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RESEARCH ARTICLE

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Dogs occupying grassy habitat near protected areas in eastern Madagascar rely on foods from forests

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[Correction added on 07 July 2023, after first online publication: The supplementary file was corrected in this version.]

Societal Impact Statement

Identifying where introduced animals fit in a food web relative to each other and to endemic species is key for biodiversity conservation planning. Using a multiproxy study of dog feces from eastern Madagascar, we infer that even dogs that spend time in derived grasslands typically eat forest-derived foods. Regardless of the time that dogs spend in cleared forest, their impacts are likely concentrated on forest-dwelling prey. If dogs in forests mostly consume threatened endemic animals (and not other introduced animals such as rats), then the exclusion of dogs from protected forests should be a priority.

Summary

- Introduced predators on islands can help control invasive species yet can also contribute to the extirpation and extinction of endemic taxa. The spread of dogs on Madagascar by ~1000 years ago coincided with the introduction of livestock and spread of grazer-adapted grasslands, and we help evaluate the extent to which modern dogs are part of novel grassland food webs.
- To infer dog diet, we identified food remains, where possible, and conducted stable isotope ratio analysis for n = 100 modern dog feces collected in derived grassland at varying distances from protected forest edges around Analamazoatra and Andasibe-Mantadia National Park in eastern Madagascar.
- Animal remains in feces and the observed range of fecal $\delta^{15}N$ values are consistent with dog meals at multiple trophic levels. However, the observed distribution of fecal $\delta^{13}C$ values suggest that few dogs in the study area consumed food derived from open C_4 grasslands.
- Existing data suggest that dogs rely primarily on C_3 consumers inhabiting forest biomes (forest-dwelling animals) for their prey, which may include endemics such as tenrecs, Malagasy rodents, and lemurs and introduced rodents such as rats. These findings indicate that dogs are not confined to the anthropogenic niche defined by grazer-adapted grasslands, but rather use and impact animal food resources associated with protected forests. Higher resolution study of dog diet

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and mobility can further clarify the potential for dogs to exploit endemic prey, compete with endemic predators, and spread disease across ecotones.

KEYWORDS
diet, dog, feces, feeding ecology, grassland, predator, stable isotope

1 | INTRODUCTION

People manage and clear Madagascar's forests (Harper et al., 2007; Kaufmann & Tsirahamba, 2006) and, in the process, have introduced an expanding multitude of plants and animals (Kolby, 2014; Kull et al., 2012). This ecological transformation is part of a long-term trend, as people brought significant changes to the island during the past millennium by contributing to the expansion of grasslands (Burney, 1987; Domic et al., 2021; Razanatsoa, 2019; Virah-Sawmy et al., 2016), the proliferation of introduced grazers (Hixon, Douglass, Crowley, et al., 2021), and the extinction of endemic megaherbivores (Burney et al., 2004; Crowley, 2010; Hansford et al., 2021). Remote sensing data from 2018 suggest that over half of the island is covered by grassland (Zhang et al., 2020), and existing data from functional ecology and paleoecology suggest that the island's grazer-adapted grassland biome is a recent phenomenon (Godfrey & Crowley, 2016; Joseph & Seymour, 2020). The distinction between novel and ancient grasslands is important, because derived grasslands tend to be ecologically depauperate (Veldman & Putz, 2011). Today, derived grasslands in Madagascar's eastern lowlands can form in as little as ~30 years (Joseph et al., 2021; Styger et al., 2007), which has led to an abundance of grasslands even in wet regions (MAP >2000 mm/yr) where natural savanna is typically scarce (Joseph et al., 2022). The associated spread of animal husbandry and derived grasslands provides compelling examples of how positive interactions among humans and introduced plants and animals can have compounding negative effects on endemic biodiversity. This type of synergy exists in other disturbed island ecosystems such as on Hawai'i, where the frugivory of introduced rodents helps spread invasive plants (e.g., Shiels, 2011).

However, negative interactions may exist also among introduced taxa, which has motivated the control of pest species through further species introductions (Messelink et al., 2008; Peacock & Abbott, 2010). Such attempts at biological control are limited by our inability to predict ecosystem-wide impacts of introduced species (Simberloff & Stiling, 1996). On Madagascar, basic research continues to highlight what may be unexpected aspects of introduced animal diets (e.g., reliance of livestock on a variety of woody and succulent plants rather than primarily grass in the arid SW; Feldt et al., 2017; Kaufmann & Tsirahamba, 2006). Research on the diverse diets of introduced predators (e.g., dogs, cats, and Indian civet) can clarify the extent to which they control populations of other introduced taxa (e.g., rats and mice), versus those of endemic prey and potential competitors in Madagascar's forests.

