements of the species (Krausman et al., 1999). The parameters that we evaluated were physiography, ground-cover height, water availability, and forage availability (Hansen, 1980).

The review of literature documented that desert bighorn sheep had occurred in at least 12 mountain ranges in Coahuila, including Sierra Los Alamos, Sierra Santa Rosalia, Sierra San Marcos y del Pino, Sierra La Paila, Picacho de San Antonio, Sierra Maderas del Carmen, Sierra de los Hechiceros, Sierra de los Aparejos, Sierra del Rey, Hacienda la Encantada, the southern portion of Sierra el Pino, and the vicinity of Sierra Mojada (Fig. 1). Hall (1981) specified that the locality of bighorn sheep on Picacho de San Antonio reported by Baker (1956) was 8.5 km east of San Lazaro, Coahuila. Hall (1981) also referred to a single individual in Boquillas Canyon on the Mexican side

of the Rio Grande, between Coahuila and Texas.

We interviewed 36 adult males from the municipalities of Cuatro Ciénegas ($n = 17$), Sierra Mojada ($n = 10$), Ocampo ($n = 5$), and Saltillo ($n = 4$). Ages of interviewees ranged from 45 to 90 years, and the mean age was 79. The largest age group ($n = 14$) was between the ages of 71 to 80 years old; there were 6 men aged 81 to 90, 7 were 61 to 70, 6 were 51 to 60, and 3 were 45 to 50 years old. Based on the interviews, we recorded 52 reports of historical occurrences of bighorn sheep. Of these, we identified 10 interviewees as actually having seen desert bighorn.

The mountain ranges identified by these men as historically occupied by desert bighorn sheep included the Sierra de la Madera, Sierra San Marcos y del Pino, Sierra la Gavia, Sierra la Fragua, Sierra el Fuste, Sierra Hechiceros, Sierra del Rey, Sierra Mojada, and Sierra Almagre (Table 1). Four of these ranges (Madera, Fragua, Almagre, and Fuste) had not been reported in the literature, and 5 ranges recorded in the literature (Alamos, Carmen, Encantada, Pino, and Paila) were not mentioned by the interviewees. However, 5 ranges (Hechiceros, Mojada, Rey, San Marcos y del Pino, and Gavia) were identified as historically occupied by desert bighorn both in the literature and in our interviews (Fig. 1).

Gilmore (1947) reported bighorn sheep remains from 2 caves in Cuatro Ciénegas, and a horn from a mountain sheep found in La Candelaria Cave that was carbon-dated to approximately 1200 A.D. (Gonzalez-Arriata, 1999). Petroglyphs depicting bighorn sheep were reported from Ejido Fruastro, in the municipality of Ramos Arizpe (R. Rodriguez, pers. comm.). R. A. Baker (pers. comm.) provided us with the only photographic evidence of a desert bighorn sheep in Coahuila. The sheep was taken on Picacho de San Antonio in 1934; this site is between Sierra San Marcos y del Pino and Sierra la Gavia near Puerto San Lazaro, Coahuila.

Free-ranging aoudad were reported from Sierra Mojada, Sierra Hechiceros, and Sierra la Fragua. Physical evidence consisted of the skull and remains of skin of an adult male that we examined, which was taken near Sierra Hechiceros. One interviewee reported having observed aoudad in the vicinity of Sierra Mojada,

