

Trends in the extinction of carnivores in Madagascar

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Abstract

Trends in the extinction of carnivores in Madagascar.— The extinction of top predators, such as mammalian carnivores can lead to dramatic changes in foodweb structure and ecosystem dynamics. Since all native Malagasy terrestrial mammalian carnivores are endemic, their extinction implies a significant loss of biodiversity in Madagascar. Here we review the literature on Madagascar's mammalian carnivores, aiming to determine which species are most likely to become extinct in the near future in view of the factors threatening their survival. We scored each factor according to its impact on the species. According to our results, the giant-striped mongoose, *Galidictis grandidieri*, is the most likely species to next become extinct. This is no surprise because this species is considered one of the rarest carnivores in the world, inhabiting only a small, threatened forest ecosystem. Our results emphasize the need for robust data about each species to help and support decision-makers implement conservation measures.

Key words: Eupleridae, Endemism, Biodiversity loss, Human impacts, Deforestation, Interspecific competition

Resumen

Tendencias de la extinción de carnívoros en Madagascar.— La extinción de los depredadores apicales, como los mamíferos carnívoros, puede conllevar cambios drásticos en la estructura de la red alimentaria y la dinámica de los ecosistemas. Dado que todos los mamíferos carnívoros terrestres autóctonos de Madagascar son endémicos, su extinción implica una pérdida notable de biodiversidad en este país. En el presente artículo examinamos las publicaciones sobre mamíferos carnívoros de Madagascar con el propósito de determinar cuáles son las especies que tienen mayor probabilidad de extinguirse en un futuro próximo, en vista de los factores que amenazan su supervivencia. Puntuamos cada factor en función de los efectos que ejerce en las especies. Según nuestros resultados, la especie que tiene más probabilidad de extinguirse es la mangosta rayada grande, *Galidictis grandidieri*, lo cual no es sorprendente porque esta especie se considera uno de los carnívoros más escasos del mundo, que habita solo en un ecosistema forestal pequeño y amenazado. Asimismo, nuestros resultados ponen de manifiesto la necesidad de disponer de datos sólidos sobre cada especie, a fin de ayudar y respaldar a las autoridades a poner en práctica medidas de conservación.

Palabras clave: Eupleridae, Endemismo, Pérdida de biodiversidad, Efectos de los humanos, Deforestación, Competencia interespecífica

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Introduction

Mammalian carnivores are susceptible to local extinction through habitat loss and fragmentation, mainly due to their fairly large distribution ranges, small population size and conflicts with humans (Woodroffe & Ginsberg, 1998; Crooks, 2002; Logan et al., 2015). Moreover, they are top predators, so their extinction can seriously affect food webs and ecosystem dynamics (Crooks, 2002). The effects of anthropogenic activities in Madagascar and their impact on carnivore populations are poorly understood (Gerber et al., 2010; Logan et al., 2015). Madagascar is one of twenty-five global biodiversity hotspots, harbouring almost 3% of the world's endemic vertebrates (Myers et al., 2000). Since all Malagasy native terrestrial mammalian carnivores are endemic (Yoder et al., 2003; Duckworth et al., 2014), their extinction would represent a significant biodiversity loss, both in Madagascar and globally.

Carnivora is one of four terrestrial mammalian orders occurring in Madagascar, but it is represented by only one family, Eupleridae (Yoder et al., 2003). This family comprises twelve species and subspecies and includes an extinct species and a newly discovered species (Albignac, 1972; Durbin et al., 2010; Goodman & Hedges, 2010). The only carnivore known to be extinct in Madagascar is the giant fossa (*Cryptoprocta spelea* Grandidier, 1902), considered a larger relative of the extant fossa, *Cryptoprocta ferox* Bennet, 1833 (Hoffman & Hawkins, 2015). The reasons for its extinction are unclear, but likely due to the loss of their main prey (such as giant lemurs) and extensive habitat destruction (Yoder et al., 2003; Goodman et al., 2004). Although the Giant fossa is the only carnivore known to be extinct in Madagascar, others extinctions may have occurred. There are also three introduced carnivore species in Madagascar: the domestic dog (*Canis familiaris* Linnaeus, 1758), the feral cat (*Felis* sp. Linnaeus, 1758), and the small Indian civet (*Viverricula indica* É. Geoffroy Saint-Hilaire, 1803) (Gerber et al., 2010; Farris et al., 2015). Co-occurrence of native and exotic carnivores may alter ecological dynamics, such as predation, competition or resource use (Hunter & Caro, 2008; Vanak & Gompper, 2010). Farris et al. (2015) identified a strong temporal overlap between native and introduced carnivores in Madagascar, with the small Indian civet presenting the greatest overlap with native Malagasy carnivores.

Here we review the ecological characteristics of Malagasy carnivores and their current threats and relevance. Our aim is to review and analyse current knowledge on the ecology, conservation and threats to Malagasy carnivores of the family Eupleridae. Based on this knowledge, we try to identify current conservation priorities and predict which species are currently more susceptible to extinction risk in the near future.

Material and methods

Literature search

This is a theoretical study based on information compiled from available literature and IUCN (International

Union for Conservation of Nature and Natural Resources) data. We restricted our search to international peer-reviewed manuscripts and books. We searched for scientific papers on the Web of Science™ database using the following keywords: 'Madagascar', Malagasy species scientific and common names, 'carnivore', 'biodiversity loss', 'deforestation', 'conservation', and scientific and common names of introduced mammalian carnivores. We reviewed 81 scientific papers and eight books. Moreover, we sourced information on the IUCN about the mammalian carnivores studied, totalling 97 references (list provided on supplemental material, table 1sS1). Furthermore, the IUCN Red List kindly provided species distribution GIS shapefiles, which were useful to calculate distribution areas and generate maps for species' distribution (fig. 1, table 1).