Most of Madagascar's modern dogs have African ancestry (Ardalan et al., 2015), and their spread to the island may have coincided with the introduction of livestock from mainland Africa. No other canids inhabited the island prior to the introduction of domesticated dogs. Radiocarbon dated dog bone recovered from archaeological and paleontological deposits across Madagascar spans the past millennium (Hixon, Douglass, Godfrey, et al., 2021), which left potential for dogs to aid human-led hunts of now-extinct megafauna (Burney et al., 2020). Today, dogs kill endemic rodents such as the Malagasy giant jumping rat (*Hypogeomys antimena*; Sommer & Hommen, 2000), occasionally stalk lemurs (Brockman et al., 2008), and help people procure forest bushmeat (including lemurs and tenrecs; Decary, 1939; Garcia & Goodman, 2003; Gardner & Davies, 2014). This can contribute to negative interactions between dogs and endemic predators such as the fosa (*Cryptoprocta ferox*), which are harassed by dogs (Kshirsagar et al., 2020; Valenta et al., 2016) and tend toward avoidance (Farris et al., 2015; Merson et al., 2019). However, dogs are also known to prey on introduced animals that can flourish in relatively open habitat (e.g., rodents and chickens), and dogs rely heavily on plant and animal scraps in human-derived food waste (Kshirsagar et al., 2020; Valenta et al., 2016). Additionally, ancient dog bone collagen (primarily from SW Madagascar) tends to be enriched in ^{13}C relative to ancient fosa collagen (Hixon, Douglass, Godfrey, et al., 2021), which suggests that dogs introduced during the past millennium tended to consume fewer forest-derived foods than fosa. It is unclear whether dogs living near Madagascar's remaining forests today rely primarily on foods from forest-dwelling taxa or on taxa in open habitat.

Evidence for modern predation by dogs can be observed directly, identified from gut or fecal remains, and inferred from the stable isotope composition of consumer tissue (e.g., bone and hair), including feces (Newsome et al., 2007). While direct observation can most accurately and precisely characterize prey diversity and abundance, inference based on analysis of intact feces and other consumer tissues provide an expedient way of estimating aspects of diet integrated over various periods of time (depending upon tissue turnover rates). Each approach has strengths and limitations. For example, through direct observation, one can estimate the number of introduced rats killed and consumed per dog per week (a parameter necessary but not sufficient for estimating dog impacts on introduced rat populations), but it is difficult to estimate whether the killed rats foraged mostly in open or closed habitat, for they are known to exploit both (Goodman, 1995). Conversely, through stable isotope analysis of dog tissue, it is possible to estimate whether most of dog diet comes from open or closed habitat, yet it is often difficult to make precise estimates of the proportion of diet that comes from a particular taxon such as introduced rats. For an initial exploration of dog diet in the

study area, we focus on the analysis of feces, which integrate diet over relatively short periods of time (Salvarina et al., 2013) and have the advantage of being easier to collect than consumer tissue such as bone, hair, or blood (Codron et al., 2007).

The precision of prey inference through fecal analysis is limited by myriad physiological and taphonomic factors including the facts that identifiable prey remains are typically scarce, and feces are highly variable in composition. While feces do contain lipids and proteins from consumed prey, they tend to include large amounts of indigestible food (e.g., cellulose) and dead bacteria. Therefore, diet quality and digestion strongly influence the composition of bulk feces and the degree to which the stable isotope content of bulk feces accurately approximates that of bulk prey tissue (Jones et al., 1979).

The stable carbon isotope ($\delta^{13}C$) content of consumer tissue is sensitive to the types of plants at the base of the food web (Codron et al., 2005). Specifically, trees and shrubs that use the C_3 photosynthesis are significantly depleted in ^{13}C relative to C_4 grasses (see Hixon, Douglass, Crowley, et al., 2021). While differences in CO_2 fixation between C_3 and C_4 plants can explain the majority of $\delta^{13}C$ variation in consumer tissues, multiple variables can account for observed $\delta^{15}N$ variation in plant and consumer tissues (Szpak, 2014). For example, soil nitrogen cycling can lead to ^{15}N enrichment in plants and their consumers, particularly in arid areas (Austin & Vitousek, 1998; Crowley et al., 2011), and consumption of foods at higher trophic levels can also lead to ^{15}N enrichment of consumer tissue (McCutchan et al., 2003).

To help characterize the diet of dogs living close to remaining forests in eastern Madagascar, we analyzed opportunistically collected dog feces across an open ecosystem characterized by C_4 grasses, adjacent to protected forest, to test the following hypotheses:

1. Dog fecal $\delta^{13}C$ values for samples collected closer to continuous forest are depleted in ^{13}C relative to samples collected from adjacent grassland and mixed grass and shrubland. This pattern in fecal stable isotope data is most parsimoniously explained by a situation in which dogs both opportunistically rely on forest taxa and move little between the place of eating and the site of defecating. We expect a broad range (>10‰) of dog fecal $\delta^{13}C$ values, consistent with the broad range of ancient dog collagen $\delta^{13}C$ values (Hixon, Douglass, Godfrey, et al., 2021) and the wide range of modern hair $\delta^{13}C$ values in another commensal omnivore (*Rattus rattus*) studied in eastern Madagascar (Dammhahn et al., 2017).
2. Dog fecal $\delta^{15}N$ values are similar across the relatively mesic forests and grasslands of eastern Madagascar. Consistent with the observed omnivory among dogs, we also expect a wide range of fecal $\delta^{15}N$ values (>6‰) and for feces in many cases to be enriched in ^{15}N relative to the tissue of potential prey (e.g., tenrecs, rodents, and chickens).
3. Dog fecal stable isotope content matches expectations based on identifiable prey remains in feces. Specifically, feces with abundant undigested cellulose reflect meals with C_4 grass that enrich bulk feces in ^{13}C, and feces with identifiable animal remains (e.g., bone, hair, claws, and feathers) come from relatively carnivorous meals that enrich bulk feces in ^{15}N. This clarifies the degree to which the two lines of dietary inference are complementary.

