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EXAMINING ANTHORPOGENIC PRESSURES ON MADGASCAR CARNIVORANS

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EXAMINING ANTHORPOGENIC PRESSURES ON MADGASCAR CARNIVORANS

BY

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MASTER OF SCIENCE THESIS

OF

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ABSTRACT

Biodiversity is increasingly threatened by anthropogenic disturbance globally. Information on the status of species and their response to changing environments is required to determine mitigation strategies before range contractions, population declines, or extinctions occur. Madagascar is a renowned biodiversity hotspot, comprising some of the highest levels of floral and faunal endemism in the world. Madagascar is also home to the most understudied family of carnivorans in the world, Eupleridae. Eupleridae is comprised of eight unique species that we currently lack fundamental knowledge about yet are of high conservation concern. Madagascar has experienced intense landscape changes from human expansion and resource extraction, especially within forested eco-regions where Eupleridae species primarily range. Conservation actions are thus hindered by a lack of clear information regarding species ecology and empirical studies evaluating species responses to on-going pressures from anthropogenic activities. Here, I examine the relative influence of intensifying landscape change and invasive carnivorans on Eupleridae through:

1) A literature review to synthesizes current information on Eupleridae life history, functional-traits, and empirical evidence of the influences of anthropogenic pressures. In addition, this review aims to help identify knowledge gaps and specify future research needs. Presented here as Manuscript 1.
2) An independent empirical study to examine the relative effects of two primary anthropogenic factors threatening carnivorans in Madagascar's eastern rainforest, the creation of forest edge from landscape change and invasive predators. To date, targeted conservation actions for Madagascar carnivorans has been hindered by a failure to understand

the relative contributions of these factors in driving species declines. Presented here as Manuscript 2.

Through this body of work, I aim to contribute pragmatic resources and empirical data on Eupleridae to guide current and future conservation practitioners.

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I owe my sanity and success to all my friends and family who make up my extended community and are too numerous to name. The support I had from all is undeniable over the last years. To my loyal companion, Indy, for the consistent reminder that a walk outside is always the answer. Thank you.

PREFACE

This thesis is prepared according to manuscript format, consisting of two manuscripts. Manuscript 1: “A synthesis of life-history, functional traits, and consequences of anthropogenic pressures on Madagascar’s threatened carnivorans, Eupleridae” has been published in *Mammal Review*, January 2021. Manuscript 2: “Rainforest carnivorans living on the edge with invasive predators” is currently in preparation for submission to *Animal Conservation*. The manuscripts are presented as submitted to the journals and may be subsequently amended for publication. Additional authors for manuscripts are listed at the beginning of each manuscript. Appendices are presented at the end of the thesis and contain data in support of this thesis that were not included in the manuscripts.

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REVIEW: A synthesis of life-history, functional traits, and consequences of anthropogenic pressures on Madagascar's threatened carnivorans, Eupleridae

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ABSTRACT

1. Madagascar's native carnivorans are an endemic monophyletic group of eight extant species belonging to the family Eupleridae. The International Union for Conservation of Nature (IUCN) currently classes seven of the species as threatened (Vulnerable or Endangered), as their populations are in decline due to intensifying anthropogenic pressures. However, little is known about these species' ecology and population trends, precluding forecasts of extinction risk. Life-history and functional traits govern species' responses to environmental pressure and can be predictive of extinction risk. Incorporating relevant trait information can vastly improve risk assessments. Yet, information on the life-history and functional traits of the Eupleridae has never been compiled into a single framework.

2. Our aims were to: 1) synthesize the current state of knowledge of the life-history and functional traits of euplerid species, 2) review empirical evidence of the effects of anthropogenic pressures on species, and 3) identify knowledge gaps and future research needs.

3. We searched the published literature to compile life-history and functional trait information and known effects of anthropogenic pressures for Eupleridae.

4. Our review indicates that Madagascar's carnivorans have high-risk life-history and functional traits that increase their vulnerability to anthropogenic pressures. Publications reported negative effects on euplerids of habitat degradation and fragmentation, logging, non-native carnivorans, disease, and hunting and retaliatory killings. However, our synthesis revealed significant knowledge gaps,

especially in species' life-history traits and in the spatial variability in most traits. For most species, we currently do not have the robust data needed to assess trait-based risk dynamics.

5. The culmination of reported traits, negative influence of ongoing anthropogenic pressures and lack of robust metrics (e.g., population trends and trait variability) indicates that euplerids are at high risk, yet may reach the cusp of extinction without notice due to significant gaps in knowledge. Future research should prioritise filling gaps in knowledge of influential traits, evaluating anthropogenic pressures, and integrating trait information to improve risk assessments and extinction forecasts.

Keywords: euplerids, extinction risk, human disturbance, Madagascar, meso-carnivorans, trait-based, understudied

INTRODUCTION

Madagascar is experiencing a biodiversity crisis. Intensifying anthropogenic disturbance has caused widespread loss, fragmentation, and degradation of native forests, resulting in high levels of threatened endemic species (Cardillo et al. 2006, Vieilledent et al. 2018). In the next 80 years, deforestation and climate change are likely to cause complete forest loss throughout Madagascar (Morelli et al. 2020). Currently, less than 50% of Madagascar's natural forest remains, and half of remaining forests are within 100 m of an edge (Vieilledent et al. 2018): there is little remaining contiguous forest that is not influenced by edge effects (Laurance et al. 2007). These landscape changes alter the structure and function of population and community dynamics (Flynn et al. 2009), reducing available habitat for species, shifting habitat use to suboptimal areas, promoting species invasions, such as by *Canis familiaris*, *Felis catus*, *Potamochoerus larvatus*, and *Rattus rattus* (Farris et al. 2015a), and introducing novel diseases (e.g. *Leptospira interrogans* and *Toxoplasma gondii;* Rasambainarivo et al. 2018). Landscape change can also increase negative interactions between humans and native species. These interactions can include livestock depredation and subsequent retaliatory killing by humans, as well as increased exposure to poaching (Ripple et al. 2016). As a result of continuing landscape changes in Madagascar, many endemic, forest-dependent fauna are listed as threatened (Critically Endangered, Endangered, or Vulnerable) despite their unknown population status (IUCN 2020).

Madagascar's native carnivorans are an endemic monophyletic group of eight species belonging to the family Eupleridae (Fig. 1). Euplerids originated from a single African ancestor approximately 18 to 24 million years ago (Yoder et al. 2003). The lack of Carnivora competition allowed the original colonisers to radiate into a broad range of niches, including mongoose-like (subfamily Galinae) and felid- or civet-like species (subfamily Euplerinea). Today, the eight extant species primarily occupy western dry deciduous forest, eastern humid rainforest, and, to a lesser extent, southern spiny forest eco-regions of Madagascar (Goodman 2013).

As top predators, euplerids play an important ecological role that influences all trophic levels, yet we know very little about their ecology (Goodman 2012, Brooke et al. 2014). This has resulted in a general lack of species-level information that is critical to a robust assessment of population status and extinction risk. For example, island-wide abundance estimates are available for only one species, *Cryptoprocta ferox* (Gerber et al. 2010, Murphy et al. 2018). Furthermore, there are no empirical estimates of population vital rates (e.g., survival and fecundity) of any species in the wild. Due to the absence of population abundances and trajectories, evidence of the effects of landscape change and subsequent anthropogenic pressures have been used to infer species' status (IUCN 2020).

Life-history and functional traits govern species' responses to environmental pressure and can be predictive of extinction risk (Williams et al. 2010). Life-history traits are the demographic parameters that determine life-time fitness, such as survival, growth, reproduction, and dispersal (Flatt & Heyland 2011), and are typically described along a slow-fast continuum. Slow species are regulated more strongly by environmental resources, while fast species are regulated by population growth rates (Fowler 1981). Functional traits are key morphological, physiological, and behavioural characteristics that define the relationships between species and the broader ecosystem in which they are embedded (Petchey & Gaston 2006). Certain unifying life-history and functional traits can thus increase species' vulnerability to environmental pressures (Purvis et al. 2000, Verde Arregoitia 2016)

Within terrestrial mammals, identified unifying high-risk traits include long gestation length, small litter size, late weaning age, late sexual maturity, large adult mass, long lifespan –all indicators of slow life history (Promislow & Harvey 1990), as well as high trophic level, small geographic range, and low population density (Fisher & Owens 2004, Fritz & Purvis 2010). Mammalian carnivorans typically have slow life histories, occur at low densities, require large areas of habitat, and suffer high human persecution rates (Cardillo et al. 2005). In unison, these traits increase their vulnerability to rapid declines from environmental or demographic perturbations and disturbance (Lande 1998).

However, species can mitigate pressures through trait plasticity (Gonzalez-Suarez & Revilla 2013). Many species readily display behavioural plasticity in temporal activity patterns and habitat use in response to external pressures. For example, urban mammals have been shown to shift their temporal activity patterns from a diurnal to nocturnal cycle to reduce temporal overlap with humans (Gaynor et al. 2018). Similarly, species may shift habitat use to avoid predation, interspecific killing or competition from non-native species (Ciach & Peksa 2019), or vary their spatial-temporal habitat use to facilitate sympatry (Karanth et al. 2017).

Predictions of Carnivora extinction risk globally have been vastly improved by considering the interaction of species biology and anthropogenic pressures (Cardillo et al. 2004). Moreover, trait-based approaches have been integrated to inform conservation planning for many taxa; including: identifying future priority conservation areas for terrestrial mammals (Brum et al. 2017) and amphibians (Becker et al. 2010), guiding conservation actions for plants under climate change (Butt & Gallagher 2018), and informing wind-farm development to reduce bird and bat species collisions (Thaxter et al. 2017). Previous reviews on threats to Madagascar biodiversity (Irwin et al. 2010) and future conservation planning (Kremen et al. 2008, Gardner 2009) have noticeably excluded the euplerids. This may be partially explained by the paucity of studies focused on the euplerid species relative to other taxa, or by the lack of any systematic review that synthesises available knowledge on any of the species. Given the widespread, serious anthropogenic threats posed to euplerids, a comprehensive review of life-history and functional traits and anthropogenic threats is needed.

Through this review, we aim to: 1) synthesise current information on the life-history and functional traits of euplerid species, 2) review empirical evidence of the effects of anthropogenic pressures on species, and 3) identify knowledge gaps and future research needs.

METHODS

We conducted a systematic literature review of all currently published or publicly available literature for euplerids in Madagascar (concluding in February 2020). We searched Web of Science (www.webofknowledge.com) and Google Scholar (scholar.google.com) using the following key word searches in singular and pairwise combination: '*Eupleridae'*, 'Madagascar', 'carnivore', 'habitat', 'invasive', 'prey', and 'disturbance', and independently searched species' colloquial, Malagasy, and taxonomic names. In addition, from each identified publication we used backward and forward citation chaining (i.e., using citations from one source to find other useful sources) to identify additional publications that were missed through the digital searches. We did not search for or include any government reports or other grey literature.

Within the literature we collected, we searched for information on the following ten life-history traits (Table 1): gestation length, litter size, sex ratio of offspring, mass at birth, weaning age, interbirth interval, age and size at sexual maturity, average lifespan, adult mass and adult body length (the last two were sex-specific where possible). We also searched for seven functional traits (Table 1): population density, feeding guild, sociality, distribution, habitat use, activity patterns, and home range size. Information on traits was sourced to a geographic location if possible (e.g., national park), and categorised into eco-regions: western dry deciduous forest, eastern humid rainforest or southern spiny forest (according to Harper et al. 2007). We specified eco-regions, since we expected traits could vary by major land-cover types (Berg & Ellers 2010). Within the literature we also searched for information on the influence of anthropogenic pressures on life-history and functional traits for all euplerids. Anthropogenic pressures included logging, habitat degradation and fragmentation, non-native carnivorans, disease, and hunting and retaliatory killings.

Finally, we summarised trait information into categories, based on how it was collected or sampled. Specifically, we identified whether information came from: 1) museum specimens (deceased specimen, a skin, halotype), 2) live captive individuals studied in a zoo or other captive facility (wild- or captive-born), 3) informal observations that were not part of a systematic study and may have no specific geographic location, 4) a formal single empirical field study of wild individuals or populations, and 5) more than one formal empirical field study of wild individuals or populations.

RESULTS: SPECIES-SPECIFIC LIFE-HISTORY AND FUNCTIONAL TRAITS

Our literature search resulted in 94 publications that met our criteria for inclusion in the review (Appendix S1). We present a summary of available information on all 17 traits in all eight species (Table 1). Information on life-history traits for most species was mostly derived from museum specimens or captive individuals. Sources of information from wild individuals were primarily from the deciduous forest (Fig. 2a). Within species, on average information was available on 75% of the seven functional traits, but only on 48% of the ten life-history traits. Functional trait information was principally from studies on wild individuals or populations (Table 1) and was geographically concentrated in the deciduous forest and rainforest eco-regions (Fig. 2b). We synthesise our findings on trait information for each species below. For details on reported life-history and functional traits by species and publication sources, see Appendices S2-S9; for a summary of density estimates for all species, see Appendix S10.

Cryptoprocta ferox (fosa, fossa)

We found 58 publications that included information on *Cryptoprocta ferox,* which was more than any other euplerid species. Information was available on all ten of the life-history traits and all seven of the functional traits (Table 1). Information on life-history traits came exclusively from captive individuals, except for body mass metrics, which were primarily from wild individuals captured in the deciduous forest. Publications on the functional traits of *Cryptoprocta ferox* were primarily from Kirindy Forest/ Centre de Formation Professionelle Forestièr (CFPF) and Kirindy-Mitea National Park in the deciduous forest and from Ranomafana National Park and Makira Natural Park-Masoala National Park in the rainforest. There is no published information available from the spiny forest, where *Cryptoprocta ferox* has been recorded.

LIFE-HISTORY TRAITS

Gestation length ranges from 42 to 90 days (measured in captive individuals only; measurement error may explain this extreme range). Females produce one litter per year, with litter size varying between two to four young, weighing approximately 80-100 g at birth. Only one study in captivity noted sex ratio of offspring for a single litter of four: three females and one male. Young are weaned at between 120 to 135 days. Adults are estimated to be sexually mature at three to four years of age. *Cryptoprocta ferox* is not known to be sexually dimorphic. Adult body mass ranges from 5.5-6.9 kg in females and from 6.1-8.6 kg in males; total body length (head-body-tail) ranges from 1357-1467 mm in females and from 1350-1532 mm in males. There is no published information available on the lifespan of *Cryptoprocta ferox* in the wild, but captive individuals are reported to live up to 17-20 years.

FUNCTIONAL TRAITS

Six studies conducted in the deciduous forest (Kirindy Forest/CFPF, Kirindy-Mitae National Park, Ankarafantsika National Park) and rainforest (Makira Natural Park-Masoala National Park and Ranomafana National Park) produced eight estimates of *Cryptoprocta ferox* density (Appendix S10). Estimates ranged from 0.18-0.25 individuals/km^2 in the deciduous forest (*n*=5), and from 0.08-0.39 individuals/km^2 in the rainforest (*n*=3). The diet of *Cryptoprocta ferox* is carnivorous and comprises lemurs, small mammals, birds, reptiles, amphibians and invertebrates. Both females and males are primarily solitary; however, males have been reported to form permanent coalitions and hunt cooperatively on occasion. The species has a promiscuous mating system, in which solitary females attract multiple males to a high tree for repeated copulation. *Cryptoprocta ferox* is cathermal, with preferences for crepuscular hours, although this may vary by geographic area. The species has been observed in deciduous forests, rainforests, and spiny forests. Habitat use varies, including wooded areas, fragmented forests, intact contiguous forest, degraded forests, and non-forested areas. *Cryptoprocta ferox* home range size in the deciduous forests from four independent publications ranges from 9.2-89 km^2. Some publications reported that male and females did not differ in home range size, while another reported that females had much smaller home ranges than males; average home range sizes are 19 and 20 km^2 for females and 55 and 35 km^2 for males, during the mating and non-mating season, respectively.

Fossa fossana (spotted fanaloka, Malagasy civet, Malagasy striped civet)

We found 25 publications that included information on six of the ten life-history traits and 6 functional traits (Table 1). Information on life-history traits was limited to metrics from captive-bred individuals, apart from morphometric data that came from one study. Nine publications provided data on functional traits throughout the rainforest, representing most of the geographic range of *Fossa fossana*. Publications informing functional traits were from Ranomafana National Park, Makira Natural Park-Masoala National Park, Anjanaharibe-Sud, Analamazaotra, and Vevembe protected forests.

LIFE-HISTORY TRAITS

Females bred in captivity produce one young per litter, with gestation lasting 82 to 90 days. Young at birth weigh approximately 65-70 g. Weaning age is 60-75 days. No information is available for the interbirth interval, although breeding is thought to occur only once a year in August or September. *Fossa fossana* is not sexually dimorphic. Captive and wild individuals have total body length measurements ranging from 610 to 714 mm, with males weighing from 1.5-2.1 kg and females 1.3-1.75 kg. There is no published information available on interbirth interval, age or size at sexual maturity or the average lifespan in either captivity or the wild.

FUNCTIONAL TRAITS

Four publications reported population densities. Estimates range from 1.38 ± 0.22 to 3.19 ± 0.55 individuals/km^2 (mean ± standard error). The diet of *Fossa fossana* is carnivorous and includes small mammals, amphibians, crustaceans, invertebrates, insects, and fish. Activity patterns are strictly nocturnal, with no reported variation. The species occurs from the most northern to the most southern protected eastern rainforests. Habitat use is variable, including areas near streams, marshes, along ridges, slopes, and valleys within non-degraded forests. Estimated home range size is 0.07-0.55 km^2 from radio-tracked individuals.

They have been observed in pairs, however, there is no published study that has examined sociality.

Eupleres goudotii (eastern falanouc, small-toothed civet)

We found 22 publications that information on one of the ten life-history traits and four of the seven functional traits (Table 1). Information on life-history traits came from a single captive individual born at a zoo, and morphometric data from four museum specimens. Eight publications provided information on functional traits of *Eupleres goudottii* from Makira Natural Park-Masoala National Park, Ranomafana National Park, and Tsitongambarika forest sites, comprising all known used eco-regions.

LIFE-HISTORY TRAITS

Evaluations of museum specimens revealed no evidence of sexual dimorphism in *Eupleres goudottii*, with total body length ranging from 675-880 mm. There is no published information on *Eupleres goudottii's* gestation length, litter size, mass at birth, sex ratio of offspring, weaning age, interbirth interval, age and size at sexual maturity or average lifespan.

FUNCTIONAL TRAITS

Eupleres goudottii is primarily a vermivore (earthworm eater), but is known to consume insects, lizards and birds. The species is nocturnal; however, it has also been described as cathermal. It is distributed throughout the rainforest and has been recorded as far north as Makira Natural Park-Masoala National Park and as far south as Ranomafana National Park.

There is no published information available on population density, sociality or home range size.

Eupleres major (western falanouc, Majors falanouc, giant falanouc)

We found 12 publications that included information on *Eupleres major*, making it the least studied species. Information was available on four of ten life-history and three of seven functional traits. Information on life-history traits were from a single captured male and four museum specimens. Six publications provided information on functional traits from three rainforest locations, Mahajanga, Ankarafantsika National Park, and Mariarano forest, comprising the only known inhabited eco-region.

LIFE-HISTORY TRAITS

In captivity, *Eupleres major* produces one young, however, it is estimated that it could produce two based on morphological features. At birth, young weigh 120-150 g. The body mass of *Eupleres major* from four museum specimens indicate a weight and length of 2-4 kg and 810-1040 mm, respectively. A single wild captured male weighed 2.4 kg and had a totally body length of 790 mm. There is no published information available for gestation length, sex ratio of offspring, weaning age, interbirth interval, age and size at sexual maturity or average life span.

FUNCTIONAL TRAITS

Eupleres major is primarily a vermivore. Activity patterns are described as nocturnal. The species is restricted to deciduous forests and has been confirmed to range from northwest Sambirano region, Ankarafantsika National Park, Mariarano, as far south as Baie-De-Baly

National Park. There is no published information on population density, sociality, habitat use or home range size.

Galidictis fasciata (broad-stripped vontsira, Malagasy broad-striped mongoose)

We found 25 publications that included information on two of ten life-history traits and five of seven functional traits. Information on life-history traits were exclusively from museum specimens. Eleven publications provided information on functional traits from rainforest and spiny forest, comprising all known inhabited eco-regions.

LIFE-HISTORY TRAITS

Two subspecies are currently recognised, *Galidictis fasciata fasciata* and *Galidictis fasciata grandidieri*, with evidence of size variation between subspecies. Morphometric data from museum specimens show that *Galidictis fasciata fasciata* has a total body length of 790-935 mm and a body mass of 520-750 g (*n*=4), and *Galidictis fasciata grandidieri* has a body length of 680-718mm and a body mass of 1000-1800 g (*n*=30). There is no published information available for gestation length, litter size, sex ratio of offspring, mass at birth, weaning age, interbirth interval, age and size at sexual maturity or average lifespan.

FUNCTIONAL TRAITS

Only two density estimates have been published, from the spiny forest: 6.23 and 7.99 individuals/km^2 for *Galidictis fasciata grandidieri*. *Galidictis fasciata fasciata* consumes small vertebrates including rodents, reptiles, amphibians and invertebrates. Rainforest camera studies found strictly nocturnal activity patterns. *Galidictis fasciata fasciata* has been recorded in two distinct eco-regions: spiny forest and rainforest. The species has been confirmed in Marojejy, Makira Natural Park-Masoala National Park, Andasibe-Mantadia National Park, and Ranomafana National Park in the rainforest and in Tsimanampetsotsa in the spiny forest. In the spiny forests, the distribution of *Galidictis fasciata fasciata* is likely to be limited by water availability Habitat use includes contiguous forests, degraded humid forests, selectively logged, disturbed environments (such as cattle-grazed areas), and primary lowland rainforest. There is no published information on home range size or sociality.

Galidia elegans (ring-tailed vontsira, Malagasy ring-tailed mongoose)

We found 24 publications that included information on seven of the ten life-history traits and all seven functional traits (Table 1). Information on life-history traits were primarily from captive individuals, though wild individuals were captured during a single field study in the rainforest. Eleven publications provided information on functional traits from four national parks and reserves, spanning much of the geographical range of *Galidia elegans* in the rainforest. No information was available on *Galidia elegans* in the deciduous forest, where they have been recorded.

LIFE-HISTORY TRAITS

In captivity, gestation length ranges from 52-90 days, with one young being produced per litter. At birth, young weigh 40-50 g and are weaned by 44-75 days. Age at sexual maturity is either one or two years. Reported body size metrics range from 560-680 mm total body length for museum specimens and 520-670 mm for wild individuals captured in Ranomafana National Park. Reported adult mass for an unknown sample source was 655-990 g; the body mass of captured female individuals from Ranomafana National Park (*n*=2) were 760 and 890 g; males (n=8) weighed 900-1085 g. No publications provided information on the sex ratio of offspring, interbirth interval or average lifespan.

FUNCTIONAL TRAITS

In Ranomafana National Park, the estimated density was 37 individuals/km^2. *Galidia elegans* has a generalist diet, consuming invertebrates, frogs, lizards, birds, and small mammals. *Galidia elegans* is strictly diurnal. Observed social structure includes mated pairs and family groups consisting of parents and their offspring. The species' known range spans the eastern rainforest, isolated areas of northern rainforest, and western deciduous forests. Habitat use includes low-land primary forests and intact forests, disturbed forest and forest edge. In the rainforest, multiple individuals may have overlapping home ranges of approximately 0.2 km^2.

Mungotictis decemlineata (bokiboky, narrow-striped mongoose)

We found 12 publications that included information on seven of the ten life-history traits and all six functional traits (Table 1). Despite the paucity of publications compared to all other euplerids, the life-history and functional traits of *Mungotictis decemlineata* are the most well-described from wild populations in congruence to eco-regions they occupy (only deciduous forest). For example, it is the only species for which we have estimated gestation length and litter size from non-captive individuals. Studies have primarily been conducted Central Menabe Protected Forests including in Kirindy forest/CFPF and north of Moradavo.

LIFE-HISTORY TRAITS

Observations of radio-tracked individuals indicate a gestation period of 74-106 days (*n*=2). In captivity, gestation length ranges from 90-105 days. Captive individuals produce one or two young per year; in the wild, observations have been of single young produced per litter. In captivity, mass at birth is 50 g and young are weaned at 60 days. Body size has been recorded in Kirindy/CFPF, Morondavo, Central Menabe Protected Forests, and at Manombo River. Information on body size indicates no sexual dimorphism. Total body length ranges from 452-620 mm. Male and female total body length has been reported to be 550 mm and 524 mm, respectively. Body mass ranges from 400-700 g; females weigh 450-740g and males 475-625g. There is no published information available on sex ratio of offspring, age at sexual maturity or average lifespan for *Mungotictis decemlineata*.

FUNCTIONAL TRAITS

Population density for *Mungotictis decemlineata* was estimated between 1-8 and 1-5 adults/km^2 in central and southern Menabe Protected Forests, respectively. *Mungotictis decemlineata* is primarily insectivorous, but also consumes small vertebrates, including lizards, frogs, birds and small mammals, and may hunt cooperatively for larger prey items, such as mouse lemurs *Microcebus spp.*. The species has strictly diurnal activity patterns. Social structure includes large gregarious groups, which may be comprised of matriarchal hierarchal family groups. *Mungotictis decemlineata* occurs only in the deciduous forest between the Tsiribihina and Mangoky Rivers. Habitat use includes dense vegetative understory, large fragmented habitat, degraded areas of xerophytic forests, and deciduous woodlands. Four estimates of home range size have been reported and are variable: 0.13-18 km^2 in Kirindy Forest/CFPF, and 1.5-2 km^2 for a ‘supergroup’ of 10 to 12 individuals in Morondava.

