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Short communication

Foraging plasticity in a highly specialized carnivore, the endangered black-footed ferret

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ABSTRACT

The extirpation of black-footed ferrets (*Mustela nigripes*) from the wild resulted from the rangewide decline of prairie dogs (*Cynomys* spp.) brought about by poisoning campaigns, the arrival of an exotic disease, and habitat loss. It is widely accepted that ferrets are an obligate, near monophagous, dietary specialist of prairie dogs and that high-density prairie dog colonies are necessary for effective recovery. To test the extent to which ferrets are dietary specialists, we measured the stable isotopic values of 321 ferrets of known age and sex as well as of their potential prey (e.g., prairie dogs, mice, ground squirrels, and rabbits). Our results confirmed that prairie dogs are the most common diet item for ferrets, although ferrets possessed greater foraging plasticity than previously reported, consuming substantial quantities of other species. The degree to which ferrets were specialized on prairie dogs differed between age–sex groups. Adult male and juvenile ferrets had equivalent diets, with prairie dogs constituting nearly 75% of their assimilated diet. In contrast, adult females obtained over one third of their diet from other species, notably mice. However, female ferrets appeared to have provisioned prairie dogs to their dependent offspring. Conservation of ferrets, one of North America's most endangered mammals, will require prairie dogs, not just as prey, but also for the prey-rich habitat that their colonies provide.

1. Introduction

Specialization is a strong predictor of extinction risk (McKinney, 1997). Dietary specialists, in particular, can be especially susceptible to population declines and extinction (Boyles and Storm, 2007). However, even for some of the most endangered and vulnerable species, quantitative assessments of diet and foraging ecology are lacking and the degree of dietary specialization is assumed even though such information can enhance conservation by improving prioritization of resources or effort, informing re-introduction programs, and guiding habitat management.

Black-footed ferrets (*Mustela nigripes*; hereafter ferrets) are widely regarded as both a habitat (Eads et al., 2011) and dietary (Powell et al., 1985) specialist of prairie dogs (*Cynomys* spp.). Due to their obligate association with prairie dogs across their distributional range, the near extinction of ferrets has been principally linked with agricultural land conversion and associated prairie dog control efforts, and the arrival of an exotic bacterial disease, plague (Lockhart et al. 2006). Since their reintroduction into the wild, research has revealed new insight into fundamental aspects of ferret biology, including life history strategies, population dynamics (Grenier et al., 2007, 2009), and habitat selection (Eads et al., 2011). However, few, and mostly anecdotal, accounts exist describing the diet and foraging ecology of ferrets. After analyzing scat samples, Campbell et al. (1987) and Sheets et al. (1972) reported that the majority (~90%) contained remains of prairie dog, but also found evidence of hares and rabbits (Sheets et al., 1972), and mice and voles (Sheets et al., 1972; Campbell et al., 1987). Ferrets have also been observed unsuccessfully pursuing songbirds (Eads, 2012). Because all published accounts of ferret dietary habits are from scat or casual observations, they are likely biased towards prairie dogs because they are larger, diurnal and, therefore, more readily observed both in field or as prey remains. Thus, the degree to which ferrets are prairie dog specialists could be overemphasized, and their reliance on other small mammal species is unclear. It is also unknown whether the strong sexual dimorphism observed in ferrets (males weighing up to 23% more than females; Santymire et al., 2012), has resulted in different foraging strategies between the sexes.

The use of stable isotopes has provided a powerful analytical tool to quantify the relative reliance of food items, especially cryptic sources, for free-ranging vertebrates (Kelly, 2000). Because dietary analysis using stable isotopes relies on the abundance of ^{13}C and ^{15}N, it avoids biases of traditional methods (e.g., scat analysis) that fail to detect highly digestible materials and measures

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assimilated, rather than excreted, diet components (Phillips, 2012). To explore the diet and foraging ecology of this endangered carnivore, we analyzed the isotopic signature of hair collected from ferrets and potential prey items, and for the first time quantified (1) the diet composition and degree to which ferrets are dietary specialists of prairie dogs and (2) potential dietary differences between age–sex groups of ferrets to explore intraspecific character displacement.

2. Methods

2.1. Study population

Historically, ferrets ranged throughout much of western North America, but after their perceived extirpation, rediscovery in the 1980s and reintroduction efforts in the 1990s, ferret populations now exist in 14 of the original 21 reintroduction sites (Jachowski et al., 2011). Shirley Basin (42°20 N 106°18 W) Wyoming is one of the most successful reintroduction sites featuring high annual population growth rates (35–59%; Grenier et al., 2007), large population size (229 individuals 95% CI = 161–298), and a broad distribution (Grenier et al., 2009).

2.2. Sample collection and preparation

From 2005 to 2011, we collected 321 hair samples (199 juveniles, 42 adult males, 80 adult females) from individual black-footed ferrets (ranging from 90 days to 5 years of age) captured in mid-August through mid-September in Shirley Basin (Grenier et al., 2009). We collected the hair from potential prey items including grasshopper mice (*Onychomys leucogaster*), deer mice (*Peromyscus maniculatus*), desert cottontails (*Sylvilagus audubonii*), thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*), Wyoming ground squirrels (*Urocitellus elegans*), and white-tailed prairie dogs (*Cynomys leucurus*) in Shirley Basin from June through September 2012. Sherman live-traps were spaced 10 m apart in a 10 × 10 array. We also conducted small mammal trapping along two transects of 100 traps spaced every 10 m adjacent to colonies. All traps were set in the evening and checked daily for 4 days. White-tailed prairie dogs (*Cynomys leucurus*) were opportunistically captured using Tomahawk live traps (Hazelhurst, WI); leporids were collected as road kills. Although ferrets have been observed unsuccessfully pursuing songbirds, they have not been detected in scat and, therefore, we did not include feathers in our analyses. Eggs of songbirds were also not sampled because hair from free-ranging ferrets would represent assimilated diet during the molt (i.e. autumn; Progulske, 1969) when eggs would be rare and likely an unimportant diet item.