Data analysis

To evaluate the risk of extinction, we generated a table whereby we averaged the standardized scores for the following factors affecting Malagasy carnivores: distribution range, species information, dietary breadth, dietary overlap, habitat breadth, strata overlap, activity pattern overlap, forested areas within distribution range in 2015, and deforestation between 2007 and 2015. Species information was estimated based on the number of references indexed internationally in which the species is evaluated (see table 1s in supplementary material). To assess dietary breadth, we put food items together in categories, namely fruits, eggs, invertebrates, amphibians and reptiles, fish, birds, lemurs, and other small mammals, and then counted how many categories of food items each species uses (table 1). Habitat breadth for each species was obtained from PANTHERIA (Jones et al., 2009). To quantify the possible ecological overlap between species, we estimated dietary, strata and activity pattern overlaps using data on diet, compiled from the literature, and data on arboreality and activity patterns, obtained from PANTHERIA (equations provided in appendix 1s in supplementary material). We assumed that more ecologically similar species would be most affected by sharing scarce resources. The distribution range was calculated in QGIS (Brighton version 2.6.0), based on shapefiles provided by the IUCN, using the Albers equal-area conical projection (EPSG: 102 022). We assessed deforestation in each species' distribution range, using QGIS, by comparing the amount of forested and non-forested areas in 2007 and 2015 (within each species' distribution range), and using the online updated data on global forest/non forest maps from ALOS PALSAR Data (Shimada et al., 2014; updated data available on http://www.eorc.jaxa.jp/ALOS/en/palsar_fnf/fnf_index.htm, June 2016). The percentage of forested areas in 2015 in each species distribution range was estimated using the same dataset. Although we are aware of the different weights that each factor may have in the ecology and probability of extinction of species, because of lack of information in the literature, we considered each factor to be of the same relevance.

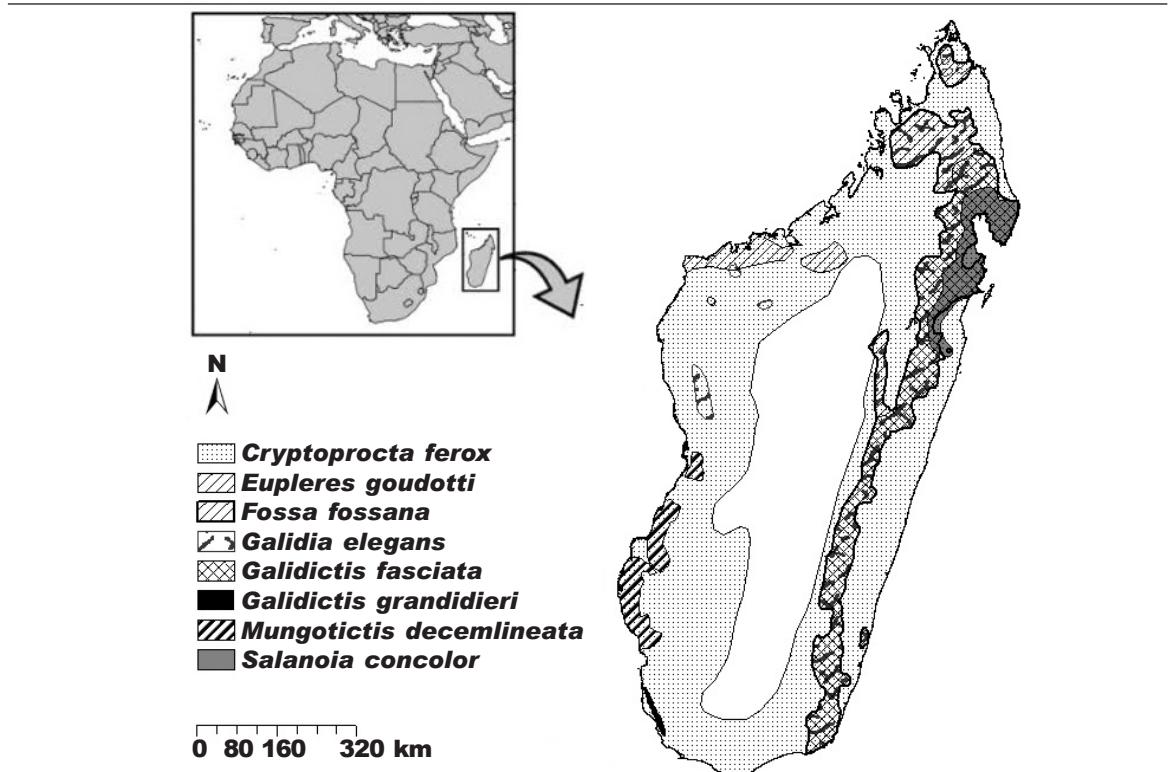


Fig. 1. Geographic distribution of the carnivore mammal species in Madagascar. Species distribution data were obtained from the IUCN Red List.

Fig. 1. Distribución geográfica de las especies de mamíferos carnívoros en Madagascar. Los datos sobre la distribución de las especies se obtuvieron de la Lista Roja de la UICN.

The scores for each factor were represented with a positive sign if the factor was favourable to conservation and a negative sign if the factor threatened conservation. Scores for each factor were standardized, resulting in variables with 0 mean and unit standard deviation, and with the most threatened species presenting the most negative score values. Scores for each factor were averaged for each species, and 95% confidence intervals were estimated for the species average scores.

Results

Species accounts

The fossa (*Cryptoprocta ferox*, Bennet, 1833) is found at low densities, in forested areas across the whole island except for the central plateau (Goodman et al., 2004; Hawkins & Racey, 2005; Hawkins & Dollar, 2008). Fossa prey on a variety of vertebrates (small mammals, lemurs, reptiles and amphibians) and occasionally feed on domestic animals such as pigs and poultry (Hawkins & Racey, 2005). Their

period of daily activity overlaps with that of *Eupleres goudotii*, *Fossa fossana*, *Galidictis fasciata*, *Viverricula indica*, and feral cats and dogs (Farris et al., 2015). Moreover, it exhibits a dietary overlap with *Galidia elegans* (Gerber et al., 2012a). With no natural predators, humans are the biggest threat for fossa as they are hunted out of fear and to protect livestock (Goodman et al., 2004; Hawkins & Racey, 2005; Hawkins & Dollar, 2008). Deforestation is destroying the formerly broad habitat of fossa (Goodman et al., 2004; Hawkins & Racey, 2005; Hawkins & Dollar, 2008).

