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Competition and Coexistence Among Canids in Maine

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Introduction

- Competition can result when species use the same food resources, leading to costly interactions (Sih et al. 1985).
- Partitioning food resources can ameliorate costs of competition (Palomares & Caro 1999). For example, carnivores may eat different amounts of animal-based protein, or they may choose different prey items, including anthropogenic foods, i.e., foods cultivated by humans and derived from plants such as corn, sugarcane, and their respective byproducts such as corn syrup (Lanszki et al. 2006; Prugh et al. 2009).
- Stable isotope analysis (SIA) can assess relative amounts of animal protein and anthropogenic food in diets (Ben-David & Flaherty 2012). N isotope values, indicated by $\delta^{15}N$, reflect the ratio of heavy to light N atoms ($^{15}N/^{14}N$) in a sample. Carnivores occupy higher trophic positions than herbivores do and thus have higher $\delta^{15}N$ values (Ben-David & Flaherty 2012). C isotope values, indicated by $\delta^{13}C$, reflect the ratio of heavy to light C atoms ($^{13}C/^{12}C$) in a sample. C_4 plants, e.g., corn and sugarcane, do not discriminate against ^{13}C, and we can detect diets containing anthropogenic foods if the natural habitat contains mainly C_3 plants (Ben-David & Flaherty 2012).
- Competition may occur among 3 canid species in Maine. Nonnative coyotes (*Canis latrans*) colonized Maine in the early 1900s, becoming the apex predator (Richens & Hugie 1974). Gray foxes (*Urocyon cineroargenteus*) were historically native to southern Maine, were extirpated, and now recolonized the region, expanding throughout the state (Bozarth et al. 2011). Native red foxes (*Vulpes vulpes*) historically occupied Maine and now overlap in range with coyotes and gray foxes (Statham et al. 2012).

