



Ecological Consequences of a Millennium of Introduced Dogs on Madagascar

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Introduced predators currently threaten endemic animals on Madagascar through predation, facilitation of human-led hunts, competition, and disease transmission, but the antiquity and past consequences of these introductions are poorly known. We use directly radiocarbon dated bones of introduced dogs (*Canis familiaris*) to test whether dogs could have aided human-led hunts of the island's extinct megafauna. We compare carbon and nitrogen isotope data from the bone collagen of dogs and endemic "fosa" (*Cryptoprocta* spp.) in central and southwestern Madagascar to test for competition between introduced and endemic predators. The distinct isotopic niches of dogs and fosa suggest that any past antagonistic relationship between these predators did not follow from predation or competition for shared prey. Radiocarbon dates confirm that dogs have been present on Madagascar for over a millennium and suggest that they at least briefly co-occurred with the island's extinct megafauna, which included giant lemurs, elephant birds, and pygmy hippopotamuses. Today, dogs share a mutualism with pastoralists who also occasionally hunt endemic vertebrates, and similar behavior is reflected in deposits at several Malagasy paleontological sites that contain dog and livestock bones along with butchered bones of extinct megafauna and extant lemurs. Dogs on Madagascar have had a wide range of diets during the past millennium, but relatively high stable carbon isotope values suggest few individuals relied primarily on forest bushmeat. Our newly generated data suggest that dogs were part of a suite of animal introductions beginning over a millennium ago that coincided with widespread landscape transformation and megafaunal extinction.

Keywords: radiocarbon dating, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, exclusion competition, predation, fosa, extinction, bushmeat

INTRODUCTION

Madagascar is a biodiversity hotspot that has repeatedly faced a variety of biological invasions over the past millennium (Middleton, 1999; Kolby, 2014; Hixon et al., submitted). A debate regarding when humans first arrived on Madagascar is ongoing, with some researchers favoring early human arrival 10,000–4,000 years ago based on rare stone tools and cutmarks on ancient elephant bird bone (Dewar et al., 2013; Hansford et al., 2018), and other researchers favoring recent arrival 1,600–1,000 years ago based on broader cultural considerations (Anderson et al., 2018). Endemic vertebrates >10 kg declined by ~950 years ago (Crowley, 2010), and over half of the island's surface is currently dedicated to pastoralism that involves introduced zebu cattle (Anonymous, 2003). Hunting, deforestation, and regional aridification help explain aspects of past extinctions (Burney et al., 2004; Virah-Sawmy et al., 2010; Crowley et al., 2017; Anderson et al., 2018; Hixon et al., 2018; Godfrey et al., 2019; Faina et al., 2021; Godfrey and Douglass, 2021), and interactions with introduced species (e.g., livestock, rodents, and predators) could have exacerbated these stressors (Dewar, 1997; Hixon et al., submitted). Globally, changes in human land use (i.e., the spread of pastoralism and commensal species) generally coincide with past environmental transformations (Stephens et al., 2019) that contribute to biotic homogenization (McKinney, 1997; McKinney and Lockwood, 1999). As part of this transformation, introduced predators can disrupt island ecosystems by facilitating human hunting, creating novel predation pressure, and competing with other predators (e.g., competition between dingoes and red foxes in Australia; Cupples et al., 2011), yet we know very little about the antiquity of introduced predators on Madagascar.

We use radiocarbon (^{14}C) and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) data from bone collagen to test the following hypotheses: (1) introduced dogs (*Canis familiaris*) preyed on lemurs, and (2) dogs competed with the island's largest endemic carnivores (*Cryptoprocta* spp., the fosa). Limited chronological overlap (as inferred from directly ^{14}C -dated dog and lemur bones) would reduce the potential for dogs to have aided hunting of extinct lemurs, and lack of isotopic niche overlap among dogs and *Cryptoprocta* spp. would diminish the potential for direct forms of competition. However, lack of dietary overlap would not necessarily exclude the possibility that dogs interacted aggressively with *Cryptoprocta* spp. or facilitated human-led hunts of prey that *Cryptoprocta* spp. also hunted. This work expands our understanding of both past megafaunal extinction and modern functional diversity of predators on Madagascar.

Madagascar's endemic family of carnivorans (Eupleridae) includes ten extant species that range in size from the ~550 g broad-striped vontsira (*Galidictis fasciata*) to the ~8.5 kg fosa (*Cryptoprocta ferox*, Wampole et al., 2021). The so-called “cave” fosa (*Cryptoprocta spelea*, thought to be extinct) was likely double the size of *C. ferox* (Goodman et al., 2004) and may still exist in remote parts of northern Madagascar (Nomenjanahary et al., 2021). All members of Eupleridae are currently threatened, and the IUCN red list currently includes *C. ferox* as vulnerable due to rapid population decline (Hawkins and Racey, 2008).

Introduced mammalian predators include dogs, cats (*Felis* spp.), and the small Indian civet (*Viverricula indica*, **Figure 1**), yet only relatively large predators (dogs and *Cryptoprocta* spp.) are reasonably well represented in Madagascar's subfossil record (Rakotozafy and Goodman, 2005; Crowley, 2010). It is not known when dogs first colonized the island (**Figure 2**, Crowley, 2010; Douglass et al., 2019), and traces of predation by dogs on subfossil bones (e.g., gnaw marks) are understudied and possibly cryptic (Brockman et al., 2008). A rare set of cave rock drawings in western Madagascar may depict a hunting scene that includes dogs, an extinct sloth lemur, and symbols that have parallels from around the Indian Ocean, but the age of these drawings is uncertain (Burney et al., 2020). Madagascar's modern dogs have primarily African ancestry (Ardalan et al., 2015), which is consistent with the Bantu origin of the most common Malagasy word for dog (amboa, Blench, 2008).

Dog diet on Madagascar is poorly characterized. Modern and historic surveys suggest dogs rely heavily on plant and animal scraps in human derived food waste (Decary, 1939; Kshirsagar et al., 2020). Yet dogs are also known to stalk lemurs (Brockman et al., 2008) and help humans hunt a variety of bushmeat (**Supplementary Dataset 2**, Decary, 1939; Garcia and Goodman, 2003; Gardner and Davies, 2014). Dogs in at least SW and NW Madagascar currently subsist largely on food scraps, and people often feed hunting dogs the innards of bushmeat (Godfrey et al., submitted, Thompson and Borgerson, pers. comm.). Dogs are popular protection animals around Ranomafana National Park, in central Madagascar (Kshirsagar et al., 2020). However, dogs can also transmit rabies and form a general nuisance while they scavenge (Rajeev et al., 2019). Some dog owners have reported that their dogs harass and kill *C. ferox* around Ranomafana (Valenta et al., 2016; Kshirsagar et al., 2020). Data from live traps and camera traps suggest that *C. ferox* avoids dogs in several national parks (**Figure 1**), which may follow from a combination of aggressive interactions and disease transmission (Dollar et al., 2007; Barcala, 2009; Gerber et al., 2012; Farris et al., 2015; Pomerantz et al., 2016; Rasambainarivo et al., 2017; Merson et al., 2019a). For example, *C. ferox* is typically cathemeral, yet individuals around Ankarafantsika in the NW and Masoala–Makira in the east tend to be primarily nocturnal, where dogs are active during the dawn and day (Farris et al., 2015; Merson et al., 2019a). Additionally, *C. ferox* captures increased following the euthanasia of dogs at Ankarafantsika (Barcala, 2009), which suggests that interactions involving dogs affect both *C. ferox* abundance and activity patterns.

