FOSSIL *MUSTELA NIGRIPES* FROM SNAKE CREEK BURIAL CAVE, NEVADA, AND IMPLICATIONS FOR BLACK-FOOTED FERRET PALEOECOLOGY

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ABSTRACT.—Morphometric measurements were used to classify 11 mustelid dentaries from Snake Creek Burial Cave (SCBC), a late Pleistocene to early Holocene–aged paleontological locality in eastern Nevada, that were undifferentiated between *Mustela nigripes* (black-footed ferret) and *Neovison vison* (American mink) due to their similar size and morphology. We, therefore, classified the SCBC fossils using 10 linear measurements of the dentary using extant *M. nigripes* and *N. vison* as proxy. Discriminant function and principal component analyses grouped the 11 unknown SCBC specimens within extant *M. nigripes* exclusively. Confirmation of *M. nigripes* at SCBC is significant because *Cynomys* spp. (their primary prey source today) have not been found at this site or other nearby Great Basin localities. Occurrence of this now-endangered taxon among the SCBC paleofauna and review of additional localities lacking *Cynomys* suggest that several geographically and temporally discrete prehistoric *M. nigripes* populations were sustained by other small mammal taxa. If this inference is true, facilitating dietary diversity in reintroduced *M. nigripes* populations could improve the species' resilience to future adversities, including anthropogenic climate change.

RESUMEN.—Se utilizó morfometría para clasificar a 11 dentarios de mustelidos del sitio Snake Creek Burial Cave (SCBC), una localidad paleontológica en el este de Nevada del Pleistoceno tardío – principios del Holoceno. Debido a su tamaño y morfología similar, los especímenes no fueron diferenciados entre *Mustela nigripes* (hurón de patas negro) y *Neovison vison* (visón americano). Consecuentemente, clasificamos los fósiles SCBC de 10 medidas lineales de los dentarios utilizando especímenes actuales *M. nigripes* y *N. vison* como representantes. El análisis discriminante y el análisis de componentes principales agruparon los 11 especímenes no identificados de SCBC dentro del *M. nigripes* actual exclusivamente. La confirmación de *M. nigripes* en SCBC es significativa porque *Cynomys* spp. (su presa principal en la actualidad) no se ha encontrado en este sitio o en otras localidades cercanas del sitio de Great Basin. La aparición de este taxón ahora en peligro de extinción entre la paleofauna de SCBC, y la revisión de otras localidades en las que *Cynomys* está ausente, sugiere que varias poblaciones prehistóricas de *M. nigripes*, geográfica y temporalmente discretas, fueron sustentadas por otros taxones de mamíferos pequeños. Si esto es cierto, incluir diversidad dietética en las poblaciones reintroducidas de *M. nigripes* podría mejorar su resiliencia ante adversidades futuras, incluyendo el cambio climático antropogénico.

Once broadly dispersed throughout the grasslands of midwestern North America, *Mustela nigripes* (black-footed ferret, hereafter referred to as BFF), an iconic predator of the prairie ecosystem, was teetering on the brink of extinction by the mid-20th century. Decreases in BFF populations were due to steadily declining viable habitat, prey reduction, and rapid disease outbreaks including sylvatic plague and canine distemper (Seal et al. 1989, Klebanoff et al. 1991, Biggins et al. 2011b). By 1987, individuals in the last known wild BFF population, consisting of 18 ferrets near Meeteetse, Wyoming, were captured to prevent the complete extinction of the species (Seal et al. 1989, Biggins et al. 1999). Despite inherent risks of breeding in captivity (Seal et al. 1989),

these efforts achieved considerable progress toward restoring BFF numbers. Captive breeding programs stabilized the living population to over 400 individuals by the 21st century (Owen et al. 2000, Lockhart et al. 2006) and established several reintroduction sites throughout the western United States (Lockhart et al. 2006). Reintroduced BFFs surpassed the number in captivity by 2002, with approximately 600 individuals living in the wild (Lockhart et al. 2006).

Objectives of BFF captive breeding programs include propagating and stabilizing ferret populations in captive and wild habitats (Seal et al. 1989, Jachowski and Lockhart 2009). Though the efforts have been successful (Jachowski and Lockhart 2009), stabilizing

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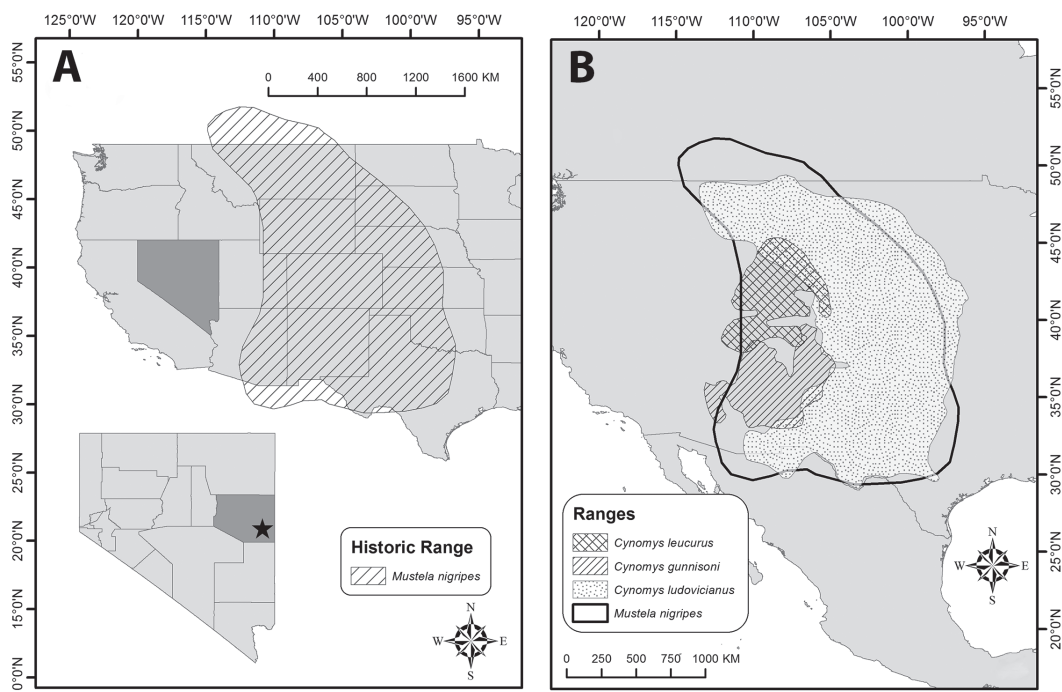[4]E-mail: n.s.fox01@gmail.com

Fig. 1. (A) The historic range of *Mustela nigripes* in western and central North America. White Pine County is highlighted in dark gray within the Nevada inset. A black star marks the general location of Snake Creek Burial Cave. (B) Historic range of *Mustela nigripes* overlapping with ranges of *Cynomys gunnisoni, C. leucurus,* and *C. ludovicianus.* Species range data are from Patterson et al. (2007).