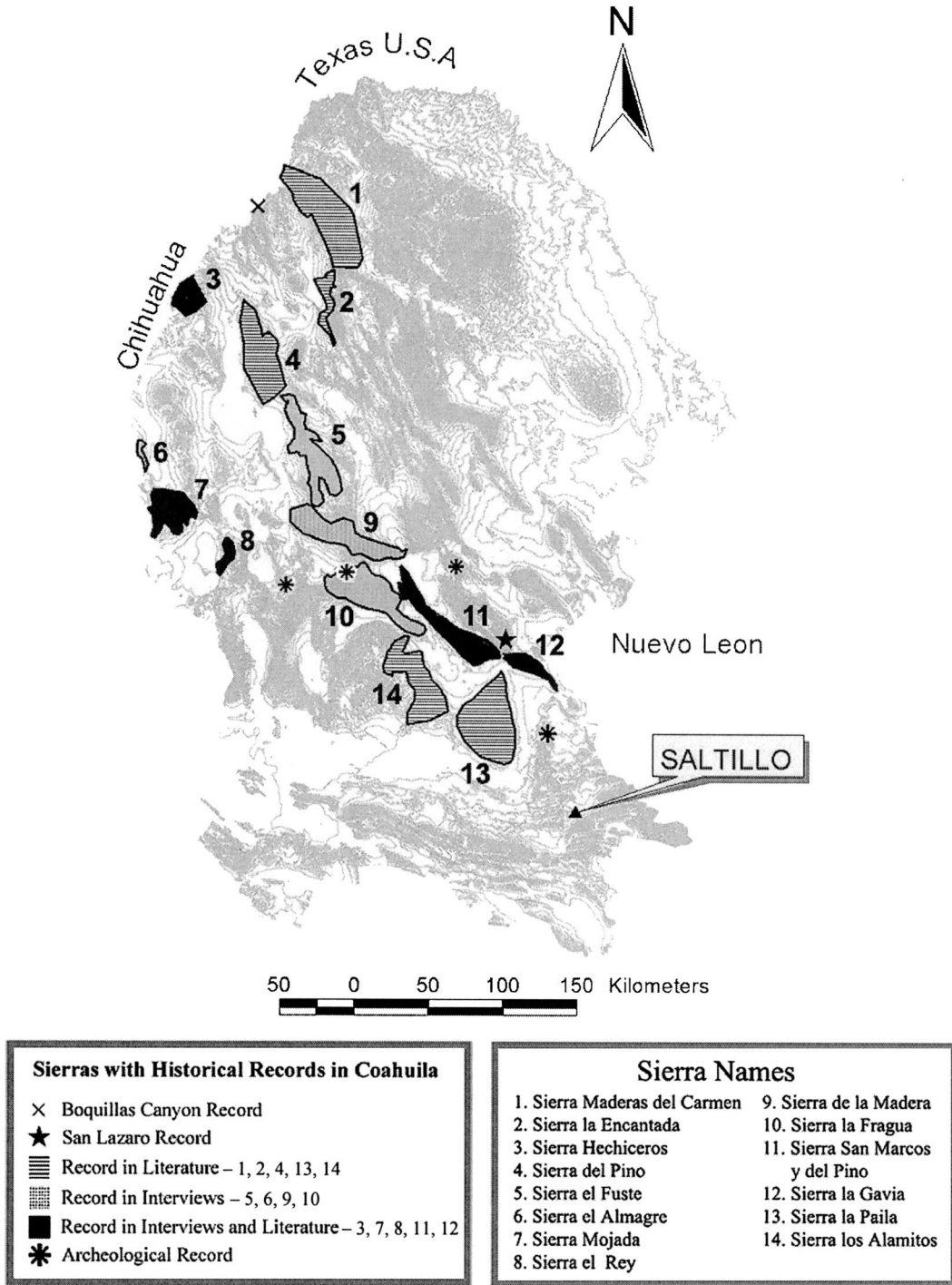


FIG. 1—Records of desert bighorn sheep (*Ovis canadensis mexicana*) in Coahuila, Mexico.

TABLE 1—Mountain ranges in Coahuila, Mexico identified by interviewees as historically occupied by desert bighorn sheep (*Ovis canadensis mexicana*) and the number of times that the species was reported, March 2003 through March 2004.

Mountain range	Reports
Sierra el Almagre	3
Sierra la Fragua	4
Sierra el Fuste	2
Sierra la Gavia (San Lazaro)	2
Sierra Hechiceros	1
Sierra de la Madera	22
Sierra San Marcos y del Pino	13
Sierra Mojada	4
Sierra el Rey	1

and a second interviewee reported seeing them in Sierra la Fragua. These reports were confirmed by correct identifications with the series of photographs.

Four habitat components are essential to desert bighorn sheep: food, water, escape terrain, and living space. Desert bighorn sheep requirements relative to living space depend on quality and quantity of food, water, escape terrain, and competition (Krausman et al., 1999). The historical desert bighorn sheep habitat in Coahuila is extensive, consisting of numerous interconnected mountain ranges extending southeasterly from the Chihuahuan border for 450 km. Few natural or artificial barriers for intermountain movements and dispersal of desert bighorn sheep exist. The habitat is characterized by steep, rocky, and broken terrain, providing the high degree of visibility preferred by bighorn sheep. Plant communities, especially at higher elevations, are relatively heterogeneous with high species diversity. The major limiting factor in many areas is the lack of permanent water.