Fossa fossana (P. L. S. Müller, 1776), also known as the Malagasy civet, is the third largest carnivore in Madagascar (Gerber et al., 2012a). It is nocturnal and distributed across the eastern territory of the island in tropical low-land and mid-altitude forests (Kerridge et al., 2003; Hawkins, 2008a). It is a generalist predator, including crustaceans, reptiles, rodents and amphibians in its diet (Goodman et al., 2003). The species' abundance has decreased due to deforestation (excessive logging or land use change for agriculture) and due to competition with other species (Hawkins, 2008a).

Table 1. Diet, activity pattern, strata of occurrence, habitat breadth and distribution range for the eight endemic carnivore species in Madagascar. Data in this table were used to estimate the factors presented in table 2 and figure 2: Fr. Fruits; Eg. Eggs; In. Insects and other arthropods; He. Herps (amphibians and reptiles); Fi. Fish; Bi. Birds; Le. Lemurs; Sm. Small mammals.

Species	Diet							
	Fr	Eg	In	He	Fi	Bi	Le	Sm
<i>Cryptoprocta ferox</i>			X	X		X	X	X
<i>Eupleres goudotii</i>			X	X		X		X
<i>Fossa fossana</i>		X	X	X			X	X
<i>Galidia elegans</i>	X	X	X	X	X		X	X
<i>Galidictis fasciata</i>			X	X			X	X
<i>Galidictis grandidieri</i>		X	X					X
<i>Mungotictis decemlineata</i>		X	X	X				X
<i>Salanoia concolor</i>			X			X		X

The taxonomic organization of the genus *Eupleres* has been widely discussed over the years. Albignac (1973) considered *Eupleres* to be monospecific and represented by two subspecies: *E. goudotii goudotii* (Doyère, 1835) and *E. goudotii major* (Lavauden, 1929). However, recently, Goodman & Helgen (2010) proposed that these subspecies could be elevated to the rank of species based on subfossil evidence. Here we consider only *Eupleres goudotii goudotii* because it is the subspecies for which most relevant information is available. The small-toothed mongoose (*Eupleres goudotii goudotii*) is thought to be very uncommon across its range, which includes the east coast and the north of Madagascar (Albignac, 1972; Dollar, 2000). Its diet consists mainly of earthworms, but it occasionally feeds on amphibians and insects (Albignac, 1972; Macdonald, 1992; Garbutt, 1999). The main threat for this species is deforestation caused by slash-and-burn agriculture, logging and charcoal production (Schreiber et al., 1989; Nowak, 1999). It is also the only species selectively hunted for bushmeat (Dollar, 2000; Logan et al., 2015). *E. g. goudotii* and *F. fossana* have highly similar activity profiles with the introduced *V. indica*, but there are considerable differences in niche requirements between these two native carnivores and *V. indica* (Farris et al., 2015).

The giant-striped mongoose (*Galidictis grandidieri*, Wozencraft, 1986) is one of the rarest carnivores in the world (Andriatsimetry et al., 2009; Marquard et al., 2011). It inhabits a small, unique spiny forest ecosystem that is threatened by human activity, and it is also preyed on by introduced dogs (Hawkins, 2008b; Marquard et al., 2011). It preys on tortoise eggs, invertebrates and some vertebrates (Andriatsimetry et al., 2009; Currylow, 2014). *G. grandidieri* co-occurs

with *C. ferox* and with the introduced civet species *V. indica*, but has no dietary overlap with the latter. Competition for food with the latter is unlikely, as *C. ferox* preys more on vertebrates than the giant-striped mongoose (Andriatsimetry et al., 2009).

The broad-striped mongoose (*Galidictis fasciata* Gmelin, 1788) is found only in the eastern rainforests of Madagascar (Garbutt, 1999; Goodman, 2003b). It is a generalist predator, feeding on rodents, small lemurs, reptiles, small amphibians and invertebrates (Garbutt, 1999; Goodman, 2003b). This species has not been extensively studied, perhaps due to their strictly nocturnal habits (Goodman & Pidgeon, 1998; Garbutt, 1999; Nowak, 1999; Goodman, 2003b). Like most Malagasy carnivores, *Galidictis fasciata* is threatened by deforestation and by direct competition with feral cats and dogs (Hawkins, 2008c; Farris et al., 2015).

The Malagasy ring-tailed mongoose (*Galidia elegans*, I. Geoffroy Saint-Hilaire, 1837) is a well-studied diurnal carnivore that has become very common in disturbed habitats (Hawkins, 2008d; Bennett et al., 2009; Farris et al., 2014). It has even been seen following groups of tourists for food waste (Hawkins, 2008c; Bennett et al., 2009; Farris et al., 2014). Three subspecies are currently recognized: *G. e. elegans* found in the eastern rainforests; a western race, *G. e. occidentalis*, found in deciduous forests in the central western parts; and a northern race, *G. e. dambreensis* (Hawkins, 2008d; Schnoell, 2012). Despite its population decline of over 20 percent in the last ten years, probably due to habitat loss, *G. elegans* occurs in secondary habitats, at forest edges, and in exotic tree plantations near native forests (Hawkins, 2008d; Irwin et al., 2010). It preys on lemurs, like *C. ferox*, *V. indica*, and feral cats and dogs, but it also consumes

Tabla 1. La alimentación, el régimen de actividad, los estratos de presencia, la amplitud del hábitat y el rango de distribución de las ocho especies endémicas de carnívoros en Madagascar. Los datos de esta tabla se emplearon para calcular los factores presentados en la tabla 2 y la figura 2: Fr. Frutos; Eg. Huevos; In. Insectos y otros artrópodos; He. Anfibios y reptiles; Fi. Peces; Bi. Aves; Le. Lemures; Sm. Pequeños mamíferos.