Madagascar's modern dogs have at least some dietary overlap with *C. ferox* that creates potential for exploitation competition (Farris et al., 2017; Merson et al., 2019a). Data from modern kill sites and *C. ferox* scat from multiple ecoregions in Madagascar indicate that they are opportunistic predators with the potential for heavy reliance on lemurs (**Supplementary Dataset 3**, Rasoloarison et al., 1995; Wright et al., 1997; Goodman et al., 1997; Dollar et al., 2007; Hawkins and Racey, 2008). Modern *C. ferox* and dogs are both known to consume sifakas (e.g., *Propithecus verreauxi*), tenrecs, rodents, birds (e.g., chicken and coua), frogs, snakes, and scraps of bushpigs and

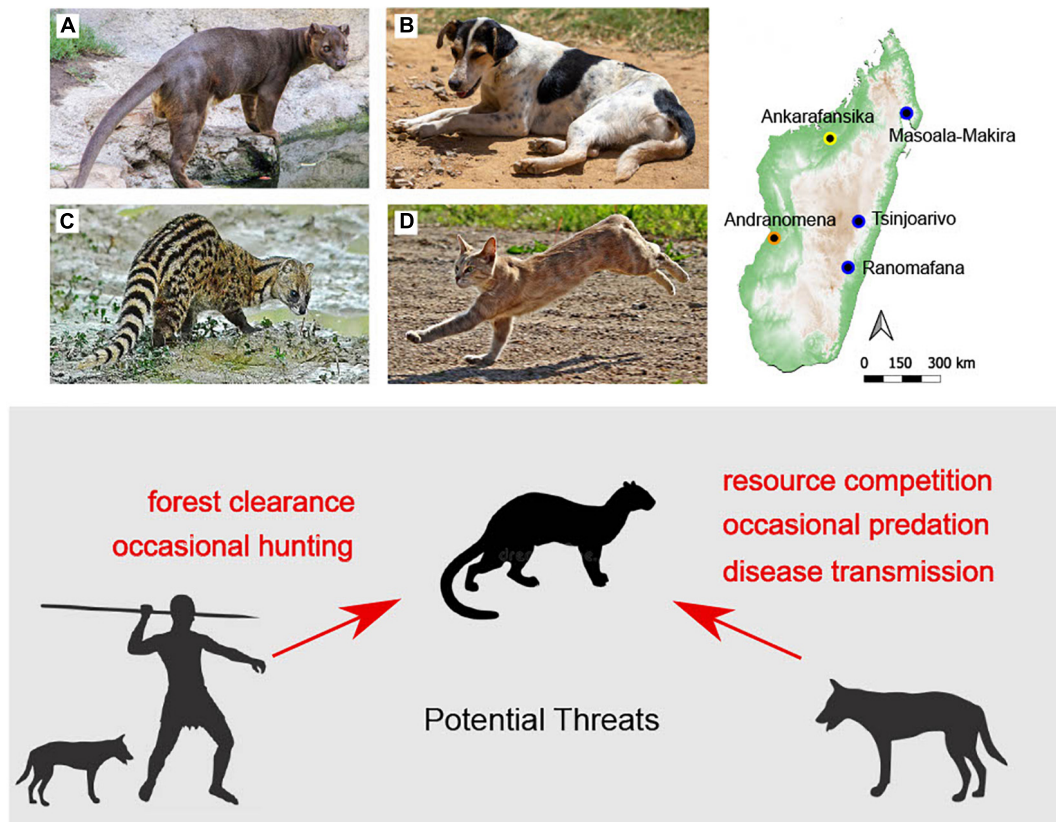


FIGURE 1 | Endemic fosa (A, *Cryptoprocta ferox*) may interact with introduced dogs (B, *Canis familiaris*), Indian civets (C, *Viverricula indica*), and cats (D, *Felis* sp.). National parks discussed in the text where antagonistic interactions between introduced and endemic predators have been observed are shown in the map at right. The ecoregion for each park is denoted using colors (orange = succulent woodland, yellow = dry deciduous forest, blue = central highlands and humid forest). Human and introduced predator threats to *C. ferox* are summarized in shaded area below.

zebu cattle (Figure 2, Decary, 1939; Rasoloarison et al., 1995; Goodman et al., 1997; Brockman et al., 2008; Hawkins and Racey, 2008; Gardner and Davies, 2014; Valenta et al., 2016). There is no published evidence for omnivory by *C. ferox* beyond possible occasional fruit consumption as a source of water during the dry season (Hawkins and Racey, 2008). Dogs raid bird and reptile nests and can engage in devastating amounts of surplus killing. Though they are typically more inefficient hunters than wild canids (Butler et al., 2004; Serpell and Barrett, 2017), their impacts can still be considerable. For example, a single stray dog killed hundreds of North Island brown kiwis (*Apteryx mantelli*, >50% of the local population) in New Zealand within a couple of months (Taborsky, 1988). The dramatic impact that dogs can have on their prey may diminish prey for *C. ferox*.

Exclusion competition between dogs and *C. ferox* follows from the potential for aggressive encounters and occurs regardless of impacts on prey populations. Dogs are avid chasers that contribute to habitat fragmentation by inducing fear and avoidance in a wide range of animals (Lenth et al., 2008; Young et al., 2011; Ritchie et al., 2014). Dogs associated with human hunters increase the potential for exclusion competition with native predators throughout Madagascar. Some evidence of the past association of dogs with human hunters (Burney et al., 2020)

suggests that there may be a history of exclusion competition between dogs and *Cryptoprocta* spp.

Radiocarbon and stable isotope data from bone collagen can give a long-term perspective on predator interactions and clarify past and ongoing processes that influence endemic biodiversity. Based on the potential association of dog bones with extinct megafauna from paleontological sites (Douglass et al., 2019), we expect some chronological overlap among these animals. We also expect some overlap in dog and *Cryptoprocta* spp. isotope values. Animals with similar diets that forage in similar habitats have tissues with similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (reviewed in Crawford et al., 2008). Carbon isotope values predominantly reflect the plants at the base of the food web (Farquhar et al., 1989; Marshall et al., 2007). Plants that use the C_3 photosynthetic pathway (primarily trees, shrubs, and herbs) tend to be depleted in ^{13}C by over 10‰ relative to plants that use the C_4 pathway (primarily grasses) or the CAM pathway (primarily succulents). Data from sympatric C_3 , C_4 , and CAM plants from SW Madagascar reflect this difference, with combined CAM and C_4 plant tissue ($\delta^{13}\text{C}$ $\mu \pm \sigma = -12.8 \pm 1.6\text{‰}$) enriched in ^{13}C by $\sim 15\text{‰}$ relative to C_3 plant tissue ($\mu \pm \sigma = -27.2 \pm 2.3\text{‰}$, Hixon et al., submitted). To a lesser extent, plant $\delta^{13}\text{C}$ values also depend on variables such as canopy cover, moisture availability, salinity, and soil microbe

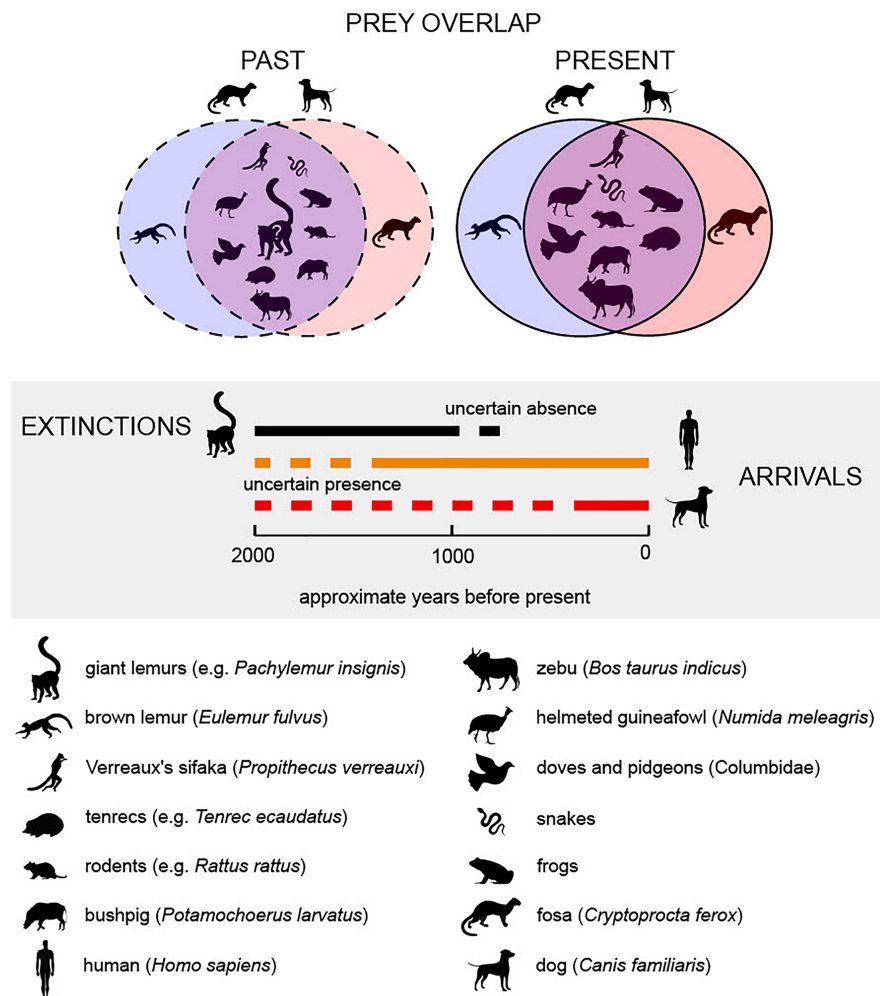


FIGURE 2 | Overlaps in dog and *C. ferox* diet (top) and chronology of extinctions and arrivals as understood before the present study (center, shaded, with uncertain occurrence prior to this publication marked with dashed lines). The spread of dogs (red bar) to Madagascar before European contact (~500 BP) has been poorly documented, and it is unknown whether they overlapped chronologically with extinct megafauna such as giant lemurs (black bar). Dogs and *C. ferox* currently scavenge and prey on many of the same animals (see in exhaustive list at bottom), but the antiquity of this dietary overlap is unknown (dashed lines). Before the present study, it was unknown whether past dogs preyed on extinct giant lemurs, yet there are abundant traces of human and mammalian carnivorous predation on extinct giant lemurs. Note that examples of exclusively dog or *C. ferox* prey are token and do not represent the diversity of predator-specific diets (see **Supplementary Datasets 2, 3**).