BFF populations has proven to be a formidable task (Clark 1986, Biggins et al. 1999). Complications of reintroduction arise from a variety of sources, including anthropogenic habitat modification, natural catastrophes, predators, niche competition, lack of obligatory prey (Hillman and Clark 1980, Clark 1986), and disease susceptibility amplified by low genetic diversity (Altizer et al. 2003, Cain et al. 2011). Of these constraints, lack of suitable habitat and continued degeneration of the primary prey species, *Cynomys* spp. (prairie dogs), are among the most significant preventable factors limiting BFF reintroduction (Jachowski and Lockhart 2009, Biggins et al. 2011a, Eads et al. 2011).

Prairie dogs are generally thought to comprise roughly 90% of extant-BFF diets. Such assumptions are established from field observations and scat analyses (Campbell et al. 1987, Klebanoff et al. 1991). Indeed, marked overlap occurs throughout the modern distributions of these taxa (Hillman and Clark 1980, Nowak 1999; Fig. 1). Extant BFFs have therefore been considered obligate to prairie dog colonies for

food and shelter (Klebanoff et al. 1991, Biggins et al. 1999, Eads et al. 2011). However, prairie dogs often host fleas carrying sylvatic plague, which has decimated historic BFF populations (Eads 2014, Shoemaker et al. 2014). This stress on historic BFF populations was exacerbated because prairie dogs are also considered agricultural pests and were frequently killed by farmers and ranchers throughout the 20th century (Anderson et al. 1986, Knowles 1988, Klebanoff et al. 1991). Degradation of prairie dog colonies resulted in habitat fragmentation and restricted gene flow, which both led to BFF population bottlenecks (Flesness 1989, Wisely et al. 2002a).

Despite their inferred obligatory relationship with prairie dogs, BFFs will occasionally exploit alternative prey. Additional species consumed include *Spermophilus* spp. (ground squirrels), *Sylvilagus* spp. (cottontail rabbits), *Peromyscus* spp. (deer mice; Hillman and Clark 1980), *Lemmiscus curtatus* (sagebrush vole), *Microtus* spp. (voles), *Lepus townsendii* (white-tailed jackrabbit; Campbell et al. 1987, Owen et al. 2000), geomyids (pocket gophers),

and *Dipodomys ordii* (Ord's kangaroo rat; Biggins et al. 2011a). Furthermore, Brickner et al. (2014) acknowledge that historic BFF consumption of prairie dogs may have been overestimated due to the more diurnal and easily observable behavior of prairie dogs relative to other rodent genera. Likewise, scatological analyses, yielding approximately 90% prairie dog elements, may have been taphonomically biased due to the comparatively robust morphology of prairie dog bones relative to smaller rodents (Brickner et al. 2014).

Recent analyses of carbon and nitrogen isotopes from BFF blood and hair materials suggest that reintroduced BFFs in Shirley Basin, Wyoming, exhibit greater foraging plasticity than was previously acknowledged (Brickner et al. 2014). Only 76%, 72%, and 61% of BFF isotope ratios from that study were associated with white-tailed prairie dog (*Cynomys leucurus*) signatures in males, juveniles, and females respectively (Brickner et al. 2014). The remainder of stable isotope signatures correlated with other small mammals, including ground squirrels and rabbits (Brickner et al. 2014). Incidentally, Shirley Basin is also the oldest (Jachowski and Lockhart 2009) and among the most successful of the BFF reintroduction sites (Brickner et al. 2014).

As with modern populations, dietary plasticity has also been noted from prehistoric BFF specimens. For example, examination of stomach contents from a well-preserved BFF mummy discovered in the Yukon Territory of Canada revealed a food bolus thought to be *Microtus* sp. (vole) based on guard hair patterns (Youngman 1994). Radiocarbon dating of this specimen produced an age of 39,560 ± 490 BP (Youngman 1994), indicating that some BFFs incorporated alternative prey to prairie dogs during the late Pleistocene. Most of our present knowledge and presumptions about BFF life history, however, are based on fragmentary (Anderson et al. 1986, Casey et al. 1986, Wisely et al. 2002a) and geographically restricted (Casey et al. 1986) observations due, in part, to the reclusive nature and sparse fossil record of BFFs.

Despite our limited knowledge of pre-bottleneck-event BFF ecology, the lifestyle of BFFs in captivity has been intensely controlled by human modifications such as prerelease conditioning, particularly during early stages of development (Vargas and Anderson 1996,

1999, Biggins et al. 1999). The extent to which these conditionings alter inherent BFF behavior is a valid concern because environmental experiences can profoundly impact young BFF predatory skills (Vargas and Anderson 1996, 1999, Biggins et al. 1999). Nevertheless, many captive breeding programs continue to precondition extant BFFs exclusively around prairie dogs as part of their prerelease protocol. Considering this discrepancy, it would be wise to broaden our knowledge of precaptive BFF ecology to facilitate optimal management techniques for recently reintroduced populations. Here we use morphometric analysis to review specimens with tentative BFF identification from Snake Creek Burial Cave (SCBC), a paleontological site in eastern Nevada that lacks prairie dog remains. From the results of this analysis and from data compiled on additional BFF localities throughout North America, we contribute to the knowledge of long-term dietary patterns of BFFs and discuss implications regarding BFF life history and management.

Site Background

Snake Creek Burial Cave is a biogeographically unique paleontological locality situated in White Pine County, Nevada (Mead and Mead 1989; Fig. 1a). The karst deposit includes a vertical sinkhole dropping 17 m into a small limestone ridge below the southern Snake Range (Heaton 1987, Mead and Mead 1989). As a natural trap, SCBC offers insight into a relatively sparse (Lawlor 1998) and inadequately understood late Pleistocene valley-bottom paleocommunity in the Great Basin (Grayson 1987, Mead and Mead 1989, Grayson 2006). Radiocarbon and uranium isotope series analyses taken from *in situ* wood and faunal remains have produced terminal Pleistocene ages from 15,100 ± 700 BP to 9460 ± 160 BP (Mead and Mead 1989, Bell and Mead 1998). Few descriptions of this chronologic unit have been reported within surrounding areas of the Great Basin, emphasizing the significance of this site (Mead and Mead 1989). Among the many species identified from this site, SCBC yields an impressive diversity of up to 8 tentatively identified mustelids including *Martes americana* (American marten), *M. nobilis* (extinct noble marten), *Mustela erminea* (ermine), *M. frenata* (long-tailed weasel), *M. nigripes*/*Neovison vison*,

TABLE 1. Ten linear measurements of the dentary included in morphometric analysis of extant *Mustela nigripes* ($n = 38$), *Neovison vison* ($n = 21$), and Snake Creek Burial Cave specimens ($n = 11$).