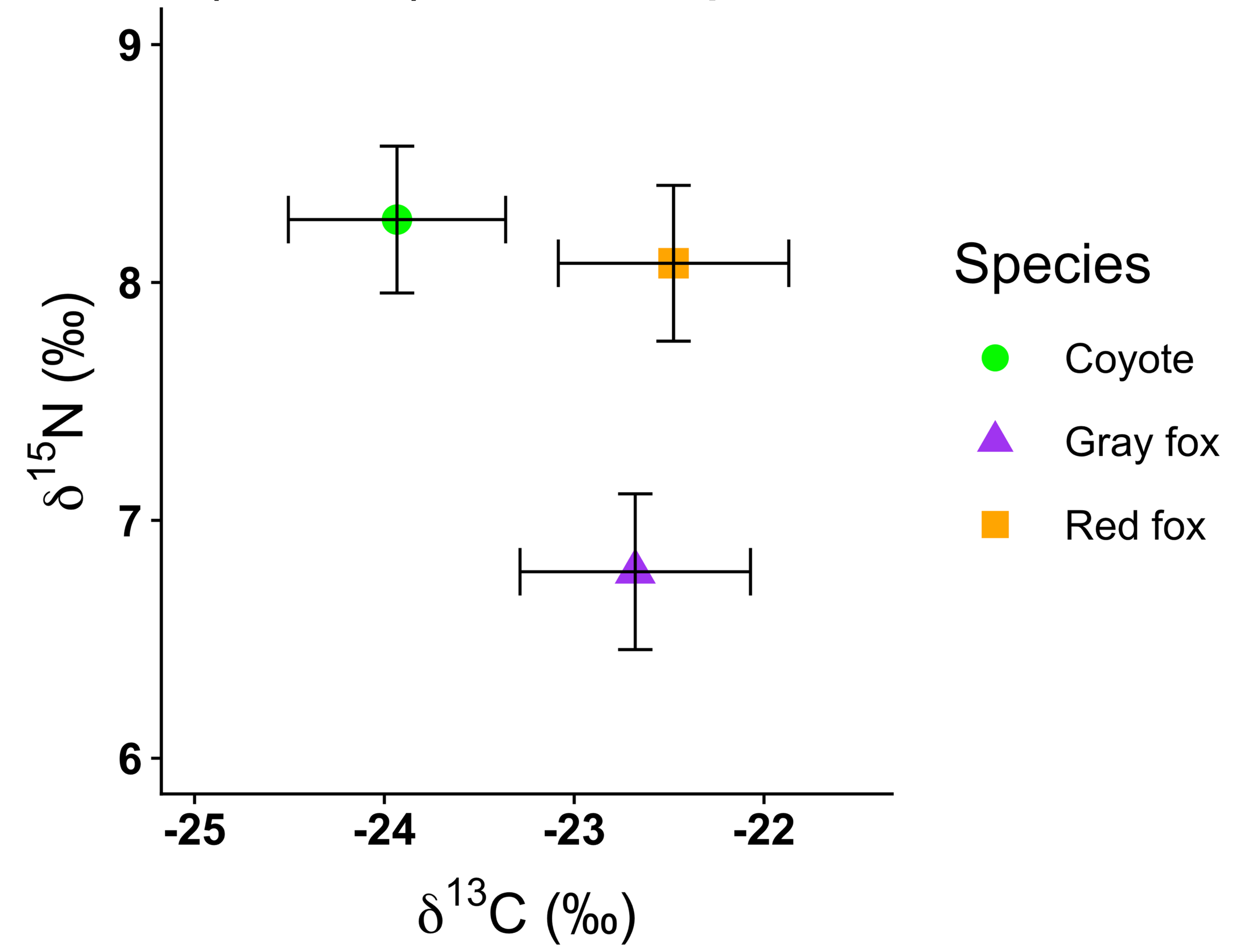
Objectives & Predictions

- To assess potential competition for food among canids by (1) comparing anthropogenic food use and relative trophic positions using SIA and (2) comparing diets using stomach contents.
- Prediction 1A: Because coyotes are apex predators and avoid humans, coyotes use anthropogenic foods the least (lowest $\delta^{13}C$).
- Prediction 1B: Because red foxes are most adapted to urban habitat (Harrison et al. 1989), they use anthropogenic foods the most (highest $\delta^{13}C$; Handler et al. 2020).
- Prediction 1C: As apex predators, coyotes occupy the highest trophic position (highest $\delta^{15}N$).
- Prediction 1D: Because gray foxes eat more plants than other canids do (Haroldson & Fritzell 1982), they occupy the lowest trophic position (lowest $\delta^{15}N$).
- Prediction 2: Because interactions with coyotes may affect habitat preferences (Harrison et al. 1989), gray foxes have the broadest diet and consume the most plants, whereas red foxes have the least diverse diet.