respiration (reviewed in Farquhar et al., 1989). These patterns are passed on to herbivores and higher order consumers over time. If both dogs and *Cryptoprocta* spp. consumed forest-dwelling herbivores (such as most of the island's extinct megaherbivores), then we would expect overlap in collagen $\delta^{13}\text{C}$ values among these groups (Godfrey and Crowley, 2016). Alternatively, if dogs regularly consumed scraps of introduced grazers (e.g., zebu cattle and ovicaprids), then we would expect dogs to have relatively high collagen $\delta^{13}\text{C}$ values and minimal overlap with *Cryptoprocta* spp.

We also expect overlap in collagen $\delta^{15}\text{N}$ values among co-occurring dogs and *Cryptoprocta* spp. Consumer tissues tend to be enriched in ^{15}N relative to diet such that each increase in trophic level corresponds to a 3–5‰ increase in collagen $\delta^{15}\text{N}$ values (Cleland, 2001; McCutchan et al., 2003;

Hyodo et al., 2010). As secondary consumers, dogs and *Cryptoprocta* spp. should have comparable $\delta^{15}\text{N}$ values, though omnivory or the preferential consumption of certain prey tissue (e.g., intestines) may reduce dog $\delta^{15}\text{N}$ values relative to *Cryptoprocta* spp. $\delta^{15}\text{N}$ values (Reid and Koch, 2017). Soil nitrogen cycling also strongly influences ecosystem $\delta^{15}\text{N}$ values and is sensitive to moisture availability (Austin and Vitousek, 1998), so both plant and consumer $\delta^{15}\text{N}$ values vary considerably among ecoregions in Madagascar (Crowley et al., 2011). Specifically, values are highest in the xerophytic spiny thicket in SW Madagascar and lowest in the humid forests in the east and north. There can also be pronounced differences among microhabitats in the same region (Crowley et al., 2012, 2014; Heck et al., 2016). Plants and animals living on saline coastal soils that are influenced by marine-derived nitrates may

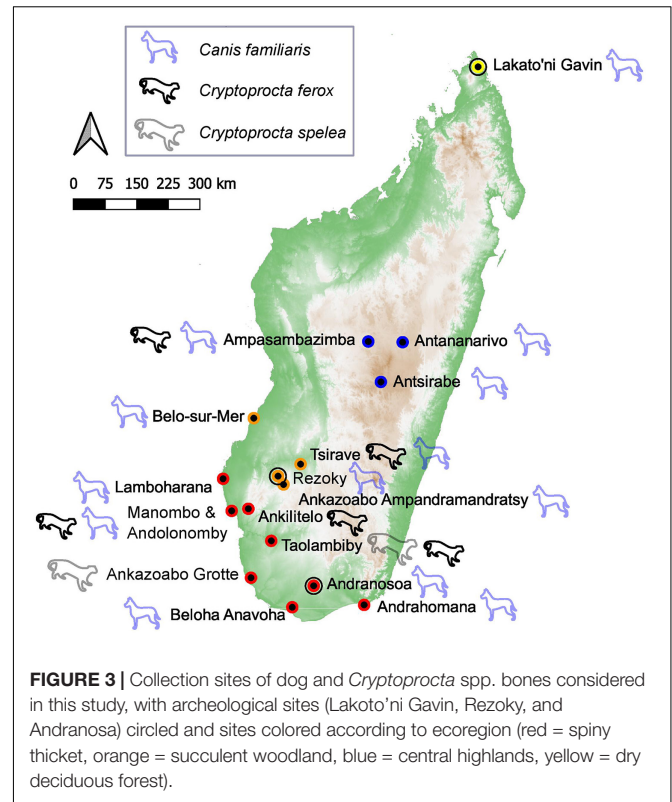
also have higher $\delta^{15}\text{N}$ values than those that live inland (Heaton, 1987; Sparks and Crowley, 2018; Mosher et al., 2020; Hixon et al., submitted). Thus, only in comparable environments can consumer $\delta^{15}\text{N}$ values be interpreted primarily in terms of diet.

MATERIALS AND METHODS

Specimen and Site Selection

Sampled dog bones come from 13 sites spread throughout Madagascar (Figure 3 and Supplementary Datasets 1, 4). We sampled all available bones from existing collections ($n = 16$ subfossils + 3 modern dog bones). Most specimens ($n = 12$) are housed at the University of Antananarivo; others are curated at the National Museum of Natural History, Paris as well as Yale University, the University of Massachusetts, Amherst, and the University of California at Santa Barbara (Supplementary Dataset 1). These bones were collected from both archeological sites (Rezoky, Andranosoa, and Lakoto'ni Gavin) and paleontological sites (e.g., Andolononby and Tsirave) that span four of Madagascar's five major ecoregions but are concentrated in the spiny thicket and succulent woodland of the southwest (Figure 3). We also analyzed two subfossil *C. ferox* bones from Taolambiby that are currently housed at the Australian National University (ANU). To augment these datasets, we compiled previously published data from five dogs (includes two modern bones, Crowley, 2010; Douglass et al., 2019), nine subfossil *C. ferox* (Crowley, 2010; Crowley and Godfrey, 2013; Crowley et al., 2017; Anderson et al., 2018), and three subfossil *C. spelea* (Crowley, 2010). Note that all subfossil *Cryptoprocta* spp. come from paleontological sites and that all but one of the previously published predators (a subfossil *C. ferox*, OxA 27174) have both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data.

To compare an estimated time of dog introduction with hunting and extinction chronologies (see section "Data Analysis" below), we also compiled previously published ^{14}C data from butchered bone of multiple endemic taxa from SW Madagascar (extinct giant lemurs, an extant lemur consumed by *C. ferox* (*P. verreauxi*), elephant birds, and pygmy hippo, (Supplementary Dataset 1) and three species of giant lemurs with relatively large sample sizes ($n \geq 20$ each, *Pachylemur insignis*, *Archaeolemur majori*, and *Palaeopropithecus ingens*, all from SW Madagascar, Supplementary Dataset 1). We focus on the arid SW, because each ecoregion has its own chronology of species introductions and extinctions, and most existing ^{14}C datasets come from this ecoregion (Crowley, 2010; Douglass et al., 2019). We focus on comparing dog and *Cryptoprocta* spp. data with those from extinct giant lemurs, because (1) there is widespread evidence that at least *Cryptoprocta* spp. and humans preyed on these animals (Meador et al., 2019; Godfrey et al., submitted), and (2) these taxa have robust ^{14}C chronologies that suggest they disappeared at approximately the same time as other megafauna such as pygmy hippos and giant tortoises (Crowley, 2010; Hixon et al., submitted). To help infer past dog and *C. ferox* diet, we compiled published lists of prey species from across the island (Supplementary Datasets 2, 3). We make stable isotope comparisons involving prey taxa within the arid SW



(Supplementary Dataset 1), and we also focus on subfossil bone, because few of our sampled specimens are modern, and some extant and introduced taxa likely shifted their diet and habitat use in response to the recent expansion of grasslands on the island (Crowley and Samonds, 2013). The previously published literature includes 298 potential prey individuals with stable isotope data from the SW, and we include unpublished records from 11 individuals in our dataset (analyzed previously by B.E.C. using approach from Sparks and Crowley, 2018). We further expanded this dataset by sampling bones from an additional 13 potential prey individuals from Taolambiby and Lamboharana/Lamboara in SW Madagascar, which brings the potential prey total to 311 individuals. During analyses, we excluded 21 previously published data from specimens that (1) lack explicit reference to bone collagen purification protocols or (2) include signs of contamination (i.e., atomic C:N > 3.5, Brock et al., 2010).