Our results concur with the report by Baker (1956) regarding the historical distribution of desert bighorn sheep in Coahuila. Subsequent authors (Leopold, 1959; Villa, 1959; Monson, 1980; Hall, 1981) referenced Baker (1956). However, from our interviews we were able to identify 4 additional areas of historical habitat not recorded in the literature: Sierra Almagre, Sierra el Fuste, Sierra de la Madera, and Sierra la Fragua. In addition, the archaeological sites at La Candelaria Cave had not been included

in documented historical occurrence of desert bighorn sheep in Coahuila.

Baker (1956) reported that the gradual disappearance of desert bighorn sheep in Coahuila was due to a combination of excessive illegal harvest, displacement, and competition with domestic livestock, particularly goats. Six of the individuals that we interviewed mentioned hunting bighorn sheep, confirming that the species was subjected to some level of harvest.

The grazing of domestic livestock, particularly sheep and goats, has been detrimental because of the transmission of fatal diseases (Foreyt and Jessup, 1985; Sandoval, 1988; Rudolph et al., 2003), which have been the principal cause for the extirpation of bighorn sheep throughout much of their native range (Gross et al., 2000).

We learned of 3 reports of direct contact between bighorn sheep and domestic sheep in Coahuila. Pablo Bernal Valdez, a 70-year-old resident of Ocampo, related the following account of an event that took place around 1935 in Sierra la Madera: "A bighorn sheep ram followed a herd of domestic sheep into a corral after they were rounded up for the night at Los Puertocitos ranch. This was observed for several days until the bighorn was finally caught and killed by a dog." Imaz (1949:507) reported the following story: "several years ago a bighorn sheep ram came down from Sierra los Alamitos, and briefly mixed with a herd of domestic sheep; something startled the ram, and he rapidly returned to the Sierra." Marsh (1937:42) mentioned an occurrence in the vicinity of Sierra la Encantada: "Several years ago a strange sheep followed a mixed herd of goats and sheep into a corral down from the mouth of Catedrales Canyon. When a man entered the corral, the animal hurtled the corral fence and fled back up the mountain side." These accounts indicate that mingling of domestic and wild sheep did occur and suggest that the transmission of disease, at least in some areas in Coahuila, was a distinct possibility. Bighorn sheep die-offs have been documented following association with domestic goats (Rudolph et al., 2003) and domestic sheep (Sandoval, 1988; Singer et al., 2000).

The archeological site at Fraustro, near Sierra la Paila, was identified by Baker (1956) as the southernmost distribution of desert big-

horn sheep in Coahuila. The site contains 16 petroglyphs depicting the heads of bighorn sheep and numerous other forms of rock art, including atlatls (spear-throwers). Similar forms of rock art can be found <20 km away in Sierra la Popa, Nuevo Leon. These sites are approximately 5,000 years old and were associated with the hunting of bighorn sheep by pre-Europeans (Murray, 1999). Undoubtedly, indigenous people took bighorn sheep, but the impact on the overall population of sheep was probably negligible.

We found unconfirmed reports of small relictual populations in Sierra del Diablo, <15 km from the Coahuila border in Chihuahua, and Sierra el Almagre, which bisects both states. It is conceivable that a few free-ranging desert bighorn sheep exist in Coahuila. A recent record from Sierra San Vicente, in northern Coahuila, consists of one photograph of the skull of a 3-year-old ram. We think that this specimen might have originated from the herd at Black Gap Wildlife Management Area ($n = 100$) or Big Bend National Park population ($n = 25$) in Texas (C. Brewer, pers. comm.).

We found no physical evidence, such as tracks, beds, droppings, skulls, or photographs, of bighorn sheep in the areas that we visited. Physical evidence was limited to a picture of a mounted head that was obtained in 1934, 8.5 km east of San Lazaro. We were unable to locate any specimens of desert bighorn sheep from Coahuila in any scientific collections.

Based on the results of our work, it was impossible to delineate the precise historical distribution of desert bighorn sheep in Coahuila. We did, however, learn that the grazing of domestic goats and subsistence hunting still persist in most areas that we visited. In addition, a potential new threat to desert bighorn, the presence of free-ranging aoudad (Simpson et al., 1978), exists in 3 areas that we visited.