2 | MATERIALS AND METHODS

2.1 | Sample collection and analysis

The subset of eastern humid forests on Madagascar that have been protected by Analamazoatra and Andasibe-Mantadia for >30 years are rich in biodiversity (Goodman, 2010). A cleared area of mixed grass and shrubland separates these forests from the highland grasslands ~20 km to the east (Bond et al., 2008). Part of the mixed grass and shrubland is a Ramsar Wetland Site (Torotorofotsy), and there is a proposal to keep some of the unprotected forest in the area as a natural resource reserve (Zahamena Ankeniheny; Figure 1). The vegetation in the study area's cleared forest has not been the subject of detailed vegetation survey. However, invasive C_4 grasses often dominate cleared habitat, and some C_3 shrubs and native taxa (e.g., bamboos) can also thrive in secondary stands (Binggeli, 2003). Madagascar includes a diverse clade of endemic C_3 grasses that may be present in sheltered pockets of otherwise cleared habitat, but these grasses tend to flourish in high mountains and forest understory (Hackel et al., 2018; Solofondranohatra et al., 2018). Where C_3 grasses are abundant, the reliance of consumers on grassy ecosystems in general cannot be readily distinguished based on consumer $\delta^{13}C$ values.

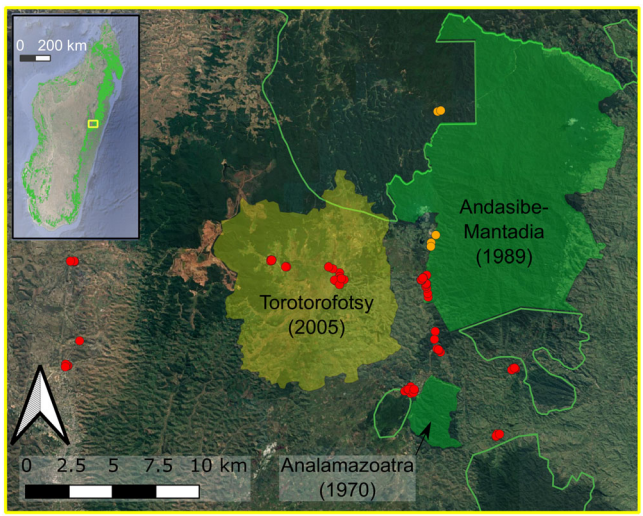


FIGURE 1 Study region illustrating dog fecal sample locations relative to national parks (Analamazoatra and Andasibe-Mantadia, established in 1970 and 1989, respectively), the Ramsar Site Wetland Site of Torotorofotsy (recognized in 2005), and the proposed natural resource reserve of Zahamena Ankeniheny (outlined in green). Only the sample locations marked in orange are >1 km from a settlement. The inset includes green areas of Madagascar that outline remaining primary vegetation (Royal Botanical Gardens, Kew). Both maps were produced over a Google Satellite base.

Over three hundred modern dog feces samples were collected opportunistically on forest margins and in the derived grassland surrounding Analamazoatra and Andasibe-Mantadia National Parks during June and July 2018. Of these samples, 100 were selected for analysis by aggregating randomly selected subsets from collection areas at different distances to the forest edge. All samples were collected within 1 km of roads, and all but six come from within 1 km of human settlement.

After collection, each fecal sample was placed in a plastic 50-ml tube and immersed in 95% ethanol. The location of each fecal sample was recorded using a handheld GPS. After ~24 h, the ethanol from each sample was decanted and transferred to a sterile 50-ml tube containing indicating silica beads topped with a sterile Kimwipe to promote desiccation. Fecal samples were then transported to the United States for analysis. As ethanol is an organic compound, it is important to note that its use in the preservation of biological samples can influence the stable isotope values of some tissues, but the magnitude of this effect on $\delta^{13}C$ and $\delta^{15}N$ tends to be small (≤~1‰) (Barrow et al., 2008; Sweeting et al., 2004). The effect of preservative treatment on fecal stable isotope values likely varies according to heterogeneous content of the feces, and existing research with orangutan feces found no effect of 99.5% ethanol treatment on fecal $\delta^{13}C$ values and only a minor effect on fecal $\delta^{15}N$ values (~0.3‰) (Tsutaya et al., 2021).

At the University of Florida and University of California at Santa Barbara, all fecal samples were visually inspected, and analysts noted the presence of plant material, animal material (bones, hair, feathers, and claws), and human trash (foil, textile, and wax). Analysis of the animal remains present in the feces included taxonomic identification whenever possible. The fecal samples contain highly fragmentary animal bones, portions of animal keratin (e.g., tenrec quills and claw coverings), and at least one bird feather. To identify the taxa represented, bone and keratin fragments were examined using a binocular microscope and/or a Dinoscope and compared to modern skeletal specimens of known taxa. Due to fragmentation, many specimens could only be identified to higher level taxonomic categories (e.g., Mammalia and Vertebrata); however, some specimens could be identified as tenrecs (species undetermined), rodents, and possibly reptiles. Additionally, the feces were X-rayed at the University of Florida's College of Veterinary Medicine to explore screening for dense remains of prey. Because most feces included at least some plant material, samples with particularly abundant plant material were also noted, which made this measure semiquantitative.