Abbreviation	Definition
TDL	Total dentary length from mandibular symphysis to condyle
DP_p3	Dentary depth at the lower third premolar
DP_m1	Dentary depth at the lower first molar
p4_H	Height of the lower fourth premolar
p4_W	Labial–lingual width of the lower fourth premolar
m1_L	Anteroposterior length of the lower first molar
m1_TalW	Labial–lingual width of the lower first molar talonid
m2_D	Diameter (greatest occlusal distance) of the lower second molar
m2_W	Labial–lingual width of the lower second molar
MTR	Length of the mandibular tooth row from lower second premolar to lower second molar

M. nivalis (least weasel), and *Gulo gulo* (wolverine). Of those species, *M. nigripes*, *M. nivalis*, and *Gulo gulo* were formerly absent from Rancholabrean-age Great Basin localities (Mead and Mead 1989).

Confirmation of BFFs at SCBC would add another locality west of this taxon's historic distribution (Mead and Mead 1989; Fig. 1a). Moreover, prairie dog materials have not been identified from this site despite extensive sorting of an estimated 30,000 vertebrate fossil specimens (Mead and Mead 1989). Preliminary descriptions of SCBC mustelids, however, acknowledged that collected materials of *M. nigripes* and "*M.*" *vison*, now *Neovison vison* (Abramov 2000, Wozencraft 2005), would benefit from reexamination since these taxa exhibit similar morphology and size (Mead and Mead 1989). The ecological implications for BFFs at a locality lacking prairie dogs warrants validating this taxon and explicitly comparing it with potential *N. vison* (hereafter referred to as mink) specimens. We aim to classify the undifferentiated SCBC mustelid dentaries housed within East Tennessee Vertebrate Paleontology (ETVP) collections to the species level, despite similarities between their potential representative taxa. In sum, objectives of this study are (1) to determine whether the 11 SCBC dentaries represent BFF, mink, or both taxa and (2) to determine, if BFFs are present at this site lacking prairie dogs, how frequently prairie dogs and other potential prey genera are represented at other BFF localities.

METHODS

Eleven fossil dentaries from SCBC previously labeled "*M. nigripes/vison*" were reevaluated using 10 linear measurements and then compared with extant BFF and mink (Table 1, Fig. 2). Fossil specimens exhibit tooth and jaw morphology, dental formula, and size indicative of the genus *Mustela* or *Neovison* (e.g., elongate m1 trigonid relative to the talonid, diminutive m2, and incipient or absent m1 metaconid; Hall 1981). BFF and mink are the only taxa (extinct or extant) that fit those criteria, and they are distinct from other North American genera within the subfamily Mustelinae such as martens (*Martes*), fishers (*Pekania*), and badgers (*Taxidea*) (Hall 1981). Moreover, BFF and mink are easily distinguishable from congeneric weasels (i.e., *M. frenata, M. erminea,* and *M. nivalis*) because they are larger and more robust overall (Hall 1981, Anderson et al. 1986). It is possible that the SCBC dentaries represent a new extinct mustelid that has not been previously recognized or described. This is unlikely, however, since no extinct members of *Mustela* or *Neovison* have been described from late Pleistocene and Holocene localities, with the exception of *N. macrodon* (formerly *M. macrodon*) from costal northeastern North America (Mead et al. 2000). Nevertheless, measures were taken to discern whether the SCBC fossils represent a third, unaccounted taxon as discussed below.

Due to the extensive geographic range and morphological variation of mink (Hall 1981, Mead et al. 2000), extant mink dentaries were sampled from several states throughout the United States, including Arkansas, Nebraska, Maine, Colorado, Alaska, and Iowa, in an effort to minimize regional and subspecies bias. Though no current BFF subspecies are acknowledged (Anderson 1989, Wozencraft 2005), morphological variation has been reported between pre- and post-bottlenecked BFFs (Wisely et al. 2002b) and in small wild populations relative to populations that experience rapid growth after reintroduction (Wisely
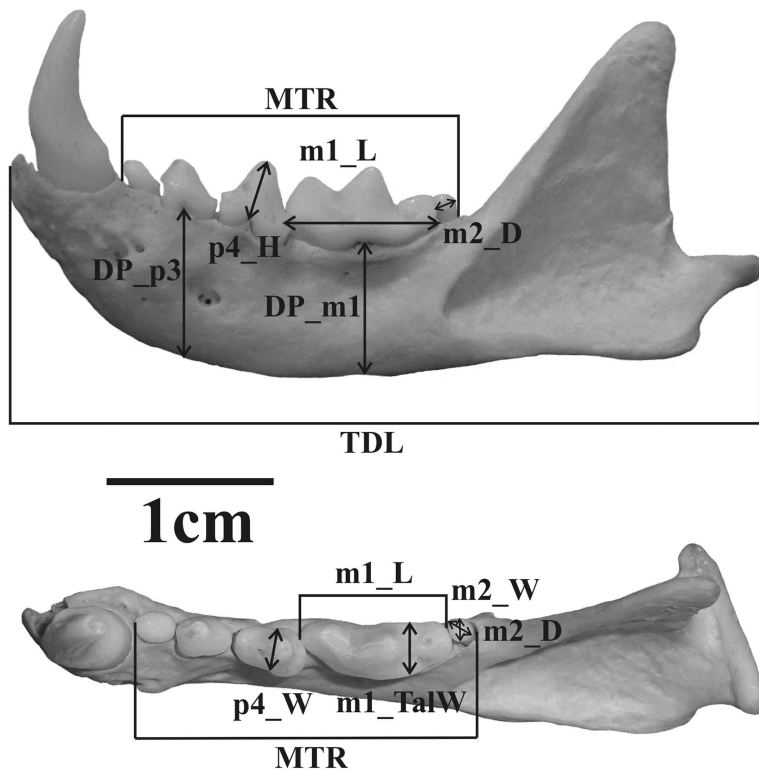
Fig. 2. Left dentary of captive-bred *Mustela nigripes* (ETVP7271), illustrating 10 linear measurements applied to extant *M. nigripes* and *Neovison vison,* as well as SCBC specimens, in lateral (top) and occlusal (bottom) views. Morphometric abbreviations are defined in Table 1.

et al. 2008). Such variation is common in founder populations due to decreased genetic diversity (Wisely et al. 2002a, Cain et al. 2011) and environmental influences such as isolation and captive breeding (Wisely et al. 2008).