^{14}C and Stable Isotope Analyses

Pretreatment of the 31 subfossil and three modern specimens took place in the Human Paleoecology and Isotope Geochemistry Laboratory at Pennsylvania State University (PSU). Prior to demineralization, bones sampled from museum collections suspected of using ink labels and conservants/consolidants such as polyvinyl acetate must go through solvent rinses to remove exogenous carbon with distinct ^{14}C content and $\delta^{13}\text{C}$ values (France et al., 2011). We sonicated museum specimens in sequential washes of methanol (MeOH), acetone, dichloromethane (DCM), and nanopure water. Samples were

sonicated in 20 mL of each fluid for 20 min. For the three modern bone samples, we removed lipids using 3× sonication in 2:1 DCM:MeOH followed by 3× rinsing in nanopure water (modified from Guiry et al., 2016).

All bones were mechanically cleaned, demineralized in 0.5 N hydrochloric acid (HCl) under refrigeration, and gelatinized in 0.01 N HCl at 60°C. Collagen from the bone of subfossil individuals was purified through ultrafiltration (14 samples, Beaumont et al., 2010; Fernandes et al., 2021) or purification with XAD resin (17 samples, **Supplementary Dataset 1**, Stafford et al., 1988, 1991; Lohse et al., 2014). When collagen is relatively intact and yields are high, ultrafiltration can purify a sample by mechanically removing the smaller (<30 kDa) fraction, which includes degraded collagen and exogenous contaminants (Higham et al., 2006). When collagen is stained or degraded, the relatively less polar contaminants (humates, in particular) can be separated chromatographically by passing the hydrolyzed sample through a column filled with XAD resin (Stafford et al., 1988).

Stable isotope data were obtained at Yale University's W.M. Keck Biotechnology Resource Laboratory, the University of Cincinnati's Stable Isotope Laboratory, and the University of New Mexico's Center for Stable Isotopes (**Supplementary Dataset 1**). Secondary standards from each lab were used to correct data using two-point normalization, and the mean accuracy of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements across runs was $\leq 0.3\text{‰}$. Standard quality assurance data indicate that the mean precision of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements across runs was ≤ 0.3 and $\leq 0.2\text{‰}$, respectively.

We confirmed sample quality and collagen preservation using percent collagen yield, atomic C:N, $\delta^{13}\text{C}$ values, and $\delta^{15}\text{N}$ values prior to AMS ^{14}C measurement (DeNiro, 1985; Van Klinken, 1999; Beaumont et al., 2010; Kennett et al., 2017). Residual contaminants can have distinct C:N and stable isotope values, and this was the case for one sample (a dog from Rezoky, sample ID "615," which was not dated and not further considered; see **Supplementary Dataset 1**). We graphitized collagen from the remaining 30 subfossil specimens at PSU and submitted graphite for ^{14}C analysis at the Pennsylvania State University AMS facility and UC Irvine's W.M. Keck Carbon Cycle AMS (**Supplementary Dataset 1**).

Data Analysis

We calibrated radiocarbon dates in OxCal 4.4 using the Southern Hemisphere calibration curve SHCal20 (Hogg et al., 2020), or the post-bomb atmospheric SH3 curve (Hua et al., 2013) for three dogs that yielded $> 14\text{C}$ modern ages (**Supplementary Dataset 1**). We used both classical frequentist and Bayesian statistical approaches to event estimation to compare estimated times of dog introduction and lemur extinctions (Buck and Bard, 2007; Bradshaw et al., 2012).

Our Bayesian approach starts with the assumption that dateable material was deposited uniformly during the past several thousand years. This assumption is conservative and underestimates the true degree of temporal overlap between introduced and extinct taxa. Extinctions actually involve a period of declining population (and decreasing rate of deposition), while introductions tend to involve a period of expanding population

(and increasing rate of deposition). Both approaches produce confidence/credible intervals for extinction and introduction events. Note that, in the case of an extinction event, the Bayesian credible interval represents the posterior probability that a species is extinct at a certain time given that it was not sampled, while the extinction confidence interval produced through the classical approach reflects the probability that a species was not sampled at a certain time because it was no longer present. We used the package "rcarbon" in R to create summed probability distributions for calibrated dates from extinct and extant fauna, and each distribution was normalized such that it integrates to one (Crema and Bevan, 2020). Note that all confidence/credible intervals for event estimation are sensitive to outliers (such as rare late occurrence data), and numerous historical accounts suggest that relict populations of extinct species may have survived until recent centuries (Godfrey, 1986; Flacourt, 1995; Burney and Ramilisonina, 1998; Nomenjanahary et al., 2021).

We follow the approach of Crowley and Godfrey (2013) to correct collagen $\delta^{13}\text{C}$ values for the Suess effect (recent enrichment of atmospheric CO_2 in ^{13}C due to the burning of fossil fuel). Specifically, we made modern and subfossil collagen $\delta^{13}\text{C}$ values comparable by adding 0.004‰ to modern data for each year that passed from 1860 to 1965 AD and 0.02‰ for each year that passed from 1965 to the time of death (if known) or sample collection (2019 most recently).

We used general linear models (GLMs, R package "glmulti," Calcagno and de Mazancourt, 2010) with corrected data to identify which variables drive variation in predator $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (i.e., taxon, time, and location, **Supplementary Tables 1, 2**). Sites with data from both dogs and *Cryptoprocta* spp. (**Figure 3**, Andolonomby, Tsirave, and Ampasambazimba) are ideal for stable isotope comparisons. For example, Tsirave dog and *C. ferox* $\delta^{15}\text{N}$ values are comparable (dog $n = 4$, $\bar{x} = 10.6\text{‰}$, *C. ferox* $n = 3$, $\bar{x} = 11.5\text{‰}$), yet Tsirave dog $\delta^{13}\text{C}$ values ($n = 4$, $\bar{x} = -9.4\text{‰}$) tend to be $\sim 10\text{‰}$ higher than *C. ferox* $\delta^{13}\text{C}$ values from this site ($n = 3$, $\bar{x} = -19.6\text{‰}$). Unfortunately, most sites include data from less than five specimens. Given limited site-specific sample sizes, we classified site location of dogs, *C. ferox*, and *C. spelea* according to coastal proximity and ecoregion. We defined coastal sites as those ≤ 10 km from the coast and inland sites as those > 10 km from the coast.

We simplified ecoregion data into two groups: SW Madagascar (including the spiny thicket and succulent woodland), and North-Central Madagascar (including the dry deciduous forest and central highlands). We combined data from the spiny thicket and succulent woodland ecoregions because they have similar climate and are both dominated by relatively xerophytic vegetation. Plants and animals from these two ecoregions have similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and are isotopically distinct from those of the relatively mesic central highlands and humid forest (Crowley et al., 2011). For similar reasons, we combine the single dog from the dry deciduous forest (PSUAMS 7663 from Lakato'ni Gavin in the far north) with the group from the central highlands. Note that only in our GLMs do we consider the limited stable isotope dataset for predators from North-Central Madagascar ($n = 5$). The rest of our analyses are focused exclusively on the SW.

We also compared $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for dogs from archeological and paleontological sites in inland SW Madagascar using t-tests. Sample sizes in these comparisons are small (archeological $n = 5$, paleontological $n = 6$), but neither $\delta^{13}\text{C}$ nor $\delta^{15}\text{N}$ values within these groups violate the t-test assumptions of normality (Shapiro-Wilk $p \geq 0.06$) or equal variance (Brown-Forsythe $p \geq 0.23$).

Uneven sampling of individuals through space and time influences the observed variance in stable isotope values for dogs and *Cryptoprocta* spp. We used Stable Isotope Bayesian Ellipses in R (SIBER) to visually inspect the breadth of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from SW Madagascar (combining spiny thicket and succulent woodland) and also compare isotopic overlap between predator genera in a way that is unbiased by sample size (Jackson et al., 2011). We consider both standard ellipse areas (SEAs, which contain ~40% of the data from each group) and ellipses that include 95% of the data from each group. Because our sample of *C. spelea* includes fewer than the recommended five specimens, we combined data from *C. spelea* and *C. ferox*. We feel this is reasonable because, within SW Madagascar, the two species have indistinguishable $\delta^{15}\text{N}$ values (Figure 6, *C. spelea* $n = 3$, $m = 14.0\text{‰}$; *C. ferox* $\delta^{15}\text{N}$ value: $n = 9$, $m = 13.9\text{‰}$, Mann-Whitney $U = 12.00$; $p = 0.85$), and $\delta^{13}\text{C}$ values (*C. spelea* $n = 3$, $m = -19.3\text{‰}$; *C. ferox* $n = 10$, $m = -18.6\text{‰}$, Mann-Whitney $U = 8.50$, $p = 0.31$). Note that the similar stable isotope values of *C. spelea* and *C. ferox* do not exclude the possibility that these species preyed on different taxa that were isotopically similar. Before analysis with SIBER, we used Shapiro-Wilk tests to confirm that *Cryptoprocta* spp. and dog $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from SW Madagascar are normally distributed ($p \geq 0.67$).