Methods

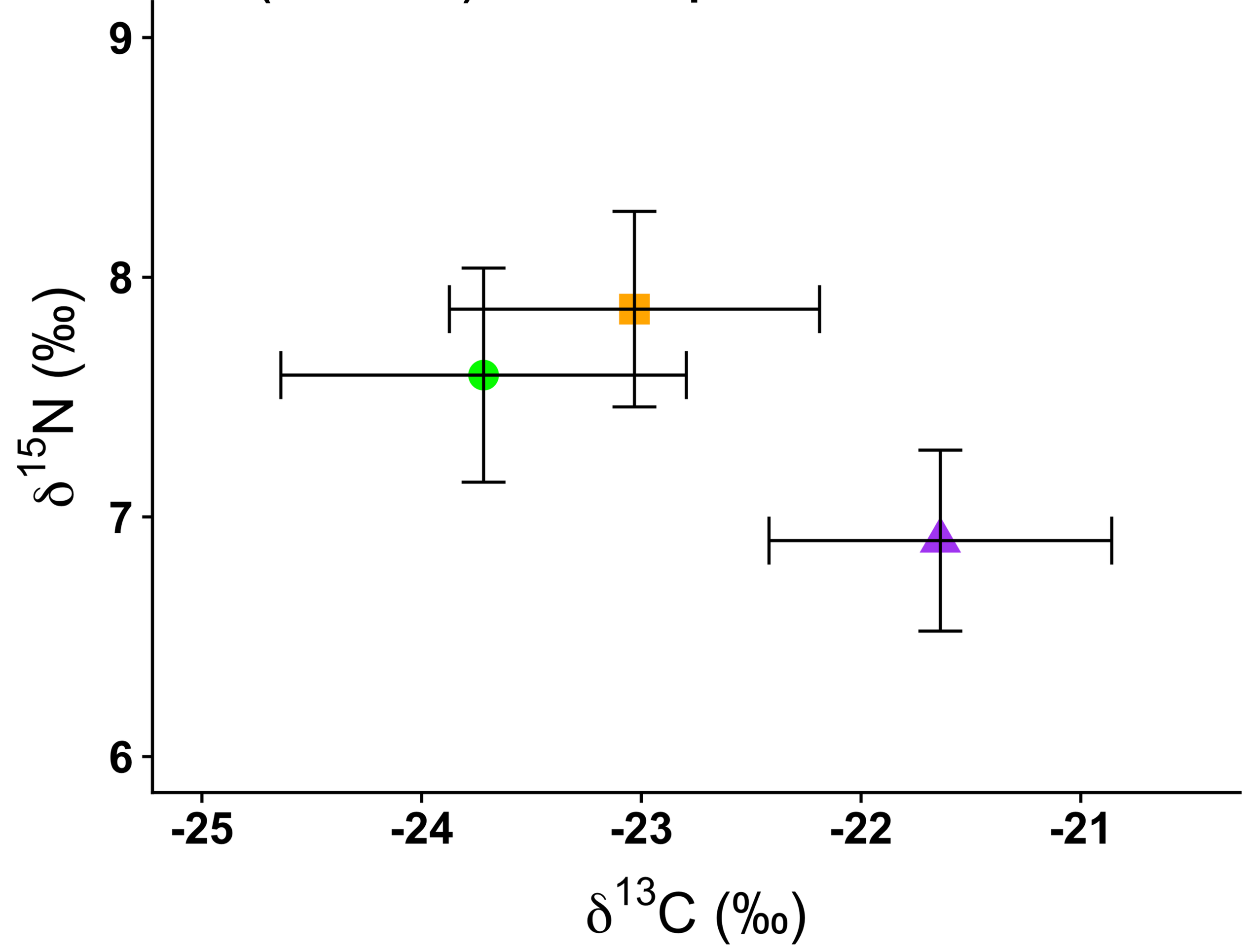
- We partnered with trappers to collect hairs, muscle tissue, and stomach contents from coyotes, red foxes, and gray foxes in fall and early winter (Oct 15 – Dec 1, 2019) in southern Maine. Canids molt in spring, and isotope values from hair reflect summer diet. Isotope values from muscle reflect fall and early winter diets in this study (Maurel et al. 1986).
- To standardize isotope analyses (Bligh & Dyer 1959), I extracted lipids from muscle samples at the University of New England.
- I sent hair and muscle samples to the Stable Isotope Facility, University of California, Davis, for quantification of $\delta^{15}N$ and $\delta^{13}C$.
- Using isotope values, I calculated kernel utilization density contours, niche overlap, and niche areas using rKIN in R (Eckrich et al. 2020).
- For each species, I identified stomach contents to the lowest taxonomic level possible: invertebrates, birds, plants, reptiles, small mammals (e.g., mice), and other mammals (i.e., hair not from small mammals).
- I calculated frequency of occurrence and relative frequency of occurrence of each prey category, generated indices of overlap among species, and compared observed diet overlap to a null distribution using EcoSimR and ggplot2 in R (Gotelli et al. 2015).

