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REVIEW

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

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#### Keywords

euplerids, extinction risk, human disturbance, Madagascar, meso-carnivores, trait-based risk, understudied

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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 classifies 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) synthesise the current state of knowledge of the lifehistory 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 from 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) indicate 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.

#### Mots clés

basé sur les traits, Eupléridés, Madagascar, méso-carnivores, perturbation humaine, risque d'extinction, sous-étudié

## **RÉSUMÉ EN FRANÇAIS**

- 1. Les carnivores indigènes de Madagascar sont un groupe monophylétique endémique de huit espèces appartenant à la famille Eupleridae. L'Union Internationale pour la Conservation de la Nature (UICN) classe actuellement sept des espèces comme menacées (vulnérables ou en danger), car leurs populations sont en déclin a cause de l'intensification des pressions anthropiques. Cependant, on en sait peu sur l'écologie et les tendances démographiques de ces espèces, ce qui exclut les prévisions de risque d'extinction. Le cycle biologique et les traits fonctionnels régissent les réponses des espèces à la pression environnementale et peuvent prédire le risque d'extinction. L'intégration d'informations pertinentes sur les caractéristiques peut considérablement améliorer les évaluations des risques. Pourtant, les informations sur la vie et les traits fonctionnels des Eupléridés n'ont jamais été compilées dans un cadre unique.
- 2. Nos objectifs sont de: 1) synthétiser l'état actuel des connaissances sur le cycle biologique et les traits fonctionnels des espèces d'Eupléridés, 2) examiner les preuves empiriques des effets des pressions anthropiques sur ces espèces, et 3) identifier les lacunes dans nos connaissances pour guider les recherches futures.
- **3**. Nous avons effectué des recherches dans la littérature publiée pour compiler des informations sur les caractéristiques biologiques, les traits fonctionnels, et les effets connus des pressions anthropiques sur les Eupléridés.
- 4. Notre étude indique que les carnivores de Madagascar ont un cycle de vie et des traits fonctionnels à haut risque qui augmentent leur vulnérabilité aux pressions anthropiques. Des publications ont signalé les effets négatifs de la dégradation et de la fragmentation de l'habitat, de l'exploitation forestière, des carnivores non indigènes, de la maladie, de la chasse, et des exécutions de représailles sur les Eupléridés. Cependant, notre synthèse a révélé des lacunes importantes dans les connaissances, en particulier dans les traits du cycle biologique des espèces et dans la variabilité spatiale de la plupart des traits. Pour la plupart des espèces, nous manquons actuellement des données nécessaires pour évaluer la dynamique des risques fondée sur les traits.
- 5. Le point culminant des caractères signalés, l'influence négative des pressions anthropiques en cours et le manque de mesures solides (par exemple, les tendances de la population et la variabilité des caractères) indiquent que les Eupléridés sont à haut risque et peuvent atteindre un niveau de disparition sans préavis en raison de lacunes importantes dans cette connaissance. Pour combler ces lacunes, les recherches futures devraient donner priorité a la connaissance des caractères influents, évaluer les pressions anthropiques et intégrer les informations sur les caractères pour améliorer les évaluations des risques et les prévisions d'extinction.

## 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, <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 18–24 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 Gallinae) and felid- or civet-like species (subfamily Eupleridae). 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 et al. 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 has 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 lifetime fitness, such as survival, growth, reproduction, and dispersal (Flatt et al. 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

Animalia						
Mammalia						
Carnivora						
Euple	ridae					
	Euple	rinae		Common name	IUCN category	
ر -	2	Cryptoprocta	spelea	giant fosa	Extinct	
			ferox	fosa	VU	
	R	Eupleres	goudotii	eastern falanouc	VU	
			major	western falanouc	EN	
	A	Fossa	fossana	fanaloka	VU	
	Galir	nae				
~		Galidia	elegans	ring-tailed vontsira	LC	
•		Galidictis	fasciata	broad-striped vontsira	VU	
		Mungotictis	decemlineata	bokiboky	EN	
	æ	Salanoia	concolor	brown-tailed vontsira	VU	

**Fig. 1.** Currently recognised species of the family Eupleridae, with Malagasy common names and the latest International Union for Conservation of Nature (IUCN) categories (VU = Vulnerable, EN = Endangered, LC = Least Concern). The eight extant species are included in this review. [Colour figure can be viewed at wileyonlinelibrary.com]

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 highrisk traits include long gestation length, small litter size, late weaning age, late sexual maturity, large adult mass, long life span – 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 (González-Suárez & 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 & Pęksa 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 life span, adult mass, and adult body length (the last two were sexspecific 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, haplotype), 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 Crypt 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 lifehistory 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 Professionnelle 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

**Table1.** Summary of available information on 10 life-history traits and seven 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). Sources of information are indicated as follows: - = none; M = museum specimen (skin or haplotype) only; C = captive individual(s) studied at zoos, born in captivity or in the wild (may include additional data from museum specimens); I = informal observation, excluded from results (no identifiable source, or observed randomly by chance; detailed information available in Appendices S2–S9); SW = single reference, wild study (trait described in only one study); MW = multiple references, wild study (trait described in more than one study).