To calculate a trophic discrimination factor, we collected hair and blood from eight adult male ferrets fed a constant diet in captivity at the Smithsonian Conservation Biology Institute's Black-Footed Ferret Conservation Center. Individuals were fed Toronto Carnivore Diet (Milliken Meat Products; Scarborough, Ontario, Canada) augmented with laboratory rats (*Rattus domesticus*). Our calculated ^{15}N discrimination factor was 3.3 ± 0.03 (±1SE), which is comparable to those previously quantified for terrestrial carnivores (Fig. 1; Caut et al., 2009; Kelly, 2000). In contrast, because lipids are ^{13}C-depleted and the captive ferret diet was lipid-rich (i.e., >25% fat) it resulted in unnaturally depleted carbon signatures and a large discrimination factor (2.7 ± 0.1; Ben-David et al., 2012; Newsome et al., 2010). Thus, we utilized the ^{13}C discrimination factor (0.6 ± 1.0) previously reported for red foxes (*Vulpes vulpes*), the only other controlled feeding trial for a terrestrial carnivore that quantified a trophic enrichment factor from whole blood (Roth and Hobson, 2000).

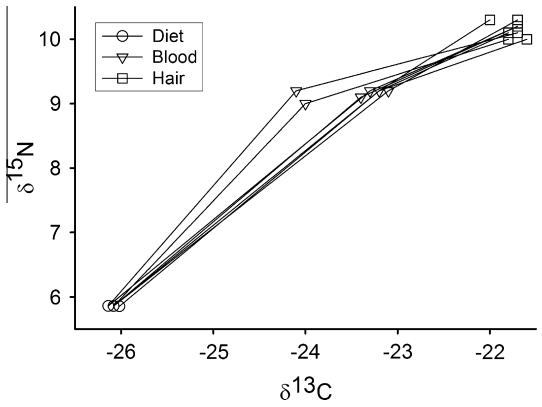

Fig. 1. δ^{13}C and δ^{15}N trophic discrimination factor for blood, hair, and diet of male captive black-footed ferrets (*Mustela nigripes*) held at Smithsonian Conservation Biology Institute (Front Royal, Virginia). Our calculated ^{15}N discrimination factor was 3.3 ± 0.03 (±1SE), which is comparable to previously quantified discrimination factors for terrestrial carnivores (Caut et al., 2009; Kelly, 2000). The high lipid content of the diet resulted in strongly depleted carbon signatures (2.7 ± 0.1) for captive ferret [15]. Consequently, we utilized the ^{13}C discrimination factor previously determined for red foxes (*Vulpes vulpes*) of 0.6 ± 1.0 (Roth and Hobson, 2000).

Hair samples were rinsed three times with 2:1 chloroform:methanol to remove surface oils and debris, homogenized, and then dried for 72 h at 55 °C following previously described methods (Pauli et al., 2009). Homogenized samples were weighed into tin combustion capsules and analyzed with a Thermo Finnigan Delta Plus XP Elemental Analyzer at the University of Wyoming Stable Isotope Facility. Results are provided as per mil (parts per thousand [‰]) ratios relative to the international standards of Peedee Belemnite (PDB; δ^{13}C) and atmospheric nitrogen (AIR; δ^{15}N) with calibrated internal laboratory standards.

2.3. Data analysis

We categorized diet items into the functional prey groups: (1) mice; (2) mid-sized mammals (i.e., ground squirrels and rabbits) and; (3) white-tailed prairie dogs (Table 1). Before quantifying the relative proportion of each prey group with mixing models, we determined whether groups were isotopically distinct with a *K* nearest-neighbor randomization test (*R* statistical software; Rosing et al., 1998). Utilizing the discrimination factors, we corrected samples of free-ranging ferrets and then estimated proportional reliance on each prey group via Bayesian-based mixing models in the package Stable Isotope Analysis in R V4 (SIAR; Parnell et al., 2010). To test our hypothesis of age- and sex-based differences in the diet of ferrets, we compared three age–sex groups: adult male, adult female and juvenile ferrets. Males and females were

Table 1
Mean δ^{13}C and δ^{15}N isotopic signatures (±1SE) of potential black-footed ferret (*Mustela nigripes*) prey groups (mice, mid-sized mammals, and prairie dogs) from Shirley Basin, Wyoming, USA.

Prey group	Species	*n*	δ^{13}C	δ^{15}N
Mice				
	Onychomys leucogaster	5	−22.6 (0.2)	10.7(0.2)
	Peromyscus maniculatus	8	−21.4 (0.7)	12.0 (1.0)
Mid-sized mammals				
	Sylvilagus audubonii	4	−22.0(0.5)	5.4 (1.1)
	Ictidomys tridecemlineatus	3	−22.0 (0.1)	8.1 (0.7)
	Urocitellus elegans	4	−22.4 (0.2)	4.4 (1.2)
Prairie dogs				
	Cynomys leucurus	17	−23.5 (0.1)	3.6 (0.3)