Salanoia concolor (brown-tailed vontsira, Malagasy brown-tailed mongoose)

We found 18 publications that included information on two of the ten life-history traits and five of the seven functional traits (Fig. 2). Information on the one life-history trait was exclusively from morphometric data from museum specimens. Four publications reported on functional traits of *Salanoia concolor* in the wild; these studies occurred in the Lac Alaotra, Betampona Natural Reserve, and Makira Natural Park-Masoala National Park, representing much of the known range of the species.

LIFE-HISTORY TRAITS

The total body length of *Salanoia concolor* in museum specimens ranges from 470-580 mm. A male and a female haplotype from Lac Alaotra were 500 and 520 mm long, respectively. Three records of the body mass of *Salanoia concolor* are: a museum specimen weighing 780 g, and the Lac Aloatra halotype male weighing 600 g, and a female weighing 675 g. There is no published information available for gestation length, litter size, sex ratio of offspring, mass at birth, weaning age, interbirth interval, age at sexual maturity or average lifespan.

FUNCTIONAL TRAITS

Salanoia concolor consumes primarily insects, invertebrates, and amphibians. Three of four studies reported activity patterns as diurnal and one as crepuscular. The distribution of the species includes Makira Natural Park-Masoala National Park, Mananara Nord, Zahamena, Lac Alaotra, and Betampona Natural Reserve. Habitat use includes low-mid altitude rainforest; *Salanoia concolor* can also occur in degraded forest, secondary vegetation, and cultivated land. Only one estimate of home range size is reported at approximately 0.2 km^2. There is no published information on population density or sociality.

RESULTS: ANTHROPOGENIC PRESSURES

There is no published information available on how anthropogenic pressures impact life-history traits for any euplerid species. Similarly, we found no study that has experimentally tested the effect of any type of anthropogenic pressure on euplerid functional traits. However, thirteen publications investigated correlations between anthropogenic pressures and three of the functional traits: density (*n*=3), habitat use (*n*=7), and activity patterns (*n*=3). We investigated correlations with the following anthropogenic pressures: introduction of non-native carnivorans, habitat degradation, habitat fragmentation, and selective logging. Additionally, we reviewed publications that examined disease risk (*n*=3) and hunting and retaliatory killings (*n*=3) of euplerids. These independent pressures can influence species' life-history traits (e.g. litter size and body mass) and functional traits, and are among the top threats to Madagascar carnivorans. Six publications are from the western deciduous forest; all remaining studies are from the eastern rainforest. Major findings in relation to anthropogenic pressures are summarised in Fig. 3.

Non-native carnivorans, habitat degradation and fragmentation, and logging

Ten of the 13 publications investigated non-native carnivorans, habitat degradation and fragmentation, and logging in relation to euplerids' functional traits; therefore, we discuss them in unison. Specific measures of anthropogenic pressure included forest fragmentation (e.g., patch size), logging activity, distances to forest edge, roads and villages, and presence of humans and non-native carnivoran species. Four publications reported on the influence of anthropogenic pressures in deciduous forest on euplerid habitat uFse (*n*=3) and temporal activity patterns (*n*=1). Nine publications reported on habitat use (*n*=5), density (*n*=2), and temporal activity patterns (*n*=2) in the rainforest. Habitat use was investigated across seasons/years (multi-season occupancy) and within a season/year (single-season occupancy). Multi-season occupancy provided insights into the processes contributing to patterns of changes in euplerid habitat use, by evaluating site-level extirpation of and colonisation by species. Single-season occupancy described patterns in habitat use within a closed time period (i.e., there was no change in the presence of a species). Habitat use is inferred as the probability of habitat use, which describes a continuous inference of what is habitat (probability of one) and what is not habitat (probability of zero), and all that lies between.

CRYPTOPROCTA FEROX

Four publications provided information on habitat degradation and/or non-native species in deciduous forests in relation to *Cryptoprocta ferox*. Habitat use is lower with the presence of *Felis catus*, but not with habitat degradation or *Canis familiaris* presence (Merson et al. 2019a). Furthermore, *Cryptoprocta ferox* utilises nocturnal hours, resulting in high temporal overlap with *Felis catus* and limited overlap with humans and *Canis familiaris* (Merson et al. 2019b). A study in Ankarafantsika National Park confirmed that *Cryptoprocta ferox* displays limited sensitivity to degraded habitat and uses networks of forest patches and corridors to navigate deforested and fragmented areas, avoiding villages (Wyza et al. 2020). However, a mark-recapture study of *Cryptoprocta ferox* had reduced capture rates in locations with *Canis familiaris* presence (Barcala 2009).

In the eastern rainforest region, *Cryptoprocta ferox* in Makira Natural Park-Masoala National Park showed significant declines in habitat use between years, but no anthropogenic variable explains local extirpation (Farris et al. 2017a). Likewise, habitat degradation and non-native carnivoran presence did not explain habitat use in a single season (Farris 2015a, b), and habitat degradation had little effect on *Cryptoprocta ferox* density (Murphy et al. 2018). However, diurnal activity of *Canis familiaris* did result in temporal shifts in the activity of *Cryptoprocta ferox* away from the daylight hours (Farris 2015c).

Similar trends were found in Ranomafana National Park, where *Cryptoprocta ferox* habitat use declined across years, correlated with increases in human presence and strong co-occurrence with *Canis familiaris (*Farris 2017a). Otherwise, *Cryptoprocta ferox* showed little sensitivity to habitat disturbance, and minor variation in density between non-degraded and degraded sites: 0.12 ± 0.05 and 0.09 ± 0.04 adults/km^2 respectively (mean ± standard error; Gerber et al. 2012a).

Cryptoprocta ferox displays high plasticity, altering both spatial and temporal activity patterns under varying environment conditions. This plasticity is likely to decrease the sensitivity of the species to habitat degradation and non-native carnivorans. Despite evidence that *Cryptoprocta ferox* may be the most adaptable of all euplerids, declines in habitat use are still present.

FOSSA FOSSANA

Habitat use by *Fossa fossana* was not found to decline across years in Makira Natural Park-Masoala National Park or Ranomafana National Park (Farris 2017a, b). However, *Fossa fossana* do display sensitivity to forest degradation and non-native carnivoran presence. In Makira Natural Park-Masoala National Park, habitat use was lower at sites with *Felis catus* presence (Farris et al. 2017a). In Ranomafana National Park, *Fossa fossana* avoids fragmented forests and occupies selectively logged forest at lower densities (1.38 ± 0.22 individuals/km^2) than unlogged forests (3.19 ± 0.55 individuals/km^2; mean ± standard error; Gerber et al. 2012a).

EUPLERES GOUDOTII

In Makira Natural Park-Masoala National Park, *Eupleres goudotii* habitat use declined across years, yet patterns of local extirpation were unexplained by either habitat degradation or non-native carnivoran presence (Farris et al. 2017a). Within years, *Eupleres goudottii* was more likely to use sites near villages where *Felis catus* was present (Farris et al. 2015b). These correlations, along with evidence of long-term declines in *Eupleres goudotii* occupancy, suggest either direct or indirect negative effects of *Felis catus* Nevertheless, we lack clear evidence because of the low detectability of *Eupleres goudotii*.

EUPLERES MAJOR

One publication shows that *Eupleres major* is less likely to occur in degraded forests than in intact forests (Merson et al. 2019a).

GALIDICTIS FASCIATA

In Makira Natural Park-Masoala National Park, *Galidictis fasciata* within-year habitat use is significantly higher closer in proximity to villages than away from them (Farris 2015a). However, habitat use declines significantly across years close to the forest edge, and is independent of non-native carnivoran habitat use (Farris et al. 2017a). This suggests that *Galidictis fasciata* is most vulnerable within edge habitat and, although lower, habitat use is likely to be more stable in forests far from the forest edge and from villages. However, we lack evidence on the casual mechanism of local extirpation at the peripheries of forests.

In Ranomafana National Park, *Galidictis fasciata* occurrence remains extremely low (probability of habitat use < 0.20) in all years. No information is available from the deciduous forest.

GALIDIA ELEGANS

In Makira Natural Park-Masoala National Park, *Galidia elegans* declined in habitat use over six years, but low detection rates precluded a multi-year assessment to understand driving factors (Farris et al. 2017a). However, within years, habitat use by *Galidia elegans* is positively associated with bird presence and understory cover, but detection rates are lower with *Felis catus* presence (Farris 2015a). These results suggest that *Felis catus* influences local activity levels of *Galidia elegans* negatively, and that *Felis catus* could be influential in explaining long-term declines in habitat use by *Galidia elegans*. In Ranomafana National Park, habitat use by *Galidia elegans* declines with increased presence of humans and *Canis familiaris* (Farris et al. 2017b). Habitat use by *Galidia elegans* is lower with increased *Felis catus* presence (Gerber et al. 2012a), and the species prefers to be active at times of the day when *Canis familiaris* and *Viverricula indica* are less active (Gerber et al. 2012b). Combined, these findings suggest that *Galidia elegans* is sensitive to non-native carnivoran presence.

MUNGOTICTIS DECEMLINEATA

In the deciduous forest of the Central Menabe Protected Forests, forest structure did not influence capture rates of *Mungotictis decemlineata*; however, captures were reduced in areas with humans or *Canis familiaris* presence (Woolaver et al. 2006).

SALANOIA CONCOLOR

Salanoia concolor showed significant declines in habitat use over six years, with local extirpation more likely closer to forest edges (Farris et al. 2017a). Over one year, habitat use by *Salanoia concolor* use was positively associated with increased bird presence. *Salanoia concolor* and *Felis catus* had high co-occurrence, using similar sites and sharing temporal activity patterns (Farris et al. 2015a, b); both species are known predators of birds. Because *Felis catus* is positively associated with forest edges, co-occurs with *Salanoia concolor*, and shares a prey source, prey-mediated effects may explain local extirpation of *Salanoia concolor* near forest edge sites.

Disease risk

We found three publications that investigated rising concerns of pathogen transmission in response to increasing presence of non-native carnivoran species with euplerids within deciduous forest and rainforest. In the deciduous forest, *Cryptoprocta ferox* tested positive for toxoplasmosis, feline calicivirus, canine distemper, and canine parvovirus. However, no mortalities were reported (Dollar 2006). In the rainforests of the Betampona Natural Reserve, patterns in habitat use indicated high potential for pathogen transmission between *Canis familiaris, Felis catus,* and euplerids (Rasambainarivo et al. 2017). However, while *Cryptoprocta ferox*, *Galidictis fasciata,* and *Galidia elegans* had confirmed exposure to both *Toxoplasma* and *Leptospira,* no evidence suggested this was due to domestic animals, and the presence of disease was lower than expected (Rasambainarivo et al. 2018). No published literature contained any additional information on disease presence, infection rates or mortality rates from pathogen exposure in euplerids.

Hunting and retaliatory killing

Hunting and retaliatory killing of euplerids have largely been studied in the eastern rainforests near Makira Natural Park-Masoala National Park. All euplerids are reported to be hunted, primarily because they are targeted; they are occasionally acquired opportunistically (Borgerson 2016). Hunting rates are higher in less degraded sites with high euplerid species richness and occurrence (Farris et al. 2015a). *Cryptoprocta ferox* has the highest reported hunting rates (*n*=90 individuals/year), followed by *Galidia elegans* (*n*=31), *Eupleres goudotii* (*n*=10), *Fossa fossana* (*n*=5) and *Galidictis fasciata* (*n*=≥2). However, others have reported that *Fossa fossana* is hunted at higher rates than any other euplerid (Borgerson 2016).

Cryptoprocta ferox has been primarily implicated in poultry depredation and there have been subsequent retaliatory killings (Merson et al. 2019c). As a result, *Cryptoprocta ferox* had the most publications that provided information on hunting and retaliatory killing. Hunting of *Cryptoprocta ferox* has been reported throughout Madagascar, including in Ankarafantsika National Park, Andranomeno Special Reserve, Ranomafana National Park, and Makira Natural Park-Masoala National Park (Golden et al. 2013, Borgerson 2016, Merson et al. 2019c). Household surveys conducted in villages near protected areas examined cases of retaliatory killing of *Cryptoprocta ferox* due to poultry predation: 2.3% of interviewed respondents claimed to attempt to kill, and of those 32% claimed to have successfully killed *Cryptoprocta ferox* (Merson et al. 2019c). In the areas surrounding Makira Natural Park-Masoala National Park, people in 57% of villages and 7% of households participate in the illegal hunting of *Cryptoprocta ferox* (Golden 2009). Given the low abundance of *Cryptoprocta ferox*, rates of hunting are likely to be unsustainable. Despite relatively few publications, reported values are good indicators of the relative commonality and high intensity of hunting pressure on euplerids.

DISCUSSION

Life-history traits

Our review of published literature on the life-history traits of Madagascar's carnivorans indicates that euplerids are skewed towards a slow life-history strategy, and possess high-risk traits (e.g., small litter size, long interbirth intervals, late sexual maturity). For example, *Galidia elegans* gives birth to a single young once a year. However, for six of the eight euplerids, information was available for seven or fewer of the ten target life-history traits, precluding assessment of their life-history strategy. Major gaps in life-history trait knowledge include: age and size at sexual maturity (unknown for 7 of the 8 species), interbirth interval (5 of 8 species), gestation length (4 of 8 species), and average lifespan (7 of 8 species).

Available life-history trait information for each species was principally from one to three publications. Most publications had small sample sizes (<5 individuals) and data were from the same or a similar study area as other studies that reported on that species. The combination of small sample size and low spatial sampling coverage across each species' geographic range suggests that our current knowledge may poorly capture the true variation in traits. Additionally, no publication provides independent information on the effects of anthropogenic pressures on life-history or functional traits (e.g., survival, fecundity). Trait variability and behavioural plasticity may be critical to understanding species resilience to environmental change (Liu et al. 2017), so for most species, we currently do not have the robust dataset required for the reliable assessment of trait-based risk dynamics.

For life-history traits, the breadth of available information originates from a few captive individuals. Captive studies are useful for quantifying gestation period, litter size, and mass at birth. Assessing these traits for wild individuals is extremely difficult and costly, and requires highly invasive techniques. However, captivity precludes any effects of extrinsic environmental factors that may lead to variation. For example, resource availability can influence reproductive patterns, such as litter size or interbirth intervals (Rauset et al. 2015). Therefore, life-history metrics from captive individuals should be considered to indicate the maximum potential for the species under ideal environmental conditions. Information on body mass and body length for half of the euplerids was reported from captured wild individuals, providing some information on variation in size within species and between sexes. However, few researchers recorded the sex and age or age class of the individuals.

We found unclear reporting of life-history trait values. Some researchers noted values of body mass, gestation period, and litter size without providing a source (i.e., there was no reference to an empirical observation or publication), and we found multiple publication sources that we believe reference the same birth. Roland Albignac produced several publications on *Cryptoprocta ferox* that reported litter size and gestation length (see Appendix S2), but seldom referenced where this information came from. In some instances, Albignac reported the same value, for example a litter size of two (Albignac 1969, 1975), but he later reported that litter sizes vary from two to four (Albignac 1984). The discrepancy of reported quantities suggests that new birthing events may have provided new insights; however, sources of information were not explicitly stated or cited. Thus, the number of publications is likely to misrepresent the true sample size for these trait values (e.g. litter size, gestation length). We identify sources of information when and label sources as unknown when appropriate in Appendices S1-S9. We encourage readers to examine the trait tables (Appendices S2-S9) and consider the sources of the reported trait information before integrating it into future analyses.

Functional traits

Functional traits were widely reported in the published literature, so that some information on most traits was provided for all euplerid species. Sampling techniques employed to study traits included remotely triggered camera traps, capture and collaring of individuals, trapping grids, and scat analysis. Notably, *Cryptoprocta ferox* had three times the number of publications of any other species. This apparent bias could be the result of preferential interest or due to the wide distribution and relatively high encounter or detection rate of this species.

Camera traps have proved to be an effective tool for studying the rare and highly cryptic euplerids, and have made the largest contributions to functional trait information across species. However, most camera-trap studies have been conducted largely in the rainforest over a single year, providing a static snapshot of species' habitat use or abundance. Multi-year studies are necessary to assess changes in species' habitat use or abundance, in order to identify mechanistic drivers of the observed dynamics (see MacKenzie et al. 2003). Currently, only two multiyear studies have been conducted, both in the eastern rainforests (Farris et al. 2017a, b).

Targeted captures and trapping grids were used in eight publications (Table 2, Appendix S11) aimed at collaring individuals to evaluate habitat use and home range size or to estimate population density. These efforts have primarily been in the western deciduous forests (*n*=5). More studies targeted *Cryptoprocta ferox* (*n*=5), whereas *Mungotictis decemlineata*, *Galidia elegans* and *Fossa fossana* each had a single study aimed at collaring or trapping. Most studies (5 of 8) had relatively small sample sizes (< 20 individuals; range of 2-54 individuals). Unfortunately, many studies did not report measures of uncertainty, such as confidence intervals or standard errors. More work is thus needed to address low capture rates and improve our knowledge by increasing the number of individuals sampled within these studies. Lastly, scat surveying was reported in four publications to inform on the diet of three euplerids: *Fossa fossana* (Goodman et al. 2003), *Galidictis fasciata* (Andriatsimietry et al. 2009) and *Cryptoprocta ferox* (Hawkins & Racey 2008). Complementary diet studies are needed to assess the ranges of prey species consumed, as scat samples can be influenced by several factors (e.g., environmental conditions) and thus may not fully represent a species' diet breadth or relative composition, or consumption rates.

Ultimately, these methodologies have improved the breadth of available information. However, few studies have been conducted that test the influence of anthropogenic pressures, principally due to the difficulty of finding comparative controls of minimally disturbed environments. The environmental conditions under which the data were collected may influence results of such studies. The underlying conditions should be given consideration when deciding if results from these studies can be generalised across a species' geographic range.

Anthropogenic pressures

Research on anthropogenic pressure on euplerids has, by necessity, explored multiple stressors at once (e.g., habitat fragmentation and invasive species), which can hamper inference to independent anthropogenic effects. The implication of this design is that while each study makes critical first steps towards providing data on functional traits, results should be applied with caution. For example, habitat use by *Fossa fossana* as reported by Farris et al. (2015b) is specific to conditions in which *Fossa fossana* is experiencing both landscape fragmentation and effects of *Canis familiaris* and *Felis catus* Therefore, it may be inappropriate to extrapolate patterns of *Fossa fossana* habitat use across the species' range, unless conditions are homogenous to the conditions of the study site or we have estimates of the independent effect size. In fact, heterogeneity in conditions exists: we found variation in top model parameters between study sites explaining *Cryptoprocta ferox* habitat use and detection probability (Gerber et al. 2012a, Farris et al. 2015a, Merson et al. 2019a). However, we also demonstrate consistent trends in species' responses to anthropogenic pressures. In Makira Natural Park-Masoala National Park and Ranomafana National Park, Farris et al. (2015a) and Gerber et al. (2012a) found negative relationships between *Felis catus* occurrence and habitat use of *Galidia elegans*. Such patterns provide strong evidence of consistent negative effects across environmental conditions, and give generalisable insights into species' sensitivities.

Information on disease risk, hunting, and retaliatory killing provides insights into mortality risks for euplerids due to anthropogenic activity. Publications on disease confirmed the presence of *Toxoplasmosis* and other diseases common in *Canis familiaris* and *Felis catus* in the native carnivoran community. Information on hunting and retaliatory killing confirmed that all euplerids are hunted and consumed, so that hunting constitutes an additional source of mortality for these species. The exact effect of the reported hunting rates on euplerids cannot be known without information on individual and population parameters, such as population density and cause-specific mortality. However, given the known patterns in euplerid life-history traits, functional traits, and declining trends in habitat use, we may infer that losses of even relatively few individuals (< 5 per year) may be highly impactful to local populations experiencing multiple anthropogenic pressures. Future studies could be improved by employing hypothesis-driven sampling designs to test the effects of hunting and retaliatory killing on functional traits.

Applications for species conservation category

The International Union for Conservation of Nature (IUCN) is the leading global source for assessing species' extinction risk. Listing category for each species is determined by using stringent criteria, such as evidence of species' range contractions, population declines, and general assessment of major environmental pressures. Rare, elusive and poorly studied species often lack geographic range and population size estimates and known trends, which can introduce uncertainty surrounding their evaluations and influence the accuracy of assessments and their listing category (Hayward et al. 2015, Ramesh et al. 2017). For example, *Cryptoprocta ferox* was downgraded to Vulnerable due to the paucity of data which precluded the species from meeting Red List standards for the Endangered category (IUCN 2020). However, through synthesising and integrating relevant life-history and functional trait information, we can decrease uncertainty through augmenting information, or we can identify specific sources of uncertainty, thus improving overall inference (Trull et al. 2018). Listing category is influential in guiding management and conservation policy and in determining both research and funding priorities (Rodrigues et al. 2006, Betts et al. 2019). Accuracy of assessments and transparency of uncertainty are pivotal. Compiling available information on functional and life-history traits, including intra-trait variation, and on responses to anthropogenic pressures is critical, yet, until now, has never been completed for euplerids.

Research priorities

The culmination of reported traits, negative influence of ongoing anthropogenic pressures and lack of robust metrics (e.g., for population trends and trait variability), indicate that euplerids are at high risk, yet may reach the cusp of extinction without notice due to significant gaps in knowledge. Based on the findings of our review, we identified four major research priorities for euplerids:

1. Fill knowledge gaps in life-history and functional traits. Research is needed on the unknown life-history traits (average life span, age at sexual maturity, interbirth interval, litter size) and functional traits (density estimates, home range size, sociality). Capturing and collaring efforts are needed to investigate vital rates (e.g., survival, fecundity), in order to understand population dynamics and the influence of resource variability on traits.
2. Conduct multi-year studies investigating anthropogenic pressures. Multi-year research is essential for assessing changes in species' habitat-use and evaluating factors influencing the observed trends.

3. Diversify studies across eco-regions and protected areas. Broadening of the spatial coverage of field studies is needed to capture spatial variation in trait information. This should be done by targeting underrepresented species in less-studied sites.
4. Integrate available life-history and functional traits into risk assessments. Research is needed to allow life-history and functional trait information to be formally integrated into risk assessments, to understand species-specific vulnerability to anthropogenic pressures, to estimate extinction risk, and to provide a clearer understanding of current and future conservation challenges.

Future research should prioritise filling gaps in our knowledge of influential traits, evaluating effects of anthropogenic pressures, and integrating trait information to improve risk assessments and extinction forecasts.

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Table 1. Summary of available information on 10 life-history traits and 7 functional traits, all species-specific and some sex-specific, from the literature; when trait information included multiple sources, we listed the best source (e.g., a study conducted in the wild would be listed if there was also a study on museum specimens).