Lastly, we plotted stable isotope data from predators and potential prey from SW Madagascar on the same graph to visually assess the potential for different patterns of predation. In this graph, we shifted predator $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values by -0.5 and -3‰ , respectively, to account for estimated offsets in stable isotope values between trophic levels (McCutchan et al., 2003), and we grouped prey species at different taxonomic levels (family and above). Large, species-specific lemur datasets are grouped according to family due to relatively similar isotopic niche spaces occupied by different species. We use higher level classification for other prey types (e.g., all birds grouped in Aves) due to limited sample sizes.

RESULTS

Chronological Data

Directly ^{14}C -dated bones suggest a brief period of overlap between dogs and extinct giant lemurs in SW Madagascar and that dogs could have been present at kill sites during times that humans butchered extinct megafauna and an extant lemur (*Propithecus verreauxi*). Limited sample sizes prevent us from meaningfully considering differences in introduction and extinction timing in different ecoregions. However, our results suggest that dogs were widespread on Madagascar by ~900 calibrated years before present (cal BP, Figure 4). The oldest ^{14}C -dated dog comes from the far northern archeological site

of Lakato'ni Gavin (Figure 3, PSUAMS 7663, $1,035 \pm 15$ ^{14}C BP, 960–810 cal BP) and is roughly contemporaneous with a dog from the archeological site of Andranosoa in the far south (PSUAMS 7623, $1,010 \pm 15$ ^{14}C BP, 930–800 cal BP). The calibrated 95% age ranges of these two individuals overlap with those of five subfossil butchered extant lemurs (*Propithecus verreauxi*) from Taolambiby and with the three youngest ^{14}C -dated extinct giant ruffed lemurs (*Pachylemur insignis*) from Tsirave (Figure 5). The youngest dated *P. insignis* from Tsirave (UCIAMS 167930, 940 ± 20 ^{14}C BP, 900–740 cal BP) postdates the two earliest dogs by less than a century, and predates the oldest dog from Tsirave by ca. 80 years (CAMS 142889, 860 ± 30 ^{14}C BP, 790–670 cal BP).

Conservative estimates for SW Madagascar suggest the introduction of dogs (approximately 1,000 years ago) roughly coincided with the population collapse and possible extinction of *Palaeopropithecus ingens*, *Archaeolemur majori*, and *P. insignis* (between about 1,100 and 700 cal BP; Figure 5). The classical 95% confidence interval for dog introduction (1,120–870 cal BP) also overlaps with the calibrated 95% age ranges for all 26 of the dated butchered bones in Figure 5. These include bones of extant *P. verreauxi* ($n = 15$), as well as extinct giant lemurs [*P. insignis* ($n = 7$) and *A. majori* ($n = 1$)], elephant birds [*Aepyornis maximus* ($n = 1$) and *Mullerornis modestus* ($n = 1$)], and a pygmy hippo [*Hippopotamus* sp. ($n = 1$)].

Stable Isotope Data

Predator collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values suggest dietary flexibility for dogs and some limited dietary overlap between *Cryptoprocta* spp. and dogs (Table 1 and Figure 6). All included predictor variables (i.e., taxon, ecoregion, coastal proximity, and time) contribute to the best fit GLMs (Supplementary Table 1) that explain variation in predator $\delta^{13}\text{C}$ values (Model 1, $n = 37$, AIC = 170.84) and $\delta^{15}\text{N}$ values (Model 2, $n = 36$, AIC = 142.04). Model 1 suggests that both *C. spelea* and *C. ferox* had low $\delta^{13}\text{C}$ values relative to dogs (Supplementary Table 2, $p = 0.007$ and $p = 0.02$, respectively). It also suggests that predator $\delta^{13}\text{C}$ values in general tend to be relatively high in SW Madagascar ($p = 0.0002$) and that they also tend to be higher at coastal sites ($p = 0.02$). Overall, predator $\delta^{13}\text{C}$ values may have decreased through time (Model 1 $p = 0.04$, Figure 7), primarily among the three *C. spelea* ($p = 0.006$). However, the model also suggests that combined predator $\delta^{13}\text{C}$ increased through time both in SW Madagascar ($p = 0.03$) and at inland sites island-wide ($p = 0.04$). Model 2 suggests that *C. ferox* have high $\delta^{15}\text{N}$ values relative to dogs (Supplementary Table 2, $p = 0.002$) and that *C. ferox* from coastal sites tend to have higher $\delta^{15}\text{N}$ values than those from inland sites ($p = 0.02$). It also suggests that both *C. spelea* and *C. ferox* $\delta^{15}\text{N}$ values increased through time ($p = 0.05$ and $p = 0.009$, respectively, Figure 7).

Standard ellipse areas (SEAs which encompass 40% of a group's data) are nearly twice as large for dogs (9.6‰^2) as they are for *Cryptoprocta* spp. in SW Madagascar (5.2‰^2 ; Figure 6). While the SEAs do not overlap, ellipses that contain ~95% of the data from each group do overlap (Figure 6). The area of overlap between the 95% ellipses accounts for ~34% of the isotopic

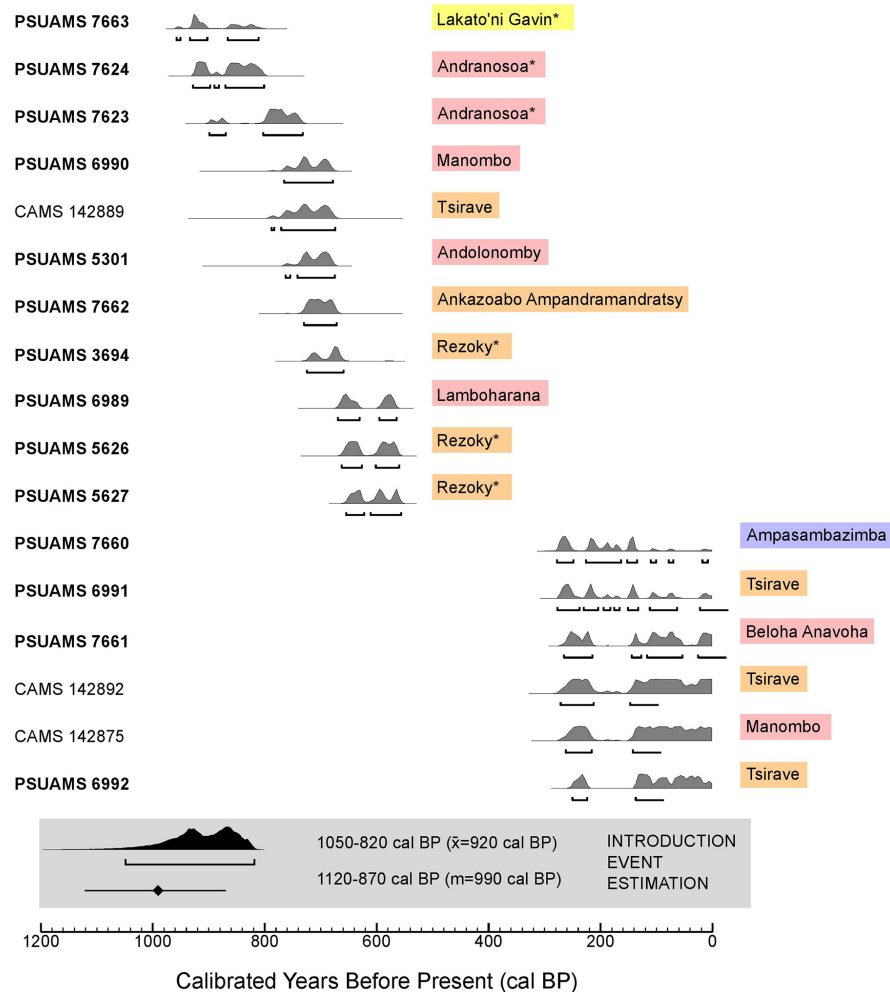


FIGURE 4 | Dog collagen ^{14}C dates calibrated in OxCal 4.4 with SHCal 20 (Hogg et al., 2020). Previously unpublished dates are bolded, sites are colored according to ecoregion (red = spiny thicket, orange = succulent woodland, blue = central highlands, yellow = dry deciduous forest), and archeological sites are marked with asterisks. Shaded box includes results from two approaches to introduction event estimation: The bracket under the Bayesian posterior probability distribution spans 95.5% of the distribution, and the diamond and associated line marks the median and 95% confidence interval estimate from the classical frequentist approach.

niche space of *Cryptoprocta* spp. but only $\sim 16\%$ of the isotopic niche space of dogs. Samples of dog and *Cryptoprocta* spp. bones integrate different amounts of time and space, but these variables alone cannot explain the relatively large isotopic niche space occupied by dogs. Specifically, the range of dates for *Cryptoprocta* spp. is about twice as great as that for dogs (Figure 7). Also, although dogs from SW Madagascar come from a greater number of sites than *Cryptoprocta* spp. ($n = 8$ vs. $n = 4$), these sites represent similar geographical spread and include both inland and coastal sites (Figure 3).