Activity pattern		Strata		Habitat Breadth	Distribution range (thousands of km ²)
Diurnal	Nocturnal	Arboreal	Terrestrial		
0.5	0.5	0.5	0.5	3	447.59
0	1	0	1	1	103.13
0	1	0	1	2	92.10
1	0	0	1	4	93.50
0.5	0.5	0	1	1	68.30
0.5	0.5	0	1	1	1.01
1	0	0.5	0.5	2	13.43
1	0	0	1	1	18.75

other small mammals, invertebrates, reptiles, fish, birds, eggs, and fruit (Nowak, 1997; Garbutt, 1999; Hawkins, 2008d; Farris et al., 2014, 2015). Its daily activity period overlaps with that of the brown-tailed mongoose, *Salanoia concolor* (Farris et al., 2014, 2015). *G. elegans* is hunted in some areas, persecuted for raiding local poultry and killed by dogs (Hawkins, 2008d). The tail of the animal is known to be used for cultural purposes by some tribal groups (Goodman, 2003a; Hawkins, 2008d).

The little-known brown-tailed mongoose, *Salanoia concolor* (I. Geoffroy Saint-Hilaire, 1837), is a diurnal species and is most frequently observed in relatively undisturbed rainforests (Hawkins et al., 2008). It feeds on small birds, mammals and coleopteran larvae (Albignac, 1972; Britt, 1999; Britt & Virkaitis, 2003). Like most Malagasy carnivores, *S. concolor* is believed to be threatened by deforestation (Hawkins et al., 2008; Farris & Kelly, 2011). This species presents high activity overlap with dogs and moderate overlap with feral cats (Farris et al., 2015). *Salanoia durrelli* is a newly-discovered species in Madagascar. It has been separated from *S. concolor* based on morphological and molecular traits (Durbin et al., 2010). Since this species is not listed in the IUCN Red List and almost no data have been published on it (at least in publicly accessible sources), we do not include it in our analyses.

The Malagasy narrow-striped mongoose (*Mungotictis decemlineata* A. Grandidier, 1867) is relatively common within a small area of the deciduous forests of Menabe in the southwest of Madagascar (Schreiber et al., 1989; Hawkins, 2008e). This species is diurnal, terrestrial and mainly insectivorous, but complements its diet with small vertebrates (Rabeantandro, 1997). Currently, the population of

M. decemlineata is threatened by predation by dogs (Hawkins, 2008e). In addition, habitat degradation caused by intensive logging and pasture conversion, and increased hunting by humans, contribute to its vulnerable status (Goodman & Raselimanana, 2003; Hawkins, 2008e).

Summary of the factors affecting Malagasy carnivore species

The scores for each factor affecting Malagasy terrestrial carnivore species were estimated and represented with either a positive or a negative sign depending on whether the factor was favourable (+) or unfavourable (-) to the conservation of the species (fig. 2). These scores were later standardized, resulting in variables with 0 mean and unit standard deviation, with the most threatened species presenting the most negative score values (table 2, fig. 3). Moreover, scores for the various factors were averaged for each species, and 95% confidence intervals were estimated for the species average scores (table 2, fig. 3).

Except for *Galidictis grandidieri*, the average level of threat did not differ significantly (fig. 3). *G. grandidieri* appears to be the species most likely to become extinct first, with all factors negatively influencing its score (Av. Std. Score = -0.77). It is followed by *M. decemlineata*, *G. fasciata*, and *S. concolor*, which also had negative average standardized scores, though these were not significant (table 2, fig. 3). *Galidia elegans* appears to be the least threatened Malagasy carnivore species (Av. Std. Score = + 0.76), unlikely to disappear from Madagascar in the near future, followed by *C. ferox*, *F. fossana*, and *E. g. goudotii*, which also had positive average standardized scores, though not significant (table 2, fig. 3).