Mean (± 95% CI) muscle isotope values of Maine canids



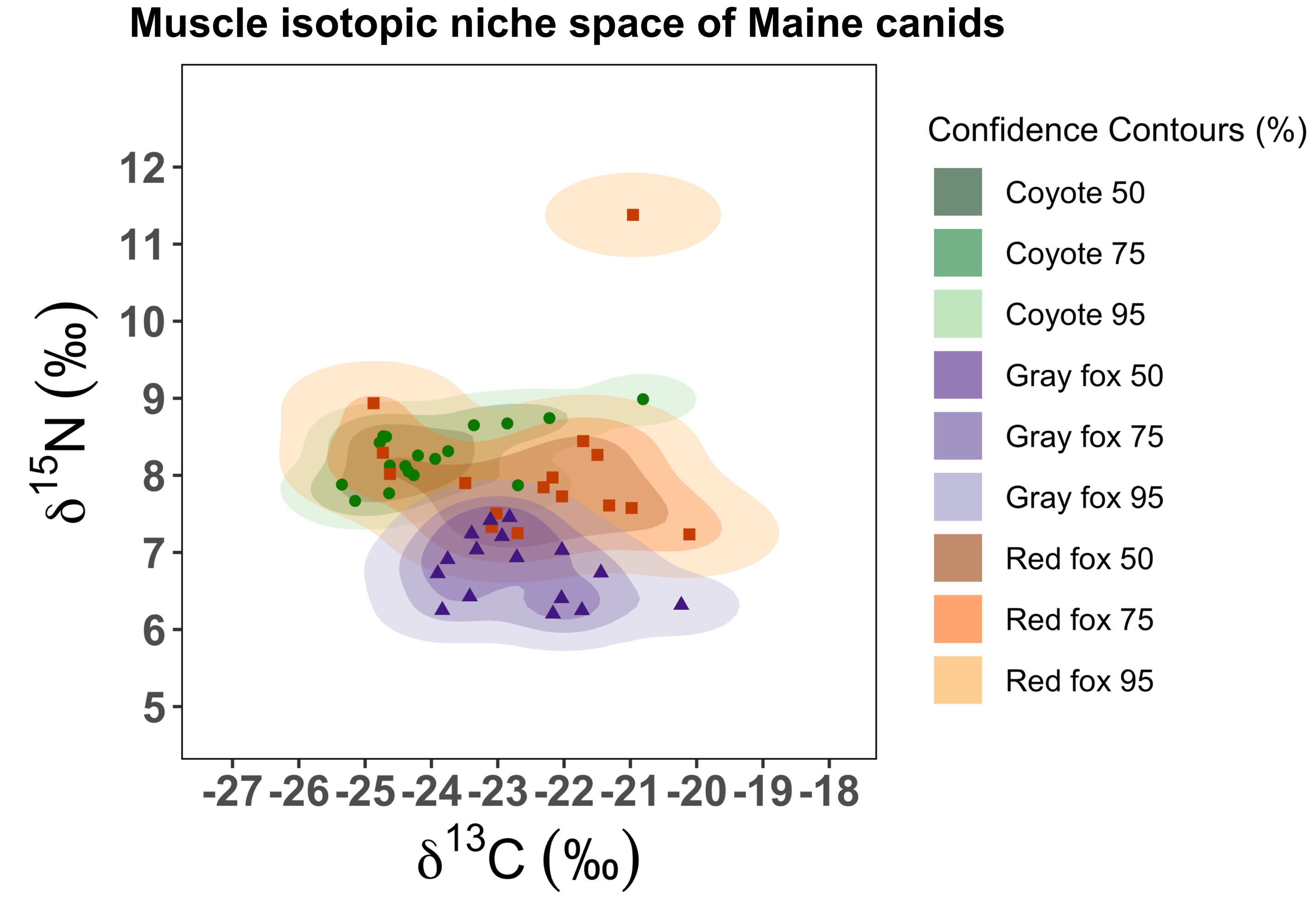
In fall & early winter, red foxes (n = 15) consumed highest amounts of anthropogenic foods; coyotes (n = 16) ate more natural foods. Coyotes & gray foxes (n = 21) held the highest and lowest relative trophic positions, respectively.