Following the approach of Codron et al. (2007), desiccated fecal samples were dried and homogenized, and the <1 mm fraction was collected for stable isotope analysis at the Human Paleoecology and Isotope Geochemistry Laboratory at the University of California at Santa Barbara. Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) and elemental (weight %C and %N) analysis was conducted at the Yale Analytical and Stable Isotope Center (YASIC) using a Thermo Delta Plus Advantage IRMS. The standard deviation across standard $\delta^{13}C$ and $\delta^{15}N$ measurements was 0.2‰ and 0.1‰, respectively (see Method S1 for details regarding data analysis).

3 | RESULTS

3.1 | Fecal dataset trends

Most fecal samples included visible plant remains (80% of total) and animal tissue (63%; Dataset S1). A minority (21%) included particularly abundant plant material, which tended to make the dried feces loosely consolidated. Hair tended to be the most abundant animal tissue (in 44% of total), but bone, claws, and a feather were also present (Figure 2). Bone and hair tend to be associated, for 73% of the samples containing bone are part of the subset that also includes hair. Animal remains in a minority of the feces (19%) could be identified at some level, and the majority of these (63%) were identified as belonging to mammals. Three samples included recognizable bones of tenrecs or rodents, and reptiles may also be present in four samples. Additionally, a minority of samples (9% of total) included human trash (foil, wax, and textiles).

The ranges of both $\delta^{13}C$ and $\delta^{15}N$ values were >10‰ (12.0‰ and 12.9‰, respectively): $\delta^{13}C$ values ($n = 100$, m = −26.8‰) ranged from −28.8‰ to −16.8‰, and $\delta^{15}N$ values ($n = 100$, m = 7.5‰) ranged from 2.6‰ to 15.5‰ (Figure 2). Distributions of fecal weight % C:N, $\delta^{13}C$, and $\delta^{15}N$ data are positively skewed and failed Shapiro–Wilk tests for normality, with test statistics (W) > 0.7 and $p < 0.001$. There is a strong positive relationship between fecal $\delta^{13}C$ and $\delta^{15}N$ values ($n = 100$, $r_s = 0.40$, $p < 0.0001$). A 5‰ increase in fecal $\delta^{13}C$ values is matched by a ~1‰ increase in fecal $\delta^{15}N$ values, but the former cannot reliably predict the latter ($r^2 = 0.08$). Weight % C:N values ($n = 100$, m = 10.1) ranged between 4.0 and 28.6.

There is no correlation between fecal $\delta^{13}C$ values and distance to forest ($n = 100$, $r_s = 0.16$, $p = 0.11$; Figures 2 and 3). The presence of animal remains and abundant plant remains best explains variability in fecal $\delta^{13}C$ values (Model 1, AIC = 451.6; Table 1 and Method S1), yet the magnitude of the effect of these factors on fecal $\delta^{13}C$ values is consistently small (<1‰). When controlling for the abundance of plant remains, Model 1 suggests that the $\delta^{13}C$ values of feces containing animal remains ($n = 48$) are insignificantly lower than those of feces that do not contain animal remains ($n = 52$, $p = 0.06$). The presence of abundant plant remains has the opposite association, with significantly higher $\delta^{13}C$ values in feces containing abundant plant remains ($n = 21$) than in feces not containing abundant plant remains ($n = 79$, $p = 0.04$). Generally, $\delta^{13}C$ data from feces with abundant plant material have a larger midspread (interval including 50% of the data) than those from feces without abundant plant material (6‰ [−27.5 to −21.5‰] as opposed to 1‰ [−27.3 to −26.3‰], respectively).

Both the presence of animal remains and distance from forest edge best explain variability in fecal $\delta^{15}N$ values (Model 2, AIC = 406.9), yet the magnitude of the effect of these variables on fecal $\delta^{15}N$ values is again consistently small (< 1‰). Model 2 suggests that, among fecal samples with animal remains present ($n = 48$), those collected relatively far from forest edges have insignificantly higher $\delta^{15}N$ values ($p = 0.07$). Though the magnitude of the gradient is small, feces collected further from the forest edge are generally relatively enriched in ^{15}N (Figures 2 and 3; $n = 100$, $r_s = 0.28$, $p = 0.006$).