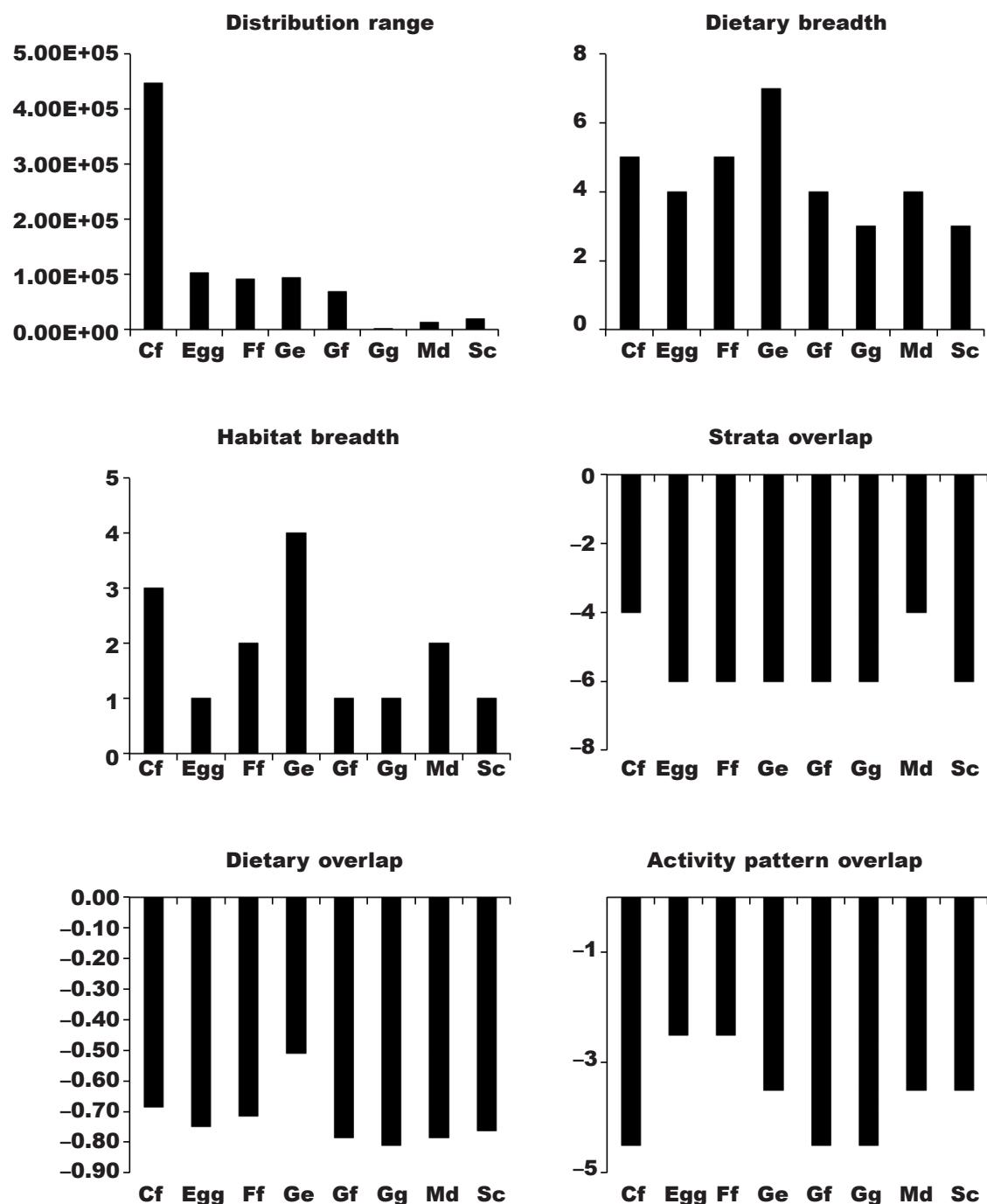
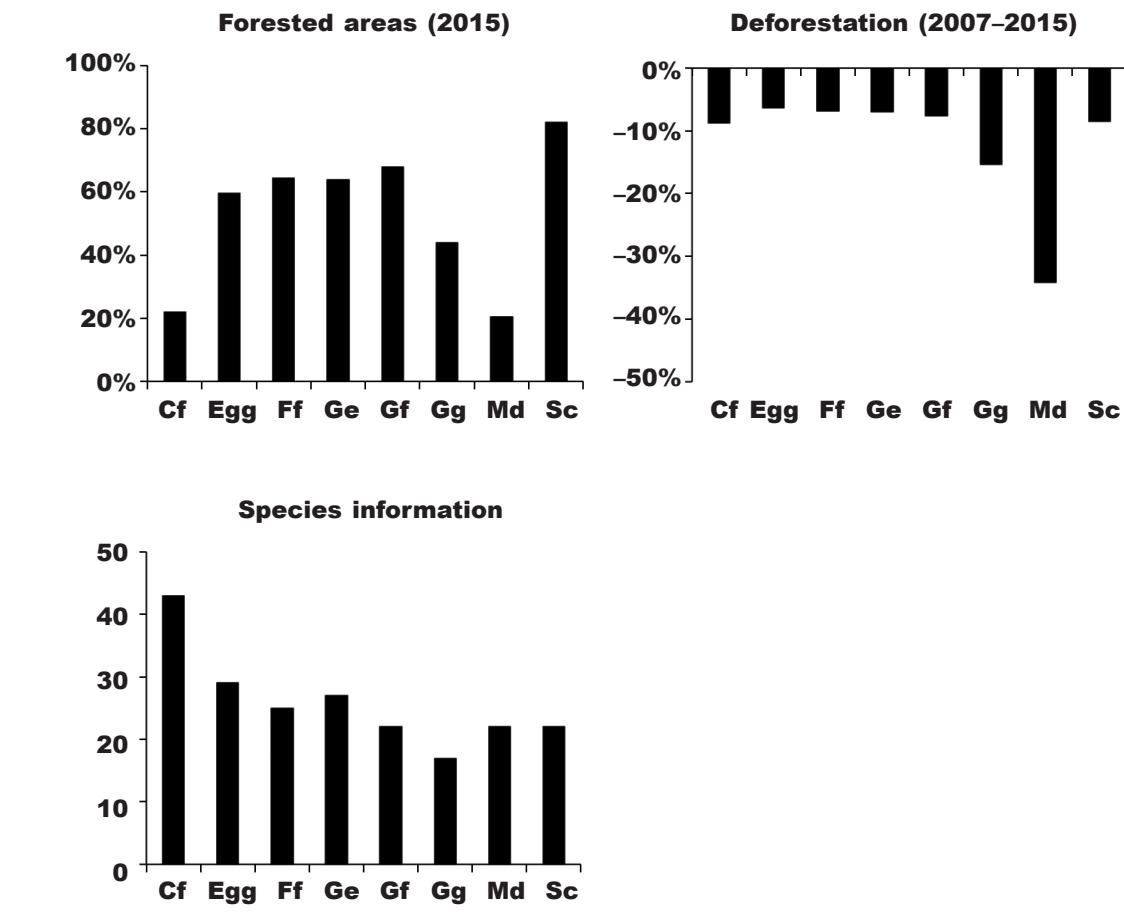


Fig. 2. Species scores (non-standardized) for factors affecting Malagasy terrestrial carnivores. Factors with an inferred negative impact are presented with negative scores while factors with a positive impact are shown with positive scores: Cf. *Cryptoprocta ferox*; Egg. *Eupleres goudotti goudotti*; Ff. *Fossa fossana*; Ge. *Galidia elegans*; Gf. *Galidictis fasciata*; Gg. *Galidictis grandidieri*; Md. *Mungotictis decemlineata*; Sc. *Salanoia concolor*.