Mean (± 95% CI) hair isotope values of Maine canids



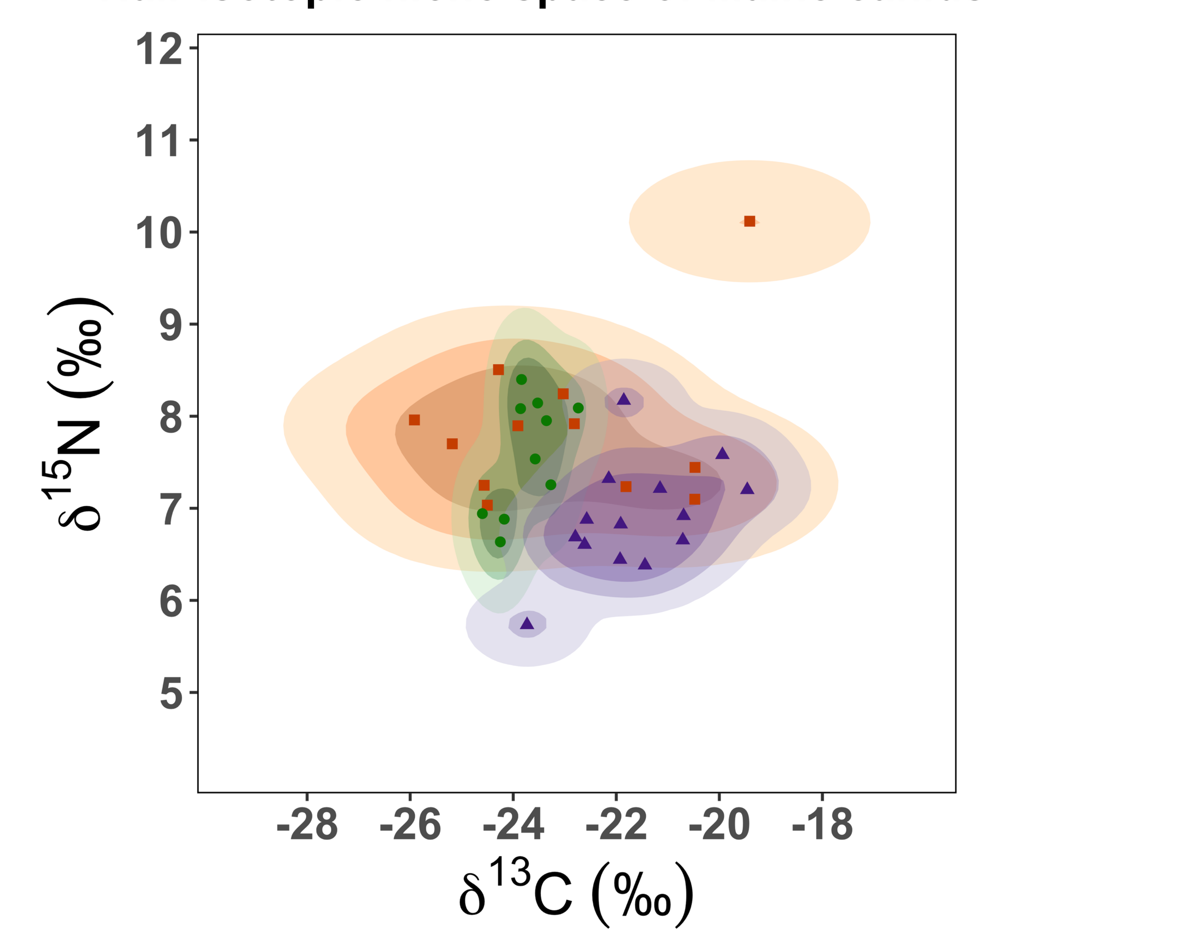
In summer, gray foxes ate the most anthropogenic foods, and coyotes consumed more natural foods. Red foxes and gray foxes held the highest and lowest relative trophic positions, respectively.