Given that desert bighorn sheep in Coahuila were near their southernmost limit of distribution, it is conceivable that they were never abundant, even prior to the arrival of Europeans. The available records, however, suggest that desert bighorn sheep occurred throughout a wide geographic area of the state. Following European settlement of the area, most populations became extinct and a few persisted to the middle of the 1900s in the most isolated and inaccessible portions of their former

range. Loss of habitat, disease introduced by domestic livestock, competition for food and space, and excessive hunting collectively contributed to the gradual extirpation of desert bighorn sheep in Coahuila.

Based on literature accounts and interviews, we conclude that desert bighorn sheep persisted in the northern part of Coahuila until approximately 1940, and in the region of Cuatro Ciénegas until the late 1950s. Apparently, the last stronghold of the subspecies was Sierra Mojada, in the extreme western portion of Coahuila along the Chihuahua border, where desert bighorn persisted until about 1970.

Desert bighorn reintroduction programs are risky, expensive, and time-consuming, both logistically and politically. The restoration of desert bighorn sheep in Coahuila will take time, perseverance, and a major commitment of resources. It is imperative that suitable habitat be available, that the probable factors responsible for the loss of the subspecies be identified, and that corrective measures be undertaken to ameliorate possible limiting factors to ensure the success of a reintroduction. Our study represents the first step toward realizing the reintroduction of free-ranging populations of desert bighorn sheep in Coahuila.

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ERYTHRISM IN THE NORTH AMERICAN BADGER, *TAXIDEA TAXUS*

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ABSTRACT—We report a second instance of erythrism in North American badgers, *Taxidea*, in western Nevada.

RESUMEN—Reportamos el segundo registro de eritrismo en el badger tajón, *Taxidea*, en el oeste de Nevada.

A dead, red-furred North American badger (*Taxidea taxus*) was found near the California-Nevada state boundary, T41N, R17E, Sec. 10, Mount Diablo Meridian, 4,700 feet (1,430 m) elevation, Washoe County, Nevada. The pelage entirely lacked blackish melanins and also lacked white markings to the extent that the facial badges and mid-dorsal striped pattern were invisible. There was an irregularly shaped white patch on the left cheek. This reddish color phase is rare in all the Carnivora, and our specimen (we have photos on file) showed intense red. The head and lower legs were bright rufous, as red as in any red fox (*Vulpes vulpes*). The nosepad and claws were nearly black. Most of the pelage resembled the horse color “strawberry roan.” There were no conspicuously pale bands on guard hairs in this roan coloration. The eyes were dried out, but seemed dark and opaque.

The habitat of this red badger, inhabited also by numerous normally colored badgers (always having short, white head stripes, as in *T. t. jeffersonii*), is basically sandy with alkali lakes. At higher elevations, there is less sage (*Artemisia tridentata*), saltbrush (*Atriplex*), and juniper (*Juniperus*), and more mixed conifers.

Our reddish badger seems only the second record of erythrism for *Taxidea* (Grinnell et al., 1937; Roest, 1961). The other reddish badger (Museum Vertebrate Zoology Specimen 19744, Berkeley) from Marin County, California, about 300 miles (about 483 km) southwest of

our specimen from Nevada (Grinnell et al., 1937) was described as “pale reddish brown” but “abnormally pallid,” with a pinkish brown substituted for the normal black or brown pigmentation. W. Z. Lidicker examined this specimen for us and added the following description: Overall, it is pale reddish. Some hairs have 2 bands, with a light tip, and what is normally a blackish band is the same color as the buffy basal band. On the flanks and rump, there are 3 bands, the middle one light brown. This pelage seems grizzled. The underparts are pale buff, except for a narrow patch of white on the mid-venter. The head markings of the typical badger are evident, with the white stripe extending a little posterior to the ears. The dark areas and “badges” are visible, but light brown, resembling the middle bands of color in the rump hairs. There is a typical white patch below and behind the eyes. The claws were light brown, but not too different from that seen in other badgers. Of particular interest, the semblance of head markings was evident, and the underfur was reddish and not pure white. Roest (1961) described a badger specimen from along the Cuyama River, in Barbara County, California, as having “partially” albinistic pelage. Its underfur was pure white, the eyes “light,” and the tips of guard hairs were “cinnamon.” This specimen also showed the semblance of head pattern, even though it lacked black or brown pigmentation. Its white dorsal stripe was discernable to the base of the

tail (long-striped badgers belong to the taxon *T. t. berlandieri*).