Fig. 2. Puntuaciones (no estandarizadas) de las especies con respecto a los factores que afectan a los carnívoros terrestres de Madagascar. Los factores que ejercen un efecto negativo se presentan con puntuaciones negativas, mientras que los que tienen un efecto positivo se muestran con puntuaciones positivas: Cf. *Cryptoprocta ferox*; Egg. *Eupleres goudotti goudotti*; Ff. *Fossa fossana*; Ge. *Galidia elegans*; Gf. *Galidictis fasciata*; Gg. *Galidictis grandidieri*; Md. *Mungotictis decemlineata*; Sc. *Salanoia concolor*.

Fig. 2. (Cont.)



Discussion

We reviewed the literature on the terrestrial carnivore mammals of Madagascar, aiming to understand which species are more likely to go extinct in the near future, taking into account the factors that might be affecting their survival. We used resources such as available literature and data on different online datasets (PANTHERIA, IUCN, ALOS PALSAR Data) to assess the major factors affecting these species. According to our results, only *Galidictis grandidieri* was revealed to be significantly more threatened. However, final score values showed four species are likely to be more threatened than the other four, with the giant-striped mongoose *Galidictis grandidieri* most likely to become extinct first. All factors seem to have a negative impact on this species' risk of extinction. This came as no surprise because *G. grandidieri* inhabits a small, unique spiny forest ecosystem that is threatened by anthropogenic impacts (Hawkins, 2008b; Marquard et al., 2011). Moreover, it is considered one of the rarest carnivores in the world, with the smallest range of all Malagasy carnivores (Andriatsimetry et al., 2009; Marquard et al., 2011). Also, this species has a narrow

dietary breadth that overlaps with both diet and activity pattern of *Cryptoprocta ferox*, while there is also a generalized lack of information on its biology (Hawkins, 2008b; Andriatsimetry et al., 2009; Currylow, 2014). Our results are in agreement with the IUCN classification, which considers *G. grandidieri* one of the most endangered Malagasy carnivore species (Hawkins, 2008b). The Malagasy narrow-striped mongoose, *Mungotictis decemlineata*, is considered Vulnerable by the IUCN (Hawkins, 2008e). Our results support this. According to the available literature and online datasets, deforestation has a devastating effect on *M. decemlineata*, with the healthiest population found within the least disturbed forest in its range, and it has one of the smallest distribution ranges of the mammalian carnivores considered here (Woolaver et al., 2006; Hawkins, 2008e). The broad-striped mongoose, *Galidictis fasciata*, is considered Near Threatened by the IUCN (Hawkins 2008c), which is not unlike findings in our analysis. *G. fasciata* has a generalist diet, consuming mammals, amphibians, reptiles, and some invertebrates (Garbutt, 1999; Goodman, 2003b), and, in addition, it presents a large distribution range (Hawkins, 2008c; our analysis). However, this spe-

Table 2. Standardized scores for each of the nine factors used to estimate the average threat score for each of the eight Malagasy carnivores. Average standardized scores (and 95% confidence intervals) are also provided for each species. Most negative average scores correspond to most threatened species, while most positive average scores correspond to least threatened species: DR. Distribution range; HB. Habitat breadth; SO. Strata overlap: APO. Activity pattern overlap; DB. Diet breadth; DO. Diet overlap; FA. Forested areas (2015); D. Deforestation (2007–2015); SI. Species information; ASS. Average standard score (\pm 95% CI).

Tabla 2. Puntuaciones estandarizadas de cada uno de los nueve factores utilizados para calcular la puntuación media de la amenaza para cada uno de los ocho carnívoros de Madagascar. También se proporciona la media de las puntuaciones estandarizadas (y los intervalos de confianza del 95%) de cada especie. La mayoría de las puntuaciones medias negativas corresponden a las especies más amenazadas, mientras que la mayoría de las puntuaciones medias positivas corresponden a las especies menos amenazadas: DR. Rango de distribución; HB. Amplitud del hábitat; SO. Superposición de estratos: APO. Superposición de patrones de actividad; DB. Ancho de la dieta; DO. Superposición de la dieta; FA. Zonas forestales (2015); D. Deforestación (2007–2015); SI. Información sobre especies; ASS. Puntuación estándar media (\pm 95% IC).

Species	DR	HB	SO	APO	DB	DO	FA	D	SI	ASS
<i>Cryptoprocta ferox</i>	2.38	1.00	1.62	-1.05	0.48	0.41	-1.39	0.32	2.19	0.66 (\pm 1.00)
<i>Eupleres g. goudotii</i>	-0.01	-0.78	-0.54	1.35	-0.29	-0.26	0.30	0.58	0.40	0.08 (\pm 0.50)
<i>Fossa fossana</i>	-0.09	0.11	-0.54	1.35	0.48	0.12	0.51	0.53	-0.11	0.26 (\pm 0.41)
<i>Galidictis fasciata</i>	-0.08	1.89	-0.54	0.15	2.02	2.25	0.49	0.51	0.14	0.76 (\pm 0.78)
<i>Galidictis grandidieri</i>	-0.25	-0.78	-0.54	-1.05	-0.29	-0.63	0.67	0.45	-0.50	-0.32 (\pm 0.43)
<i>Mungotictis decemlineata</i>	-0.72	-0.78	-0.54	-1.05	-1.06	-0.88	-0.41	-0.38	-1.13	-0.77 (\pm 0.22)
<i>Salanoia concolor</i>	-0.63	0.11	1.62	0.15	-0.29	-0.63	-1.46	-2.36	-0.50	-0.44 (\pm 0.85)
	-0.60	-0.78	-0.54	0.15	-1.06	-0.38	1.31	0.35	-0.50	-0.23 (\pm 0.55)