Muscle isotopic niche space of Maine canids



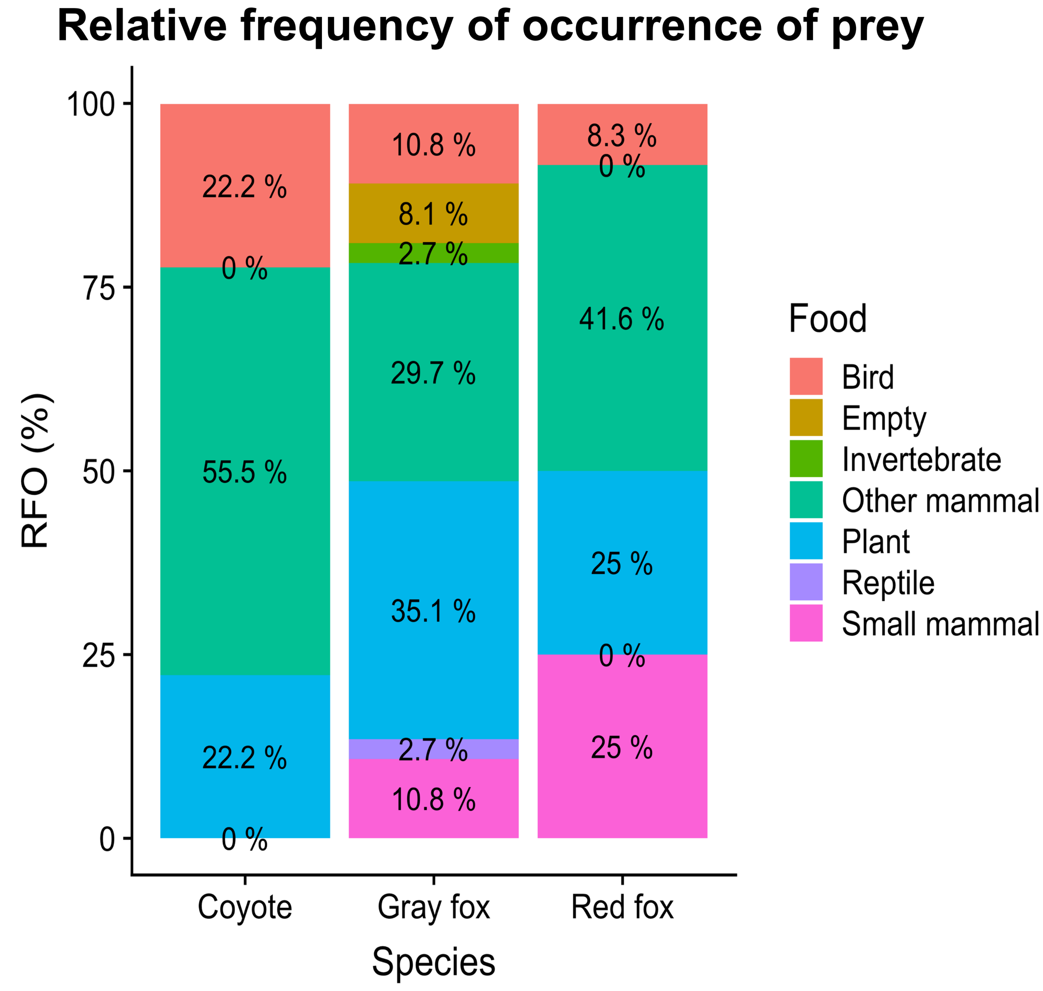
In fall and early winter, red foxes had the largest niche areas at all contours. Coyotes had the smallest niche areas, except for the 95% contour where gray foxes had a slightly smaller niche area. Core overlaps (50% contour): coyote-red fox: 35.7%; coyote-gray fox: 0%; red fox-coyote: 15.5%; red fox-gray fox: 0.7%; gray fox-coyote: 0%; gray fox-red fox: 1.2%.