	C. ferox	F. fossana	E. goudotii	E. major	G. fasciata	G. elegans	M. decemlineata	S. concolor
Life-history traits								
Gestation length (days)	С	С	_	-	_	С	MW	_
Litter size	С	С	_	С	_	С	SW	_
Sex ratio of offspring	С	_	_	-	_	-	-	_
Mass at birth (g)	С	С	_	С	_	С	С	_
Weaning age (days)	С	С	_	-	_	С	С	_
Interbirth interval	С	_	_	-	_	С	SW	_
Age (years) and size at sexual maturity	С	-	_	-	-	I	I	-
Average life span (years)	С	_	-	_	-	-	I	-
Body mass (kg): unknown sex	MW	MW	I	I	Μ	MW	MW	Μ
Body mass (kg): male	MW	MW	-	SW	_	MW	SW	Μ
Body mass (kg): female	MW	MW	-	_	-	MW	SW	Μ
Body length (mm): unknown sex	MW	MW	Μ	Μ	Μ	MW	MW	Μ
Body length (mm): male	MW	_	-	SW	_	_	MW	Μ
Body length (mm): female	MW	_	-	SW	-	-	MW	Μ
Functional traits								
Population density (individuals/km <sup>2</sup> )	MW	MW	_	-	SW	SW	SW	_
Feeding guild	MW	MW	С	SW	SW	MW	I	MW
Sociality	MW	I	_	-	_	MW	MW	_
Distribution	MW	MW	MW	MW	MW	MW	MW	MW
Habitat use	MW	MW	SW	I	MW	MW	SW	MW
Activity patterns	MW	MW	MW	MW	MW	MW	MW	MW
Home range size (km <sup>2</sup> )	MW	SW	_	_	_	SW	MW	SW





Ecoregion: 📕 deciduous forest 📕 rainforest 📒 spiny forest

Fig. 2. Numbers of studies on wild individuals or populations of each species in the family Eupleridae in each eco-region, providing information on life-history traits (a) and functional traits (b). [Colour figure can be viewed at wileyonlinelibrary.com]

this extreme range). Females produce one litter per year, with litter size varying between two and 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 and 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 to 6.9 kg in females and from 6.1 to 8.6 kg in males; total body length (head-body-tail) ranges from 1357 to 1467 mm in females and from 1350 to 1532 mm in males. There is no published information available on the life span 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 Mitea 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 to 0.25 individuals/km<sup>2</sup> in the deciduous forest (n = 5), and from 0.08 to 0.39 individuals/km<sup>2</sup> 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 cathemeral, 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 to 89 km<sup>2</sup>. 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<sup>2</sup> for females and 55 and 35 km<sup>2</sup> 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 six 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 82–90 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 life span in either captivity or the wild.

#### FUNCTIONAL TRAITS

Four publications reported population densities. Estimates range from  $1.38 \pm 0.22$  to  $3.19 \pm 0.55$  individuals/km<sup>2</sup> (mean  $\pm$  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  $0.07-0.55 \text{ km}^2$  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 have 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 to 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 life span.

#### 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 cathemeral. 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, major 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 was 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 indicates 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 total 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.

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#### 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 was 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 680-718 mm 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 life span.

#### FUNCTIONAL TRAITS

Only two density estimates have been published, from the spiny forest: 6.23 and 7.99 individuals/km<sup>2</sup> 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 was 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 geographic 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 to 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 to 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) was 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 life span.

#### FUNCTIONAL TRAITS

In Ranomafana National Park, the estimated density was 37 individuals/km<sup>2</sup>. *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 lowland 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<sup>2</sup>.

## *Mungotictis decemlineata* (bokiboky, narrow-striped mongoose)

We found 12 publications that included information on seven of the ten life-history traits and all functional traits (Table 1). Despite the paucity of publications compared with 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 Morondava.

#### 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 to 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 Forest/ CFPF, Morondava, Central Menabe Protected Forests, and at Manombo River. Information on body size indicates no sexual dimorphism. Total body length ranges from 452 to 620 mm. Male and female total body length has been reported to be 550 mm and 524 mm, respectively. Body mass ranges from 400 to 700 g; females weigh 450-740 g and males 475-625 g. There is no published information available on sex ratio of offspring, age at sexual maturity, or average life span for Mungotictis decemlineata.

#### FUNCTIONAL TRAITS

Population density for Mungotictis decemlineata was estimated between 1-8 and 1-5 adults/km<sup>2</sup> 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<sup>2</sup> in Kirindy Forest/CFPF, and 1.5-2 km<sup>2</sup> for a 'supergroup' of 10-12 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 lifehistory 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 to 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 as follows: a museum specimen weighing 780 g, the Lac Alaotra haplotype 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 life span.

#### 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<sup>2</sup>. 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, 13 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 nonnative 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.



**Fig. 3.** Key studies on consequences of anthropogenic pressures for euplerids on Madagascar. Anthropogenic pressures investigated in the studies are denoted by black icons, locations of studies are indicated on the map and denoted by reference numbers 1-8; affected species are listed. Protected areas in Madagascar are shown within each eco-region. Major findings from publications with resulting consequences of pressures on euplerids are summarised. For detailed findings by species, see Appendices S2–S9. [Colour figure can be viewed at wileyonlinelibrary.com]

These independent pressures can influence species' lifehistory 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 nonnative carnivoran species. Four publications reported on the influence of anthropogenic pressures in deciduous forest on euplerid habitat use (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 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 et al. 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 et al. 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 et al. 2015a). Otherwise, *Cryptoprocta ferox* showed little sensitivity to habitat disturbance, and minor variation in density between non-degraded and degraded sites:  $0.12 \pm 0.05$  and  $0.09 \pm 0.04$  adults/km<sup>2</sup>, respectively (mean  $\pm$  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 et al. 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<sup>2</sup>) than unlogged forests (3.19 ± 0.55 individuals/km<sup>2</sup>; 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 et al. 2015a). However, habitat use declined significantly across years close to the forest edge, and was 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 was positively associated with bird presence and understory cover, but detection rates were lower with Felis catus presence (Farris et al. 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 declined 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*  $(n = \ge 2)$ . 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 the following: 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 life span (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 lifehistory 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.

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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 S2-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, 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 multi-year 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 homogeneous 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 causespecific 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,

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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.
- 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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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

- 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. Mungoticitis 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.