	C. ferox	*F. fossana*	*E. goudotii*	*E. major*	*G. elegans*	*G. fasciata*	*M. decimerliata*	*S. concolor*
Life history traits								
Gestation length	🟩	🟩	⬜	⬜	🟩	⬜	⬛	⬜
Litter size	🟩	🟩	⬜	🟩	🟩	⬜	🟦	⬜
Sex ratio of offspring	🟩	⬜	⬜	⬜	⬜	⬜	⬜	⬜
Mass at birth	🟩	🟩	⬜	🟩	🟩	⬜	🟩	⬜
Weaning age	🟩	🟩	⬜	⬜	🟩	⬜	🟩	⬜
Interbirth interval	🟩	⬜	⬜	⬜	⬜	⬜	🟦	⬜
Age- & size at sexual maturity	🟩	⬜	⬜	⬜	🟢	⬜	🟢	⬜
Male	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
Female	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
Average lifespan	🟩	⬜	⬜	⬜	⬜	⬜	🟢	⬜
Body Mass Unknown sex	⬛	⬛	🟨	🟢	⬛	🟨	⬛	🟨
Male	⬛	⬛	⬜	🟦	⬛	⬜	🟦	🟨
Female	⬛	⬛	⬜	⬜	⬛	⬜	🟦	🟨
Body length: Unknown sex	⬛	⬛	⬜	🟨	⬛	🟨	⬛	🟨
Male	⬛	⬜	⬜	🟦	⬜	⬜	⬛	🟨
Female	⬛	⬜	⬜	⬜	⬜	⬜	⬛	🟨
Functional traits								
Population density	🟦	⬛	⬜	⬜	🟦	🟦	🟦	⬜
Feeding guild	⬛	⬛	🟩	🟦	⬛	🟦	🟢	⬛
Sociality	⬛	🟢	⬜	⬜	⬛	⬜	⬛	⬜
Range distribution	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛
Habitat Use	⬛	⬛	🟦	⬜	⬛	⬛	🟦	⬛
Activity patterns	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛
Home Range	🟦	🟦	⬜	⬜	🟢	⬜	⬛	🟦

Source of Information

⬜	None
🟨	Museum specimen only[1]
🟩	Captive individual (s)[2]
🟢	Informal observation(s)[3]
🟦	Single reference, wild study[4]
⬛	Multiple references, wild individual/population[5]

[1] Museum specimen: a skin or halotype

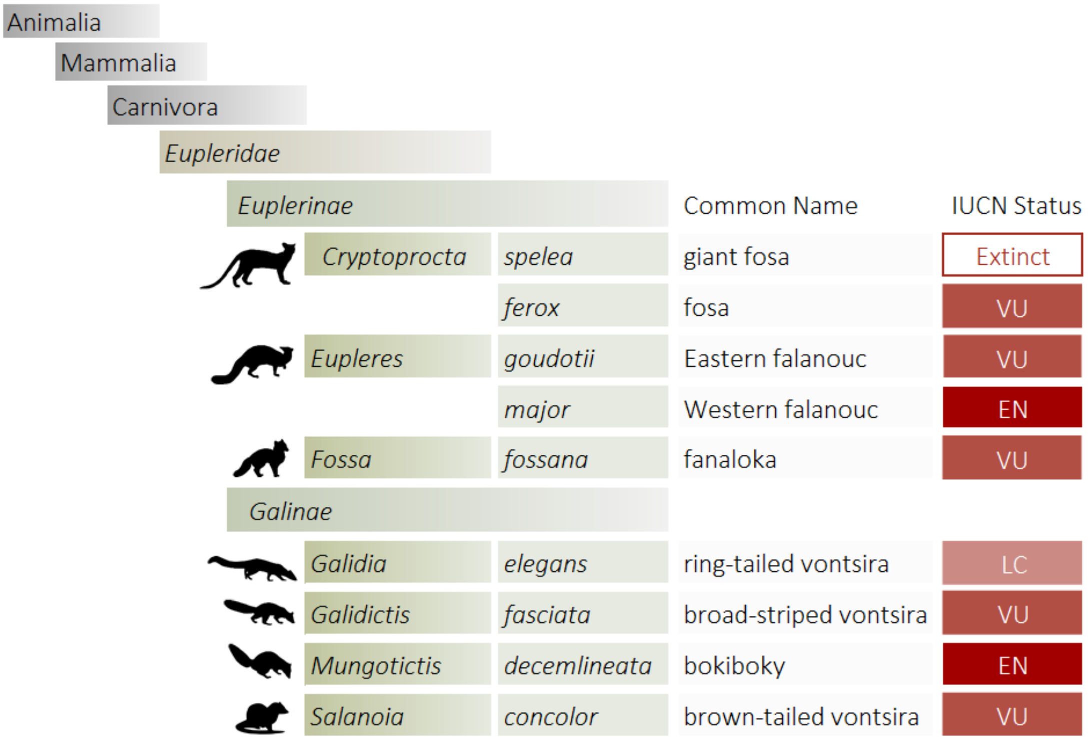
[2] Captive individuals: indviduals who are studied at zoos, either captive or wild born; trait may include additional museum specimens

[3] Informal observaton(s): stated within the literature with no idenifiable source or was observed randomly by chance

[4] Single reference wild study: only one study initiate that directly examined trait

[5] Multiple references from published wild population: greater than one study that directlyexamined the trait in wild non-captive invididuals or populations

Figure 1. Currently recognized species of family Eupleridae, including Malagasy common names and latest IUCN status (VU = vulnerable, EN = endangered, LC = least concern)



Animalia
Mammalia
Carnivora
Eupleridae

Euplerinae		Common Name	IUCN Status
Cryptoprocta	*spelea*	giant fosa	Extinct
	ferox	fosa	VU
Eupleres	*goudotii*	Eastern falanouc	VU
	major	Western falanouc	EN
Fossa	*fossana*	fanaloka	VU
Galinae			
Galidia	*elegans*	ring-tailed vontsira	LC
Galidictis	*fasciata*	broad-striped vontsira	VU
Mungotictis	*decemlineata*	bokiboky	EN
Salanoia	*concolor*	brown-tailed vontsira	VU

Figure 2. Distribution of publications by species and eco-regions for life-history traits (A) and functional traits (B) for literature reporting on wild individuals or populations

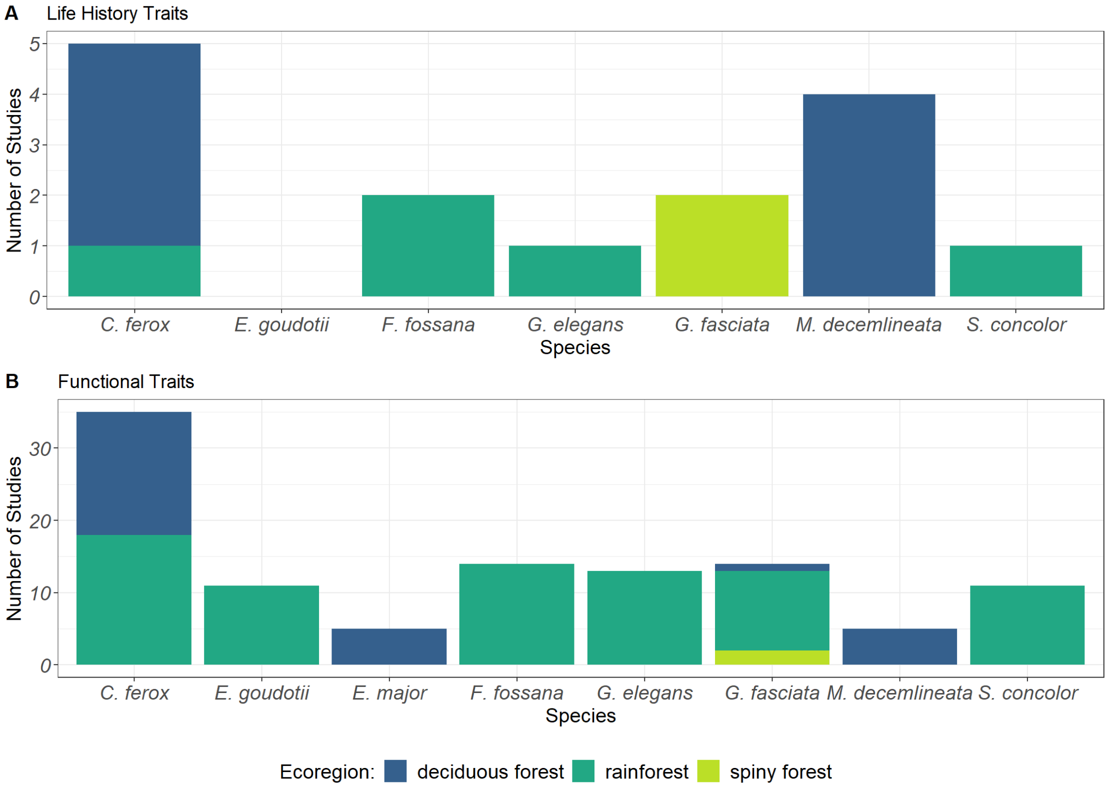
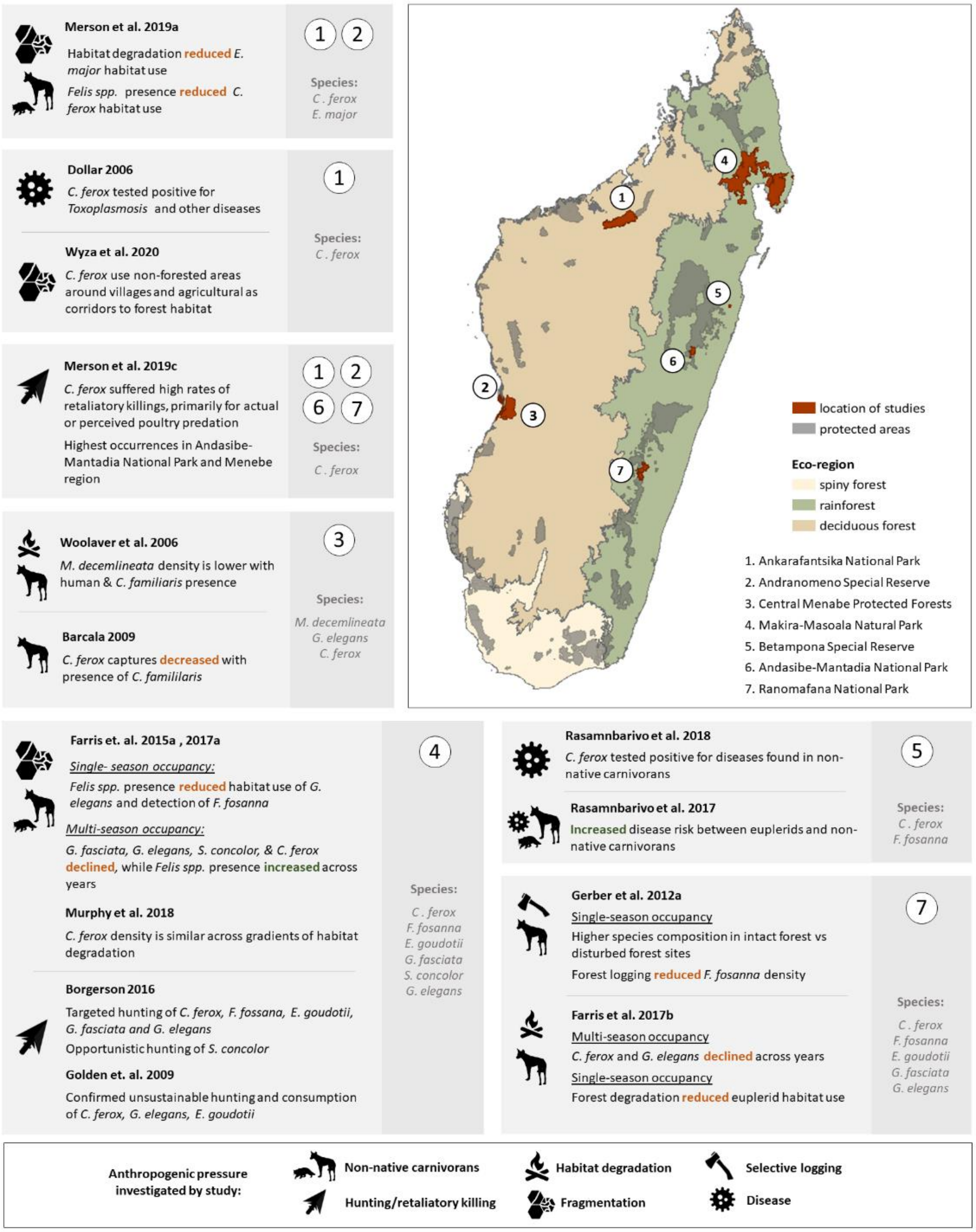


Figure 3. Key studies on consequences of anthropogenic disturbance for euplerids. Anthropogenic pressure investigated in the study are denoted by black icons, location of study is denoted by a reference number (1-8) and coordinates to the inset map, and species investigate are listed in grey. Location of study sites are in red, all protected areas in Madagascar are in gray within each eco-region. Major findings for publications with a resulting consequence of pressures on euplerids is summarized in the grey boxes. For detailed findings by species see Appendices S2-S9.



Merson et al. 2019a

Habitat degradation reduced *E. major* habitat use

Felis spp. presence reduced *C. ferox* habitat use

① ②

Species: *C. ferox*, *E. major*

Dollar 2006

C. ferox tested positive for *Toxoplasmosis* and other diseases

Wyza et al. 2020

C. ferox use non-forested areas around villages and agricultural as corridors to forest habitat

①

Species: *C. ferox*

Merson et al. 2019c

C. ferox suffered high rates of retaliatory killings, primarily for actual or perceived poultry predation

Highest occurrences in Andasibe-Mantadia National Park and Menebe region

① ② ⑥ ⑦

Species: *C. ferox*

Woolaver et al. 2006

M. decemlineata density is lower with human & *C. familiaris* presence

Barcala 2009

C. ferox captures decreased with presence of *C. famililaris*

③

Species: *M. decemlineata*, *G. elegans*, *C. ferox*

Farris et. al. 2015a , 2017a

Single- season occupancy:

Felis spp. presence reduced habitat use of *G. elegans* and detection of *F. fosanna*

Multi-season occupancy:

G. fasciata, G. elegans, S. concolor, & C. ferox declined, while *Felis spp.* presence increased across years

Murphy et al. 2018

C. ferox density is similar across gradients of habitat degradation

Borgerson 2016

Targeted hunting of *C. ferox, F. fossana, E. goudotii, G. fasciata and G. elegans*

Opportunistic hunting of *S. concolor*

Golden et. al. 2009

Confirmed unsustainable hunting and consumption of *C. ferox, G. elegans, E. goudotii*

④

Species: *C. ferox*, *F. fosanna*, *E. goudotii*, *G. fasciata*, *S. concolor*, *G. elegans*

Rasamnbarivo et al. 2018

C. ferox tested positive for diseases found in non-native carnivorans

Rasamnbarivo et al. 2017

Increased disease risk between euplerids and non-native carnivorans

⑤

Species: *C. ferox*, *F. fosanna*

Gerber et al. 2012a

Single-season occupancy

Higher species composition in intact forest vs disturbed forest sites

Forest logging reduced *F. fosanna* density

Farris et al. 2017b

Multi-season occupancy

C. ferox and *G. elegans* declined across years

Single-season occupancy

Forest degradation reduced euplerid habitat use

⑦

Species: *C. ferox*, *F. fosanna*, *E. goudotii*, *G. fasciata*, *G. elegans*

Anthropogenic pressure investigated by study:

- Non-native carnivorans
- Hunting/retaliatory killing
- Habitat degradation
- Fragmentation
- Selective logging
- Disease

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website. *https://doi.org/10.1111/mam.12234*

Appendix S1. Literature reviewed
Appendix S2. *Cryptoprocta ferox* trait tables
Appendix S3. *Fosa fossana* trait tables
Appendix S4. *Eupleres goudotii* trait tables
Appendix S5. *Eupleres major* trait tables
Appendix S6. *Galidictis fasciata* trait tables
Appendix S7. *Galidia elegans* trait tables
Appendix S8. *Mungotictis decemlineata* trait tables
Appendix S9. *Salanoia concolor* trait tables
Appendix S10. Summary of all reported density estimates
Appendix S11. Capture events used to estimate density and home range size

MANUSCRIPT 2

Forest carnivorans living on the edge with invasive predators

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Abstract

Forest edge and invasive predators have been identified as two primary threats to carnivore populations, globally. These pressures are often found in unison, facilitated by anthropogenic activities (e.g., fragmentation), and together may have a greater influence then when they occur separately. To date, targeted conservation actions for Madagascar carnivorans has been hindered by a failure to understand the relative contributions of these factors in driving species declines. We conducted a camera survey along the edge of intact continuous protected rainforests in eastern Madagascar to evaluate the extent of invasive predators and forest edge separately and in combination on native carnivoran spatial use. We hypothesized that changes at the forest edge interact with invasive predator relative activity or co-occurrence to reduce carnivore spatial use near the forest edge and separately have less influence. In contrast to findings in fragmented and degraded forests of Madagascar, our study found little evidence that habitat degradation from hard forest edge and invasive predators separately or in combination indiscriminately reduced native carnivoran spatial use in continuous intact forest. We found some support that at the forest edge, vegetational changes of increasing shrub cover and co-occurrence with dogs, degrades habitat and reduces spatial use of three of four native carnivorans. Instead, we found that proximity to villages, especially with high invasive predator activity (free-ranging cats) is of primary concern and mitigation is required. However, native carnivorans showed variable sensitivities to examined pressures and our results support the necessity of species-specific management actions to maximize conservation outcomes. Our results highlight the importance of evaluating the extent to which interactions between pressures are occurring in studies aimed at assessing species risk under multiple threats. By conducting these empirical evaluations, practitioners can improve mitigation efforts using evidence-based actions to target the primary contributing pressure(s).

Key-words: camera trap, cats, co-occurrence, dogs, edge effects, habitat degradation, meso-carnivorans, rainforest

1 | Introduction:

Forest dependent carnivorans are under pressure from the proliferation of forest edges and free-ranging dogs and cats. Forest edges have increased around the world due to intensified human activity from agriculture, resource extraction and human expansion (Haddad et al., 2015). Dogs and cats are the world's most abundant and widespread invasive, intraguild mammalian competitors (Woodroffe & Ginsberg, 1998; Gompper et al. 2014). Forest edge and invasive predator effects can independently influence community and population dynamics, or in unison, result in additive or interactive effects (Didham et al., 2007; Doherty et al., 2015). Identifying the relative impacts of each is essential for developing targeted actions at or near forest edges to maximize conservation outcomes, such as the protection of threatened species.

Wide-ranging global forest fragmentation has led to high proportions of forests near a hard forest edge - abrupt transition in landscape from forest to non-forested, including human dominated and natural landscape (Taubert et al., 2018). The creation of forest edge results in abiotic and biotic changes, importantly, microclimate (e.g. humidity, air temperature; Magnago et al., 2015) and vegetation structure (e.g. shrub cover, canopy cover, canopy height; Didham & Lawton, 1999). These changes can reduce habitat suitability for species across trophic levels, triggering population declines and community shifts at the peripheries of forest boundaries (Laurance & Yensen, 1991; Pfeifer et al., 2017). Whether such changes lead to an ‘edge effect’ can be understood by measuring changes in populations or communities near the forest edge relative to the interior forest (Harper et al., 2005). Forest edge effects from human activities are predicted to be comparatively worse for carnivorans compared to other taxonomic groups, given their large range requirements, low densities, and propensity for human-wildlife conflict (Woodroffe & Ginsberg, 1998). Edge effects have been shown to negatively impact carnivore survival (Balme, Slotow & Hunter, 2010), population density (Revilla, Palomares & Delibes, 2001), spatial use (Kuehl & Clark, 2002), and increase their risk to human persecution (Woodroffe & Ginsberg, 1998); however, species responses are variable due to numerous abiotic and biotic factors that produce edge effects (Kiffner, Stoner & Caro, 2013; Pfeifer et al., 2017).

Free-ranging dogs and cats may themselves be considered an edge effect (Lacerda, Tomas & Marinho-Filho, 2009). Dogs and cats are more active near forest edges and anthropogenic activity centers (e.g., human settlements, roads; Farris et al., 2015a; Paschoal et al., 2018). However, they can also occupy interior forest, either accompanying humans or occurring alone (Farris et al., 2015b,c; Paschoal et al., 2016). Presence of dogs and cats negatively impact native species through predation, competition, fear-mediated behavioral effects, and disease transmission (Medina et al., 2011; Gompper, 2014; Lessa et al., 2016;). Outcomes of such interactions include reduced spatial use (Revilla, Palomares & Delibes, 2001; Vanak & Gompper, 2010), temporal activity shifts (Gerber, Karpanty & Randrianantenaina, 2012a), increased mortality from intraguild killings (Silva-Rodriguez, Ortega-Solis & Jimenez, 2010), and reduced fitness from harassment (Young et al., 2011). Such growing evidence of the negative effects of free-ranging dogs and cats on native wildlife worldwide has raised concerns in both wildlife management and conservation fields (Hughes & Macdonald, 2013; Loss, Will & Marra, 2013; Weston et al. 2014; Doherty et al., 2016, 2017).

While studies have shown that invasive predators influence the habitat use of native species, evaluating the extent to which this influence is additive or interactive with structural changes to forests near the edge is essential to identifying the degree of these conservation issues and for developing management actions. Habitat features including vegetation structure, proximity to anthropogenic centers, and prevalence of trails influence invasive predator behavior and alter invasive-native interactions (Sepúlveda et al., 2015). For example, in forested areas dogs are known to select for bare ground, trails and roads for movement and avoid dense vegetation (Sepulveda et al., 2015; Farris et al., 2015b). In such cases, native predators may be "shielded" from direct negative interactions with dogs when fine-scale shrub cover is high. Conversely, cats have shown higher use in areas with high shrub cover, where prey availability is often higher (Recio et al., 2014). Thus, within high shrub cover environments cats may influence native carnivorans to a greater extent, directly (predation) and indirectly (prey-mediated). Investigating the influence of free ranging dogs and cats and habitat structure on carnivorans is much needed, particularly in areas with high conservation value threatened by rapid habitat degradation (Vanak & Gompper, 2010). Such areas include islands, where high levels of endemism and species richness is coupled with large human impacts (Kier et al., 2009). Forest dependent medium-large bodied mammals living on islands are at highest risk of extinction and largely understudied (Brooke et al., 2014; Tilman et al., 2017).

Forest regions of the island of Madagascar are a biodiversity hotspot and a global priority for the protection of mammalian carnivorans (DiMinin et al., 2016). Forest edge effects and introduced free-ranging dogs and cats are two primary threats to all endemic forest dependent carnivorans of Madagascar (IUCN 2020). Recently, research has investigated how forest fragmentation, degradation, dogs, cats or a combination influence carnivore spatial or temporal activity (Wampole, Farris & Gerber, 2021). No research has examined the hard-edge interface between human dominated landscapes and natural intact forested landscapes, where the extent of each pressures can be evaluated independently, importantly at boundaries of large protected forest - the last strongholds of viable native carnivoran populations (Gerber, Karpanty & Randrianantenaina, 2012b; Murphy et al., 2018).

Our study aimed to quantify the separate and combined influence of invasive predators (i.e., dogs and cats) and hard forest edge on Madagascar's native carnivoran spatial use. We hypothesized native carnivoran spatial use is influenced by both invasive predators and changes in habitat (specifically vegetation structure) from hard forest edge; and that in combination, invasive predators and forest edges interact, causing a greater negative effect together than their combined additive effects. We evaluated our hypothesis by estimating the magnitude (e.g., effect size) of separate single pressures from invasive predators and forest edges and their combined effects (additive or interactive) using an occupancy modeling framework (MacKenzie et al., 2017). We expected that invasive predators and forest edge could influence native carnivorans at two scales, their relative activity (probability of detection) and occupancy (probability of occurrence). We used single-season, single-species (MacKenzie et al., 2002) and multi-species co-occurrence models (Rota et al., 2016) to test the respective hypotheses that native carnivoran spatial use is negatively affected by 1) invasive predator relative activity and forest edge variables, and 2) invasive predator occurrence and forest edge variables.

2 | Materials & Methods:

2.1 | Study Site

We conducted field surveys during the cool-dry season (June – October 2019), within and bordering Mantadia National Park in the eastern humid rainforest of Alaotra-Mangoro Region, Madagascar. Mantadia is approximately 100 km^2 and is one of the last remaining large expanses of intact rainforest in Madagascar. Forest outside of the park boundaries have experienced intense logging, tavy (slash and burn agriculture), and mining, resulting in small remnants of highly fragmented, and degraded forest stands (McConnell, Sweeny & Mulley, 2004). Our study covered roughly a 50 km^2 area near the western edge of Mantadia (Figure 1). The southern edge of our study area contained hard forest edge, delineated by a national park road. Villages adjacent to the road are surrounded by agricultural fields and house free ranging (unconfined/unleashed) cats *Felis spp*. and dogs *Canis famililaris*. The northern edge of Mantadia is intact continuous forest that intersects community protected forest (Torotofotsy) with outlying small settlements and footpaths to large village communities outside the park boundary to the west. Five species of native carnivoran's distributional range include Mantadia and were expected to be observed during our survey (IUCN 2020): *Cryptoprocta ferox* (fosa), *Fossa fossana* (spotted fanaloka), *Eupleres goudotii* (eastern falanouc), *Galidictis fasciata* (broad-striped vontsira), and *Galidia elegans* (ring-tailed vontsira).

2.2 | Camera Trap Survey & Image Processing

We established 78 sites, approximately 500 m apart, on existing trails spanning from the hard forest edge to the interior forest. At each site, we placed one remote trail camera (Browning- Strike Force Pro XD) 20-30 cm off the ground, operating continuously throughout the day. We processed images using software Digikam (www.digikam.org) to identify species detected. We created detection histories for each species using camtrapR (v2.0.2, Niedballa et al., 2016) in the R programing language (R Core team, 2020). We set occasion lengths as 1-day intervals. We considered a 30-minute time difference between photographs of the same species at the same site to be an independent detection event (Gerber, Karpanty & Randrianantenaina, 2012b).

2.3 | Forest Edge and Ancillary Model Covariates

For each camera site, we measured vegetation cover at two scales: site (50 m) and landscape (1000 m). Site-level (SL) metrics were calculated using the point intercept method (Canfield, 1941). We quantified the percent cover at each site by recording the presence of down/dead, ground, shrub, and canopy cover - open, low, mid, and high, following Gerber, Karpanty & Randrianantenaina, 2012a (Supporting Information, S1). Landscape level (LL) cover type was obtained from Landsat 4-5 imagery, 30 x 30 m resolution (acquired October 10, 2018) and classified using methodology from Freitas, Mellow & Cruz (2005); percent cover was calculated using the R package landscapemetrics with a 1000 m site buffer (v.1 .4.4; Hesselbarth et al., 2019). Lastly, we calculated the Euclidean distance to the nearest village and hard forest edge from each camera site.

We defined a hard forest edge boundary using our vegetation classification data, drawing a polyline along the intersection of canopy and non-canopy vegetation classifications using ArcGIS (10.6.1; ESRI 2011). To assess potential edge variables, we tested for a linear relationship between quantified vegetation structure metrics (SL and LL) and distance to hard edge (Supporting Information, S2). We found three structural vegetation metrics that had an observed independent linear variation as distance from a hard forest edge increased, thus capturing alternative types of potential vegetational edge effects: percent shrub (*shrub*, SL), percent open canopy (*open canopy*, LL), and percent high canopy (*high canopy*, LL). Near the forest edge *shrub* and *open canopy* were higher, and *high canopy* lower. We also consider distance to hard forest edge (*forest edge*) as a potential variable, which represents unexplained variation in habitat use as distance from the edge increases. Lastly, we established two ancillary metrics to forest edge; distance to village (*village*) and human trap success (human; as the sum of independent detection events per site, scaled by the number of days the site was sampled), previously found to be important predictors and provide an alternative to our hypotheses. All variables are supported in the literature as predictors of native carnivoran habitat use, prey availability and/or species interactions (Table 1).