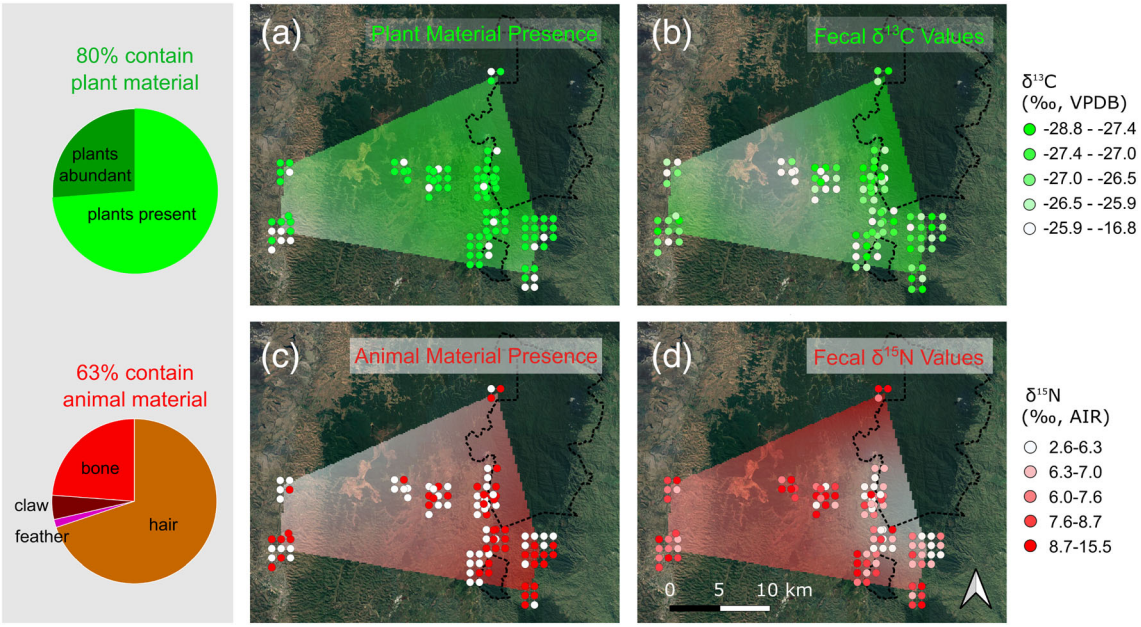
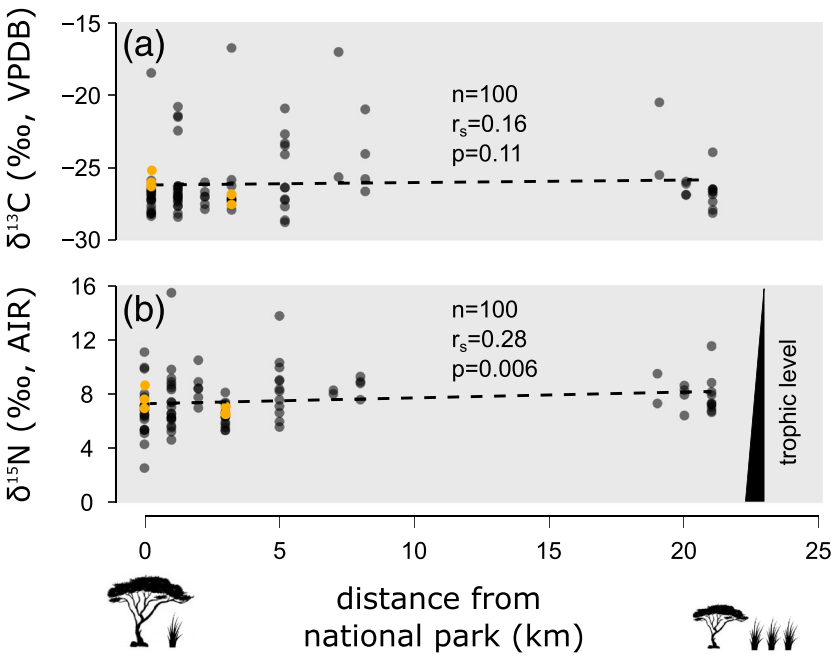


FIGURE 2 Map insets around study area showing the presence of different materials visible in dog feces (colored points in (a) and (c)) and $\delta^{13}C$ and $\delta^{15}N$ values from bulk feces (color in (b) and (d) graduated according to categories with equal sample size). Stable isotope data are given relative to internationally accepted standards. Spatial tendencies in each small multiple are illustrated through colored surfaces in each case (generated using a Bayesian approach in the IsoMemo application AverageR). Because feces come from sampled clusters, the points are displaced to form gridded clusters. The inset maps are placed over a Google Satellite base map, and notes on material present in the fecal samples are provided in pie charts to the left.

FIGURE 3 Dog fecal $\delta^{13}C$ data (a) and $\delta^{15}N$ data (b) according to distance to the forests of Analamazoatra and Andasibe-Mantadia National Parks, with samples collected >1 km from settlements marked in yellow.



The presence of animal remains, trash, and abundant plants and interactions between the presence of trash and abundant plants best explains variability in fecal C:N values (Model 3, AIC = 595.8; Table 1). Model 3 suggests that the C:N values of feces containing trash ($n = 9$) tends to be significantly greater than those without trash ($n = 91$, $p = 0.01$).

3.2 | Comparisons with plants and animals

The distribution of dog fecal $\delta^{13}C$ values overlaps primarily with the distribution of $\delta^{13}C$ values of C_3 plants (Method S1 and Dataset S2). The assumption of herbivory among dogs gives a maximum estimate of C_4 food web reliance by dogs (Figure 4a), yet the estimated median

TABLE 1 Description of linear models discussed in the text

Model terms[a]	δ^{13}C Model 1 AIC = 451.6	δ^{15}N Model 2 AIC = 406.9	C:N Model 3 AIC = 595.8
Distance	0.56	0.81	0.60
Abundant Plants	0.89	0.46	0.75
Animals	0.80	0.66	0.84
Trash	0.52	0.59	0.93
Animals × Distance	0.12	0.38	0.18
Trash × Abundant Plants	0.11	0.10	0.54

Notes: See Table S1 for model outputs. Each model includes the terms highlighted in grey. Within each dataset, glmulti considers all possible models and ranks them according to an information criterion (AIC in our case). The model-averaged importance of each term within each model reflects the support of the variable across all possible versions of the model. These values are given in corresponding cells.