Dogs generally tend to have higher $\delta^{13}\text{C}$ values and lower $\delta^{15}\text{N}$ values than *Cryptoprocta* spp., but dogs from inland archeological sites in SW Madagascar (Rezoky & Andranosoa) tend to have $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that are relatively comparable with those of *Cryptoprocta* spp. (Figures 6, 7). Specifically, the mean (± 1 SD) $\delta^{13}\text{C}$ value for dogs from inland archeological sites in SW Madagascar ($n = 5$, $\bar{x} = -14.9 \pm 1.4\text{‰}$) is significantly lower than the mean value for dogs from inland paleontological sites

in this region [$n = 6$, $\bar{x} = -11.1 \pm 3.3\text{‰}$, $t(9) = 2.42$, $p = 0.04$]. However, limited sample sizes and limited contemporary samples from archeological and paleontological sites may confound this comparison, since dog $\delta^{13}\text{C}$ values across inland SW sites significantly increased during the past millennium ($n = 11$, $r_{\text{Spearman}} = 0.60$, $p = 0.05$, Figure 7). Additionally, the mean $\delta^{15}\text{N}$ value for dog collagen from archeological sites in this region ($n = 5$, $\bar{x} = 13.3 \pm 0.8\text{‰}$) is apparently, yet insignificantly, higher than the mean value for dogs from inland paleontological sites [$n = 6$, $\bar{x} = 11.9 \pm 2.4\text{‰}$, $t(9) = 1.26$, $p = 0.24$].

DISCUSSION

Brief overlap in directly dated introduced dogs and extinct megafauna means that we cannot reject the hypothesis that dogs could have helped humans hunt giant lemurs and possibly other megafauna at least $\sim 1,000$ years ago. Dogs have had diverse diets that are largely distinct from *Cryptoprocta* spp. diets and

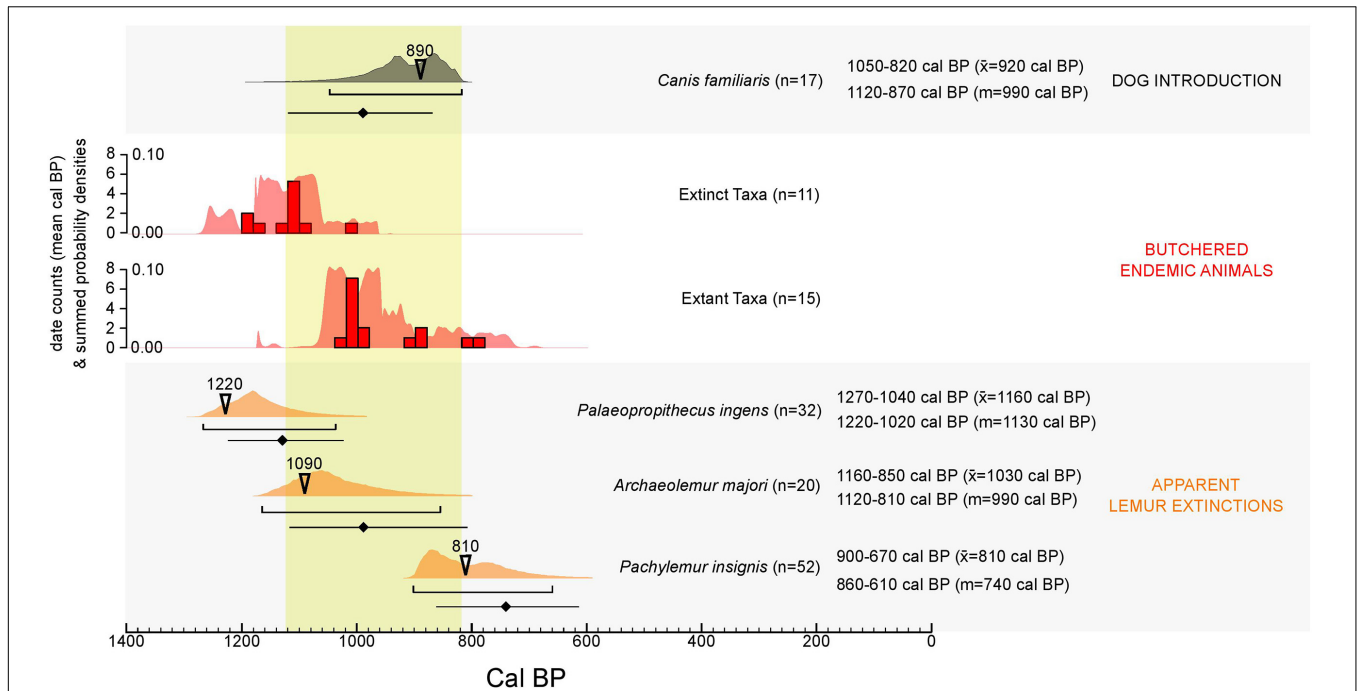


FIGURE 5 | Dog introduction event estimate compared to dates from butchered endemic animal bone and giant lemur extinction event estimation. Numbered arrowheads mark the mean calibrated date from the oldest recognized dog and youngest recognized giant lemur belonging to each taxon. See **Figure 4** for explanation of confidence intervals for event estimation. Note that extinction confidence intervals consider only data from purified collagen. Dates from butchered animal bone are binned in 20-year intervals (saturated color) and are also displayed through summed probability distribution overlays (unsaturated color). Butchered extinct taxa represented in the histogram include *Pachylemur insignis*, *Archaeolemur majori*, *Hippopotamus* sp., *Aepyornis maximus*, and *Mullerornis modestus*. All of these taxa disappear from the subfossil record by ~800 cal BP (Crowley, 2010). Butchered extant taxa in the histogram include only *P. verreauxi*.

TABLE 1 | Descriptive statistics for island-wide *Canis familiaris* and *Cryptoprocta* spp. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and age data.

Taxon	n	$\bar{x}$	SD	Range	[min, max]
$\delta^{13}\text{C}$ (‰, VPDB)					
<i>Canis familiaris</i>	23	-13.5	3.0	12.4	[-20.4, -8.0]
<i>Cryptoprocta</i> spp.	14	-18.9	1.1	4.0	[-21.0, -17.0]
$\delta^{15}\text{N}$ (‰, AIR)					
<i>Canis familiaris</i>	23	12.3	1.8	6.6	[9.1, 15.7]
<i>Cryptoprocta</i> spp.	13	13.6	1.6	5.1	[11.2, 16.3]
Age (mean cal BP)					
<i>Canis familiaris</i>	23	NA	NA	959	[890, -69]
<i>Cryptoprocta</i> spp.	14	NA	NA	2,280	[3,280, 1,000]

Note that the range within each group includes both spatial and temporal variability (Figures 6, 7), and the $\delta^{13}\text{C}$ values for the six modern dogs were corrected for the Suess Effect (following Crowley and Godfrey, 2013) so that they are comparable with subfossil collagen values.

include only minor inputs from forest-dwelling species, which is inconsistent with the hypothesis that dogs competed with *Cryptoprocta* spp. (Figures 6, 8). Nevertheless, dogs could have contributed to interference competition with endemic predators.

The introduction of dogs coincided with expanding human presence on Madagascar, which included the significant growth and movement of Malagasy populations (Pierron et al., 2017), the rise of the island's earliest urban center (Radimilahy, 1998), and

the expansion of trade down the west coast of the island (Dewar and Wright, 1993; Boivin et al., 2013). Early trade connections between East Africa and Madagascar are consistent with the primarily African ancestry of Madagascar's dogs (Ardalan et al., 2015). However, given that the earliest directly ^{14}C -dated dog (from Lakato'ni Gavin) slightly preceded the appearance of SE Asian rice and cotton in the region (Crowther et al., 2016), the potential for multiple past dog introductions should be considered through analysis of ancient DNA, if possible.