cies' diet and activity pattern overlap with both native and introduced carnivores living in the same area as *G. Fasciata* that can have a negative impact on its risk of extinction (Hawkins, 2008c; Farris et al., 2015). The brown-tailed mongoose (*Salanoia concolor*) is considered Vulnerable by the IUCN (Hawkins et al., 2008), again supported by our analysis. This species is highly negatively affected by lack of information, small distribution range and habitat breadth, and restricted diet that overlaps with several other species (Farris et al., 2015; our analysis). Although there is currently no evidence of predation by humans or competition with exotic carnivores, *S. concolor* has been found to be absent from sites where feral cats occur (Albignac, 1972; Hawkins et al., 2008; Farris et al., 2012). As

there is little information on *S. concolor*, the IUCN recognizes the need to reevaluate the extent of threats to the species, which might warrant reclassification from Vulnerable to Endangered (Hawkins et al., 2008).

The ring-tailed mongoose, *Galidictis elegans*, is considered Least Concern by the IUCN (Hawkins, 2008d), in agreement with our analysis. Its widespread distribution range occurs in a number of protected areas and forested fragments (Hawkins, 2008d). This species also has a large variety of prey in its diet, but it has a high dietary overlap with both native and exotic species (Hawkins, 2008d; Farris et al., 2014, 2015; our analysis). In contrast with our findings, the fossa (*Cryptoprocta ferox*) is considered Vulnerable by the IUCN (Hawkins & Dollar, 2008). Although it

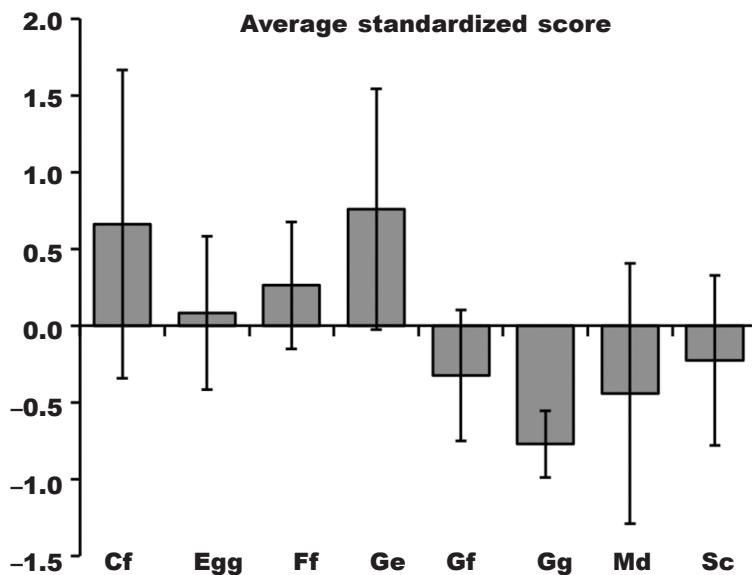


Fig. 3. Mean standardized scores per species, averaged across all scores for all factors (table 2), with 95% confidence intervals: Cf. *Cryptoprocta ferox*; Egg. *Eupleres goudotii goudotii*; Ff. *Fossa fossana*; Ge. *Galidia elegans*; Gf. *Galidictis fasciata*; Gg. *Galidictis grandidieri*; Md. *Mungotictis decemlineata*; Sc. *Salanoia concolor*.

Fig. 3. Puntuaciones medias estandarizadas por especie, teniendo en cuenta las puntuaciones de todos los factores (tabla 2), con intervalos de confianza del 95 %): Cf. *Cryptoprocta ferox*; Egg. *Eupleres goudotii goudotii*; Ff. *Fossa fossana*; Ge. *Galidia elegans*; Gf. *Galidictis fasciata*; Gg. *Galidictis grandidieri*; Md. *Mungotictis decemlineata*; Sc. *Salanoia concolor*.

seems that *C. ferox* is one of the least threatened Malagasy carnivore species according to our results, we acknowledge its vulnerability, mainly caused by its ecological overlap with all native and introduced carnivores, and human-related conflicts (Hawkins & Dollar, 2008; Gerber et al., 2012a; Farris et al., 2015; Logan et al., 2015). It is of considerable concern that deforestation is destroying the habitat of the formerly widely distributed *C. ferox* (Goodman et al., 2004; Hawkins & Racey, 2005). Nevertheless, fossa is a well-studied, generalist predator, with a high distribution range (Albignac, 1972; Goodman et al., 1997; Hawkins & Racey, 2008; Gerber et al., 2012a; Farris et al., 2015). The Malagasy civet (*Fossa fossana*) is considered Near Threatened by the IUCN (Hawkins, 2008a). According to our results and online datasets, although its distribution range is one of the largest, it has a high dietary and activity overlap with other carnivore species (Farris et al., 2015). Moreover, this species appears to be particularly sensitive to forest disturbance, as it is absent from fragmented rainforests, does not occupy human-dominated landscapes, and is considered to be intolerant to degraded forests (Kerridge et al., 2003; Gerber et al., 2012b). Lastly, the small-toothed mongoose (*Eupleres goudotii goudotii*), is considered Endangered by the IUCN (Dollar, 2000), but not in our results. However, we acknowledge that it

is sensitive to habitat destruction due to deforestation, and that its narrow dietary niche overlaps with those of *F. fossana* and *C. ferox* (Albignac, 1972; Schreiber et al., 1989; Macdonald, 1992; Garbutt, 1999; Nowak, 1999; Dollar, 2000; Logan et al., 2015).

One of the major concerns for Malagasy species is deforestation. Harper et al. (2007) reported that, since the 1950s, forest coverage on Madagascar had declined by 40%. Deforestation has altered carnivore assemblages, with contiguous rainforests harbouring the greatest number of native species (Gerber et al., 2012b). Despite conservation efforts, deforestation rates remain high, with its consequent negative impacts on biodiversity, soil compaction and erosion, water and carbon cycles (Erdmann, 2003; Raik, 2007). Economic interests and political lobbying, such as the state's forest concession policy (Jarosz, 1993; Klein, 2002), also contribute to the high rates of deforestation. Decisions by politicians in the 1920s led to the massive destruction of some of the most easily accessible forests on the island (Jarosz, 1993).