[a]"Distance" = distance between sample collection point and a protected area, "Abundant Plants" = presence of abundant plants in feces, "Animals" = presence of animal prey in feces, "Trash" = presence of trash in feces.

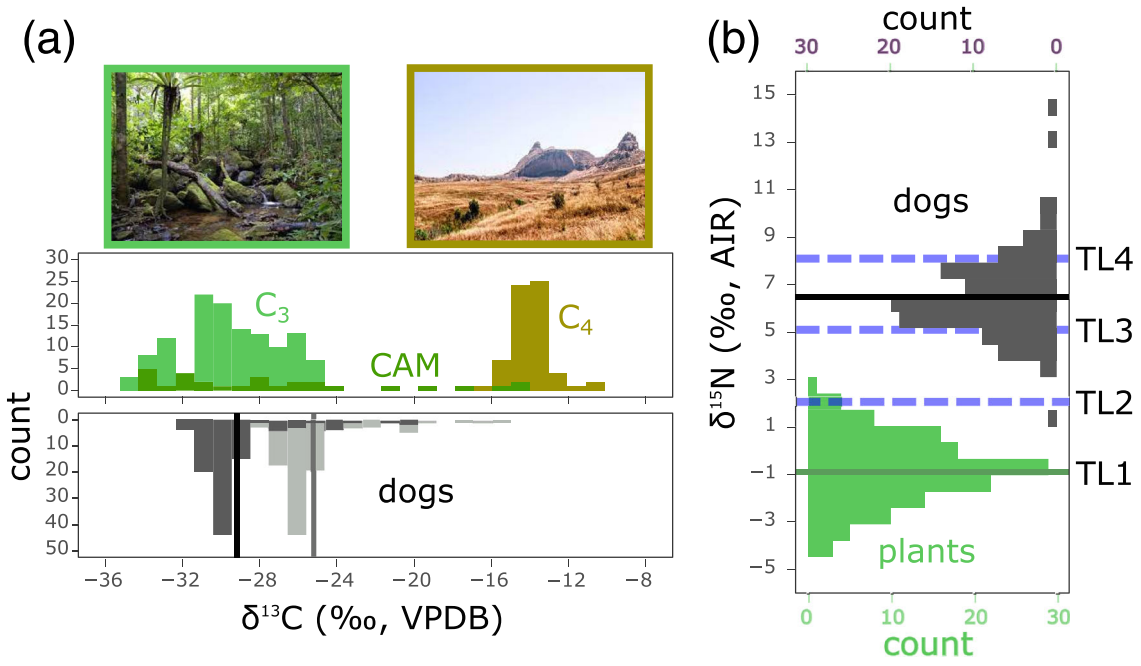


FIGURE 4 (a) Histograms showing C_3, CAM, and C_4 plant δ^{13}C data relative to dog fecal δ^{13}C data corrected to be comparable with plant isotope data assuming that dogs are primarily herbivorous (light gray) and carnivorous (dark gray). Means of δ^{13}C values are marked with bold vertical lines. (b) Histograms showing C_3 plant δ^{15}N data (collected near the study site) relative to dog fecal δ^{15}N data corrected to estimate the δ^{15}N values of the corresponding diet. Means are marked with bold horizontal lines, and dashed blue lines approximate trophic level (TL) estimates on the δ^{15}N scale.

δ^{13}C value of dog bulk diet in this case ($n = 100$, m = −26.0‰) falls below the Suess-corrected C_4 plant δ^{13}C value ($n = 61$, m = −14.0‰) by more than 10‰. The assumption that dogs are secondary consumers makes the estimated median δ^{13}C value of their diet (m = −30.0‰) almost indistinguishable from the median Suess-corrected C_3 plant δ^{13}C value (m = −30.5‰). Approximately 7‰ separates the median estimated dog diet δ^{15}N value ($n = 100$, m = 6.3‰) from the median C_3 plant δ^{15}N value ($n = 135$, m = −0.8‰).

Roughly approximated bulk diet stable isotope values (as inferred from available data from feces, hair, and bone) suggest that modern dog diet around Andasibe is depleted in ^{13}C by ~10‰ relative to ancient dog diet in southwest Madagascar and is also depleted in ^{13}C relative to the ancient diets of fosa and cattle in the southwest (Figure 5, Method S1, and Datasets S3 and S4). Estimated dog diet δ^{13}C values are also lower than those of introduced mice (*Mus musculus*) in the eastern study region. However, the dietary δ^{13}C values estimated from the dog fecal δ^{13}C values are comparable with those of a variety of forest-dwelling taxa in the region, including endemic rodents, tenrecs, and lemurs. The central tendency of the estimated isotopic composition of dog diet is comparable to that of both introduced black rats (*R. rattus*) and the insectivorous shrew tenrec (*Microgale pusilla*).