Extant BFF dentaries were sampled from the Wyoming Captive Breeding program. However, all captive-bred BFFs exhibit similar genotypic and phenotypic diversity due to yearly trading among breeding facilities. We selected specimens housed within ETVP collections because they were more accessible and abundant than historic specimens. Individuals with prominent dental pathologies, a common condition in captive-bred animals, were not included. Though slight morphological variation exists between captive-bred and historic BFFs, captive-bred specimens are assumed to be more similar to fossil individuals of the same species than to other taxa and should serve as adequate proxies for the purpose of discriminating against mink, given that intraspecific variation tends to be greatly surpassed

by interspecific differences (e.g., assumptions in Wallace 2006).

Linear measurements were obtained from 21 wild mink and 38 captive-bred BFF dentaries that were housed within ETVP collections (Fig. 2). An independent-sample *t* test was conducted using the total length of the dentary (TDL) of these extant specimens to determine whether variation between taxa could be explained by size exclusively. The *t* test was not significant (t [30.02] $= 1.74$, $P = 0.92$), confirming that these species cannot be discriminated without additional variables. Mandibular characters were therefore selected based on observable points of interspecific variation, as noted in previous studies (e.g., Anderson 1977, Anderson et al. 1986, Mead et al. 2000), and were measured using digital calipers (Mitutoyo Absolute IP67).

Measurements were taken twice to the nearest 0.01 mm. The average of these measurements was only recorded when the 2 measurements were within 0.1 mm of each

TABLE 2. Linear measurements for Snake Creek Burial Cave dentaries ($n = 11$). All measurements are in millimeters. Morphometric abbreviations are defined in Table 1.

NAUQSP #	Side	TDL	DP_p3	DP_m1	p4_H	p4_W	m1_L	m1_TalW	m2_D	m2_W
8711/115B	Left	41.19[a]	9.80	8.25			8.77	2.39		
8711/116B	Left	42.67	10.01	8.88	3.31	2.49	8.55	2.38	1.62	1.66
8711/117B	Right	42.12	9.17	8.20	3.56	2.35	9.02	2.39		
8711/118B	Right	39.75	8.97	8.53	3.03	2.27	7.91	2.30		
8711/119B	Left	39.38	8.90	8.35	2.94	2.25	7.85	2.31		
8711/120B	Right	42.36	9.68	8.52			8.66	2.36		
8711/121B	Left	38.99[a]		7.76	3.23	2.22	8.10	2.40		
8711/122B	Left	40.21	8.75	7.61	3.51	2.57	8.61	2.31		
8711/123B	Right	35.07	7.87	6.91	3.18	2.07	7.98	2.14		
8711/124B	Right	42.73	8.85	7.77			9.03	2.58		
8711/125B	Left	37.59[a]	8.01	5.61	2.83	1.94				

[a]Total dentary length (TDL) estimates for incomplete specimens averaged across complete SCBC specimens posteriorly from the p3 alveolar ridge (77.9% of TDL).

other. We ensured that only adult extant individuals (of both sexes) were included by only measuring specimens that lacked visible cranial sutures and that had fully erupted permanent lower dentition. Measurements were taken from left dentaries, unless only right features were available. All variables (Table 1) were standardized over the length of the dentary to reduce interspecific size bias prior to statistical analysis. Because of the condition of the specimens, TDL measurements were only attainable from 8 of the 11 SCBC specimens. TDL was estimated for the remaining 3 by measuring from the p3 alveolar ridge to the mandibular condyle. The percentage of that measurement relative to TDL was then averaged across complete SCBC specimens (77.9%) and used to estimate TDL of incomplete specimens (measurements obtained from all fossil specimens are shown in Table 2).

Only one SCBC specimen retained an m2, and no fossils retained a complete lower tooth row (p2–m2). Consequently, lower tooth row was removed as an independent variable in subsequent analyses. Other degraded or absent features were replaced with group averages to facilitate a single stepwise discriminant analysis (SDA) and principle component analysis (PCA) encompassing all extant and fossil specimens (Fig. 3). SDA was also conducted for each fossil specimen individually, using only variables from preserved features, to ensure that the standardization did not alter classification outcomes.

Stepwise discriminant analyses were conducted (SPSS version 24) to determine whether measured dentary characters (Table 1) could effectively separate extant BFF from mink and subsequently classify the 11 SCBC specimens entered as unknowns. Mahalanobis distance, the squared distance from the mean centroid of each species group, was also calculated. Fossils with low distance values, within or near the range of variation exhibited by their SDA-assigned species group, were considered to have high classification confidence (e.g., McGuire 2011). Principal component analyses were conducted using the same morphological variables included in SDA to ensure that the SDA training set (extant BFF and mink) did not generate a false classification dichotomy. That is, fossil specimens representing a taxon discreet from the training set should separate from these extant species in isolated morphospace. Lastly, we surveyed the literature for reports of prehistoric BFF sites across North America. We summarize those data, as well as the presence/absence of prairie dogs, 7 other rodent genera, and 2 lagomorph genera at those sites, of which the other rodents and lagomorphs may have functioned as alternative BFF prey (Hillman and Clark 1980, Campbell et al. 1987, Biggins et al. 2011a). Fossil assemblage data were obtained for 25 BFF localities and 4 additional localities published with "cf. *Mustela nigripes*" or "*Mustela* cf. *M. nigripes*" materials (Table 3).