Early introduced dogs could have aided past human-led hunts of extant lemurs like *P. verreauxi* and megafauna that went extinct within the past millennium (Crowley, 2010; Hixon et al., submitted), but isotope data suggest that these kills did not form the bulk of dog diet (Figure 8). Most extinct megafauna browsed woody C_3 vegetation (Crowley and Samonds, 2013; Godfrey and Crowley, 2016; Crowley et al., 2021; Hixon et al., submitted). A modern dog from Antsirabe does have an exceptionally low $\delta^{13}\text{C}$ value (-20.4‰) and relatively high $\delta^{15}\text{N}$ value (15.7‰), which may indicate that it relied heavily on forest bushmeat. However, the wide range of dog $\delta^{13}\text{C}$ values likely reflects a continuum of reliance on agropastoralist-supplied foods (based on C_4 or CAM plants), which is also observed in modern free-roaming dogs (Valenta et al., 2016). Consumption of scraps from butchered grazing livestock (e.g., zebu cattle) could have contributed to relatively high dog $\delta^{13}\text{C}$ values (Figure 8), particularly at archeological sites that include bones of dogs as

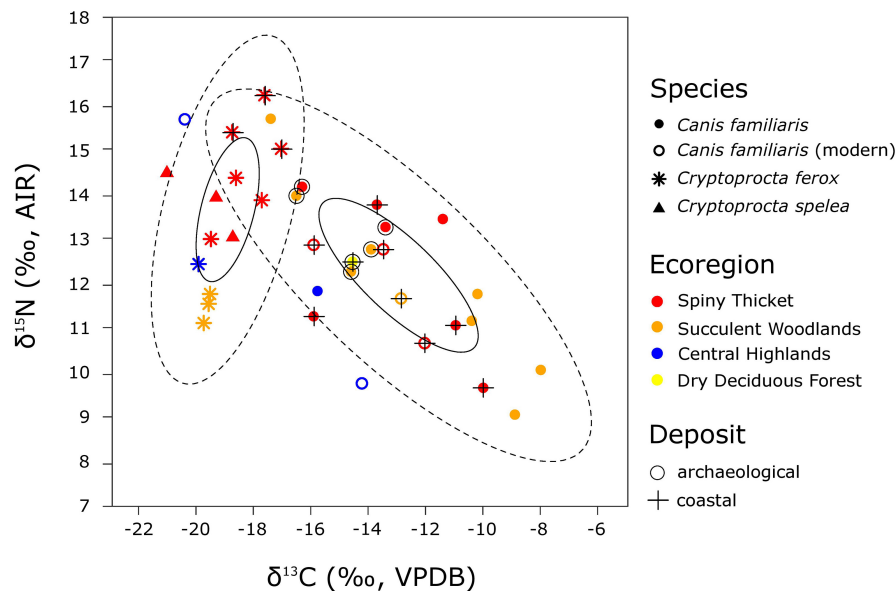


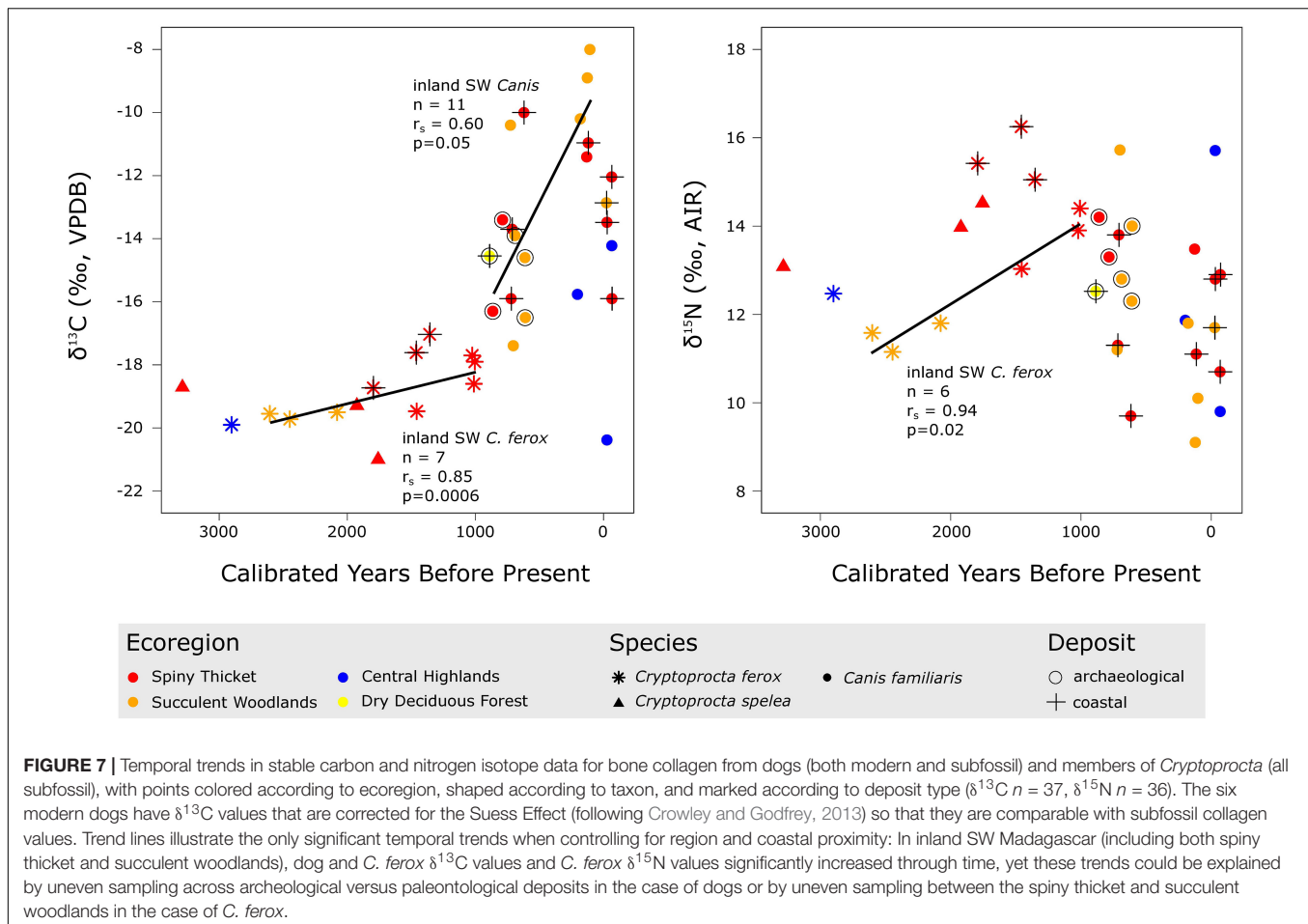
FIGURE 6 | Stable carbon and nitrogen isotope data for bone collagen from dogs (both modern and subfossil) and members of *Cryptoprocta* (all subfossil), with points colored according to ecoregion, shaped according to taxon, and marked according to deposit type ($n = 36$). For each genus, ellipses outline approximately 95% of the data (dashed) and 40% of the data (solid) from only the SW ecoregions (spiny thicket and succulent woodlands, *Canis* $n = 19$, *Cryptoprocta* $n = 12$). Island-wide, average calibrated dates for *C. spelea* specimens ($n = 3$) range from 3,280 to 1,760 cal BP, those for *C. ferox* ($n = 10$) range from 2,900 to 1,010 cal BP, and those for dogs ($n = 23$) span from 890 cal BP to the present. The six modern dogs have $\delta^{13}\text{C}$ values that are corrected for the Suess Effect (following Crowley and Godfrey, 2013) so that they are comparable with subfossil collagen values.

well as livestock (Vérin and Battistini, 1971; Rasamuel, 1984; Hixon et al., submitted). However, rather counterintuitively, dogs from inland archeological sites in the arid SW tend to have lower $\delta^{13}\text{C}$ values than those from inland paleontological sites where they were less likely to be associated with pastoralists. The relatively low $\delta^{13}\text{C}$ values of dogs from archeological sites could be explained by reliance on provisioned scraps from ovicaprids that browsed on a wide range of vegetation (Hixon et al., submitted) or from endemic, forest-dwelling game hunted by humans in forests dominated by C_3 plants (Figure 8; Decary, 1939). Archeological bone deposits in SW Madagascar tend to be highly fragmentary and may include traces of scavenging (Vérin and Battistini, 1971; Douglass et al., 2018). There are abundant marks of mammalian carnivorous predation and scavenging on the bones of extinct giant lemurs at paleontological sites (Meador et al., 2019, also at Taolambiby, Clark, pers. comm.), and the possibility that both *Cryptoprocta* spp. and dogs contributed to these patterns of gnaw marks on relatively recent bones cannot be excluded.