2.4 | Invasive predator model inclusion specification

For the single-species occupancy model, we modeled the parameters ψ (probability of occurrence) and p (probability of detection; a measure of relative activity) to investigate species spatial use. We quantified invasive predator's relative activity using dog and cat trap success (*dog* and *cat*, respectively). We included *dog* and *cat* as variables modeling ψ and p for each native carnivoran. The advantage of the single-species model is that it allows the consideration of a small amount of site activity by invasive predators to not have a large effect on native species spatial use, while a lot of use might reduce native species relative activity or occurrence.

For the multi-species co-occurrence model, invasive predator presence/absence was treated explicitly in the model and could affect native species occupancy and relative activity. The advantage of the co-occurrence model is that we can jointly consider variation in detection of invasive and native species but assume that native carnivorans will respond to the occurrence of an invasive predator similarly at any relative activity level.

2.5 | Occupancy Models

2.5.1 | Single-species Model

We examined the influence of invasive predator relative activity and forest edge, by constructing a set of 14 competing global models (8 additive, 6 interactive) and 2 additional global models (Supporting Information, S3). We first created eight global models that modeled ψ as an additive effect of invasive predator relative activity and forest edge variables. We paired each invasive predator variable (*dog*, *cat*) with each forest edge variable (*shrub, open canopy, high canopy, forest edge*) separately by global model, as forest edge variables represent competing hypotheses about types of structural edge effects. We then created six global models that modeled ψ as an interaction between invasive predators and forest edge variables on native carnivorans, by combining *shrub* and *forest edge* separately with each invasive predator (*dog, cat*). We had no a priori knowledge to justify inclusion of interaction terms between invasive predators and canopy cover variables (*open canopy, high canopy*) for Madagascar carnivorans, thus we excluded these combinations from consideration (Supporting Information, S4). The result was a set of competing models of plausible interactions of vegetation structure and invasive predators on carnivoran spatial use supported by the literature (Table 1).

Lastly, we generated two competing global models, representing an alternative hypothesis, that native carnivoran occupancy was influenced by proximity to a village and not explained by forest edge variables; we therefore modeled ψ as an additive and interactive effect of *village* and invasive predators (*dog*, *cat*). For all global models, we modeled p by forest edge with each invasive predator (*dog*, *cat*), and included ancillary variables, *human* and *village*, to account for variation in relative activity (p) unrelated to our hypotheses.

We generated all possible combinations of each global model while holding forest edge variables constant (*shrub, open canopy, high canopy, forest edge*) using “dredge” in the R package MuMIN (v.1.43.17; Bartoń et al., 2020). We then generated all possible combinations of invasive predator relative activity (*dog*, *cat*), excluding forest edge variables. Our complete model set of 960 models included all possible combinations of singular, additive, and interactive influences of hypothesized forest edge effects and each invasive predator on native carnivoran occupancy. Due to the small sample size for the broad-striped vontsira, we removed interaction terms and restricted models to include no more than two variables on ψ or p in any given model (n=114 models). Prior to model fitting, all covariates were log transformed then scaled and centered, reducing the effects of outliers, improving model convergence, and providing meaningful comparison between estimated coefficients. Covariates were tested for multicollinearity (Supporting Information, S2) and were found to all have a correlation coefficient < 0.2, except human and dog site-level detection rates at 0.58. We compared models using Akaike Information

Criterion corrected for small sample size (AICc; Burnham and Anderson, 2002). All analyses were done in the R programming language and models were fit using the package unmarked (v. 1.0.0; Fiske & Chandler, 2011).

We quantified the strength of variables that represent absolute importance of forest edge and invasive predator influence using model averaged coefficients that provide a weighted effect size (Galipaud, Gillingham & Dechaume-Moncharmont, 2017, Supporting Information, S5). We summarized coefficient size by small (0.1-0.5), medium (0.5-1.0), and large (>1.00) effects. Covariates were standardized; thus, a medium effect would have a 0.5 to 1-unit change in standard deviation. For comparative purposes, we also report the sum of Akaike weights (*sw*) by variable as additional support of coefficient relative importance, following standard practice (Supporting Information, S7; Burnham & Anderson 2002) despite current debate concerning its utility (Galipaud, Gillingham & Dechaume-Moncharmont, 2014, 2017; Giam & Olden, 2016). Lastly, we assessed the effects of invasive predators and forest edge variables using model averaged predictions, accounting for model selection uncertainty (Burnham & Anderson, 2004); note that model averaged predictions are not predictions from model averaged coefficients (Galipaud, Gillingham & Dechaume-Moncharmont, 2017).

2.5.2 | Multispecies Model

We evaluated the influence of invasive predator co-occurrence on native carnivoran spatial use, independently and in combination with potential forest edge variables. For each native carnivoran, we considered the influence of two species co-occurrence (native carnivorans and – dogs only (native+dog), – cats only (native+cat), – dogs and cats (native + dog + cat) and three species co-occurrence (native carnivoran, dogs and cats;

native*dog*cat). We also included an independent model, which excluded any influence of species interactions (Supporting Information, S3). Following Rota et al., 2016, we modeled species co-occurrence as natural parameters (*f*), quantified as the log odds of species occupancy. For example, when considering 2 species (dog and fosa) co-occurrence varying by *shrub*, we specify f's as ratios of combinations of fosa only occupancy probability (ψ_{10}), dog only (ψ_{01}), dog and fosa (ψ_{11}), and no occurrence (ψ_{00}), which are linked to covariates as a linear model as,

$$f_1 = \log\left(\frac{\psi_{10}}{\psi_{00}}\right) = \alpha_0 + \alpha_1 shrub$$

$$f_2 = \log\left(\frac{\psi_{01}}{\psi_{00}}\right) = \beta_0 + \beta_1 shrub$$

$$f_{12} = \log\left(\frac{\psi_{11}\psi_{01}}{\psi_{10}\psi_{01}}\right) = \gamma_0 + \gamma_1 shrub$$

where α_0, β_0, and γ_0 are intercepts and α_1, β_1, and γ_1 are slope parameters associated with *shrub*. From the natural parameters, we can derive a conditional probability using the inverse-logit link to examine variation in fosa occupancy, conditional on the occurrence of dogs across varying measures of shrub as:

$$P\ (fosa\ |dog) = logit^{\ -1}((\alpha 0 + \gamma 0) + (\alpha 1 + \gamma 1\ )\ \times\ shrub)$$

For each native species, we modeled natural parameters of marginal occurrence (occurrence without species interactions; e.g., f_1 and f_2), using variables found to be have medium or large absolute importance from our single-species model results. We modeled environmental covariates on species interactions (e.g., f_{12}) based on important predictor variables from previous studies and considered here (shrub, forest edge, village; Table 1). We created 17 competing models, for fosa, fanaloka, and falanouc, which included marginal, pairwise and three-species co-occurrence models. These models represented our specific hypotheses in the ways in which native carnivoran spatial use could be influenced by invasive predator occurrence separately or in combination with forest edge variables (*forest edge, shrub*) and our alternative hypothesis *village*. Due to data sparsity, we fit only pairwise co-occurrence models to examine broad-striped vontsira spatial use, resulting, in six competing models. Low detection of the ring-tailed vontsira resulted in excluding them from this analysis; we only report naïve occupancy. We compared models using AICc and evaluated top model coefficients to determine relative support for the separate and combined influences of invasive predator occurrence and hypothesized forest edge effects. Models were fit using the package unmarked (Fiske & Chandler, 2011).

3 | Results

3.1 | Survey

We sampled for a total of 9396 trap nights (n=78 sites) and captured 1341 independent detections of target species. Fanaloka were the most frequently detected species (n=538), followed by falanouc (n=276), dogs (n=248), fosa (n=161), cats (n=76), broad-striped vontsira (n=29) and ring-tailed vontsira (n=13). Ring-tailed vontsira naïve occupancy was 0.08. We detected native carnivorans at different frequencies, separately and in combination with invasive predators near and far from a forest edge, providing appropriate combinations to test our hypotheses (Supporting Information, S6).

3.2 | Single species occupancy model

We found little evidence to support our hypothesis that native species occurrence was driven by an interaction between invasive predator relative activity and forest edge variables (Figure 2; Supporting Information, S7, S8). Specifically, we found no medium or large interaction effects with these variables for any species. We found some support that *dog* and *shrub* in combination influenced native carnivoran occupancy. Specifically, we found a small negative effect of *dog* and *shrub* on fanaloka occurrence with lower occupancy at sites with higher dog relative activity and percent shrub cover. We also found support for a small positive effect of the interaction of *cat* and *forest edge* on fosa occurrence, however, this effect was much less supported compared to the large positive effect of only *forest edge* (Figure 3A). We found no evidence that forest edge variables separately influenced carnivoran occupancy, except for the fosa (*forest edge*). We also found no clear evidence that invasive predator relative activity separately influenced native carnivoran occupancy. We did find support of our alternative hypothesis of an interaction between invasive predator relative activity and *village* for falanouc and fanaloka (Figure 2, Figure 3B-C). Lastly, we found a small positive effect of *village* alone on broad-striped occupancy.

We found invasive predator relative activity influenced native carnivoran activity (*p*), such as *dog* having a large negative effect on falanouc activity and a small effect on fosa activity (Figure 2). *Cat* had a medium positive effect on falanouc activity, but we found no effect on activity for any other native carnivoran. We also found support that native carnivoran activity is influenced by *forest edge*, in that *forest edge* had a medium positive effect on fanaloka and falanouc activity. *Village* had contrasting effects on native carnivorans, as we found a medium negative effect on falanouc activity, a small positive effect on fanaloka, and a medium positive effect on broad-striped vontsira activity. Lastly, *human* had a small positive effect on fosa and fanaloka, and a medium effect on broad-striped vontsira. See Supporting Information, S9 for plots of medium and large effects for each species.

3.3 | Multispecies occupancy model

Support for the relative separate and combined effects of forest edge effects and invasive predator co-occurrence was variable among species (Table 2; Supporting Information, S10). We found no clear support (independent co-occurrence model was most supported) that fosa occupancy is influenced by co-occurrence with invasive predators (Figure 4A). The second top model supported dogs and *shrub* in combination interact to reduce fosa occupancy (β = -0.743, SE=0.362, p=0.040; Table 2; Figure 5). We found support that fanaloka occupancy is positively influenced by dogs but declines with high shrub cover (β = -0.7145, SE=0.314, p=0.03). However, this does not result in a meaningful decline in fanaloka occupancy (Figure 4B). We also found model support that falanouc occupancy is largely influenced by co-occurrence with dogs in shrub cover (β = -1.008, SE= 0.373, $p < 0.01$; Figure 4C). We found no clear support for any variation in broad-striped vontsira occupancy (Figure 4D). Across species, we saw a similar trend in response of native carnivorans to dog co-occurrence within high shrub cover sites, however the strength of species response was variable, with 3 of 4 species reducing occurrence in response (Figure 5).

4 | Discussion

Forest degradation in Madagascar facilitates invasive predators which jointly result in reduced occurrence or extirpation of native carnivorans (Gerber, Karpanty & Randrianantenaina, 2012a; Farris et al., 2015c, 2017a,b). Additionally, research has highlighted pressures on native carnivorans at peripheries of intact protected forests

(Wampole, Farris & Gerber, 2021). However, we found little evidence that habitat degradation from hard forest edge and invasive predators separately or in combination indiscriminately reduce native carnivoran spatial use in a continuous intact forest. Interspecific variation was evident in both the magnitude and direction of native carnivoran responses to pressures. We found native carnivoran response was dependent on cat activity and not occurrence alone. Conversely, dog occurrence impacted native species spatial use irrespective of their relative activity.

Our results support that continuous forest habitat can buffer native carnivorans from the negative effects of invasive predators and forest edge effects. For example, the overall high occupancy of broad-striped vontsira irrespective of proximity to the forest edge or invasive predator contrasts with prior findings in Makira Natural Park (Farris et al., 2017a). Support for our hypothesis was only present for interactive influences of dog co-occurrence in dominant shrub cover (Figure 5) and meaningful declines in occupancy were only evident for the falanouc. Notably, our results for falanouc and fanaloka in continuous forest were similar to findings from fragmented forests, with reduced occupancy at dog occupied sites near highly degraded forest edge (Farris et al., 2015c).

Within disturbed forest systems, increased prevalence of invasive predators has been linked to reduced spatial use and temporal shifts in native carnivorans (Wampole, Farris & Gerber, 2021). In a single-season survey we found in continuous forest invasive predator co-occurrence and relative activity alone is not associated with considerable declines in occupancy or local extirpation of most native carnivorans. Of all species, the falanouc displayed the most immediate sensitivity to invasive predators alone. In response to increased dog and cat activity, falanouc reduced their activity when dogs were present, but increased their activity in the presence of cats. Additionally, dog activity had a small negative influence on fosa, which has been observed previously (Farris et al., 2015c).

Structural vegetation changes at the forest edge did not influence native carnivoran spatial use alone in our study. Instead we found distance to hard forest edge has a larger influence. Fosa, the furthest ranging and largest species, had a strong negative relationship with distance from a hard edge, but not in response to any measured vegetation structures. Fosa have been shown to utilize forest edge habitat to move between forest fragments while avoiding villages (Wyza et al., 2020). Despite use of forest edge within fragmented landscapes, fosa occupancy has declined (Farris et al., 2017a). We suggest, that without incentive to utilize edge for movement between patches, fosa avoid use of hard forest edge habitat, where it may be risky to occupy (Woodruff & Ginsburg, 2010). Similarly, falanouc and fanaloka had reduced activity near the edge. Their smaller-range requirements may limit the necessity to completely avoid the forest edge.

Overall, we found little support for our main hypotheses, with small to zero estimated effects from examined pressures separately or in combination in both single-species and multi-species models. It is possible that co-occurrence alone isn’t capturing species sensitivities to invasive predators except under extreme pressure (e.g. low-quality habitat and intense invasive predator activity). Simulation studies indicate that co-occurrence models from presence-absence data provide weak signals of negative effects, especially for smaller samples sizes, and could reduce the observed magnitude of invasive predator co-occurrence on native carnivorans (Blanchet, Caxelles & Gravel, 2020). However, we conducted one of the largest continuous camera surveys with explicit spatial design to account for examined separate and combine pressures on carnivorans to date in a single season using both single-species and multi-species co-occurrence models. By doing so, in the single-species model we captured effects of invasive predators that may otherwise go undetected in a co-occurrence model without explicit consideration of the relative activity of invasive predators and vise-versa. Single and multispecies models found different responses by native carnivorans to invasive predators, highlighting the importance of evaluating both when determining interspecies effects.

Prior, multi-season analyses show that invasive predators or forest degradation from increased edge and vegetation changes, either singularly or acting jointly, can result in spatial exclusion or reduced occupancy of native species (Farris et al., 2017a,b). However, we did not find similar negative responses of native carnivorans at hard forest edge of continuous intact forest. However, we conducted our research over a single season, capturing a snapshot of the current spatial use of carnivorans, precluding assessment of possible shifting dynamics, especially if pressures are intensifying. We found larger effects of invasive predator relative activity and evidence of strong co-occurrence (e.g. fanaloka-dog, falanouc-cat). Future multi-season research is required to test how invasive predator's activity influences native carnivoran occupancy across years.

We found more support for our alternative hypothesis that proximity of human settlements (*village*) drive changes in carnivoran spatial use more than vegetational forest edge effects and facilitate greater impacts by invasive predators. Falanouc and fanaloka occupancy was reduced at sites near villages with high cat activity, where prey-mediated effects maybe occurring. Important links between prey trap success (bird and small mammals), invasive predators, and native carnivorans (falanouc, fanaloka) near villages have been observed in fragmented systems (Farris et al., 2015c). Additionally, villages or anthropogenic centers are known to present extra risk to species, either through hunting or persecution (Merson et al., 2018) or represent variable disturbances that species may select against (Sévêque et. al., 2020).

Our survey revealed alarmingly few observations of the smallest resident carnivorans, the broad-striped vontsira and the ring-tailed vontsira. We found broad-striped vontsira had the lowest detection rate of evaluated carnivorans. Such low detection reduces statistical power to evaluate species spatial use. For example, we were unable to conduct a formal analysis for the ring-tailed vontsira, and we were unable to test for interactive effects for the broad-striped vontsira in our single-species model. Future studies should aim to conduct species specific surveys, where targeted efforts can be made to increase species detection.

4.1 | Management Implication

The combination of anthropogenic pressures from forest edge, specifically intense shrub cover and villages at the peripheries of intact continuous forests and relatively high invasive predator's activity appear to be the greatest threat to native carnivorans. Of less concern is when the pressures occur separately. Our study provides important evidence that protection of intact continuous forests is imperative for species conservation and is currently providing refuge for native carnivorans from intensifying anthropogenic pressures at the peripheries of forest habitat. Continued protection of large, intact continuous forest is essential.

We identified that species differ in their relative sensitives to pressures from invasive predators and forest edges. Our results support the necessity of species-specific management actions. We suggest the following based on our findings:

Fosa *(Cryptoprocta ferox):* Hard forest edge results in significantly reduced spatial use by fosa at approximately 500 m from a hard forest edge. Buffer zones should be established between protected area boundaries and hard forest edge to provide the full effective area of protected forests for fosa. Our results support previous recommendations that large intact protected areas are required to maintain fosa populations (Gerber, Karpanty & Randrianantenaina, 2012b).

Fanaloka (*Fossa fossana*) Fanaloka avoid sites with high cat activity near villages. Cats should be managed to limit their activity within the forest near villages. Fanaloka showed a negative response to dogs when co-occurring at forest edge sites with high shrub. Dogs should be restricted at the forest edge containing high levels of shrub cover. Additionally, the strong trend in co-occurrence of dogs is worrisome and multi-year surveys are recommended to monitor possible latent effects of dogs on fanaloka overtime.

Falanouc (*Eupleres goudotti*): Dogs negatively affect falanouc site use and correspond with spatial exclusion in degraded, high shrub areas. Dogs should be prevented from co-occurring with falanouc across all environmental gradients. Falanouc use forest near villages, but reduce use when cat activity is high. Conversely, we found higher use in core forest with higher cat activity. We suspect potential prey-mediated effects may be occurring. Species specific research is needed to examine the falanouc habitat use in relation to cat activity and prey abundance near villages.

Broad-striped vontsira (*Galidictis fasciata*): Species specific research is needed to understand the drivers of broad-striped vontsira spatial use.

4.2 | Policy Recommendation

Lastly, our findings indicate that conservation policy/practices which establish a minimum of 500m buffer zones between communities and protected forest edges for sustainable resource use would be impactful to mitigating pressures on species at the peripheries of park boundaries. To improve conditions for native carnivores, buffer zones would need to include forest habitat, maintain shrub cover below 50 percent and minimize use by invasive predator (dog presence/cat activity). Invasive predators could be minimized either through reducing free-roaming behavior of dogs and cats or decreasing abundance near villages and within highly degraded habitat. Free spay and neuter clinics are offered to communities surrounding protected areas and can help reduce propagule pressure from free-roaming dogs and cats if local communities/individual are willing to participate. Ultimately establishment of sustainable buffer zones would require support and joint partnerships from community leaders/organizers and park authorities to create equitable policy and program implementation (Budhathoki 2004).

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Table 1. Covariate descriptions and literature support for use in occupancy models investigating native Madagascar carnivore spatial use. Hypothesis represents categories of competing models tested with each corresponding covariate model on occurrence probability (ψ) and/or detection probability (p; a measure of relative activity) as indicated by model parameter column.

Hypothesis	Covariate	Description	Reference	Model Parameter
forest edge	*forest edge*	Euclidean distance from each site to nearest forest edge boundary	Farris 2017a,b; Ross *et al.* 2020	ψ, p
	shrub	percent shrub at site, measured by point center quarter	Farris et al, 2015b,c, 2017; Stanton *et al.* 2018[2]	ψ,p
	open canopy	percent open canopy landscape at 1000 m buffer from categorized Landsat imagery	Whitworth *et al.* 2019[1]	ψ
	high canopy	percent high canopy landscape at 1000 m buffer from categorized Landsat imagery	Whitworth *et al.* 2019[1]	ψ
invasive predator	*dog*	trap success	Farris *et al.* 2017a,b, Merson *et al.* 2019	ψ, p
	cat	trap success	Farris *et al.* 2015c, Gerber *et al.* 2012b	ψ, p
ancillary	*human*	number of independent detections of humans	Farris 2017a	ψ, p
	village	Euclidean distance from each site to nearest village	Farris 2017a	ψ, p
interaction	*shrub*cat*	interaction of percent shrub at site and cat trap success	Farris *et al.* 2014, 2015b,c Recio *et al.* 2014[1]	ψ

*shrub*dog*	interaction of percent shrub at site and dog trap success	Sepúlveda *et al.* 2015	ψ
*forest edge*cat*	interaction of distance to forest edge and cat trap success	Farris *et al.* 2017b; Merson *et al.* 2019; Ross *et al.* 2020	ψ
*forest edge*dog*	interaction of distance to forest edge and dog trap success	Farris *et al.* 2015c; Merson *et al.* 2019	ψ
*village*cat*	interaction of distance to village and cat trap success	Farris *et al.* 2017a,b Gerber *et al.* 2012b; Paschoal *et al.* 2018[1]	ψ
*village*dog*	interaction of distance to village edge and dog trap success	Farris *et al.* 2015b; Farris et al 2016	ψ

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[1] Outside Madagascar but within tropical rainforest eco-regions

[2] Global meta-analysis

Table 2. Comparison of top models from single-season multispecies occupancy analyses. Co-occurrence occupancy models (ψ_C) estimate the influence of invasive predators on native carnivoran occupancy and independent occurrence models (ψ_M) assume no influence of invasive predators on native carnivoran occupancy. ψ_C with environmental variable, indicate support for an interaction between invasive predator and the environmental variable (e.g. ~dog:shrub). Evidence ratios indicate the level of support for the top model relative to the model in that row, for each species.

	Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt	Evidence Ratio
fosa	ψ_M	13	3103.62	0.00	1.00	0.33	-1535.96	0.33	-
	ψ_C (dog:shrub)	15	3104.16	0.55	0.76	0.25	-1533.21	0.58	1.32
	ψ_C (dog)	14	3105.77	2.15	0.34	0.11	-1535.55	0.69	3.82
fanaloka	ψ_C (dog:shrub)	17	4783.26	0.00	1.00	0.41	-2369.53	0.41	-
	ψ_C (dog)	16	4784.85	1.59	0.45	0.19	-2371.96	0.60	2.21
falanouc	ψ_C (dog:shrub)	14	3579.80	0.00	1.00	0.54	-1772.57	0.54	-
	ψ_M	12	3582.39	2.59	0.27	0.15	-1776.80	0.69	3.65
broad-striped vontsira	ψ_M	12	2019.47	0.00	1.00	0.44	-995.33	0.44	-
	ψ_C (dog:shrub)	14	2021.95	2.49	0.29	0.13	-993.64	0.57	3.47
	ψ_C (cat)	13	2022.30	2.83	0.24	0.11	-995.31	0.67	4.13
	ψ_C (dog)	13	2022.35	2.88	0.24	0.10	-995.33	0.78	4.23

Figure 1. Study area map indicating 1) Madagascar with remaining forest (2014), 2) Mantadia National Park and surrounding forest, and 3) study area and camera trap locations in relationship to distance from the hard forest edge (2018).

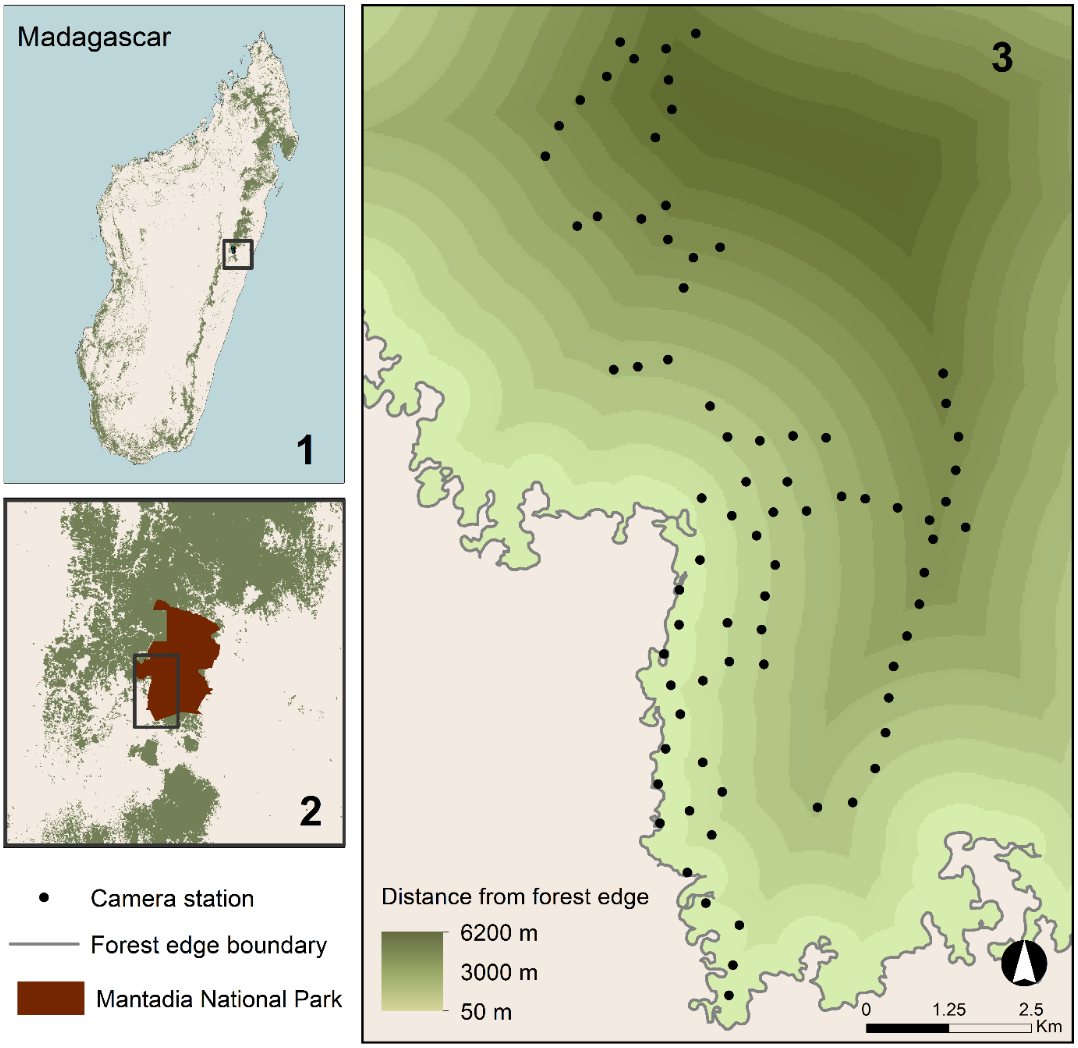


Figure 2. Model averaged coefficient effect sizes for separate and combined pressures on A) native carnivoran occurrence (*ψ*) and B) relative activity (*p*). Colors indicate the categorical effect size (regardless of sign) and value indicates the coefficient estimate. Single variables (e.g., cat) indicate a main effect that is not conditional on another variable, while combined variables (e.g., cat:forest edge) indicate an interaction effect. Larger weighted effect sizes indicate more support for the interaction of single variable being important; equal size effects between interactions and single variables indicate uncertainty.