RESULTS

The SDA function generated a statistically significant difference between extant BFF and mink ($P < 0.001$, Wilks' lambda = 0.034). Results yielded 100% predicted group memberships for both original and cross-validated cases and generated a single function (eigenvalue = 28.66) that accounted for 100% of the total variance. Variables selected by the SDA,
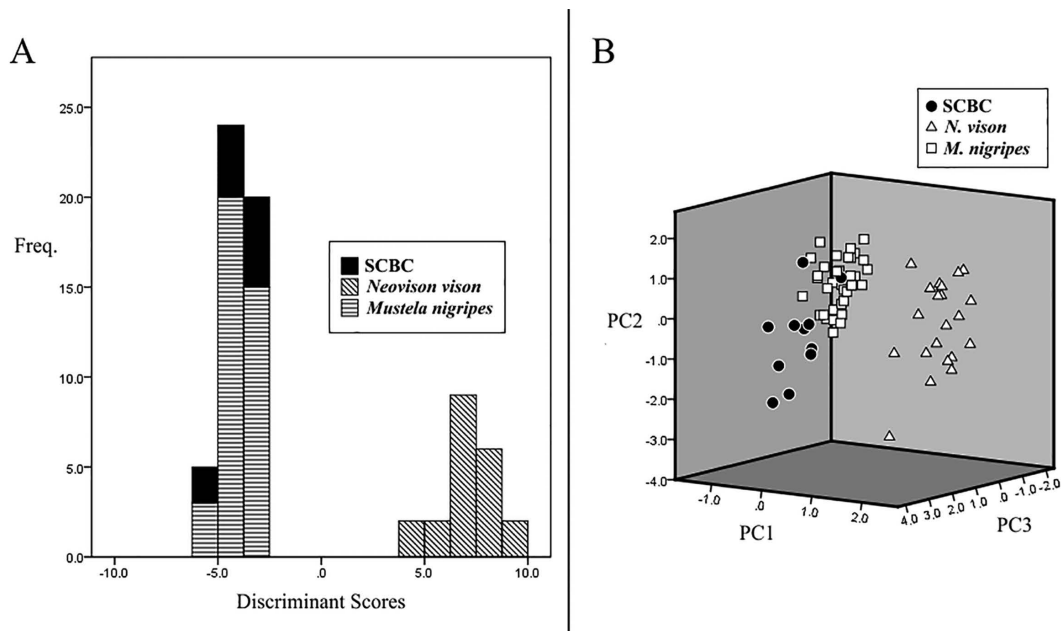
Fig. 3. (A) Stepwise discriminant scores ($P < 0.001$, Wilks' lambda = 0.034) for extant *Neovison vison* ($n = 21$), extant *Mustela nigripes* ($n = 38$), and Snake Creek Burial Cave fossils ($n = 11$). The range of fossil Mahalanobis distance values ($n = 11$) relative to the mean centroid of extant training sets was 0.06–3.32 for BFF and 92.04–164.17 for mink. Reported values are from group-run (missing character–averaged) data, though distances from analysis of individually preserved fossil characters were similar. (B) First 3 principal component scores for the same *N. vison, M. nigripes,* and Snake Creek Burial Cave fossils illustrated in panel A. The first 3 components explained 82.9% of data variance (55.4%, 14.6%, and 12.9% for PC1, PC2, and PC3, respectively).

in descending significance, were width of the m1 talonid, m1 length, dentary depth at the p3, and m2 width. The first 2 components of the PCA explained 72.6% of data variance and generated discreet clusters for BFF and mink, with more intraspecific variation exhibited in the latter taxon. Subsequent to training analyses, both the individual SDA (i.e., one fossil specimen per analysis using only variables preserved from that fossil) and the group-run SDA (i.e., all fossil specimens with missing variables averaged; Fig. 3a) classified fossil specimens within extant BFFs exclusively. All SCBC specimens exhibited low Mahalanobis distances relative to the mean centroid of extant BFFs (average distance from mean = 1.16, range 0.06–3.32, $n = 11$). Those values were approximately 2 orders of magnitude greater relative to the mean centroid of extant mink (average distance from mean = 123.76, range 92.04–164.17). Fossil specimens also clustered within, or near, extant BFF morphospace in the PCA (Fig. 3b). The first 3 principal components that included extant BFF, extant

mink, and the 11 SCBC fossils explained 82.9% of data variance, at 55.4%, 14.6%, and 12.9% respectively.

DISCUSSION

Classification

Significant characters for discriminating extant BFF and mink in SDA (i.e., m1 talonid, m1 length, dentary depth at the p3, and m2 width) support interspecific differences between these taxa as mentioned in the literature. For example, Anderson et al. (1986) noted that the m1 talonid is narrower in BFFs than in mink. Those authors also observed thicker mandibles and a smaller m2 in BFFs relative to mink (Anderson et al. 1986). Though PCA of dentary variables grouped fossil specimens in close morphospace with extant BFFs, the SCBC population exhibited a broader range of individual variation as illustrated by their distribution along the first 3 principle components (Fig. 3b) and by their Mahalanobis distances relative to the mean centroid of

TABLE 3. Twenty-nine North American localities yielding *Mustela nigripes* materials (including *M.* cf. *nigripes*). Localities are listed by descending latitude with presence (X), absence (—), or cf. identifications of potential prey genera. State and province locations (Prov.) follow standard abbreviations. See footnotes for additional abbreviations.

Site	Prov.	Age	C.	D.	L.	Le.	Ma.	Mi.	P.	S.	Sy.	T.	References
Old Crow River	YU	LPL	—	—	—	X	—	X	—	X	—	—	Harington 1978, Youngman 1994
Sixty Mile River	YU	LPL	—	—	—	—	—	cf.	—	X	—	—	Harington 1978, Youngman 1994
Hunker Creek	YU	LPL	—	—	—	—	—	—	—	X	—	—	Harington 1978, Youngman 1994
January Cave	AB	LPL	X	—	cf.	X	X	X	X	X	—	X	Burns 1991
Medicine Hat	AB	LPL	X	—	—	X	—	X	—	X	X	X	Harington 1978, Stalker and Churcher 1982
Spotted Bear	SD	LHO	X	—	—	X	—	X	—	—	X	—	Hurt 1953
Jaguar Cave	ID	LPL	X	—	—	X	X	X	X	X	X	X	Kurtén and Anderson 1972
Swanson	SD	LHO	X	—	—	—	—	—	—	—	X	X	Hurt 1951
Little Canyon Creek Cave	WY	EHO	—	—	X	X	X	X	X	—	—	X	Walker 1987
Little Canyon Creek Cave	WY	LPL	—	—	X	X	X	X	X	—	—	X	Walker 1987
Moonshiner	ID	EHO	X	—	X	X	X	X	X	X	X	X	White et al. 1984
Smith Falls Local Fauna	NE	LPL	X	—	—	X	X	X	X	X	X	X	Voorhies and Corner 1985
Duck Point	ID	LPL	X	—	X	X	—	X	X	X	X	X	McDonald 1998
Little Box Elder Cave	WY	EHO	X	—	X	X	X	X	X	X	X	X	Anderson 1968, Walker 1987
Little Box Elder Cave	WY	LPL	X	—	X	X	X	X	X	X	X	X	Anderson 1968, Walker 1987
Graves/Potter[a]	NE	LPL	X	—	—	X	—	X	—	X	X	X	Cavin 2004
Chimney Rock Animal Trap	CO	LPL	X	—	—	—	X	X	X	X	X	X	Hager 1972
Highway 74	NE	MPL	X	X	—	—	—	X	—	X	—	—	Martin and Martin 1995
Cathedral Cave	NV	MPL	—	—	X	X	X	X	X	X	X	X	Jass 2007, Jass and Bell 2011
Snake Creek Burial Cave	NV	LPL	—	—	X	X	X	X	—	X	cf.	—	Heaton 1987, Mead and Mead 1989, Bell and Mead 1998
Porcupine Cave[c]	CO	MPL	X	—	X	X	X	X	X	X	X	X	Barnosky and Bell 2004
Cudahy Ash Mine[b]	KS	MPL	X	—	—	—	—	X	X	X	X	X	Hibbard 1970, Anderson et al. 1986
Atlatl Cave[a]	NM	LHO	X	—	—	X	—	—	X	—	X	—	Lyman 1980
Isleta Caves	NM	LPL/EHO	X	X	X	X	X	X	X	X	X	X	Harris and Findley 1964, Harris 1993
Fort Washita[a]	OK	LHO	—	—	—	—	—	—	—	X	X	—	Penman 1975
Moore Pit	TX	LPL	—	X	X	—	—	X	X	X	X	—	Slaughter 1966, Anderson et al. 1986
Burnet Cave	NM	LPL	X	X	X	X	X	X	X	—	X	X	Schultz and Howard 1935, Harris 1993
Big Manhole Cave	NM	LPL	—	—	—	X	X	X	X	X	X	X	Harris 1993
Jimenez Cave	MX	LPL	X	X	X	X	—	X	X	X	X	X	Messing 1986