Hair isotopic niche space of Maine canids



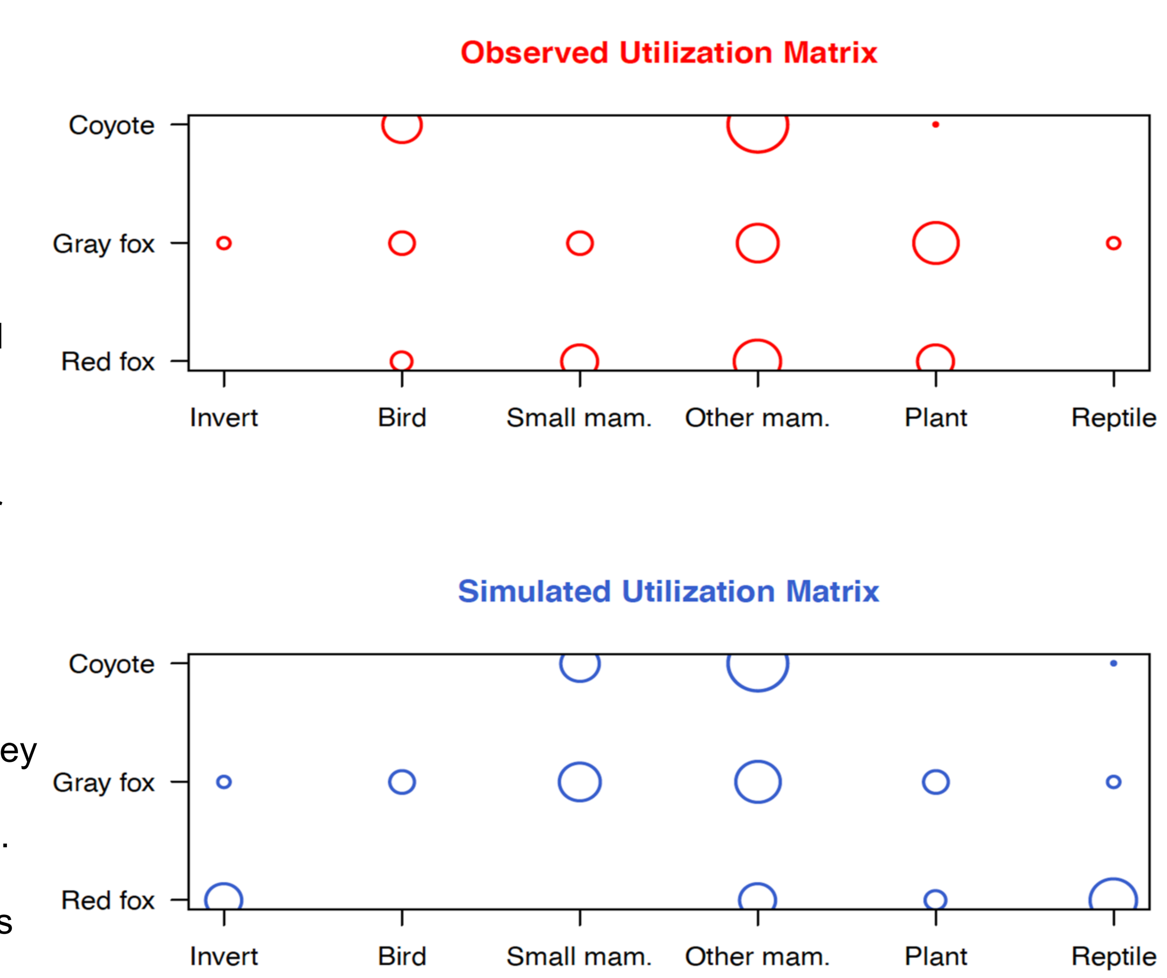
In summer, red foxes had the largest niche areas and coyotes had the smallest niche areas at all contours. Core overlaps (50% contour): coyote-red fox: 81.5%; coyote-gray fox: 0%; red fox-coyote: 21.3%; red fox-gray fox: 12.6%; gray fox-red fox: 27.6%; gray fox-coyote: 0%.

Relative frequency of occurrence of prey



(LEFT)
Relative frequency of occurrence of prey items in stomachs from fall and early winter for coyotes (n = 5), red foxes (n = 7), and gray foxes (n = 17). Gray foxes had the broadest diet and coyotes had the narrowest diet. Fox diets were most similar (alpha = 0.92; p = 0.041). Gray fox – coyote diets were least similar (alpha = 0.65; p = 0.224).