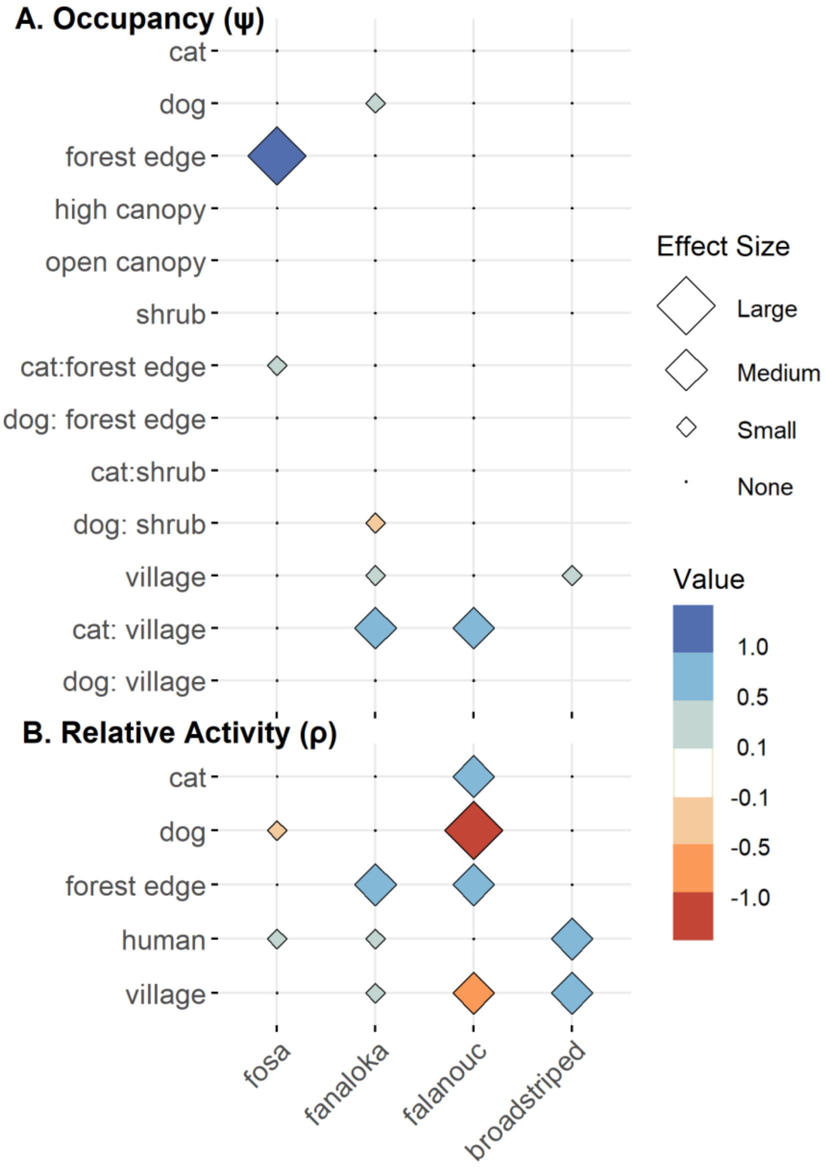


Figure 3. Single-season, single species model averaged predictions for medium-large effects on native carnivoran occupancy.

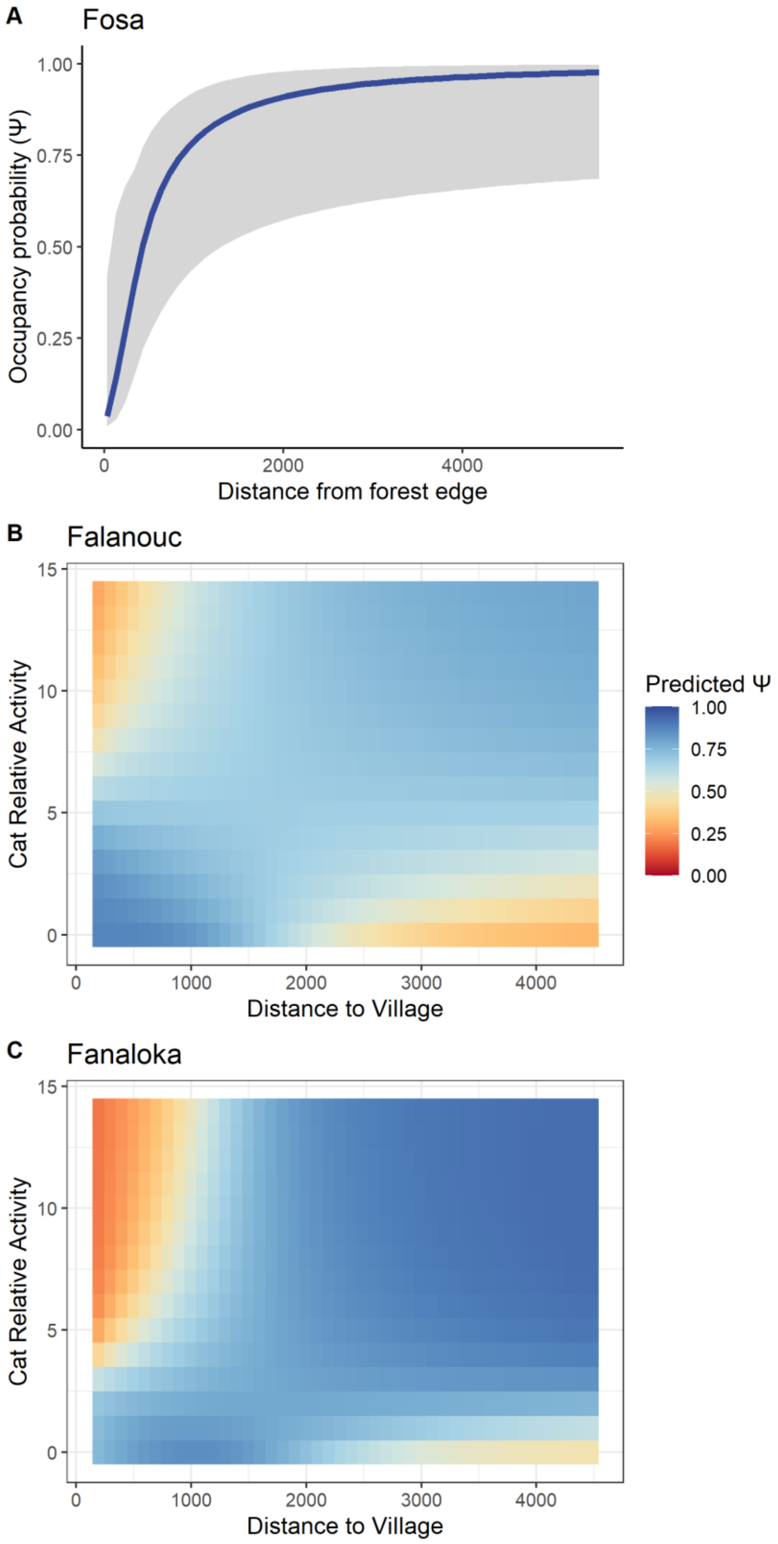


Figure 4. Conditional occupancy probability of each native carnivoran with respect to invasive species presence from the top multi-species occupancy models. The condition absent (orange)/present (blue) refers to the invasive predator in the top model, with 95% confidence intervals (shaded area).

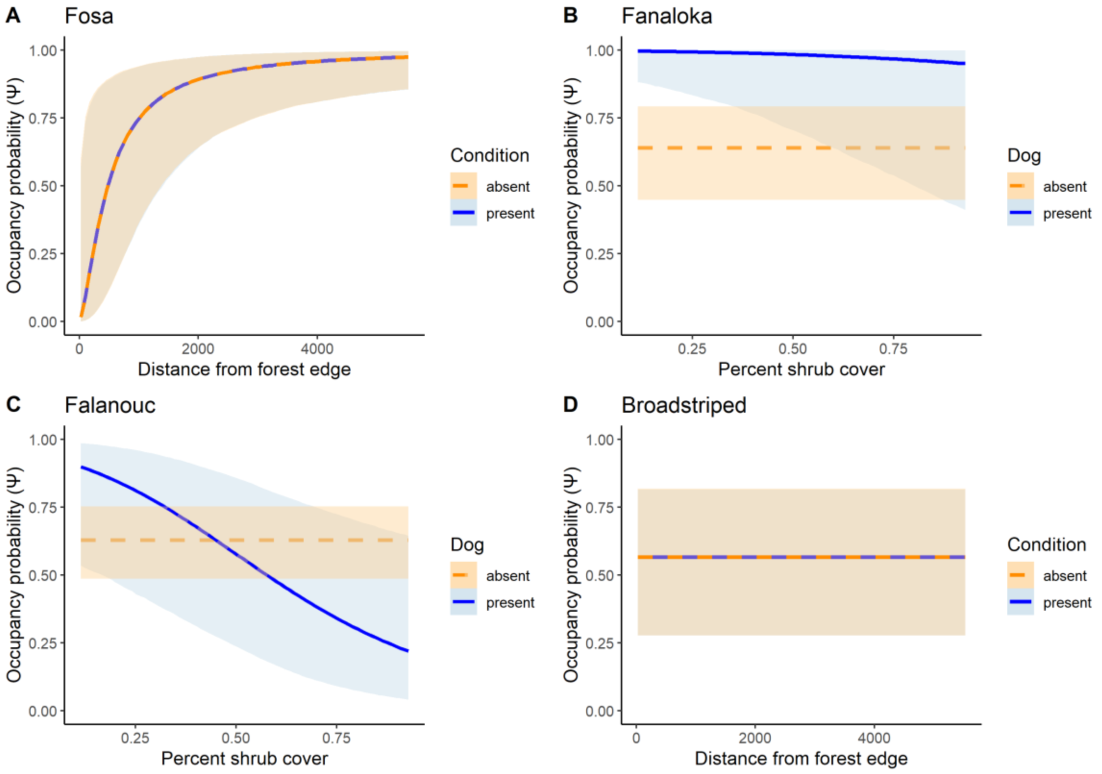
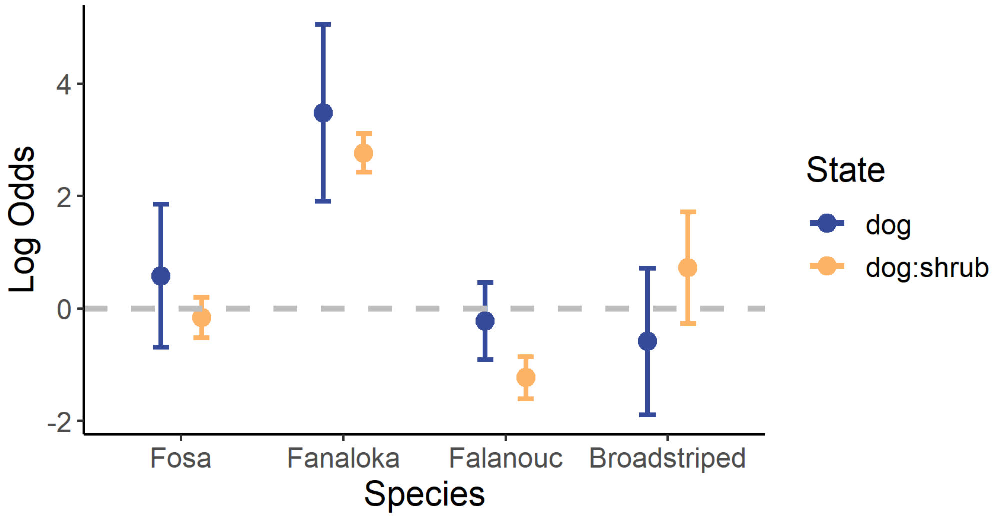


Figure 5. Comparison of the effect of dog co-occurrence at mean percent shrub cover (blue) and dog co-occurrence at one standard deviation above the mean (yellow) on native carnivoran occupancy. The points (blue and yellow) represent the mean change in native carnivoran occupancy on the log odds scale from the estimated marginal occupancy (grey line) along with 95% confidence intervals.



Supporting Information

Appendix S1

Vegetation Sampling Protocols

Methodology

We walked a 10 m perpendicular line at 0 (camera location), 25, and 50 m in three cardinal directions N, SE, SW (corresponding to 0, 120, 240 degrees) recording vegetation cover at every 2 m point for a total of 70 points at each site. Vegetation structure criterion is specified in below in Table 1.

Table 1. Criteria used to determine vegetation structure at each sampling point.

Vegetation structure	**metric criteria**
down/dead cover	≥ 15 cm DBH
ground cover	0 - 0.5 m
shrub cover	0.5 - 5m
low tree canopy cover	0 - 5 m
mid tree canopy cover	5 - 15 m
high tree canopy cover	≥ 15m

Appendix S2

Covariate Correlation Tests & Vegetation Linear Regression Plots

Table 1. Correlation coefficients or each pairwise covariate combination. No covariates with greater than 0.40 correlation coefficient was included in any single model.

	forest edge	**village**	**shrub**	**open canopy**	**high canopy**	**dog**	**cat**	**human**
forest edge	NA	0.40	-0.42	-0.39	0.31	0.37	-0.17	0.23
village	0.40	NA	-0.06	-0.38	0.38	-0.22	-0.29	-0.22
shrub	-0.42	-0.06	NA	0.06	-0.01	-0.12	0.21	0.03
open canopy	-0.39	-0.38	0.06	NA	-0.89	-0.01	0.15	0.06
high canopy	0.31	0.38	-0.01	-0.89	NA	-0.09	-0.25	-0.03
dog	0.37	-0.22	-0.12	-0.01	-0.09	NA	0.12	0.58
cat	-0.17	-0.29	0.21	0.15	-0.25	0.12	NA	0.09
human	0.23	-0.22	0.03	0.06	-0.03	0.58	0.09	NA

Table 2. Results from linear models of the relationship between distance from forest edge and vegetation covariates.

Covariate	*Estimate*	*Std. Error*	*t- value*	*Pr(>|t|)*
shrub	-0.4175	0.1042	-4.0054	0.0001
high canopy	0.3085	0.1091	2.8274	0.0060
open canopy	-0.3936	0.1054	-3.7325	0.0004

Figure 1. Plots of linear relationship of distance from forest edge and vegetation covariates. Shrub was quantified at the site level, whereas open canopy and high canopy were calculated at the landscape level (1000m buffer).

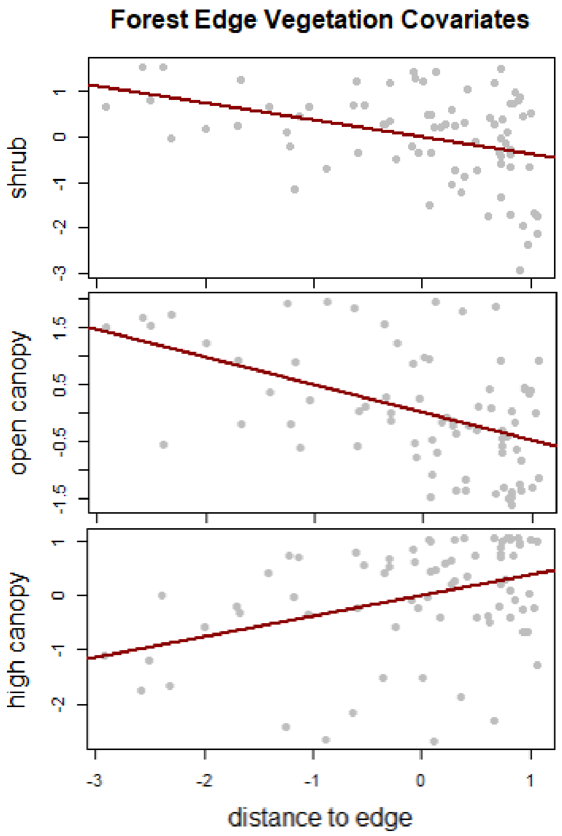


Table 3. Pearson's correlation coefficient for pairwise test of collinearity across spatial scales for each landscape metric class (PLAND 1, PLAND 2, PLAND 3). Percent land-cover (PLAND) was highly collinear across spatial scales (lsm.250, lsm.500, lsm.1000) for all metrics (250, 500, 1000 meter buffer) of canopy cover.

No Canopy (PLAND 1)

	lsm.250	lsm.500	lsm.1000
lsm.250	NA	0.925662	0.807037
lsm.500	0.925662	NA	0.933235
lsm.1000	0.807037	0.933235	NA

Low:Mid Canopy (PLAND 2)

	lsm.250	lsm.500	lsm.1000
lsm.250	NA	0.919182	0.848569
lsm.500	0.919182	NA	0.935643
lsm.1000	0.848569	0.935643	NA

Mid:High Canopy (PLAND 3)

	lsm.250	lsm.500	lsm.1000
lsm.250	NA	0.933271	0.796162
lsm.500	0.933271	NA	0.928534
lsm.1000	0.796162	0.928534	NA

Figure 2. Boxplot for examined vegetation structure metric at each evaluated spatial scale (250, 500 and 100m buffer).

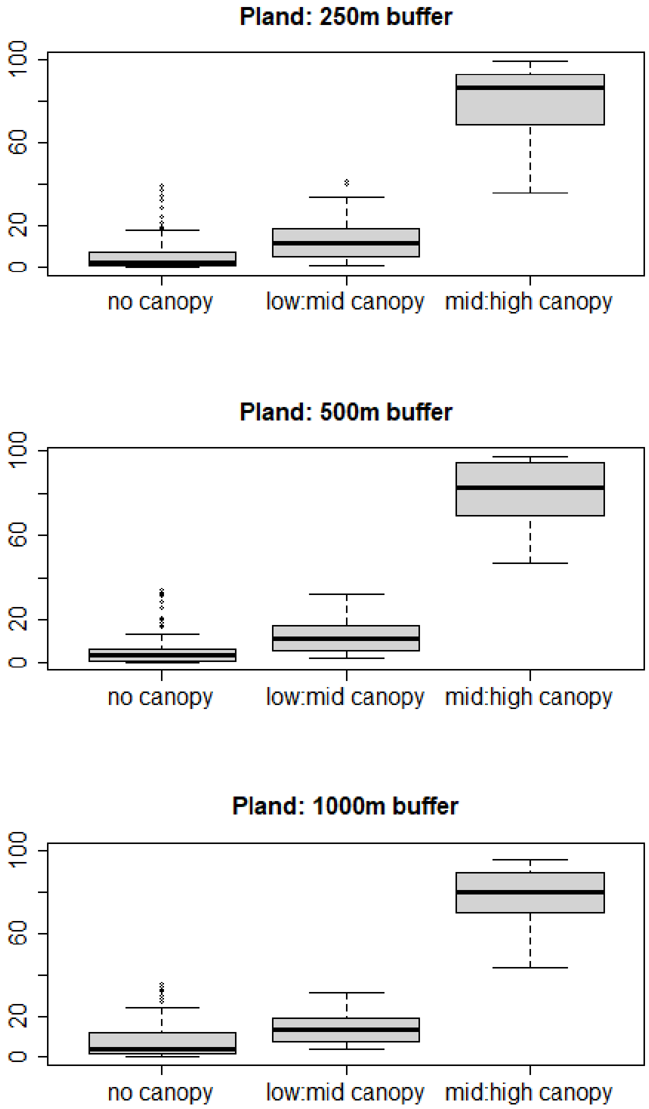
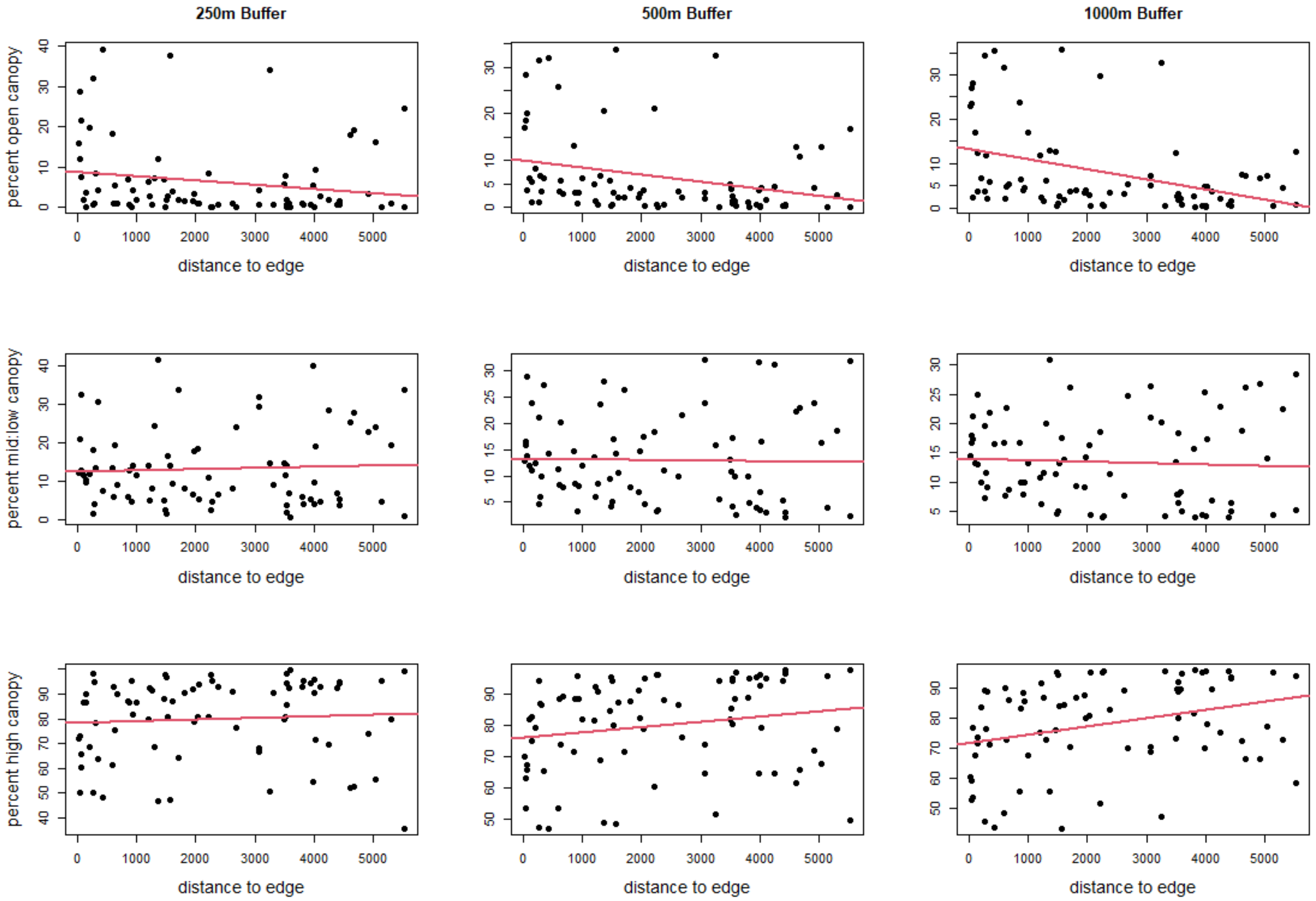


Figure 3. Results of linear model (red line) of observer vegetation metrics (black points) across spatial scales.



Appendix S3

Model Lists for Single- and Multi-Species Occupancy Models

Table 1. Single-species, single-season occupancy model, competing global model list. Each global model was used to generate all possible combinations of each global model(G) while holding ψ forest edge variables constant (*shrub, open canopy, high canopy, forest edge)* within each competing global model, allowing to test all possible combinations of (p) simultaneously with ψ, which has been shown to improve model estimates, than when estimated separately (Doherty et al. 2012).