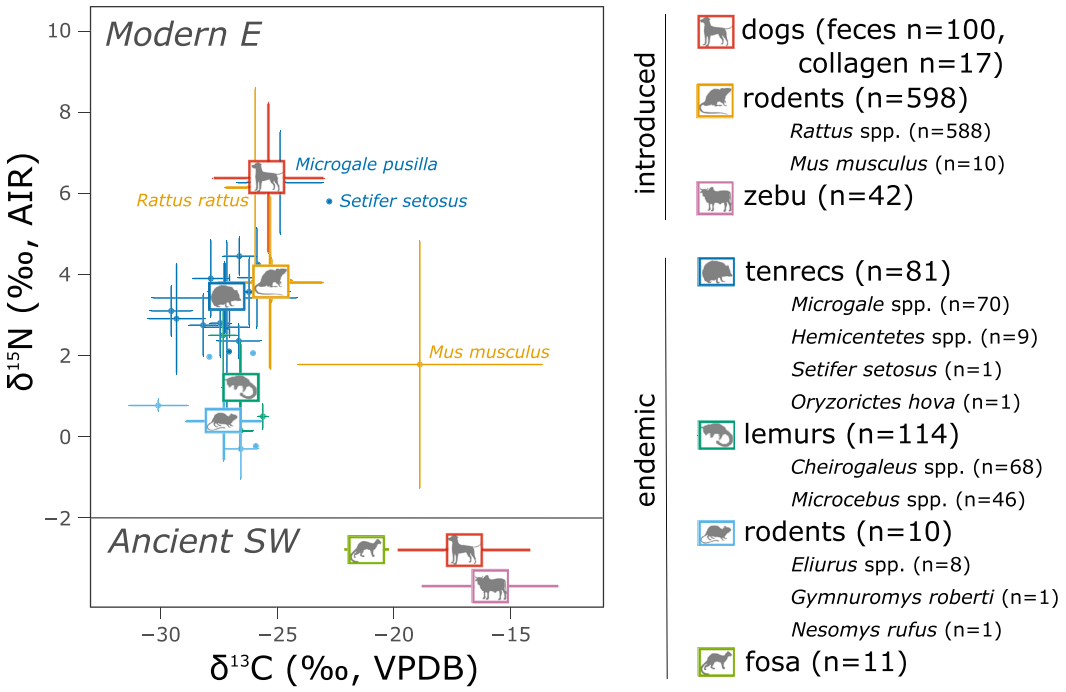


FIGURE 5 Stable isotope data from dogs and other introduced taxa (warm colors) and endemic taxa that are potential prey or competitors (cool colors). Analyzed tissues include feces (dogs in present study), fur (all other taxa in top frame, modern and from eastern Madagascar: "Modern E"), and subfossil bone collagen (ancient specimens in bottom frame all from SW Madagascar: "Ancient SW"), and all data are corrected to approximate the isotopic composition of diet (Dataset S4). For groups that include multiple species (e.g., tenrecs in dark blue), the animal icon and lines mark the weighted mean and standard deviation for the group. Each species has its own mean and standard deviation given as relatively faint points and lines (when $n > 1$). Note that both $\delta^{13}C$ and $\delta^{15}N$ data from modern specimens within 150 km of the eastern study area (top frame) are shown against only the $\delta^{13}C$ data from ancient specimens from the southwest (spanning the past ~3000 years).

4 | DISCUSSION

Fecal data suggest that dogs in the study region are omnivores that primarily rely on C_3-based food webs, with a relatively small reliance on C_4 grasslands. The fecal $\delta^{13}C$ data are inconsistent with the expectation that dogs closer to the forest have feces relatively depleted in ^{13}C. However, the observed range of fecal $\delta^{15}N$ values are consistent with the expectation of omnivory. The correspondence between fecal remains and stable isotope data is generally weak and highlights the strengths and limitations of each approach to dietary inference.

4.1 | Dietary inference

The distribution of dog fecal $\delta^{13}C$ values suggests that very few dogs relied on meals from C_4 grasslands. Given the wide distribution of CAM epiphytes, it is unlikely that they significantly ^{13}C enriched or depleted the diet of omnivores in the study area. If anything, the consumption and defecation of relatively indigestible tissue (presumably dominated by C_4 grasses) does seem to enrich dog feces in ^{13}C, but the magnitude of this effect is minor (Model 1). The reliance of modern dogs on C_3-based food webs contrasts with existing data from ancient bone, which suggest that both ancient dogs and zebu cattle in southwest Madagascar relied to a greater extent on food webs based on C_4 grasslands and CAM succulents. This contrast likely follows from differences in vegetation composition (with xerophytic plants more abundant in the southwest) and attests to dietary flexibility in dogs.

The variability of dog fecal $\delta^{13}C$ values is poorly explained by distance to forest, and dogs with relatively high fecal $\delta^{13}C$ values occur on forest margins. There are multiple plausible explanations for the absence of a correlation between fecal $\delta^{13}C$ values and distance to forest. Dog meals in the derived grassland that covers most of the study region may come from food webs based on C_3 shrubs, and reliance on food webs involving C_3 grasses may similarly deplete dog feces in ^{13}C. Also, dogs can traverse the study region in a day and can live in villages on the margin of protected areas. Consequently, movement could easily explain why feces relatively depleted in ^{13}C could be widespread in a C_4 grassland and conversely why some feces enriched in ^{13}C are present on the margin of C_3 forests. Additional behavioral studies and proxies of mobility (e.g., radio collar or Sr isotope work) could help resolve this possibility.