In *Taxidea*, most of the body fur typically is a mixture of black, brown, reddish, and yellowish colors. Usually the head markings are nearly black, as are the eyes hidden by the markings. Rusty brown or ochraceous underfur and some pelages with reddish subterminal banding are not uncommon in western badgers, which also might show creamy yellow underfur in some geographic regions (Long, 1972; Long and Killingley, 1983). The 3 aforementioned reddish badgers ranged from pale white with a reddish cinnamon suffusion and with a pale head pattern, to reddish tan with a semblance of brownish pattern, to bright rufous and roan with no sign of a pattern. In raccoons (*Procyon lotor*), some specimens of which have diluted melanins that obscure facial markings, and include albinism, the albinism was shown to result from 2 genes, and yellow-tan and golden-red pelages resulted from other genes (Long and Hogan, 1988). In these abnormal raccoons, masks and tail rings were absent or dim, possibly due to penetrance and variable epistasis. In the 3 badger specimens discussed here, the one from Nevada was unique in entirely lacking the head pattern and in having intense rufous pelage on the feet and head. It resembled the Marin County badger in lacking white underfur and resembled both of the other recorded badgers in having a reddish suffusion.

A literature search for erythrism provided few other examples. Grinnell et al. (1937) mentioned a skunk (?*Mephitis*). Hall (1951) examined 5,457 specimens of weasels, of which "a large share" was skulls without skins, and that large sample yielded only 3 erythristic specimens, none of which resembled our badger. One showed dilution of brown dorsally, with ventral color spotted over the rump and back; apparently, the ventral color was unchanged. The second had the buff-yellow (not red) color of the underparts expanded onto "each foreleg, the axillary regions, and a saddle-shaped area over the shoulders." The third weasel was white, resembling winter color, but had a faint wash of "ochraceous or reddish color." This weasel seems much like the albinistic badger of Roest (1961), except the eyes were normally dark, the white was purest on the top of the head and nape, (which normally are the

darkest brown), some facial markings are present, and the black tail tip was missing. These 3 weasels all represented *Mustela frenata*. Pitt (1921) described much the same coloration in pole cats (*M. putorius*) and ferrets (*M. furo*). The erythrism was "certainly dominant over albinism" and recessive to "black-brown" (melanin) coloration. This would follow the genetic patterns seen in the raccoon (Long and Hogan, 1988).

Even in numerous style names for mutant selected ranch mink (*M. vison*), to our knowledge there is no erythrism recorded. If we consider the color red that has become well established in carnivoran species, there is the fox group, especially *V. vulpes* (but the underparts are pure white) and the lesser panda (*Ailurus*), which has white markings on the head. The definition of erythrism was blurred further by comments such as those by Hall (1951) that the erythristic condition is seen in the pelage of some northwestern races. Badgers of the subspecies *T. t. jeffersonii* and many western specimens in the Mexican taxon *T. t. berlandieri* have richly ochraceous or reddish underfur, but the guard hairs show no reduction of melanin. The definition of erythrism should be a mutant form; that is, it has a probable genetic basis, showing the reduction of melanin and an abundance of reddish color over most parts of the body, dark eyes (not pink), and some obscuring of facial or body patterns. The last might be unnecessary as part of the definition.

The frequency of erythrism in carnivores and in *Taxidea* was reported rare (Roest, 1961). As for ascertaining the frequency quantitatively in the badger, which has only one species in the genus *Taxidea*, one of us (Long, 1972) examined more than 1,000 badgers in the United States Museum of Natural History in his revision of the genus. The data were recorded on file, in the University of Wisconsin Museum of Natural History, on the Smithsonian data cards used then. The cards contain mostly external, cranial, and dental measurements, but there are also careful notations on stripe length, facial pattern, color of pelage, bleaching, and molt for 735 skins. Adding other counts (University of Illinois, 28 specimens; University of Kansas, approximately 70; and University of Wisconsin-Stevens Point, 10), and subsequent examination of badgers from Minnesota and the University of Wisconsin-Madison, Long

found no albinism or erythrism in about 1,000 skins. It seems likely that Roest (1961) and Grinnell et al. (1937) had examined numerous badgers from California, because they found the 2 aforementioned badgers noteworthy. The study by Long (1972) included 145 skins from Nevada and California, from the region our red specimen was found.

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