Current knowledge on the majority of species is scarce and measures to improve this (such as ecological studies or monitoring programs) should be prioritized. For example, we found that the giant-striped mongoose *G. grandidieri* was most likely to be next to become extinct but current knowledge on this species

(as for *M. decemlineata*, *S. concolor*, *G. fasciata* and *F. fossana*) is limited. This means that, although *G. grandidieri* was considered the most vulnerable in our analysis, there is some uncertainty associated with this outcome. Lack of knowledge on human–animal conflicts greatly inhibited our analysis, with no data available for *F. fossana*, *G. fasciata* and *G. grandidieri*. Additionally, information on the species' prey status is also missing for *G. elegans*, so these two important factors were not taken into consideration in the final analysis for each species. It is clear that our current level of knowledge on species can influence our risk evaluations and the probability of a species going extinct. We strongly believe that if knowledge gaps are filled, better management actions can be taken to mitigate the most pressing threats. It should also be borne in mind that lack of knowledge is a threat in itself, as it is harder to preserve the unknown.

In conclusion, Malagasy terrestrial mammalian carnivores are at risk of extinction. There is an immediate need to increase the size of protected areas across all Madagascar's forested ecosystems (Gerber et al., 2012b). Conservation measures such as community-based actions are already contributing to the protection of *C. ferox* (Jones et al., 2008). A recent assessment across the tropics has shown that well-designed community-based conservation approaches, despite their possible flaws, often result in synergistic economic and ecological gains (Brooks et al., 2012). Emphasis should also be placed on the need for conservation legislation to be strictly enforced. Finally, knowledge on each and every species is essential to correctly implement conservation measures and to support decision makers in formulating and enacting management plans.

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Supplementary material

Appendix 1s. Equations used for the estimation of dietary, strata and activity pattern overlap.

Apéndice 1s. Ecuaciones utilizadas para la estimación de la dieta, los estratos y el patrón de actividad.

Dietary overlap

The dietary overlap of a species, relatively to other species, was estimated has the sum of the overlap (weighted by the maximum possible number of overlapping species) for each of the food items in its diet, weighted by the diet breadth (i.e. the number of different items on that species diet).

$$\text{Dietary_overlap} = \sum_i^n \left[\frac{1}{\text{Dietary_breadth}} \times \frac{\text{Overlapping_species}}{\text{Max_overlap}} \right]$$

were *dietary_breadth* is the number of different food items, *overlapping_species*, the number of other species eating the same item; and *max_overlap*, the maximum number of species that could overlap (i.e. seven species)

Strata overlap

The strata overlap of species *n* was estimated as the sum of the products between species *n* scores (for arboreal and terrestrial strata) and all other *i* species scores (for arboreal and terrestrial strata).

$$\text{Strata_overlap}_n = \sum_i^{n-1} [(Arb_n \times Arb_i) + (Ter_n \times Ter_i)]$$

were *Arb* is the score of arboreal strata for species *n* and *i* (0; 0.5 or 1); and *Ter* is the score of terrestrial strata for species *n* and *i* (0; 0.5 or 1)

Activity pattern overlap

The activity pattern overlap of species *n* was estimated as the sum of the products between species *n* scores (for diurnal and nocturnal activity) and all other *i* species scores (for diurnal and nocturnal activity). Cathameral species were coded as 50% diurnal and 50% nocturnal.

$$\text{Activity_pattern_overlap}_n = \sum_i^{n-1} [(Di_n \times Di_i) + (No_n \times No_i)]$$

were *Di* is the score of diurnal activity for species *n* and *i* (0; 0.5 or 1); and *No* is the score of nocturnal strata for species *n* and *i* (0; 0.5 or 1)

Table 1s. List of references consulted in this study, with reference to species addressed and to the type of information available in each listed reference: D. Diet; C. Competition; M/O. Madagascar/other. Species codes: Cf. *Cryptoprocta ferox*; Eg. *Eupleres goudotii*; Ff. *Fossa fossana*; Ge. *Galidia elegans*; Gf. *Galidictis fasciata*; Gg. *Galidictis grandidieri*; Md. *Mungotictis decemlineata*; Sc. *Salanoia concolor*.

Tabla 1s. Lista de las referencias consultadas en este estudio, con referencia a las especies que mencionan y el tipo de información disponible en cada una de ellas: D. Dieta; C. Competencia; M/O. Madagascar/otros. (Para los códigos de las especies, véase arriba).

Table 1s. (Cont.)

Table 1s. (Cont.)

References	Cf	Eg	Ff	Ge	Gf	Gg	Md	Sc	D	C	M/O
Noss et al. (1996)											X
Nowak (1999)	X	X	X	X	X	X	X	X	X		
Paemelaere & Dobson (2011)					X						
Rabeantoandro (1997)								X			
Raik (2007)											X
Ravoahangy et al. (2011)	X	X			X						
Razafimahaimodison (2003)					X			X			X
Razafindratsima (2014)											X
Scales (2012)								X			X
Schipper et al. (2008)	X	X	X		X		X	X			
Schneider & Kappeler (2014)	X	X	X								
Schnoell (2012)					X						
Schreiber et al. (1989)	X	X			X		X	X	X		
Shimada (2014)											X
Tilman et al. (1994)											X
Vanak & Gompper (2010)											X
Van Vuuren et al. (2012)	X						X				
Watson et al. (2004)											X
Woodroffe & Ginsberg (1998)											X
Woolaver et al. (2006)							X				
Yoder et al. (2003)	X	X						X			
Totals	44	30	26	28	23	18	23	23	18	20	37

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