Model #	ψ	p
G1	~ *forest edge* + *dog*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G2	~ *forest edge* + *cat*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G3	~ *shrub* + *dog*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G4	~ *shrub* + *cat*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G5	~ *open canopy* + *dog*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G6	~ *open canopy* + *cat*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G7	~ *high canopy* + *dog*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G8	~ *high canopy* + *cat*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G9	~ *village* + *dog*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G10	~ *village* + *cat*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G11	~ *shrub* * *dog*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G12	~ *shrub* * *cat*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G13	~ *forest edge* * *cat*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G14	~ *forest edge* * *dog*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G15	~ *village* * *cat*	~ *forest edge* + *village* + *human* + *cat* + *dog*
G16	~ *village* * *dog*	~ *forest edge* + *village* + *human* + *cat* + *dog*

Doherty, P. F., White, G. C., & Burnham, K. P. (2012). Comparison of model building and selection strategies. *Journal of Ornithology*, *152*(S2), 317–323. https://doi.org/10.1007/s10336-010-0598-5

Table 2. Multi-species occupancy model framework testing competing hypotheses on the influence of invasive predator co-occurrence independent or in combination with predicted pressures. We examined four competing models for each native-invasive predator pairing: the influence of invasive predator co-occurrence alone, or in combination with *shrub*, *forest edge* and *village*.

	Natural parameters						
Competing Hypothesis	**native (f_1)**	**dog (f_2)**	**cat (f_3)**	**native:dog (f_{12})**	**native:cat (f_{13})**	**dog:cat (f_{23})**	**native:dog:cat (f_{123})**
Independent: invasive predator co-occurrence does not affect native carnivoran occupancy	~1 *	~ *village*	~1	0	0	0	0
Dog co-occurrence							
independent of vegetation structure	~1 *	~ *village*	~1	~1	0	0	0
dependent on proximity to a forest edge	~1 *	~ *village*	~1	~*forest edge*	0	0	0
dependent of percent shrub	~1 *	~ *village*	~1	~ *shrub*	0	0	0
dependent on proximity to a village	~1 *	~ *village*	~1	~ village	0	0	0
Cat co-occurrence							
independent of vegetation structure	~1 *	~ *village*	~1	0	~1	0	0
dependent on proximity to a forest edge	~1 *	~ *village*	~1	0	~*forest edge*	0	0
dependent of percent shrub	~1 *	~ *village*	~1	0	~ *shrub*	0	0
dependent on proximity to a village	~1 *	~ *village*	~1	0	~ village	0	0
Dog or Cat co-occurrence							
independent of vegetation structure	~1 *	~ *village*	~1	~1	~1	0	0
dependent on proximity to a forest edge	~1 *	~ *village*	~1	~*forest edge*	~*forest edge*	0	0
dependent of percent shrub	~1 *	~ *village*	~1	~ *shrub*	~ *shrub*	0	0
dependent on proximity to a village	~1 *	~ *village*	~1	~ village	~ village	0	0
Dog and Cat co-occurrence							
independent of vegetation structure	~1 *	~ *village*	~1	0	0	~1	~1
dependent on proximity to a forest edge	~1 *	~ *village*	~1	0	0	~1	~*forest edge*

dependent of percent shrub	~1 *	~ *village*	~1	0	0	~1	~ village
dependent on proximity to a village	~1 *	~ *village*	~1	0	0	~1	~ *shrub*

~1* indicates that native carnivoran (f1) parameter was modeled by species specific variables determined to have medium or large relative effect from single-species model average coefficient findings

Appendix S4

Literature support for included interaction terms

How invasive predators interact with native carnivorans can depend on their behavior or fine-scale habitat use. Habitat features including vegetation structure, proximity to anthropogenic centers, and prevalence of trails influence invasive predator behavior/movement and alter invasive-native interactions directly (spatial-exclusion) or indirectly (prey-mediated effects). We therefore included interaction terms between invasive predators and environmental variables that could have direct effects on native or invasive carnivore habitat use and movement/behavior or indirect effects by prey-mediated influences based on our literature search for Madagascar carnivorans or for similar tropical forest carnivorans elsewhere.

Interaction	**Rationale for interaction**	**Reference**	**Parameter**
*shrub*cat*	movement, prey-mediated	Farris et al. 2014, 2015b,c Recio et al. 2014[1]	ψ
*shrub*dog*	movement, chase	Sepúlveda et al. 2015	ψ
*forest edge*dog*	habitat use, movement	Farris et al. 2017b; Merson et al. 2019; Ross et al. 2020	ψ
*forest edge*cat*	habitat use, movement, prey mediated	Farris et al. 2015c; Merson et al. 2019	ψ
*village*dog*	habitat use, behavior	Farris et al. 2017a,b Gerber et al. 2012b; Paschoal et al. 2018[1]	ψ
*village*cat*	habitat use, behavior	Farris et al. 2015b; Farris et al 2016	ψ

[1] Outside Madagascar but within tropical rainforest eco-regions

[2] Global meta-analysis

Specific Findings

Behavior/movement/habitat use

Farris et al. 2016: *Shrub* has been an important predictor in fine-scale habitat use of dogs, cats, and native carnivores.

Farris et al. 2015b, 2016: Cats have higher habitat use (higher occupancy and trap success) near *villages*

Farris et al. 2014: Understory cover (such as shrub) best explained dog and cat habitat use (occupancy).

Farris et al 2017a,b: *Dog* habitat use is higher near villages and forest edge.

Gerber et al. 2012: Dogs have higher habitat use (occupancy) near villages

Merson et al. 2019: *Forest edge* has been an important predictor of invasive predator(*cat/dog*). Native carnivoran(fosa) occupancy as negatively associated with cats.

Paschoal et al. 2018: Dogs use protected forest areas for longer periods of time near villages (higher housing density).

Ross et al. 2020: Forest and edge best explained habitat use (occupancy) of dogs.

Sepulveda et al. 2015: Dogs are known to select for bare ground, trails and roads for movement and avoid dense vegetation. Forest was an important barrier to dog movement likely due to dense understory vegetation dominant in the temperate rainforest.

Prey Mediated

Bajaru et al. 2019: shrub cover has been an important predictor of prey availability for small mammal and ground nesting birds.

Farris et al. 2015c: Bird trap success was the most important variable for predicting carnivore occupancy across species (see Table 4; S1 Table) with a positive relationship for three natives and a negative relationship for feral cat (see Fig 2a).

Farris et al. 2016: Cats preferentially select for areas used by ground nesting birds. Cat occupancy best explained by small mammal trap success. Small mammal trap success was highest in non-degraded sites. Bird trap success was highest in

Farris et al. 2017b: Bird and small mammal trap success significantly declines across years with dramatic increases in cats (trap success and occupancy).

Merson et al. 2019: Cat occupancy was negatively associated with birds.

Recio et al. 2014: Cats have shown higher use in areas with high shrub cover, where prey availability is often higher.

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Appendix S5

Model Averaging Coefficients

Case Study

This case study is intended to describe how to compare absolute and relative support of model averaged coefficients when comparing models with additive and interaction combinations of variables. An issue with the common implementation of this comparison is that the main effects mean different things in a model with and without interactions. Model averaging main effects across these models does not make sense.

Model 1: y $= \beta_0 + \beta_1 \times x_1 + \beta_2 \times x_2$

Model 2: y $= \beta_0 + \beta_1 \times x_1 + \beta_2 \times x_2 + \beta_3 \times (x_1 \times x_2)$

In the above models, the interpretation of β_1 and β_2 are quite different. In model 1, β_1 is the main effect of x_1, but when there is an interaction included with x_1 (Model 2) then β_1 is the conditional effect of $x_2 = 0$. If the x variables have been standardized (centered and scaled) then β_1 would be the effect at the mean level of β_2. As the coefficient for an interaction approaches zero ($\beta_3 \to 0$), the main effects of additive and interaction models will become the same. Thus, the conditional effects of an interaction model becomes the main effects.

Below, we will simulate data and model average coefficients in three sections to demonstrate how to compare additive and interaction effects when model averaging where there is model selection uncertainty. Our goal is to examine the absolute and relative size of coefficients to examine support for 1) no effects, 2) additive combinations, and 3) interactions. We will shrink interaction effects by including zeros for coefficients in additive models where they are not present. We will also shrink the main effects of the the additive models (without interactions) by replacing the conditional effects (β_1 and β_2 of Model 2) in the interaction models with zeros.

When there is strong support for an interaction (large coefficient and high AIC weight) then model averaged coefficients will be be large. However, the main effects will be shrink towards zero. When there is strong support for an additive combination of variables (not interaction) then the interaction coefficients will be shrunk to zero and the main effects will not be.

Section 1

```
###################################
#Setup workspace
rm(list=ls())
options(warn=-1)
library(glmulti)
```

```
## Loading required package: rJava

## Loading required package: leaps
```

```
library(MuMIn)
library(stringr)

#Simulate covariate data that is standardized
```

```
n=100 #sample size
set.seed(343)
x1=rnorm(n,0,1)
x2=rnorm(n,0,1)
x3=rnorm(n,0,1)

#Create design matrices for interaction combination (without x3)
X=model.matrix(~x1*x2)

#True coefficients
beta=t(matrix(c(1,-1,1,-0.5),ncol=4))
beta
```

```
##      [,1]
## [1,]  1.0
## [2,] -1.0
## [3,]  1.0
## [4,] -0.5
```

```
#Simulate data with interaction model
set.seed(444)
probs=plogis(X%*%beta)
y=rbinom(n,1,prob = probs)

###############################
#Fit all pairwise subsets with additive and interactions
out <-glmulti(y ~ x1+x2+x3,
            level = 2,                # interactions considered
            method = "h",             # Exhaustive search
            crit = "aicc",            # AIC as criteria
            marginality=TRUE,         # Does not allow interactions without their main effects
            confsetsize = 100,        # Keep 100 best models
            plotty = F, report = F,   # No plot or interim reports
            fitfunction = "glm",
            family="binomial")

#Model combination formulas
out@formulas[[1]]
```

```
## y ~ 1 + x1 + x2 + x2:x1
## <environment: 0x000000006a298c88>
```

```
#Using common model averaging techniques
model.avg(out@objects)
```

```
##
## Call:
## model.avg(object = out@objects)
##
## Component models:
## '124'    '1234'   '12'     '12345'  '12346'  '123'    '123456' '1235'
## '1236'   '12356'  '2'      '23'     '236'    '1'      '13'     '135'
## '(Null)' '3'
##
## Coefficients:
##        (Intercept)         x1        x2      x1:x2         x3      x1:x3
```

```
## full     0.9125088 -0.9372772 1.578953 -0.7618143 0.04155389 0.02449997
## subset   0.9125088 -0.9456913 1.578970 -0.9405995 0.10511718 0.22794215
##             x2:x3
## full   0.02276045
## subset 0.21397166
```

Using the "full" (includes zeros where variables are not included with models) model averaging we conflate the main effects of an additive only model and the conditional effects of an interaction model. However, the model averaged interaction coefficients are fine. They are shrunk towards zero when an additive model is supported, which is appropriate.

```
#extract coefs
coefs=model.avg(out@objects)

#Find the interaction coefs
index.interaction=apply(matrix(colnames(coefs$coefficients)),1,
                        FUN=function(x){str_detect(x, ":", negate = FALSE)})

#These are correct model average interaction coefficients that are shrunk towards zero
coefs$coefficients[1,which(as.integer(index.interaction)==1)]
```

```
##       x1:x2       x1:x3       x2:x3
## -0.76181427  0.02449997  0.02276045
```

```
#Extract coefficients and AIC model weights
table.coef=model.sel(out@objects)

#Get the "main effects" coefficients
main=table.coef[,which(as.integer(index.interaction)==0)[-1]]
main
```

```
##            x1       x2         x3
## 1  -0.9681986 1.634448         NA
## 2  -0.9659855 1.652044 0.07041358
## 3  -0.8762019 1.285679         NA
## 4  -0.9519252 1.658775 0.08219832
## 5  -0.9369653 1.640052 0.14377201
## 6  -0.8714892 1.305886 0.10759699
## 7  -0.9278828 1.646006 0.13869858
## 8  -0.8686022 1.402221 0.16101669
## 9  -0.8240215 1.375681 0.21515616
## 10 -0.8246939 1.432390 0.22864391
## 11         NA 1.288910         NA
## 12         NA 1.312582 0.14519499
## 13         NA 1.393757 0.29354152
## 14 -0.7877819       NA         NA
## 15 -0.7858081       NA 0.02331682
## 16 -0.7959542       NA 0.01164817
## 17         NA       NA         NA
## 18         NA       NA 0.08314656
```

```
#Identify models with interaction with x1,x2, and x3
index.x1=unlist(lapply(out@formulas,FUN=function(x){str_detect(paste(c(x)), "x1:|:x1", negate = FALSE)}
index.x2=unlist(lapply(out@formulas,FUN=function(x){str_detect(paste(c(x)), "x2:|:x2", negate = FALSE)}
index.x3=unlist(lapply(out@formulas,FUN=function(x){str_detect(paste(c(x)), "x3:|:x3", negate = FALSE)}

#Loop through models and change main effects to zero when they are involved in an interaction
```

```
for(i in 1:length(index.x1)){
  if(index.x1[i]==TRUE){main[i,1]=0}
  if(index.x2[i]==TRUE){main[i,2]=0}
  if(index.x3[i]==TRUE){main[i,3]=0}
}

#Main coefs only with zeros where interactions are involved
main
```

```
##             x1       x2         x3
## 1    0.0000000 0.000000         NA
## 2    0.0000000 0.000000 0.07041358
## 3   -0.8762019 1.285679         NA
## 4    0.0000000 0.000000 0.00000000
## 5    0.0000000 0.000000 0.00000000
## 6   -0.8714892 1.305886 0.10759699
## 7    0.0000000 0.000000 0.00000000
## 8    0.0000000 1.402221 0.00000000
## 9   -0.8240215 0.000000 0.00000000
## 10   0.0000000 0.000000 0.00000000
## 11          NA 1.288910         NA
## 12          NA 1.312582 0.14519499
## 13          NA 0.000000 0.00000000
## 14  -0.7877819       NA         NA
## 15  -0.7858081       NA 0.02331682
## 16   0.0000000       NA 0.00000000
## 17          NA       NA         NA
## 18          NA       NA 0.08314656
```

```
#Replace NA's with zeros
index.na=which(is.na(main),arr.ind=TRUE)
main[index.na]=0

#Extract AIC Weights
weights=table.coef[,13]

#Multiply each column by the weights and sum
#This is the model averaged main effects for additive models only shrunk towards zero
colSums(main*weights)
```

```
##          x1          x2          x3
## -0.13475214  0.21470702  0.01624797
```

```
#Combine main and interaction coefs.
shrunk.coefs=c(colSums(main*weights),coefs$coefficients[1,index.interaction])
shrunk.coefs
```

```
##          x1          x2          x3       x1:x2       x1:x3       x2:x3
## -0.13475214  0.21470702  0.01624797 -0.76181427  0.02449997  0.02276045
```

RESULTS: There is a large effect for the interaction b/w x1 and x2, which makes sense as this is was included in the model used to simulate the data. The main effect of x3 is near zero and has little support; this is good because it was not in the model used to simulate the data.

The main effects of x1 and x2 are not small and thus are showing some support, suggesting that the variables of x1 and x2 are important and that there is some model selection uncertainty as to whether the additive of interaction models are more supported.

Section 2

We will do the same thing as above but we will use a generating model that has no interaction

```
#Create design matrices for additive combination (without x3)
X=model.matrix(~x1+x2)

#True coefficients
beta=t(matrix(c(1,-1,1),ncol=3))

#Simulate data without an interaction model
set.seed(441)
probs=plogis(X%*%beta)
y=rbinom(n,1,prob = probs)

###############################
#Fit all pairwise subsets with additive and interactions
out <-glmulti(y ~ x1+x2+x3,
            level = 2,               # interactions considered
            method = "h",            # Exhaustive search
            crit = "aicc",          # AIC as criteria
            marginality=TRUE,       # Does not allow interactions without their main effects
            confsetsize = 100,         # Keep 100 best models
            plotty = F, report = F,  # No plot or interim reports
            fitfunction = "glm",
            family="binomial")

#Model combinations
out@formulas[[1]]
```

```
## y ~ 1 + x1 + x2
## <environment: 0x000000006f57a968>
```

```
#Common model averaging technique
model.avg(out@objects)
```

```
##
## Call:
## model.avg(object = out@objects)
##
## Component models:
## '12'      '124'     '123'     '1236'    '12346'   '1234'    '2'       '1235'
## '12356'   '123456'  '12345'   '23'      '236'     '1'       '13'      '135'
## '(Null)'  '3'
##
## Coefficients:
##        (Intercept)         x1        x2      x1:x2         x3      x2:x3
## full     0.9318296 -0.6970534 0.9456015 -0.1136675 -0.0286494 -0.1396366
## subset   0.9318296 -0.7519887 0.9485912 -0.3537265 -0.0604429 -0.5802912
##                x1:x3
## full   -0.0005656213
## subset -0.0051181695
```

Using the "full" model averaging we conflate the main effects of an additive only model and the conditional effects of an interaction model. However, the model averaged interaction coefficients are however fine. They are shrunk towards zero when an additive model is supported, which is appropriate.

```r
coefs=model.avg(out@objects)

#Find the interaction coefs
index.interaction=apply(matrix(colnames(coefs$coefficients)),1,
                        FUN=function(x){str_detect(x, ":", negate = FALSE)})

#These are correct and appropriate model average interaction coefficients that are shrunk towards zero
coefs$coefficients[1,which(as.integer(index.interaction)==1)]
```

```
##         x1:x2         x2:x3         x1:x3
## -0.1136675172 -0.1396366286 -0.0005656213
```

```r
#Extract coefficients and AIC model weights
table.coef=model.sel(out@objects)

#Get the "main effects" coefficients
main=table.coef[,which(as.integer(index.interaction)==0)[-1]]
main
```

```
##            x1        x2           x3
## 1  -0.7185566 0.9229127           NA
## 2  -0.7369367 0.9743794           NA
## 3  -0.7165831 0.9271801  0.045577587
## 4  -0.8232767 0.9169838 -0.127496371
## 5  -0.8505427 1.0599922 -0.207247601
## 6  -0.7364263 0.9750851  0.006653906
## 7          NA 0.9430102           NA
## 8  -0.7199731 0.9147466  0.038251175
## 9  -0.8284163 0.9296402 -0.123886623
## 10 -0.8534151 1.0670045 -0.206256050
## 11 -0.7416183 0.9635341 -0.001134781
## 12         NA 0.9500071  0.078015381
## 13         NA 0.9618855 -0.026204775
## 14 -0.6955713        NA           NA
## 15 -0.6952520        NA  0.003527729
## 16 -0.7330818        NA -0.022290701
## 17         NA        NA           NA
## 18         NA        NA  0.059949175
```

```r
#Identify models with interaction with x1,x2, and x3
index.x1=unlist(lapply(out@formulas,FUN=function(x){str_detect(paste(c(x)), "x1:|:x1", negate = FALSE)}
index.x2=unlist(lapply(out@formulas,FUN=function(x){str_detect(paste(c(x)), "x2:|:x2", negate = FALSE)}
index.x3=unlist(lapply(out@formulas,FUN=function(x){str_detect(paste(c(x)), "x3:|:x3", negate = FALSE)}

#Loop through models and change main effects to zero when they are involved in an interaction
for(i in 1:length(index.x1)){
  if(index.x1[i]==TRUE){main[i,1]=0}
  if(index.x2[i]==TRUE){main[i,2]=0}
  if(index.x3[i]==TRUE){main[i,3]=0}
}

#Main coefs only with zeros where interactions are involved
main
```

```
##            x1        x2          x3
## 1  -0.7185566 0.9229127          NA
```

```
## 2   0.0000000 0.0000000          NA
## 3  -0.7165831 0.9271801 0.045577587
## 4  -0.8232767 0.0000000 0.000000000
## 5   0.0000000 0.0000000 0.000000000
## 6   0.0000000 0.0000000 0.006653906
## 7          NA 0.9430102          NA
## 8   0.0000000 0.9147466 0.000000000
## 9   0.0000000 0.0000000 0.000000000
## 10  0.0000000 0.0000000 0.000000000
## 11  0.0000000 0.0000000 0.000000000
## 12         NA 0.9500071 0.078015381
## 13         NA 0.0000000 0.000000000
## 14 -0.6955713        NA          NA
## 15 -0.6952520        NA 0.003527729
## 16  0.0000000        NA 0.000000000
## 17         NA        NA          NA
## 18         NA        NA 0.059949175
```

```
#Replace NA's with zeros
index.na=which(is.na(main),arr.ind=TRUE)
main[index.na]=0

#Extract AIC Weights
weights=table.coef[,13]

#Multiply each column by the weights and sum
#This is the model averaged main effects for additive models only shrunk towards zero
colSums(main*weights)
```

```
##           x1           x2           x3
## -0.394662719  0.484222048  0.006607056
```

```
#Combine main and interaction coefs.
shrunk.coefs=c(colSums(main*weights),coefs$coefficients[1,which(as.integer(index.interaction)==1)])
shrunk.coefs
```

```
##            x1            x2            x3         x1:x2         x2:x3
## -0.3946627189  0.4842220479  0.0066070557 -0.1136675172 -0.1396366286
##         x1:x3
## -0.0005656213
```

RESULT: There is strong support for large effects of additive combinations of x1 and x2, but not so for x3, which makes sense as x3 was not in the generating model.

There is some support for an interaction between x1:x2 and x2:x3 but these effects are smaller than the main effects. Thus, there is some model selection uncertainty.

Section 3

We will do the same thing as above (again) but we will use a generating model that has no interaction and increase the sample size and thus reduce model selection uncertainty.

```
n=1000 #sample size
set.seed(11343)
x1=rnorm(n,0,1)
x2=rnorm(n,0,1)
```

```
x3=rnorm(n,0,1)

#Create design matrices for addtive combination (without x3)
X=model.matrix(~x1+x2)

#coefficients
beta=t(matrix(c(1,-1,1),ncol=3))

#Simulate data with interaction model
set.seed(444)
probs=plogis(X%*%beta)
y=rbinom(n,1,prob = probs)

###############################
#Fit all pairwise subsets with additive and interactions
out <-glmulti(y ~ x1+x2+x3,
            level = 2,               # interactions considered
            method = "h",            # Exhaustive search
            crit = "aicc",          # AIC as criteria
            marginality=TRUE,       #Does not allow interactions without main effects
            confsetsize = 100,         # Keep 100 best models
            plotty = F, report = F,  # No plot or interim reports
            fitfunction = "glm",
            family="binomial")

#Model combinations
out@formulas[[1]]
```

```
## y ~ 1 + x1 + x2
## <environment: 0x0000000019120f20>
```

```
#Common model averaging technique
model.avg(out@objects)
```

```
##
## Call:
## model.avg(object = out@objects)
##
## Component models:
## '12'     '123'    '124'    '1235'   '1234'   '1236'   '12345'  '12356'
## '12346'  '123456' '1'      '13'     '135'    '2'      '23'     '236'
## '(Null)' '3'
##
## Coefficients:
##         (Intercept)        x1       x2         x3       x1:x2      x1:x3
## full      0.9655858 -1.056101 1.000433 0.02172400 -0.01221763 0.01511691
## subset    0.9655858 -1.056101 1.000433 0.04431799 -0.04203913 0.08513802
##              x2:x3
## full   -0.001191094
## subset -0.009036990
```

Using the “full” model averaging we conflate the main effects of an additive only model and the conditional effects of an interaction model. However, the model averaged interaction coefficients are however fine. They are shrunk towards zero when an additive model is supported, which is appropriate.

```r
coefs=model.avg(out@objects)

#Find the interaction coefs
index.interaction=apply(matrix(colnames(coefs$coefficients)),1,
                        FUN=function(x){str_detect(x, ":", negate = FALSE)})

#These are correct and appropriate model average interaction coefficients that are shrunk towards zero
coefs$coefficients[1,which(as.integer(index.interaction)==1)]
```

```
##        x1:x2        x1:x3        x2:x3
## -0.012217634  0.015116906 -0.001191094
```

```r
#Extract coefficients and AIC model weights
table.coef=model.sel(out@objects)

#Get the "main effects" coefficients
main=table.coef[,which(as.integer(index.interaction)==0)[-1]]
main
```

```
##            x1        x2         x3
## 1  -1.0536293 0.9980896         NA
## 2  -1.0539992 0.9964708 0.05204669
## 3  -1.0620354 1.0070860         NA
## 4  -1.0529049 0.9996820 0.03330442
## 5  -1.0621589 1.0051481 0.05107180
## 6  -1.0540315 0.9964079 0.05178052
## 7  -1.0615335 1.0086528 0.03152347
## 8  -1.0539871 0.9994152 0.02784513
## 9  -1.0621618 1.0051381 0.05103391
## 10 -1.0624478 1.0083165 0.02608064
## 11 -0.8794112        NA         NA
## 12 -0.8799916        NA 0.08194561
## 13 -0.8797676        NA 0.06950357
## 14         NA 0.8134253         NA
## 15         NA 0.8112748 0.04229115
## 16         NA 0.8130887 0.04908210
## 17         NA        NA         NA
## 18         NA        NA 0.07625837
```

```r
#Identify models with interaction with x1,x2, and x3
index.x1=unlist(lapply(out@formulas,FUN=function(x){str_detect(paste(c(x)), "x1:|:x1", negate = FALSE)}
index.x2=unlist(lapply(out@formulas,FUN=function(x){str_detect(paste(c(x)), "x2:|:x2", negate = FALSE)}
index.x3=unlist(lapply(out@formulas,FUN=function(x){str_detect(paste(c(x)), "x3:|:x3", negate = FALSE)}

#Loop through models and change main effects to zero when they are involved in an interaction
for(i in 1:length(index.x1)){
  if(index.x1[i]==TRUE){main[i,1]=0}
  if(index.x2[i]==TRUE){main[i,2]=0}
  if(index.x3[i]==TRUE){main[i,3]=0}
}

#Main coefs only with zeros where interactions are involved
main
```

```
##            x1        x2         x3
## 1  -1.0536293 0.9980896         NA
```

```
## 2  -1.0539992 0.9964708 0.05204669
## 3   0.0000000 0.0000000         NA
## 4   0.0000000 0.9996820 0.00000000
## 5   0.0000000 0.0000000 0.05107180
## 6  -1.0540315 0.0000000 0.00000000
## 7   0.0000000 0.0000000 0.00000000
## 8   0.0000000 0.0000000 0.00000000
## 9   0.0000000 0.0000000 0.00000000
## 10  0.0000000 0.0000000 0.00000000
## 11 -0.8794112        NA         NA
## 12 -0.8799916        NA 0.08194561
## 13  0.0000000        NA 0.00000000
## 14         NA 0.8134253         NA
## 15         NA 0.8112748 0.04229115
## 16         NA 0.0000000 0.00000000
## 17         NA        NA         NA
## 18         NA        NA 0.07625837
```

```r
#Replace NA's with zeros
index.na=which(is.na(main),arr.ind=TRUE)
main[index.na]=0

#Extract AIC Weights
weights=table.coef[,13]

#Multiply each column by the weights and sum
#This is the model averaged main effects for additive models only shrunk towards zero
colSums(main*weights)
```

```
##         x1         x2         x3 
## -0.6148174  0.6144215  0.0118643
```

```r
#Combine main and interaction coefs.
shrunk.coefs=c(colSums(main*weights),coefs$coefficients[1,which(as.integer(index.interaction)==1)])
shrunk.coefs
```

```
##           x1           x2           x3        x1:x2        x1:x3        x2:x3 
## -0.614817352  0.614421479  0.011864300 -0.012217634  0.015116906 -0.001191094
```

RESULTS: With a much much larger sample size, the interaction coefs are much closer to zero and there is more clear support for the additive combinations of x1 and x2.