^acf. *Mustela nigripes* identification.

^bConflicting *M. nigripes* identifications: *M. nigripes* (Hibbard 1970), cf. *Neovison vison* (Anderson et al. 1986)

^cAge estimates vary considerably among different Porcupine Cave excavations and faunas (<1,000,000 to >600,000 BP; Barnosky and Bell 2004). That range transcends the early and middle Pleistocene, but will be grouped as middle Pleistocene for the purpose of this study. The Porcupine Cave list in this table represents Pit fauna level one (<550,000 to >600,000 BP) (Barnosky and Bell 2004; Figs. 7.1–7.3), which was chosen because (1) Porcupine Cave stratigraphy is best understood from its excavation and (2) it has the greatest diversity of small mammal taxa (included in this survey) associated with *M. nigripes*. However, *M. nigripes* has been found in other Porcupine Cave deposits including the Velvet Room and Badger Room. Small mammals associated with *M. nigripes* from those faunas may be dissimilar from the genera marked present above.

Taxon abbreviations: C. = *Cynomys* spp., D. = *Dipodomys* spp., L. =*Lemmiscus curtatus*, Le. = *Lepus* spp., Ma. = *Marmota* spp., Mi. = *Microtus* spp., P. = *Peromyscus* spp., S. = *Spermophilus* spp., Sy. = *Sylvilagus* spp., T. = *Thomomys* spp.

Age abbreviations: LHO = late Holocene (5000 BP–present), EHO = early Holocene (10,000–5000 BP), LPL = late Pleistocene (126,000–10,000 BP), MPL = middle Pleistocene (781,000–126,000 BP). Note that radiometric dates are not available for all localities; some (e.g., Porcupine Cave and Duck Point) are grouped according to biochronologic age correlations.
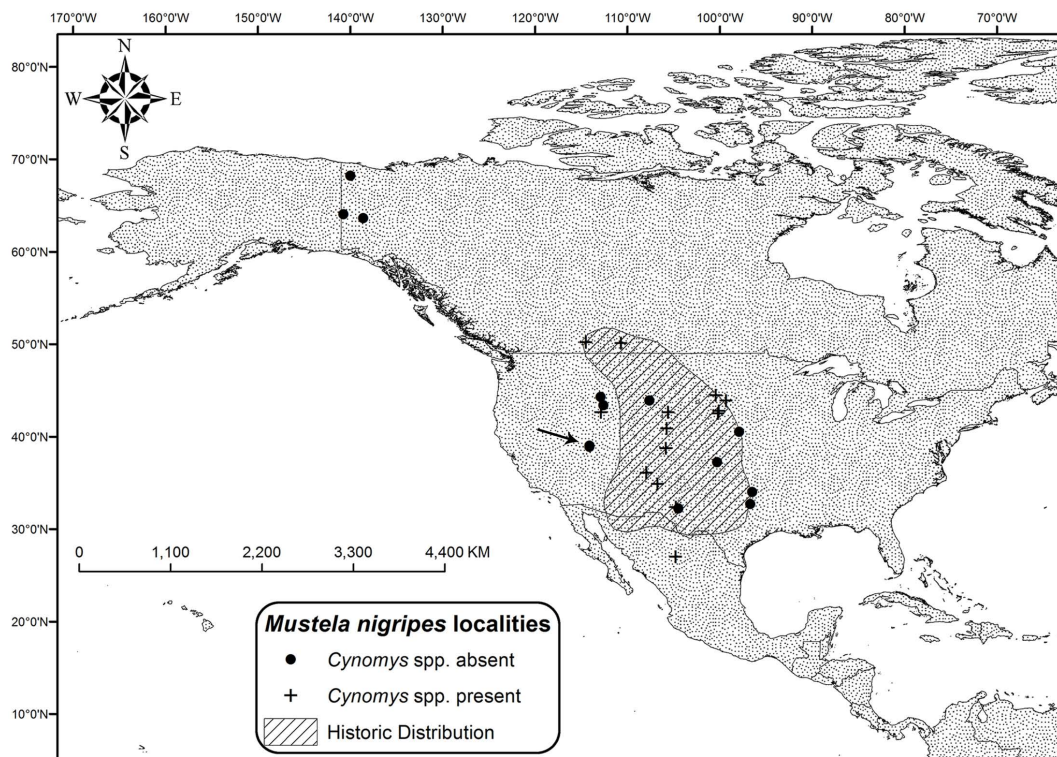
Fig. 4. Twenty-nine Pleistocene–Holocene North American localities with *Mustela nigripes* (cf. included) as listed in Table 3. Sites are labeled according to the presence or absence of *Cynomys* spp. Snake Creek Burial Cave and Cathedral Cave (overlapping) are indicated by the black arrow. Species range data are from Patterson et al. (2007).

extant BFF (extant BFF range 0–2.44, $n = 38$; fossil range 0.06–3.32, $n = 11$). While this observation may be due to temporal differences in deposition or generations between individuals, relatively extensive variation was also observed in the Mahalanobis distances of extant mink relative to their mean centroid (range 0.01–7.76, $n = 21$) and in their PCA distribution (Fig. 3b). Captive (extant) BFFs exhibited markedly less intraspecific variation, as illustrated by dense PCA clustering (Fig. 3b) and more constrained Mahalanobis distances, which may reflect morphological uniformity due to limited genetic variation after their population bottlenecking, as mentioned (Wisely et al. 2002a, Cain et al. 2011). Additionally, minor morphological differences between extant and prehistoric BFF specimens could reflect habitat differences between the late Pleistocene biome of eastern Nevada and the captive environments of BFFs today (e.g., Wisely et al. 2008). Thus, more robust studies that include historic and prehistoric BFFs and

encompass greater geographic and temporal ranges, such as ancient DNA analysis and 3D geometric morphometrics, may be warranted to elucidate potential drivers of this species' morphological and genetic changes through time.