(RIGHT)
Observed and simulated utilization matrices based on frequency of occurrence of prey items in fall and early winter showing resource partitioning. Coyotes, red foxes, and gray foxes competed for prey items (overlap index = 0.77; p = 0.022).



Conclusions

✓ 1A) Based on stable isotope values, coyotes are less likely to compete for anthropogenic foods and instead consume natural food items in fall, early winter, and summer.

✓ 1B) Based on stable isotope values, red foxes may utilize anthropogenic foods in fall and early winter as food availability declines and competition increases. Conversely, in summer when food is more available, red foxes may switch to natural foods such as small mammals and berries (Major & Sherburne 1987).

✗ 1B) Based on stable isotope values, gray foxes may compete with red foxes for anthropogenic foods in fall and early winter. In contrast, gray foxes may utilize anthropogenic foods throughout summer as a means of partitioning resources and reducing competition.

✓ 1C) Based on stable isotope values, coyotes appear to eat more animal protein in fall and early winter. Red foxes may reduce competition with coyotes by utilizing anthropogenic foods.

✗ 1C) Based on stable isotope values, coyotes appear to reduce the proportion of animal prey in their diet in summer, consistent with previous diet analyses in Maine (Major & Sherburne 1987).

✓ 1D & 2) Based on all data, gray foxes have the broadest diet, eat more plants, and occupy the lowest relative trophic position.

✗ 2B) Based on all data, red foxes do not have the least diverse diet but may be more prone to diet specialization.

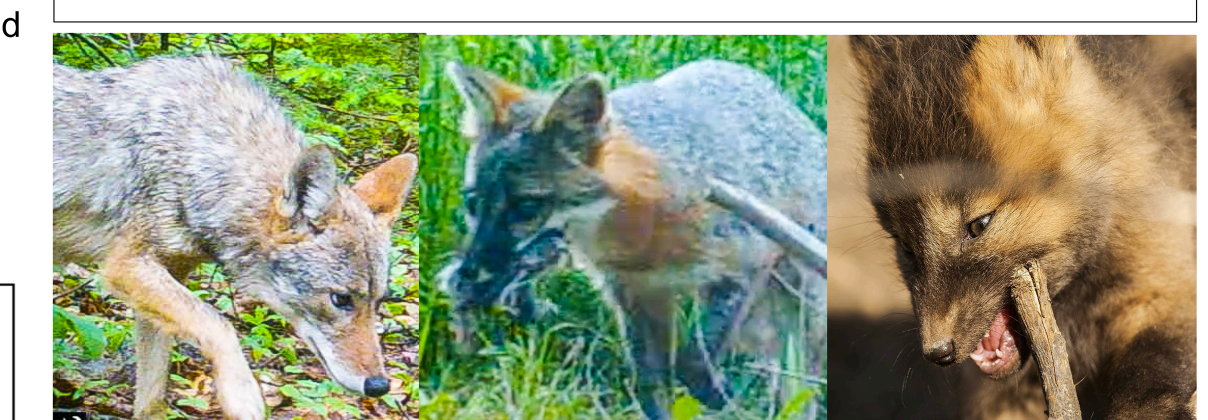
Diet overlap appears to be greatest in summer when food resources are higher versus in fall and early winter when food resources are lower. Stomach contents suggest that all species compete in fall and early winter. Red foxes are the only canid that have core niche overlap with both competitors.

Red foxes may be subject to exploitative competition with gray foxes particularly in fall and early winter. Red foxes may be subject to interference and exploitative competition with coyotes in fall, early winter, and summer.

Gray foxes and coyotes may not compete with one another as heavily as they do with red foxes. Additionally, gray foxes are not as susceptible as red foxes to predation by coyotes because gray fox can climb trees (Haroldson & Fritzell 1982).

We did not collect fine scale spatial data, though all three species have relatively large home ranges and are habitat and diet generalists (Haroldson & Fritzell 1982; Major & Sherburne 1987).

The costs of competitive interactions appear highest for the native red fox among canids in Maine.



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Acknowledgements

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