Simulation of Model Averaging Coefficients

Simulation

We will conduct a simulation study to investigate the effects of model averaging coefficients to indicate support for an additive or interaction effect between variables. If a model does not include the interaction than the interaction coefficient will be zero. We will shrink the main effects by changing the conditional effects (i.e., non-interaction coefficients) of the interaction model to be zero. This way, the main and conditional effects are not mixed and are shrunk to zero when not supported by Akaike weight.

In the first section we will use a generating model that includes an interaction and in the second section we will use a generating model that excludes an interaction. Thus, the first section should should show support for an interaction and not the main effects. The reverse should be true for the second section.

The generating model of the first section is $y_i \sim \text{Binomial}(1, p_i)$
$logit(p_i) = \beta_0 + \beta_1 \times x_1 + \beta_2 \times x_2 + \beta_3 \times (x_1 \times x_2)$

The generating model of the second section is $y_i \sim \text{Binomial}(1, p_i)$
$logit(p_i) = \beta_0 + \beta_1 \times x_1 + \beta_2 \times x_2$

Section 1

```
###################################
#Setup workspace
rm(list=ls())
options(warn=-1)
library(glmulti)
```

```
## Loading required package: rJava

## Loading required package: leaps
```

```
library(MuMIn)
library(stringr)
library(vioplot)
```

```
## Loading required package: sm

## Package 'sm', version 2.2-5.6: type help(sm) for summary information

## Loading required package: zoo

##
## Attaching package: 'zoo'

## The following objects are masked from 'package:base':
##
##     as.Date, as.Date.numeric
```

```
#Simulate standardized covariate data
n=200 #sample size
set.seed(1343)
x1=rnorm(n,0,1)
x2=rnorm(n,0,1)


#Generating model design matrix
X=model.matrix(~x1*x2)

#True coefficients
beta=t(matrix(c(-0.5,0.1,0.1,0.5),ncol=4))

#True probabilities
probs=plogis(X%*%beta)

#how many data sets to simulate
n.data=1000

#Save the shrunk coeficients
shrunk.coefs.save=matrix(NA, nrow=n.data,ncol=4)
colnames(shrunk.coefs.save)=c("Int","x1","x2","x1:x2")

#START LOOP
for(z in 1:n.data){

  #Simulate data with interaction model
  set.seed(1000+z)
  y=rbinom(n,1,prob = probs)


  #Fit all pairwise subsets with additive and interactions
  out <-glmulti(y ~ x1+x2,
              level = 2,               # interactions considered
              method = "h",            # Exhaustive search
              crit = "aicc",          # AIC as criteria
              marginality=TRUE,       #Do not allow interactions without main effects
              confsetsize = 100,         # Keep 100 best models
              plotty = F, report = F,  # No plot or interim reports
              fitfunction = "glm",
              family="binomial")

  coefs=model.avg(out@objects)


  #Extract coefficients and AIC model weights
  table.coef=model.sel(out@objects)

  #Extract the coeficients
  table.coef2=table.coef[,1:4]

  #Identify models with interaction with x1,x2, and x3
  index.x1=unlist(lapply(out@formulas,FUN=function(x){
```

```
    str_detect(paste(c(x)), "x1:|:x1", negate = FALSE)}))
  index.x2=unlist(lapply(out@formulas,FUN=function(x){
    str_detect(paste(c(x)), "x2:|:x2", negate = FALSE)}))

#Loop through and change main effects to zero when they are involved in an interaction
  for(i in 1:length(index.x1)){
    if(index.x1[i]==TRUE){table.coef2[i,2]=0}
    if(index.x2[i]==TRUE){table.coef2[i,3]=0}
  }

  #Main coefs only with zeros where interactions are involved
  table.coef2

  #Replace NA's with zeros
  index.na=which(is.na(table.coef2),arr.ind=TRUE)
  table.coef2[index.na]=0

  #Extract AIC Weights
  weights=matrix(table.coef[,'weight'])

#Multiply each column by the weights and sum
shrunk.coefs=t(table.coef2)%*%weights

#save the output
shrunk.coefs.save[z,]=shrunk.coefs

#Print progress
if(z%%100==0) cat(z, " "); flush.console()
}
```

```
## 100  200  300  400  500  600  700  800  900  1000
```

```
#END LOOP
```

Section 2

```
#Generating model design matrix
X=model.matrix(~x1+x2)

#True coefficients
beta=t(matrix(c(-0.5,0.5,0.5),ncol=3))

#True probabilities
probs=plogis(X%*%beta)

#how many data sets to simulate
n.data=1000

#Save the shrunk coeficients
shrunk.coefs.save2=matrix(NA, nrow=n.data,ncol=4)
colnames(shrunk.coefs.save2)=c("Int","x1","x2","x1:x2")

#START LOOP
```

```r
for(z in 1:n.data){

  #Simulate data with interaction model
  set.seed(1000+z)
  y=rbinom(n,1,prob = probs)


  #Fit all pairwise subsets with additive and interactions
  out <-glmulti(y ~ x1+x2,
              level = 2,               # interactions considered
              method = "h",            # Exhaustive search
              crit = "aicc",          # AIC as criteria
              marginality=TRUE,       #Do not allow interactions without main effects
              confsetsize = 100,         # Keep 100 best models
              plotty = F, report = F,  # No plot or interim reports
              fitfunction = "glm",
              family="binomial")

  coefs=model.avg(out@objects)


  #Extract coefficients and AIC model weights
  table.coef=model.sel(out@objects)

  #Extract the coeficients
  table.coef2=table.coef[,1:4]

  #Identify models with interaction with x1,x2, and x3
  index.x1=unlist(lapply(out@formulas,FUN=function(x){
    str_detect(paste(c(x)), "x1:|:x1", negate = FALSE)}))
  index.x2=unlist(lapply(out@formulas,FUN=function(x){
    str_detect(paste(c(x)), "x2:|:x2", negate = FALSE)}))

  #Loop through and change main effects to zero when they are involved in an interaction
  for(i in 1:length(index.x1)){
    if(index.x1[i]==TRUE){table.coef2[i,2]=0}
    if(index.x2[i]==TRUE){table.coef2[i,3]=0}
  }

  #Main coefs only with zeros where interactions are involved
  table.coef2

  #Replace NA's with zeros
  index.na=which(is.na(table.coef2),arr.ind=TRUE)
  table.coef2[index.na]=0

  #Extract AIC Weights
  weights=matrix(table.coef[,'weight'])

#Multiply each column by the weights and sum
shrunk.coefs=t(table.coef2)%*%weights

#save the output
```

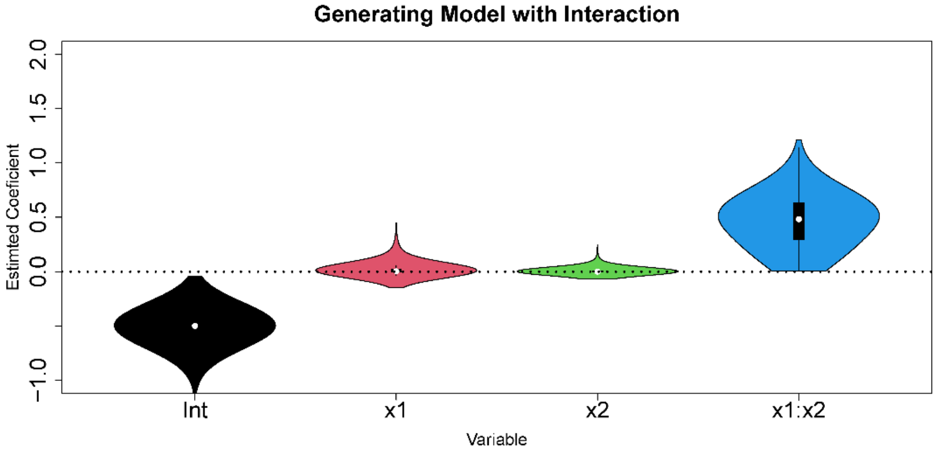
```
shrunk.coefs.save2[z,]=shrunk.coefs

#Print progress
if(z%%100==0) cat(z, " "); flush.console()
}
```

```
## 100  200  300  400  500  600  700  800  900  1000
```

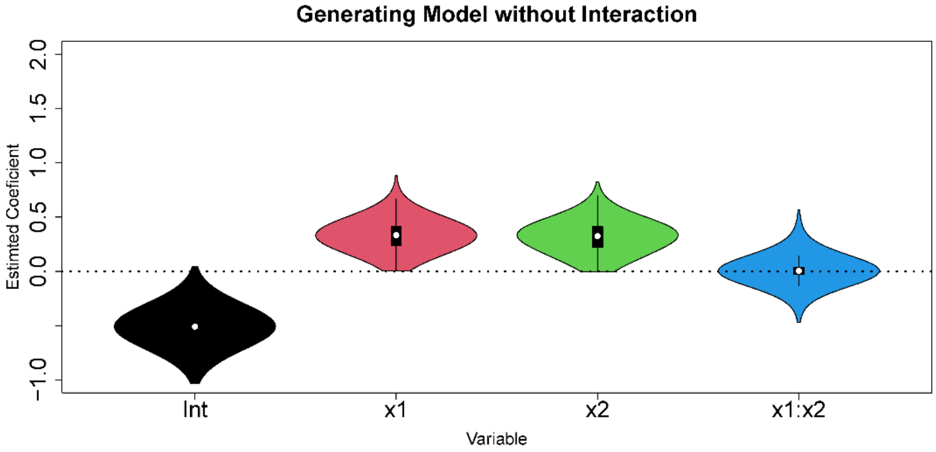
```
#END LOOP
```

##Plotting Results

```
#Plot the estimated shrunk coefficients
par(mfrow=c(2,1),cex.main=2,cex.axis=2,cex.lab=1.5)
vioplot(shrunk.coefs.save,use.cols = TRUE,col=1:4,xlab="Variable",ylab="Estimted Coeficient",
        ylim=c(-1,2),main="Generating Model with Interaction")
abline(h=0,lwd=3,col=1,lty=3)
vioplot(shrunk.coefs.save2,use.cols = TRUE,col=1:4,xlab="Variable",ylab="Estimted Coeficient",
        ylim=c(-1,2),main="Generating Model without Interaction")
abline(h=0,lwd=3,col=1,lty=3)
```



Generating Model with Interaction

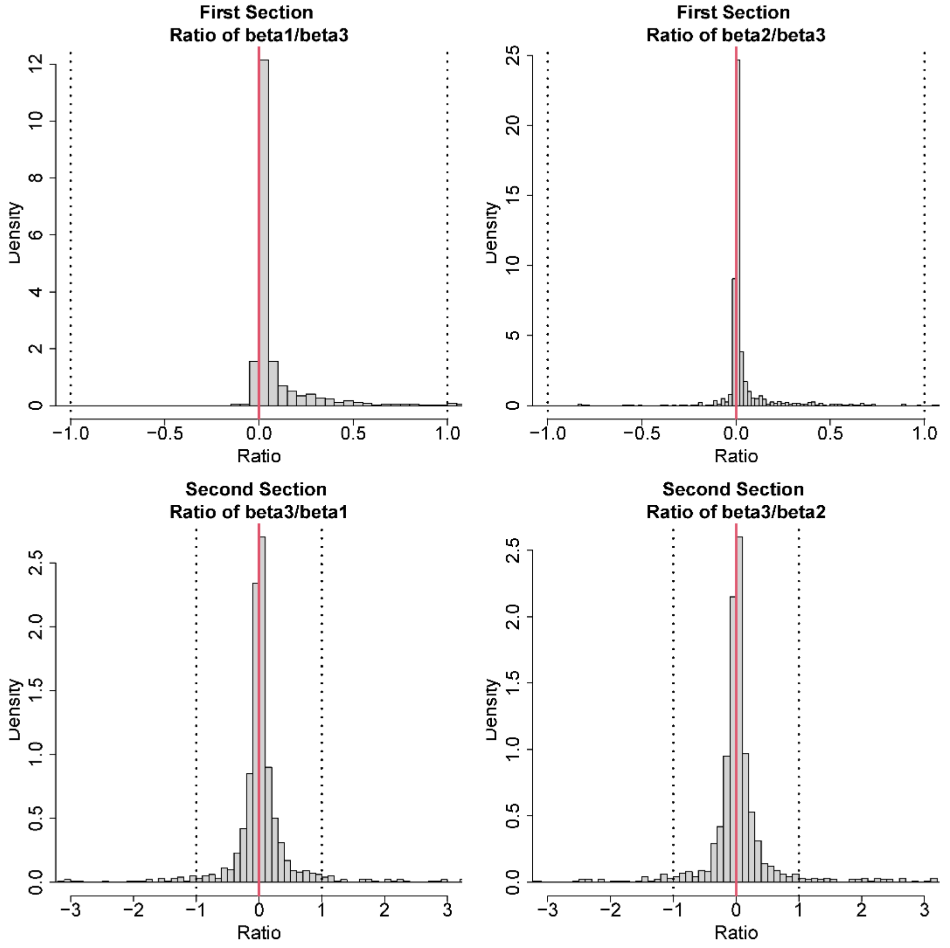


Generating Model without Interaction

Both plots indicate that the respective coefficients are appropriately being shrunk towards zero, indicating support for an interaction in the top figure and support for no interaction in the bottom figure. The variability for each coefficient will ultimately depend on the sample size of the data and size of the estimated coefficients. But generally, this type of approach captures the intended inference of providing support for additive or interaction effects without conflating main and conditional effects.

```
#Plot ratios of estimated coefficients for each section results
par(mfrow=c(2,2),cex.main=2,cex.axis=2,cex.lab=2)
a=(shrunk.coefs.save[,2])/(shrunk.coefs.save[,4])
hist(a,breaks=1000,xlim=c(-1,1),freq=FALSE,xlab="Ratio",
     main="First Section \nRatio of beta1/beta3")
abline(v=0,lwd=3,col=2,lty=1)
abline(v=-1,lwd=3,col=1,lty=3)
abline(v=1,lwd=3,col=1,lty=3)
```

```
b=(shrunk.coefs.save[,3])/(shrunk.coefs.save[,4])
hist(b,xlim=c(-1,1),breaks=1000,freq=FALSE,xlab="Ratio",
     main="First Section \nRatio of beta2/beta3")
abline(v=0,lwd=3,col=2,lty=1)
abline(v=-1,lwd=3,col=1,lty=3)
abline(v=1,lwd=3,col=1,lty=3)


a=(shrunk.coefs.save2[,4])/(shrunk.coefs.save2[,2])
hist(a,breaks=1000,xlim=c(-3,3),freq=FALSE,xlab="Ratio",
     main="Second Section \nRatio of beta3/beta1")
abline(v=0,lwd=3,col=2,lty=1)
abline(v=-1,lwd=3,col=1,lty=3)
abline(v=1,lwd=3,col=1,lty=3)

b=(shrunk.coefs.save2[,4])/(shrunk.coefs.save2[,3])
hist(b,xlim=c(-3,3),breaks=1000,freq=FALSE,xlab="Ratio",
     main="Second Section \nRatio of beta3/beta2")
abline(v=0,lwd=3,col=2,lty=1)
abline(v=-1,lwd=3,col=1,lty=3)
abline(v=1,lwd=3,col=1,lty=3)
```



The ratio is between an estimated coefficient expected to be zero (numerator) and an estimated coefficient expected to not be zero (denominator). Thus, we expect most plotted ratio values will be at or close to zero. Positive or negative values indicate that an estimated coefficient that should be zero is not at zero. \

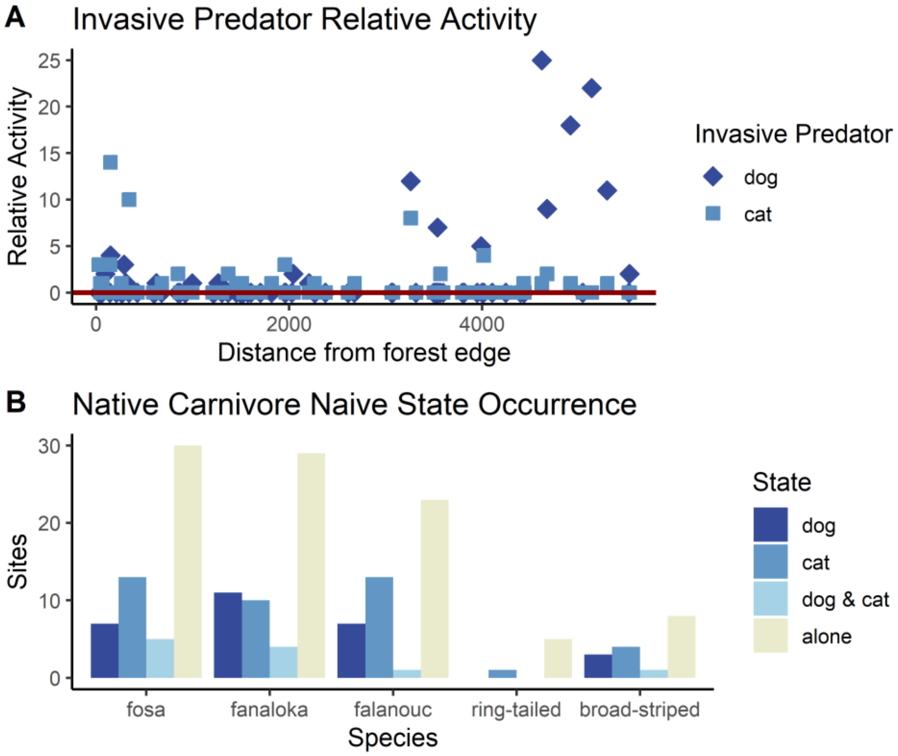
Values lower than -1 or greater than 1 indicate greater support for an incorrect inference. For example, if the generating model included an interaction and the ratio between β_2 and β_3 is greater than one, it indicates more support for an additive combination than an interaction because the interaction effect (β_3) is smaller than main effect (β_2). Overall, we see that most values are near zero

Appendix S6

Survey Results:

Invasive Predator Relative Activity & Co-occurrence Distributions

We examined detections of native carnivorans and invasive predators to verify our sampled observations had a representative distribution to preform our analysis. To test our hypotheses, we required variation in invasive predator detections across distance to forest edge, and site co-occurrence with native carnivorans (e.g. native carnivoran with dog, with cat, with dog and cat, and alone). We therefore checked for the distribution of invasive predator (dog, cat) relative activity across distance to forest edge (A) and examined native carnivoran naïve state occurrence with invasive predators (B). We determined in both instances we had a reasonable sample size and distribution to test our hypotheses on the separate and combined effects of invasive predators and forest edge for three native carnivorans (fosa, fanaloka, falanouc). However, we had a more limited sample size for the broad-striped vontsira which reduced our statistical power to estimate interaction parameters. We therefore did not model any interaction terms for the broad-striped vontsira. Lastly, our initial examinational also revealed a limited sample size and variable state distribution of the ring-tailed vontsira, we therefore did not include ring-tailed vontsira in either single- and multi- species analyses.



Appendix S7
Model Average Coefficients

Model averaged coefficients and sums of Akaike weights (sw) for single season single species occupancy analysis. Higher coefficient values for single variables (e.g., cats) indicate more support for independent effects, while higher values of combined variables (e.g., cats:forest edge) indicate more support of an interaction effect.

Hypothesis	***ψ***	**fosa**	***sw***	**fanaloka**	***sw***	**falanouc**	***sw***	**broad-striped**	***sw***
Invasive Predator	*cats*	0.039	0.120	-0.045	0.084	-0.054	0.128	0.000	0.003
	dogs	0.060	0.118	0.154	0.179	-0.022	0.058	0.000	0.003
Forest Edge	*forest edge*	1.306	0.869	0.009	0.022	-0.016	0.061	0.067	0.064
	high canopy	-0.005	0.005	0.007	0.020	-0.016	0.063	-0.008	0.012
	open canopy	0.001	0.003	-0.011	0.027	0.014	0.061	0.004	0.008
	shrub	-0.007	0.003	-0.006	0.019	0.006	0.042	-0.001	0.005
Interaction	*cats: forest edge*	0.386	0.076	0.013	0.016	0.009	0.019	-	-
	cats: shrub	0.000	0.000	-0.024	0.025	-0.044	0.056	-	-
	dogs: forest edge	-0.001	0.033	0.000	0.001	0.000	0.002	-	-
	dogs: shrub	0.000	0.000	-0.194	0.039	-0.020	0.014	-	-
Alternative	*village*	0.001	0.003	0.229	0.253	0.002	0.043	0.266	0.178
	cats: village	0.000	0.000	0.858	0.464	0.586	0.496	-	-
	dogs: village	0.000	0.000	0.054	0.076	0.001	0.002	-	-

Relative Activity	***p***	**fosa**	***sw***	**fanaloka**	***sw***	**falanouc**	***sw***	**broad-striped**	***sw***
	cats	0.032	0.344	0.013	0.263	0.641	1.000	0.001	0.006
	dogs	-0.433	1.000	0.001	0.242	-1.058	1.000	0.059	0.111
	forest edge	0.047	0.314	0.821	1.000	0.834	1.000	0.078	0.085
	human	0.440	1.000	0.313	1.000	-0.016	0.270	0.870	0.890
	village	-0.065	0.397	0.132	0.741	-0.614	1.000	0.785	0.622

Appendix S8
Single-Season Single-Species Occupancy Model Results

Results for each native carnivores single-season single species occupancy models. Reportered are all models that had a model weight equal to or greater than two percent. Bolded coeffcient values indicate a p-value < 0.05.