Data herein support the presence of BFF within the SCBC paleofauna. Conversely, the occurrence of mink is not supported. The mustelid diversity of SCBC is now reduced to 7 species, though smaller fossils of the subfamily Mustelinae (e.g., *Mustela erminea*) may benefit from reexamination as well. This locality represents one of at least 8 prehistoric sites west of historic distributions of both BFF and prairie dogs that contain the former taxon, yet lack the latter (Anderson et al. 1986, Owen et al. 2000; Fig. 4). The minimum number of individual BFFs at SCBC is 6, since 6 of the 11 specimens represent left dentaries (Table 2). Therefore, Snake Creek Burial Cave has the most BFF specimens reported at a fossil locality lacking *Cynomys* (Anderson et al. 1986). It also represents the farthest westward

occurrence of this taxon within the contiguous United States, aside from Cathedral Cave located approximately 40 km north of SCBC (Owen et al. 2000; Fig. 4). SCBC and Cathedral Cave represent the only 2 BFF localities known from the physiographic Great Basin, a region where no prairie dog fossils have been reported (Owen et al. 2000, Grayson 2006).

Prehistoric Locality Review

In addition to SCBC, Anderson et al. (1986) noted that 11 of 21 other prehistoric sites containing BFF materials lacked *Cynomys* spp., though other rodents and lagomorphs were often present and abundant. Likewise, Owen et al. (2000) acknowledged that while BFFs and prairie dogs are assumed to have an obligate predator-prey relationship, at least 42% of Pleistocene and early Holocene localities yielding BFFs remain unassociated with prairie dog materials. From those data, and from the lack of prairie dogs at several BFF localities west of the historic distribution of prairie dogs, Owen et al. (2000) argued that current relationships between prairie dogs and BFFs are likely secondary effects of BFF colonization in regions heavily populated by prairie dogs. Those authors inferred that modern interactions between these taxa must have been established within the last 800,000 years based on dates from the oldest known locality lacking prairie dogs at that time, Cathedral Cave, biochronologically dated between 750,000 and 850,000 BP (Owen et al. 2000). However, a more recent uranium series radioisotope analysis of flowstones sampled from Room Two of Cathedral Cave dated it between 146,020 ± 2584 BP and 153,700 ± 6400 BP, suggesting that the fauna is considerably younger than previously estimated (Jass and Bell 2011). Occurrence of BFFs at SCBC, a locality near Cathedral Cave that lacks prairie dogs and yields upper age limits of 15,100 ± 700 BP, supports and refines the paleoecological inferences proposed by Owen et al. (2000). Combined, these data imply that within discrete provinces of the Great Basin, close interactions between BFFs and prairie dogs had not yet been established as recently as about 15,000 BP or later. However, 2 discrete spatial and temporal data points are insufficient for generating broad paleoecological conclusions concerning these taxa.

Given the discrepancy between historic and prehistoric BFF and prairie dog relationships and the limited prehistoric information available concerning these taxa within the Great Basin, we surveyed the literature for additional localities to determine which small mammals were frequently associated with BFFs at other spatial and temporal intervals. Data collected across sites (Table 3) are in general agreement with the findings of Anderson et al. (1986) and Owen et al. (2000). Of the 25 definitive prehistoric BFF localities evaluated throughout North America, 11 lack documented association with prairie dogs (44%), yet many are associated with other rodents and lagomorphs. Ratios were similar when 4 additional "cf. *Mustela nigripes*" sites were included: 13 of those 29 sites (about 45%) lack prairie dogs (Table 3). Literature data (Fig. 5) illustrate an inverse relationship between several rodent and lagomorph genera present among BFF localities from different age intervals. Prairie dogs and *Sylvilagus* spp. were comparatively underrepresented across BFF sites until the late Holocene (Table 3, Fig. 5). Conversely, *Spermophilus* spp., *Microtus* spp., and *Thomomys* spp. are relatively common at Pleistocene sites, yet decrease in representation among Holocene sites (Table 3, Fig. 5). Percentages of rodent and lagomorph genera present across all BFF sites (taxa designated as cf. not included) are as follows: *Microtus*, 84%; *Spermophilus*, 80%; *Lepus*, 72%; *Peromyscus*, 68%; *Sylvilagus*, 68%; *Thomomys*, 68%; *Marmota*, 60%; *Cynomys*, 56%; *Lemmiscus*, 48%; and *Dipodomys*, 16% (Table 3).