The distribution of dog fecal $\delta^{15}N$ values is consistent with meals at multiple trophic levels (Figure 4b). The widespread plant remains in dog feces may be somewhat unexpected, yet this is consistent with modern observations of dog diet (Sueda et al., 2008) and genetic evidence that domestic dogs have experienced selection for starch digestion (Axelsson et al., 2013). Animal remains present in feces

(particularly bones and claws) indicate some level of carnivory and further suggest that at least some dog meals included rodents, tenrecs, or reptiles. Despite the significant tendency for dogs further from the forest edge to have feces enriched in ^{15}N (Model 2; Figure 3), there is little evidence to support the idea that dog meals further from the forest included more animal tissue. This is because (1) the magnitude of the fecal $\delta^{15}N$ gradient (Figure 3b) is small relative to the overall range of fecal $\delta^{15}N$ values and (2) animal remains, if anything, were more widespread in feces collected close to the forest edge (Figure 2c). The depletion of feces in ^{15}N closer to the forest could easily be the product of most dog diets close to the forest edge coming from relatively mesic habitat with lower $\delta^{15}N$ baseline. This issue of baseline may also help explain why dog feces enriched in ^{13}C (indicating greater reliance on dry-adapted C_4 plants) tend to be enriched in ^{15}N.

Existing data suggest that dogs and introduced rats have meals that are isotopically similar. However, the taxonomic resolution of the dietary inference possible through fecal $\delta^{13}C$ and $\delta^{15}N$ values is limited by both the variable composition of feces, limited separation among potential prey taxa, and missing data from taxa that may contribute significantly to dog diet (e.g., chickens and reptiles; Kshirsagar et al., 2020). This is particularly true for the broad ranges of rat hair stable isotope values, which will complicate any attempt to estimate the proportion of rats in predator diet based solely on bulk tissue $\delta^{13}C$ and $\delta^{15}N$ values. Though introduced rats and dogs have diets that are isotopically similar, dog fecal stable isotope signatures could easily follow from combinations of tissue from introduced mice and rats. Alternatively, existing data suggest that the majority of dog meals could have also included tenrec tissue. The scarce identifiable animal remains present in feces make it difficult to distinguish among these possibilities, but complementary prior information regarding diet (e.g., through behavioral or molecular studies and stable isotope values from multiple consumer tissues) could improve the resolution of dietary inference. The details of dog diet are an important area of future research given that they determine whether the impacts of dogs on particular endemic taxa are positive or negative.

4.2 | Implications

The introduction of dogs on Madagascar was associated with the spread of grasslands and introduced grazers like zebu cattle ~1000 years ago. However, many dogs that currently live in derived grassland close to modern forests have little reliance on foods derived from C_4 grasses. This increases the potential for negative interactions between dogs and endemic prey and potential competitors. Dogs could easily contribute to habitat fragmentation by harassing endemic prey and aiding human-led hunts (Brockman et al., 2008; Garcia & Goodman, 2003; Kshirsagar et al., 2020), but the extent to which dogs themselves kill animals versus scavenge animal remains is poorly known. Higher resolution study of dog diet can further help clarify the extent to which dogs control populations of other introduced taxa that also rely on the island's forests (e.g., rats).

As with past research involving rats in the study area, we observe a mismatch between the fecal $\delta^{13}C$ data and the sites where feces were collected. Specifically, Dammhahn et al. (2017) previously used soil and plant samples in the study region to note that food webs in open habitat (anthropogenic steppe and agricultural fields) tend to be enriched in ^{13}C relative to those in closed forests. However, we note that dog fecal $\delta^{13}C$ values are independent of the distance that separates the feces from the nearest protected primary forest. Thus, as with rats, we suggest that the evident mobility of dogs between open and closed habitats increases their potential to share zoonotic diseases and parasites with endemic taxa. In SW Madagascar, dogs and other introduced animals are known to harbor ectoparasites with bacterial pathogens such as *Rickettsia* spp. (Ehlers et al., 2020). Future pathogen and stable isotope analyses may clarify whether isotopic traces of mobility among introduced animal populations are positively associated with disease transmission. Greater detail in our understanding of dog feeding ecology will help wildlife management teams assess when, where, and how it is best to control dog populations in and around forests for the conservation of endemic biodiversity.

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CONFLICT OF INTEREST

We declare we have no conflicts of interest.

AUTHOR CONTRIBUTIONS

S.W.H., K.V., J.K., and Z.F. planned and designed the research. K.V., M.N., S.C., D.M., and C.F. conducted fieldwork, and S.W.H., K.V., and S.F. conducted labwork. S.W.H. and K.V. wrote the manuscript, and all coauthors commented on the manuscript.

DATA AVAILABILITY STATEMENT

All data are provided in Datasets S1–S4, and all details regarding data collection and analysis are provided in the manuscript and Method S1.

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