Past exploitation competition between dogs and *Cryptoprocta* spp. seems unlikely given that isotope data suggest ancient *Cryptoprocta* spp. consumed mostly forest dwelling animals (e.g., lemurs), while dogs have relied more heavily on prey from relatively open habitats (e.g., scraps from the food of agropastoral communities). Dogs may be replacing endemic predators around human communities today (Farris et al., 2016), but the distinct diets of dogs and *Cryptoprocta* spp. suggest that dogs are not fulfilling the ecological role of *Cryptoprocta* spp. In particular, the distinct isotopic niches of dogs and *Cryptoprocta*

spp. suggest that any past antagonistic relationship between these predators did not follow from predation or competition for shared prey. Instead, dogs could have antagonized *Cryptoprocta* spp. through exclusion competition by chasing shared prey, creating a landscape of fear, and thus contributing to habitat fragmentation (Laundré et al., 2010). The directly ^{14}C -dated subfossil record for *C. spelea* is sparse ($n = 3$), yet recent accounts of what may be *C. spelea* still living in the far north of Madagascar (Nomenjanahary et al., 2021) suggest that there may be a history of interaction between dogs and *C. spelea*. Dogs may occasionally prey on *C. ferox* (Valenta et al., 2016), yet comparable $\delta^{15}\text{N}$ values for dogs and *C. ferox* suggest that dogs have not routinely consumed endemic predators, such as *C. ferox*, or other introduced predators, such as cats, during the past millennium (Figure 8). The observation that dogs rarely prey on cats is consistent with the modern observation that both exotic predators are often simultaneously abundant (Farris et al., 2014).

Although there was limited dietary overlap between *C. ferox* and dogs ~1,000 years ago, this may have expanded during the past millennium as *C. ferox* came into more frequent contact with human modified landscapes that tend to have higher plant and animal $\delta^{13}\text{C}$ values. Palynological and geochemical records from much of Madagascar document the expansion of grasslands favored by livestock and dogs during the past millennium (Burney, 1987; Crowley and Samonds, 2013; Burns et al., 2016; Virah-Sawmy et al., 2016; Domic et al., 2021). Future stable isotope work with modern and subfossil *C. ferox* individuals that span the past millennium can test this possibility. *C. ferox* continues to hunt in shrinking forest fragments but may partly



exploit the expanding anthropogenic niche, as documented in other taxa such as vervet monkeys (*Chlorocebus pygerythrus*) on mainland Africa (e.g., Loudon et al., 2014). *Cryptoprocta ferox* is known to navigate deforested areas (Wyza et al., 2020), and there are numerous recent accounts of *C. ferox* raiding poultry and controlling introduced rat populations (Merson et al., 2019b).

Ongoing efforts try to control dog populations, yet dogs are only part of the picture. A growing body of directly ^{14}C -dated specimens of introduced animals suggests that dogs became established on Madagascar at approximately the same time as introduced herbivores (zebu cattle and ovicaprids, Hixon et al., submitted) and at possibly the same time as cats (Sauther et al., 2020). Genetic data from Madagascar's modern cats indicate that their ancestors colonized the island from the Arabian Sea region within the past millennium (Sauther et al., 2020). Similar to dogs, cats are a successful invasive predator on numerous islands (Medina et al., 2011; Nogales et al., 2013). However, unlike dogs, cats may be a closer functional replacement for *Cryptoprocta* spp. since they also climb trees. Cats successfully prey on a large variety of endemic species on Madagascar (Brockman et al., 2008; Merson, 2017) and are difficult for endemic predators to avoid (Gerber et al., 2012). Existing $\delta^{13}\text{C}$ data from four cats in SW Madagascar (Figure 8) could suggest that they consumed different prey than *Cryptoprocta* spp., but the available

sample size is quite small. Though cats are well-represented in archeological deposits of ~1,000 years ago on the island of Mayotte (~330 km NW of Madagascar), subfossil felid remains are unfortunately very scarce in Madagascar's paleontological and archeological deposits (Petit, 1933; Chanudet, 1975). The analysis of additional cat remains would better clarify when cats arrived on Madagascar and how their diets compared to those of other predators.

Madagascar's ecosystems continue to face new species introductions (e.g., Asian toads; Kolby, 2014) and shifts in land use (e.g., cash cropping; Réau, 2002) that threaten endemic biodiversity. The suite of past animal introductions that included dogs and livestock coincided with a pulse of megafaunal extinction and constituted an early turning point in Malagasy socio-ecological history. This situation is analogous to the colonization of Remote Oceania by people with a "transported landscape" that included dogs, pigs, rats, and chickens (Anderson, 2009). During the brief co-occurrence of dogs, introduced livestock, and endemic megafauna on Madagascar, pastoralists both relied on their livestock and opportunistically hunted endemic animals (Vérin and Battistini, 1971; Rasamuel, 1984). Introduced animals compounded negative impacts of humans on endemic fauna. Livestock provided a reliable food supply for growing human

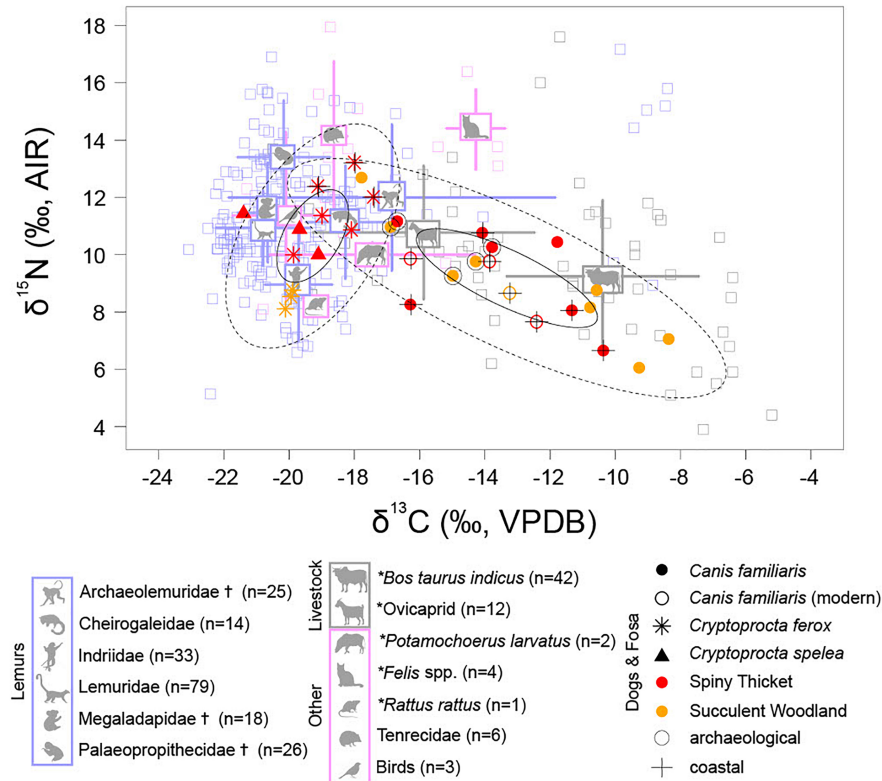


FIGURE 8 | Stable carbon and nitrogen isotope data for bone collagen from dogs (both modern and subfossil) and members of *Cryptoprocta* (all subfossil) collected in SW Madagascar, with points colored according to ecoregion, shaped according to taxon, and marked according to deposit type ($n = 36$, see **Figure 5** explanation of ellipses fitted to dog and *Cryptoprocta* spp. data). Stable isotope data from the bone collagen of lemurs, livestock, and other animals collected in SW Madagascar are plotted for reference, with icons marking means and lines marking standard deviations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Note that extinct families of giant lemurs are marked with (†), introduced taxa are marked with (*), and modern individuals (including six modern dogs) have $\delta^{13}\text{C}$ values that are corrected for the Suess Effect (following Crowley and Godfrey, 2013) so that they are comparable with subfossil collagen values. Also note that dog and *Cryptoprocta* spp. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are shifted by -0.5 and -3‰ , respectively, to account for estimated offsets in stable isotope values between trophic levels (McCutchan et al., 2003). Thus, the dog and *Cryptoprocta* spp. points approximate the isotopic composition of their diet.

populations (Pierron et al., 2017), and we have shown here that dogs could have aided human-led hunts and contributed to habitat fragmentation during the past millennium. However, forest-dwelling endemic animals contributed relatively little to dog diet. The colonization of Madagascar by pastoralists and introduced predators likely had dramatic environmental consequences and formed what can be considered the first step in the biotic homogenization of the island.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the work focuses on ancient vertebrates.

AUTHOR CONTRIBUTIONS

SWH, DK, KD, BC, LG, LR, and HW designed the research. SWH, KD, LE, and BC performed the analyses. SWH, KD, LG, BC, LR, GC, AA, SH, and HW aided sample collection and identification. SWH and DK wrote the manuscript. All authors edited the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.689559/full#supplementary-material>

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