Two issues warrant further examination. First, is the absence of prairie dogs at so many BFF localities real or only an artifact of the fossil record? Differential research methodologies (e.g., sampling extent, collection bias, and identification criteria), taphonomic effects, spatial variation, temporal unconformities, and time averaging should all be factored in when interpreting prehistoric assemblages (Lyman 2008, Varela et al. 2011). Due to these constraints, species absences should be evaluated with particular caution, given the likelihood of generating erroneous or misleading information (Lyman 2008, Varela et al. 2011). However, studies have shown that cave assemblages, which represent the majority of BFF sites, are generally indicative of past mammalian communities despite potential time-averaging
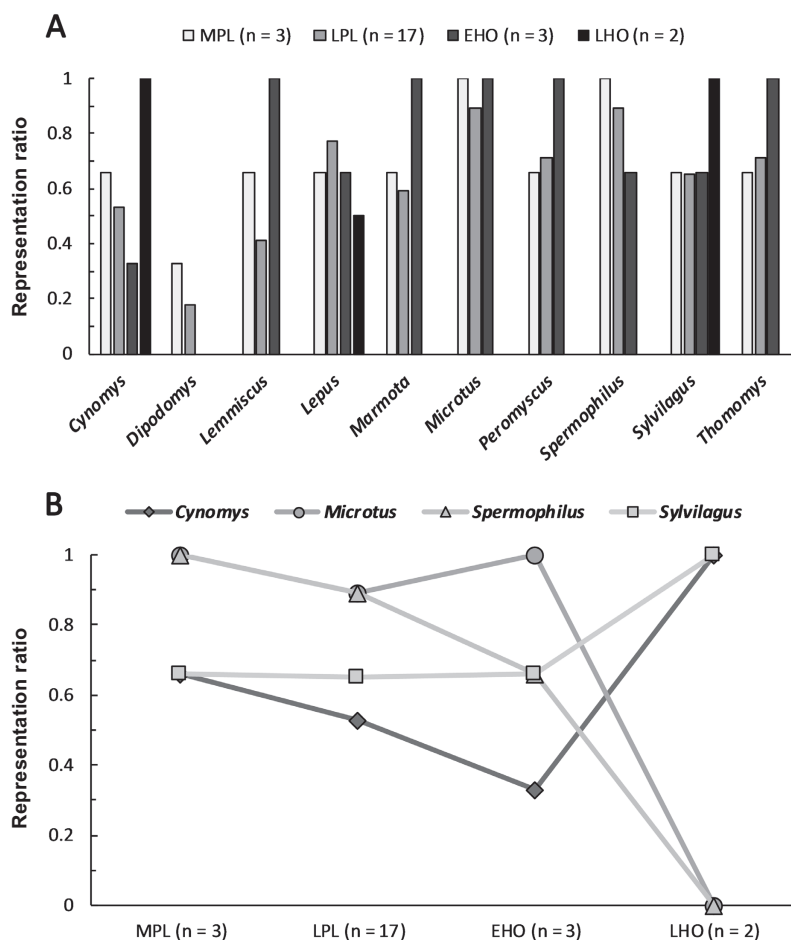
Fig. 5. (**A**) Representation ratios (localities present/total localities) of 10 rodent genera among 25 sites with *Mustela nigripes.* Data were compiled from presence-absence representation as depicted in Table 3 (cf. *Mustela nigripes* localities not included). Localities are grouped by middle Pleistocene (MPL), late Pleistocene (LPL), early Holocene (EHO) or late Holocene (LHO) ages according to data provided in the literature and the definitions given in Table 3. Note that Isleta Caves, a late Pleistocene/early Holocene site, was grouped as late Pleistocene for the purpose of this study because Pleistocene-indicative taxa (e.g., *Camelops*) were recovered there. *Mustela nigripes* identification from Cudahy Ash Mine follows the cf. *Neovison vison* diagnosis of Anderson et al. (1986), and is not included. (**B**) Plot of *Cynomys* spp., *Microtus* spp., *Spermophilus* spp., and *Sylvilagus* spp. representation among 25 *M. nigripes* localities. Taxa are plotted according to the same age, site, and identification criteria as in panel A.

effects (e.g., Hadly 1999, Terry 2010). It also seems unlikely that taphonomic events would preserve small rodents such as *Microtus* and not the comparatively larger and more robust elements of prairie dogs. Localities preserving small rodents should, therefore, also preserve prairie dogs if they were present in an assemblage.

Second, what caused changes in relative abundance of prey through time? One possible explanation could include the geographic and temporal spread of bison across North Amer-

ica. Large grazers, and prairie dogs, are known to have a profound impact on prairie ecosystems (Kotliar et al. 1999, Truett et al. 2001). Extant prairie dog colonies, in particular, thrive in short and mixed grasses (Knowles 1988, Benedict et al. 1996, Truett et al. 2001). Such environments are facilitated by the grazing of cattle and bison (Truett et al. 2001). Conversely, rodents such as *Spermophilus* and *Microtus* are able to colonize taller, less disturbed vegetation (Benedict et al. 1996, and references therein). Given that the Rancholabrean North American

Land Mammal Age is defined by the presence of *Bison* sp. in North American assemblages and is typically characterized by additional fauna existing between about 210,000 BP and 9500 BP (Bell et al. 2004), it seems reasonable that increased representation of prairie dogs among BFF localities after the Pleistocene could have been facilitated by the spread of bison and later cattle throughout North American grasslands. Though exact driving mechanisms are unknown, studies have shown positive spatial relationships between bison and cattle grazing selection and prairie dog colony distribution (e.g., Chipault and Detling 2013, and references therein). Indeed, 80% and 77% of the BFF sites from the Rancholabrean Age and younger that were found in this literature search (Table 3) also yield *Bison* or *Bos* elements (cf. *M. nigripes* sites included and excluded, respectively). These concepts remain speculative, however, until detailed analysis of the drivers of change in rodent diversity among sites and over time can be undertaken. Nevertheless, a marked temporal shift in prey representation is conspicuous among these data, and certainly warrants further examination.

Ecological Implications

Many historical records indicate a close relationship between extant BFFs and prairie dogs (Casey et al. 1985), whereas fossil evidence suggests that this relationship was not equally facilitated across their geographic and temporal range (e.g., Anderson et al. 1986, Owen et al. 2000). We confirm that BFFs were present at SCBC, a well-sampled late Pleistocene paleontological locality, despite the absence of identifiable prairie dog material from this site. Data from this study and the literature imply that, in some locations, BFF diets were dissimilar and possibly more diverse in the past than at present, or as historically acknowledged. Moreover, prairie dogs were unlikely a major aspect of BFF diet in some of these locations.

Such evidence can be applied to modern conservation efforts, given that highly specialized species are generally more vulnerable to extinction (Boyles and Storm 2007, Brickner et al. 2014), especially during periods of rapid environmental change (e.g., Miller et al. 2005). For example, obligate specialists may have difficulties tracking their ecological niche in response to environmental changes if the taxon they rely on has low dispersal ability (Gilman et al. 2010). Those constraints are applicable to BFF reintroduction because prairie dogs are poor intercolony dispersers (Garrett and Franklin 1988, Slobodchikoff et al. 2009), which could limit BFFs' ability to track habitat changes due to the effects of anthropogenic climate change. Therefore, as a consequence of their reduced genetic diversity (Wisely et al. 2002a) and extreme dietary specialization (Campbell et al. 1987), reintroduced BFFs may be at greater risk of extinction than other species that demonstrate extreme niche specialization or that have endured a population bottleneck (Cain et al. 2011).

In light of these data, and as noted by Brickner et al. (2014), it may not be coincidence that BFFs from Shirley Basin, Wyoming, are among the most successfully reintroduced ferret populations, given their mosaic of consumed prey species. This study does not suggest that BFFs should be precluded from hunting prairie dogs. However, facilitating exposure to greater prey diversity may fortify their resilience when faced with future ecological adversities such as plague (e.g., Shoemaker et al. 2014) or climate change. Indirect impacts such as predator-prey interactions of other prairie taxa should be considered as well (e.g., Eads et al. 2015). Therefore, we advocate performing systematic analyses to monitor the consumption, interactions, and general sustainability of additional rodents and lagomorphs at BFF reintroduction sites.

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