Fosa

Model #	ψ (Int)	*dog*	*forest edge*	*cat*	*village*	*shrub*	*open canopy*	*high canopy*	*dog* shrub*	*cat* shrub*	*cat* forest edge*	*dog* forest edge*	*dog* village*	*cat* village*	*p* (Int)	*cat*	*dog*	*forest edge*	*human*	*village*	df	logLik	AICc	delta	weight
75	**2.095**	-	**1.455**	-	-	-	-	-	-	-	-	-	-	-	**-3.723**	-	**-0.405**	-	**0.454**	-	5	-708.83	1428.49	0.00	0.09
201	**2.094**	-	**1.455**	-	-	-	-	-	-	-	-	-	-	-	**-3.723**	-	**-0.405**	-	**0.454**	-	5	-708.83	1428.49	0.00	0.09
202	**2.143**	-	**1.486**	-	-	-	-	-	-	-	-	-	-	-	**-3.726**	0.105	**-0.421**	-	**0.450**	-	6	-708.06	1429.30	0.81	0.06
76	**2.143**	-	**1.486**	-	-	-	-	-	-	-	-	-	-	-	**-3.726**	0.105	**-0.421**	-	**0.450**	-	6	-708.06	1429.30	0.81	0.06
217	**2.156**	-	**1.529**	-	-	-	-	-	-	-	-	-	-	-	**-3.712**	-	**-0.437**	-	**0.426**	-0.124	6	-708.17	1429.53	1.04	0.05
91	**2.156**	-	**1.529**	-	-	-	-	-	-	-	-	-	-	-	**-3.712**	-	**-0.437**	-	**0.426**	-0.124	6	-708.17	1429.53	1.04	0.05
95	**2.362**	-	**1.560**	-	-	-	-	-	-	-	-	-	-	-	**-3.774**	-	**-0.491**	0.214	**0.409**	-0.242	7	-707.33	1430.26	1.77	0.04
221	**2.363**	-	**1.560**	-	-	-	-	-	-	-	-	-	-	-	**-3.774**	-	**-0.491**	0.214	**0.409**	-0.242	7	-707.33	1430.26	1.77	0.04
232	**2.093**	-	**1.529**	0.301	-	-	-	-	-	-	-	-	-	-	**-3.720**	-	**-0.408**	-	**0.452**	-	6	-708.59	1430.36	1.87	0.03
107	**2.164**	0.510	**1.449**	-	-	-	-	-	-	-	-	-	-	-	**-3.719**	-	**-0.411**	-	**0.452**	-	6	-708.61	1430.41	1.92	0.03
205	**2.113**	-	**1.445**	-	-	-	-	-	-	-	-	-	-	-	**-3.734**	-	**-0.408**	0.033	**0.455**	-	6	-708.80	1430.78	2.29	0.03
79	**2.113**	-	**1.445**	-	-	-	-	-	-	-	-	-	-	-	**-3.734**	-	**-0.408**	0.033	**0.455**	-	6	-708.80	1430.78	2.29	0.03
771	**6.732**	-	4.181	8.531	-	-	-	-	-	-	5.050	-	-	-	**-3.737**	-	**-0.404**	-	**0.463**	-	7	-707.74	1431.07	2.58	0.02
218	**2.177**	-	**1.531**	-	-	-	-	-	-	-	-	-	-	-	**-3.719**	0.078	**-0.439**	-	**0.433**	-0.085	7	-707.80	1431.19	2.70	0.02
92	**2.177**	-	**1.531**	-	-	-	-	-	-	-	-	-	-	-	**-3.719**	0.078	**-0.439**	-	**0.433**	-0.085	7	-707.80	1431.19	2.70	0.02
108	**2.169**	0.414	**1.476**	-	-	-	-	-	-	-	-	-	-	-	**-3.721**	0.102	**-0.425**	-	**0.448**	-	7	-707.89	1431.38	2.89	0.02
248	**2.158**	-	**1.606**	0.301	-	-	-	-	-	-	-	-	-	-	**-3.710**	-	**-0.440**	-	**0.425**	-0.125	7	-707.92	1431.44	2.95	0.02

Fanaloka

Model #	ψInt	*dog*	*forest edge*	*cat*	*village*	*shrub*	*open canopy*	*high canopy*	*dog* shrub*	*cat* shrub*	*cat* forest edge*	*dog* forest edge*	*dog* village*	*cat* village*	*p* Int	*cat*	*dog*	*forest edge*	*human*	*village*	df	logLik	AICc	delta	weight
957	**1.493**	-	-	0.313	**1.202**	-	-	-	-	-	-	-	-	1.843	**-2.661**	-	-	**0.796**	**0.335**	**0.171**	8	-1542.74	3103.57	0.00	0.19
958	**1.492**	-	-	0.310	**1.210**	-	-	-	-	-	-	-	-	1.858	**-2.646**	0.058	-	**0.787**	**0.328**	**0.171**	9	-1542.42	3105.48	1.91	0.07
941	**1.470**	-	-	0.334	**1.249**	-	-	-	-	-	-	-	-	1.844	**-2.612**	-	-	**0.861**	**0.253**	-	7	-1545.01	3105.62	2.05	0.07
317	**1.224**	0.913	-	-	**1.029**	-	-	-	-	-	-	-	-	-	**-2.666**	-	-	**0.809**	**0.332**	**0.169**	7	-1545.03	3105.65	2.09	0.07
959	**1.493**	-	-	0.314	**1.203**	-	-	-	-	-	-	-	-	1.847	**-2.662**	-	0.023	**0.772**	**0.331**	**0.190**	9	-1542.64	3105.93	2.37	0.06
925	**1.637**	1.822	-	-	**1.241**	-	-	-	-	-	-	-	0.720	-	**-2.669**	-	-	**0.812**	**0.332**	**0.170**	8	-1541.50	3107.09	3.53	0.03
942	**1.469**	-	-	0.330	**1.255**	-	-	-	-	-	-	-	-	1.856	**-2.597**	0.059	-	**0.853**	**0.246**	-	8	-1544.68	3107.44	3.87	0.03
301	**1.205**	0.919	-	-	**1.060**	-	-	-	-	-	-	-	-	-	**-2.618**	-	-	**0.873**	**0.251**	-	6	-1547.24	3107.67	4.10	0.02
943	**1.473**	-	-	0.330	**1.241**	-	-	-	-	-	-	-	-	1.839	**-2.618**	-	-0.029	**0.881**	**0.270**	-	8	-1544.81	3107.70	4.13	0.02
318	**1.211**	0.899	-	-	**1.041**	-	-	-	-	-	-	-	-	-	**-2.655**	0.039	-	**0.802**	**0.326**	**0.168**	8	-1544.89	3107.86	4.30	0.02
960	**1.492**	-	-	0.311	**1.210**	-	-	-	-	-	-	-	-	1.861	**-2.647**	0.056	0.019	**0.768**	**0.325**	**0.188**	10	-1542.35	3107.98	4.41	0.02
319	**1.221**	0.909	-	-	**1.030**	-	-	-	-	-	-	-	-	-	**-2.667**	-	0.018	**0.790**	**0.328**	**0.184**	8	-1544.96	3108.02	4.45	0.02

Falanouc

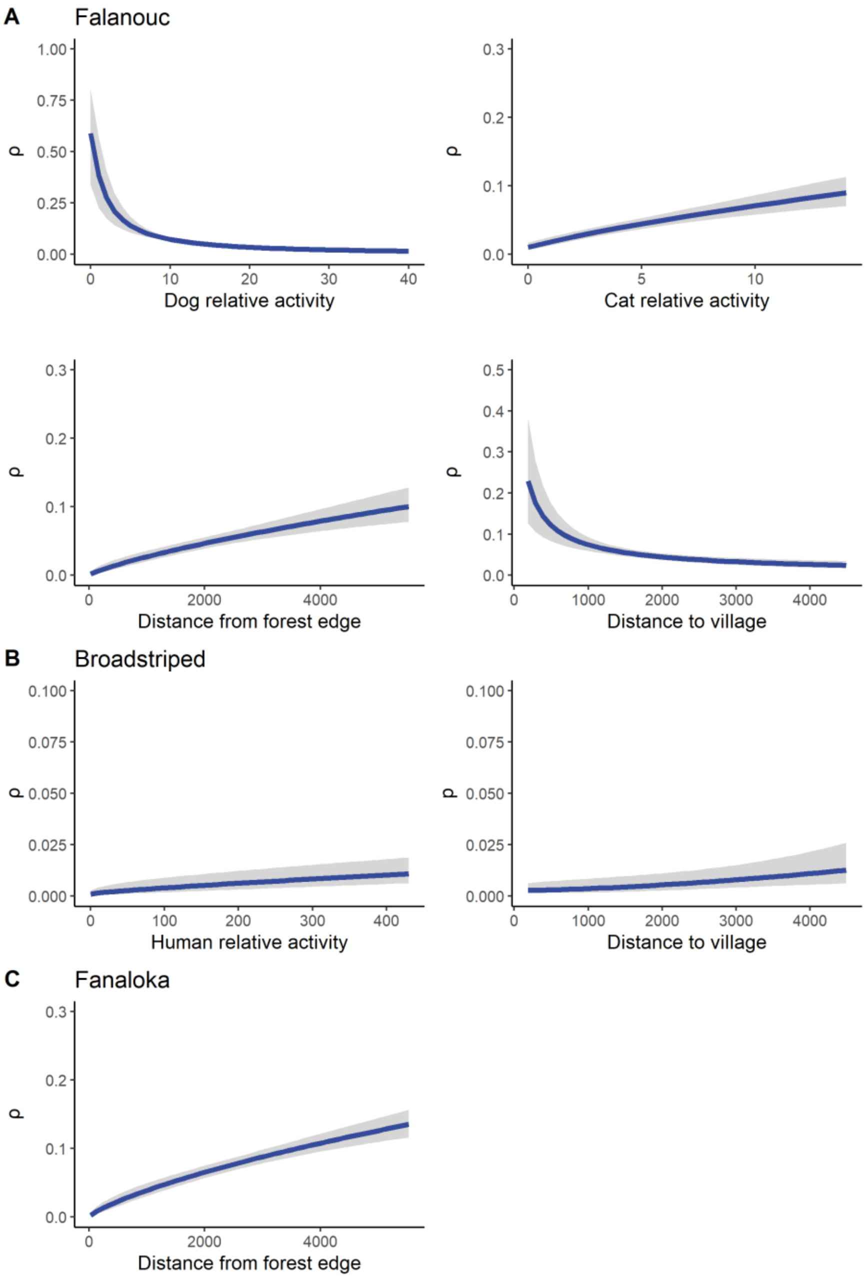
Model #	ψInt	*dog*	*forest edge*	*cat*	*village*	*shrub*	*open canopy*	*high canopy*	*dog* shrub*	*cat* shrub*	*cat* forest edge*	*dog* forest edge*	*dog* village*	*cat* village*	*p* Int	*cat*	*dog*	*forest edge*	*human*	*village*	df	logLik	AICc	delta	weight
950	**0.931**	-	-	0.287	0.032	-	-	-	-	-	-	-	-	**1.178**	**-3.017**	**0.639**	**-1.076**	**0.826**	-	**-0.603**	9	-932.04	1884.73	0.00	0.36
958	**0.940**	-	-	0.280	0.020	-	-	-	-	-	-	-	-	**1.187**	**-3.018**	**0.652**	**-1.076**	**0.871**	-0.061	**-0.639**	10	-931.74	1886.76	2.03	0.13
823	**0.651**	-	-	-0.029	-	0.097	-	-	-	-0.794	-	-	-	-	**-3.019**	**0.637**	**-1.082**	**0.821**	-	**-0.609**	9	-934.21	1889.07	4.33	0.04
152	0.480	-	-	-	-	-	-	-	-	-	-	-	-	-	**-3.001**	**0.632**	**-1.044**	**0.812**	-	**-0.606**	6	-938.30	1889.78	5.04	0.03
24	0.480	-	-	-	-	-	-	-	-	-	-	-	-	-	**-3.001**	**0.632**	**-1.044**	**0.812**	-	**-0.606**	6	-938.30	1889.78	5.04	0.03
184	0.510	-	-	-0.363	-	-	-	-	-	-	-	-	-	-	**-3.005**	**0.639**	**-1.049**	**0.817**	-	**-0.612**	7	-937.17	1889.93	5.20	0.03

Broad-striped vontsira

Model #	ψ Int	*dog*	*forest edge*	*cat*	*village*	*shrub*	*open canopy*	*high canopy*	*p* Int	*cat*	*dog*	*forest edge*	*human*	*village*	df	logLik	AICc	delta	weight
16	0.097	-	-	-	-	-	-	-	**-5.557**	-	-	-	**1.084**	**1.280**	4	-165.453	339.454	0.000	0.302
45	0.097	-	-	-	-	-	-	-	**-5.557**	-	-	-	**1.084**	**1.280**	4	-165.453	339.454	0.000	0.302
63	-0.087	-	-	-	1.567	-	-	-	**-5.044**	-	-	-	**0.845**	-	4	-166.870	342.288	2.834	0.073
70	-0.087	-	-	-	1.567	-	-	-	**-5.044**	-	-	-	**0.845**	-	4	-166.870	342.288	2.834	0.073
40	-0.104	-	-	-	-	-	-	-	**-5.280**	-	-	**0.929**	**0.635**	-	4	-167.657	343.863	4.408	0.033
11	-0.104	-	-	-	-	-	-	-	**-5.280**	-	-	**0.929**	**0.635**	-	4	-167.657	343.863	4.408	0.033
56	-0.775	-	**1.088**	-	-	-	-	-	**-4.732**	-	-	-	**0.686**	-	4	-168.142	344.832	5.377	0.020
27	-0.775	-	**1.088**	-	-	-	-	-	**-4.732**	-	-	-	**0.686**	-	4	-168.142	344.832	5.377	0.020

Appendix S9
Prediction Plots of the Important Variables on Native carnivoran Relative Activity

Prediction plots for medium and large effects on native carnivoran relative activity (p) determined from model averaged coefficient from single-season, single-species occupancy model. No medium or large effects were found for the fosa. Falanouc (A) relative activity was influences by *dog*, *cat*, *forest edge*, and *village*. Broad-striped vontsira (B) relatively activity was influenced by *human* and *village*. Fanaloka relative activity was influence by *forest edge*.



Appendix S10
Single-season Multispecies Occupancy Model Results

Co-occurrence occupancy models are indicated by ψ_C, where independent occurrence models, are indicated with ψ_M. Co-occurrence models support the influence of invasive predator on native carnivoran occupancy. Independent models support no influence of invasive predator on native carnivoran occupancy. ψ_C with environmental variable, indicate support for an interaction between invasive predator and the environmental variable (e.g. ~dog:shrub). Evidence ratios indicate the level of support for the top model relative to the model in that row, for each species

Fosa

Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt	Evidence Ratios
ψ_M	13	3103.62	0.00	1.00	0.33	-1535.96	0.33	-
ψ_C (dog:shrub)	15	3104.16	0.55	0.76	0.25	-1533.21	0.58	1.32
ψ_C (dog)	14	3105.77	2.15	0.34	0.11	-1535.55	0.69	3.82
ψ_C (cat)	14	3106.51	2.90	0.24	0.08	-1535.92	0.77	5.55
ψ_C (dog:village)	15	3107.15	3.53	0.17	0.06	-1534.70	0.83	7.61
ψ_C (dog:forest edge)	15	3108.21	4.60	0.10	0.03	-1535.23	0.86	12.98
ψ_C (dog+cat)	15	3108.81	5.20	0.07	0.02	-1535.53	0.88	17.51
ψ_C (dog:cat:forest edge)	16	3109.30	5.69	0.06	0.02	-1534.19	0.90	22.37
ψ_C (cat:forest edge)	15	3109.41	5.80	0.06	0.02	-1535.84	0.92	23.66
ψ_C (dog:cat)	15	3109.48	5.87	0.05	0.02	-1535.87	0.94	24.53
ψ_C (cat:shrub)	15	3109.58	5.96	0.05	0.02	-1535.92	0.96	25.69
ψ_C (cat:village)	15	3109.58	5.96	0.05	0.02	-1535.92	0.97	25.69
ψ_C (dog:shrub+cat:shrub)	17	3110.44	6.83	0.03	0.01	-1533.12	0.98	39.57
ψ_C (dog:cat:shrub)	16	3110.74	7.13	0.03	0.01	-1534.91	0.99	46.06
ψ_C (dog:cat:village)	16	3112.64	9.02	0.01	0.00	-1535.86	1.00	118.78
ψ_C (dog:village + cat:village)	17	3113.42	9.81	0.01	0.00	-1534.61	1.00	175.75
ψ_C (dog: forest edge + cat:forest edge)	17	3114.45	10.84	0.00	0.00	-1535.13	1.00	294.25

Fanaloka

Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt	Evidence Ratios
ψ_C (dog:shrub)	17	4783.26	0.00	1.00	0.41	-2369.53	0.41	-
ψ_C (dog)	16	4784.85	1.59	0.45	0.19	-2371.96	0.60	2.21
ψ_C (dog:forest edge)	17	4786.32	3.06	0.22	0.09	-2371.06	0.69	6.05
ψ_C (dog:shrub+cat:shrub)	19	4787.09	3.83	0.15	0.06	-2367.99	0.75	8.89
ψ_C (dog+cat)	17	4787.15	3.89	0.14	0.06	-2371.48	0.81	9.15
ψ_C (dog:village + cat:village)	19	4787.45	4.19	0.12	0.05	-2368.17	0.86	10.63
ψ_C (dog: forest edge + cat:forest edge)	19	4787.88	4.61	0.10	0.04	-2368.39	0.90	13.15
ψ_C (cat:village)	17	4787.92	4.66	0.10	0.04	-2371.86	0.94	13.46
ψ_C (dog:village)	17	4788.08	4.82	0.09	0.04	-2371.94	0.97	14.58
ψ_M	15	4791.31	8.05	0.02	0.01	-2376.78	0.98	73.13
ψ_C (cat:forest edge)	17	4791.56	8.30	0.02	0.01	-2373.68	0.99	82.85
ψ_C (cat:shrub)	17	4792.70	9.44	0.01	0.00	-2374.25	0.99	146.74
ψ_C (dog:cat:forest edge)	18	4792.99	9.72	0.01	0.00	-2372.70	0.99	169.16
ψ_C (cat)	16	4793.08	9.82	0.01	0.00	-2376.08	1.00	177.66
ψ_C (dog:cat:shrub)	18	4794.93	11.67	0.00	0.00	-2373.67	1.00	447.05
ψ_C (dog:cat:village)	18	4795.41	12.15	0.00	0.00	-2373.91	1.00	567.83
ψ_C (dog:cat)	17	4797.72	14.46	0.00	0.00	-2376.76	1.00	1802.90

Falanouc

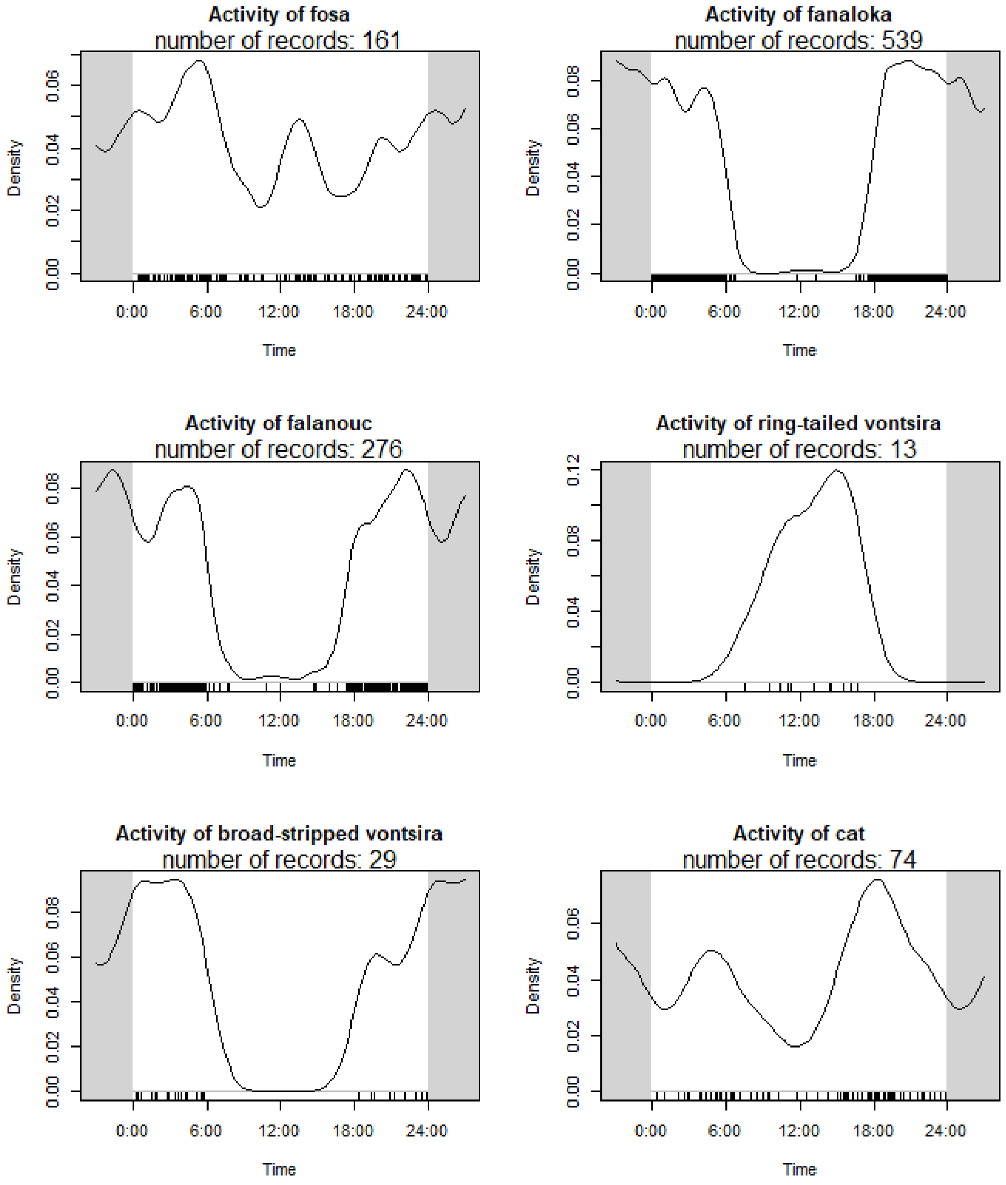
Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL	CumWt	Evidence Ratios
ψ_C (dog:shrub)	14	3579.80	0.00	1.00	0.54	-1772.57	0.54	-
ψ_M	12	3582.39	2.59	0.27	0.15	-1776.80	0.69	3.65
ψ_C (dog:cat:shrub)	15	3584.07	4.27	0.12	0.06	-1773.16	0.75	8.46
ψ_C (dog)	13	3584.91	5.11	0.08	0.04	-1776.61	0.79	12.87
ψ_C (cat)	13	3585.12	5.32	0.07	0.04	-1776.72	0.83	14.33
ψ_C (dog:cat)	14	3585.27	5.47	0.06	0.03	-1775.30	0.86	15.42
ψ_C (cat:village)	14	3585.97	6.17	0.05	0.02	-1775.65	0.89	21.85
ψ_C (dog:shrub+cat:shrub)	16	3586.02	6.22	0.04	0.02	-1772.55	0.91	22.46
ψ_C (dog:cat:forest edge)	15	3586.43	6.64	0.04	0.02	-1774.35	0.93	27.59
ψ_C (dog:cat:village)	15	3586.97	7.17	0.03	0.01	-1774.61	0.95	36.07
ψ_C (dog:forest edge)	14	3587.42	7.62	0.02	0.01	-1776.37	0.96	45.06
ψ_C (dog:village)	14	3587.43	7.63	0.02	0.01	-1776.38	0.97	45.36
ψ_C (dog+cat)	14	3587.71	7.91	0.02	0.01	-1776.52	0.98	52.27
ψ_C (cat:shrub)	14	3588.00	8.20	0.02	0.01	-1776.67	0.99	60.27
ψ_C (cat:forest edge)	14	3588.10	8.30	0.02	0.01	-1776.72	1.00	63.37
ψ_C (dog:village + cat:village)	16	3592.15	12.35	0.00	0.00	-1775.62	1.00	480.87
ψ_C (dog: forest edge + cat:forest edge)	16	3593.23	13.43	0.00	0.00	-1776.16	1.00	825.67

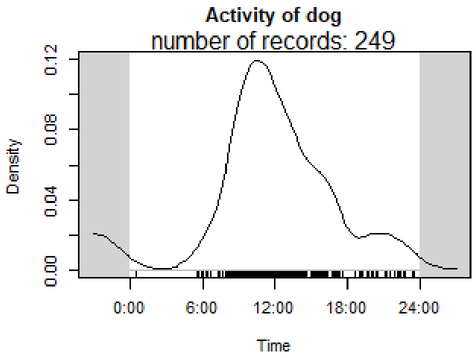
Broad-striped vontsira

Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL	CumWt	Evidence Ratios
ψ_M	12	2019.47	0.00	1.00	0.44	-995.33	0.44	-
ψ_C (dog:shrub)	14	2021.95	2.49	0.29	0.13	-993.64	0.57	3.47
ψ_C (cat)	13	2022.30	2.83	0.24	0.11	-995.31	0.67	4.13
ψ_C (dog)	13	2022.35	2.88	0.24	0.10	-995.33	0.78	4.23
ψ_C (dog:forest edge)	14	2023.08	3.61	0.16	0.07	-994.21	0.85	6.09
ψ_C (cat:village)	14	2024.28	4.81	0.09	0.04	-994.81	0.89	11.09
ψ_C (cat:shrub)	14	2024.94	5.47	0.06	0.03	-995.14	0.92	15.44
ψ_C (cat:forest edge)	14	2025.28	5.81	0.05	0.02	-995.30	0.94	18.28
ψ_C (dog:cat)	14	2025.28	5.81	0.05	0.02	-995.31	0.96	18.29
ψ_C (dog:village)	14	2025.28	5.82	0.05	0.02	-995.31	0.99	18.32
ψ_C (dog:shrub+cat:shrub)	16	2027.77	8.31	0.02	0.01	-993.43	0.99	63.67
ψ_C (dog: forest edge + cat:forest edge)	16	2028.92	9.45	0.01	0.00	-994.00	1.00	112.84
ψ_C (dog:village + cat:village)	16	2030.28	10.82	0.00	0.00	-994.68	1.00	223.40

APPENDICES

Appendix 1. Activity density plots of native carnivorans, invasive predators, and humans included in our analyses for Manuscript 2.




Activity of dog
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Density
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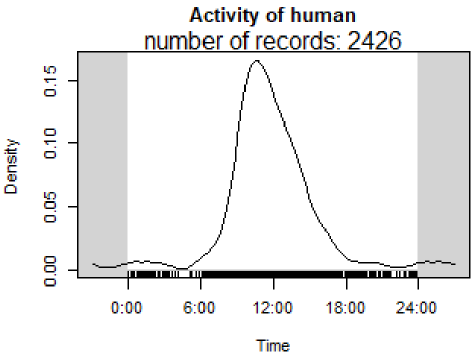
0.04
0.08
0.12
0:00
6:00
12:00
18:00
24:00
Time


Activity of human
number of records: 2426
Density
0.00
0.05
0.10
0.15
0:00
6:00
12:00
18:00
24:00
Time