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Introduced rat assemblage affects feral cat threat to biodiversity in French Polynesian islands

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Abstract :

Context:

Invasive feral cats strongly threaten native fauna on islands worldwide. The impact of feral cat populations is assumed to be higher in the presence of introduced rodents and may also vary according to an island's rodent species assemblage.

Aims:

This study assessed feral cat impacts on island biodiversity in French Polynesian islands harbouring differing assemblages of rat species, by investigating their abundance and trophic ecology.

Methods:

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We focused on the following six human-inhabited islands of three archipelagos in French Polynesia (South Pacific) with differing rat species assemblages: Tahiti and Moorea, Ua Huka and Tahuata, Rurutu and Rimatara. We studied (1) cat abundance, by setting up camera traps during 15 consecutive days to provide an abundance index, the general index (GI) or mean number of virtual captures per camera per occasion, and (2) cat diet, by performing macroscopic analyses of scat samples to determine the frequency of occurrence (FO) of prey categories.

Key results:

Our study showed previously unreported patterns of cat-abundance index for the Society archipelago, with a GI of 0.30 ± 0.12 in Tahiti and 0.02 ± 0.02 in Moorea; for the Marquesas, with a GI of 0.75 ± 0.20 in Ua Huka and 0.20 ± 0.06 in Tahuata; and for the Austral, with a GI of 0.06 ± 0.04 in Rurutu and 0.19 ± 0.05 in Rimatara. Feral cats are shown to prey strongly on introduced rodents (FO = 91.3%), arthropods (37.8%), squamates (18.6%) and birds (13.3%) in our study sites. FO of birds are particularly high in Rimatara (31.9%) and Ua Huka (16.8%). Conclusions: We demonstrated that feral cats represent a serious threat to biodiversity in French Polynesian islands, with 15 species preyed on, including eight endemic birds, four of them being considered threatened by the IUCN Red List. Surprisingly, relative abundances of feral cats were higher both on islands harbouring only one rat species (Ua Huka, with only Rattus exulans) and on islands free of black rats. This finding raises questions regarding the ‘hyperpredation’ hypothesis for multi-invaded island ecosystems.

Implications:

This study on islands with differing assemblages of introduced rodents demonstrated the need for invasive predator studies in multi-invaded ecosystems, so as to improve bird conservation and guide management strategies and site prioritisation.

Keywords : camera-trap monitoring, diet, endemic bird species, Felis catus, invasive predator, multi-invaded ecosystems, Pacific island conservation, Rattus spp

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Introduction

Invasive populations of the feral cat *Felis catus* strongly threaten the native fauna on islands worldwide (Doherty et al. 2016). In the Pacific region, where islands have high proportions of endemic animal species, several studies have pointed out the urgent need to investigate cat presence and predation pressure (Bonnaud et al. 2011, Nogales et al. 2013, Palmas et al. 2017). French Polynesia, located in the South Pacific, is one of the geographical areas still lacking reliable data on feral cat ecology and impacts (Bonnaud et al. 2010). The scientific community has called for this gap to be filled rapidly because of the exceptional conservation stakes, including a high extinction risk to endemic animal species (Medina et al. 2011, Palmas et al. 2017, Spatz et al. 2017). French Polynesia belongs to one of the world's 36 biodiversity hotspots, namely the "Polynesia-Micronesia Hotspot" (Myers et al. 2000, Harrison and Ness 2017). These diverse islands, ranging from high volcanic islands to atolls, harbour unique biodiversity, particularly in terms of terrestrial avifauna. This includes 27 endemic bird species, some now limited to small and localised populations and exhibiting strong decline during the past decades (Monnet et al. 1993, Thibault and Meyer 2001, Thibault and Cibois 2017).

Domestic cats were first introduced into French Polynesia by Europeans around 1773 (Newell 2010). Feral individuals are currently present in most habitat types (low elevation coastal forests, valley rainforests, dry to mesic ridge forests, montane cloud forest above 1,000 m asl, Meyer and Palmas in press) of many inhabited atolls, even including high volcanic islands (Legros 2011). However, little is known about their abundance and their impacts on native fauna. Although it has been suggested that many bird species are threatened by feral cat populations in French Polynesia (Holyoak and Thibault 1984, Thibault and Guyot 1988, Seitre and Seitre 1992), there has so far been little tangible information or strong direct evidence of predation pressure and impact. Feral cats are suspected of having contributed to the extinction of at least five species of land birds belonging to the genus *Prosobonia* (sandpiper, Scolopacidae), *Ptilinopus* (fruit dove, Columbidae), *Porphyrio* (swamphen, Rallidae) and *Pomarea* (monarch flycatcher, Monarchidae) in French Polynesia (Thibault and Guyot 1988, Doherty et al. 2016, Thibault and Cibois 2017).

The scarcity of published data on the impacts of feral cat populations on native and endemic island fauna constitutes a major barrier to the development of appropriate conservation strategies in French Polynesia (Meyer et al. 2018, Palmas et al. 2019). Preliminary data on the diet of feral cats were collected between 2009 and 2018 in three high volcanic islands of the Society archipelago, namely Moorea (Wilcox and Spotswood 2011), Tahiti (Zarzoso-Lacoste 2008) and Raiatea (Faulquier 2014), in Ua Huka in the Marquesas (*unpublished data*), and in the raised atoll of Niau in the Tuamotu (Zarzoso-Lacoste et al. 2016, 2019). Except for Niau, however, these data are not abundant and robust enough to allow scientists or land managers to draw solid conclusions on the diversity and intensity of cat impacts. Nevertheless, these preliminary studies revealed predation by feral cats on birds, notably on at least three native seabird species: the Tahiti petrel *Pseudobulweria rostrata* in Moorea (Wilcox and Spotswood 2011) and in Raiatea (Faulquier 2014), the Baillon's or tropical shearwater *Puffinus bailloni* (formerly called *P. lherminieri*, Audubon's shearwater) and the greater crested tern *Thalasseus bergii* (syn. *Sterna bergii*) in Niau (Zarzoso-Lacoste et al. 2019). The study in Niau also highlighted feral cat predation on two terrestrial endemic species, the Atoll fruit-dove *Ptilinopus coralensis* and the Tuamotu reed warbler *Acrocephalus atyphus* (Zarzoso-Lacoste et al. 2016).

The impact of feral cat populations is assumed to be higher in the presence of introduced mammalian prey species, particularly introduced rodents (Courchamp et al. 1999). Rodents constitute a stable and abundant resource that can help sustain high feral cat abundance (Smith and Quin 1996), thereby exacerbating predation pressure on native wildlife via the "hyperpredation" process (Courchamp et al. 1999, Ringler et al. 2015). This theory predicts that a formerly introduced prey species, well adapted to high predation pressure, could indirectly induce the extinction of an indigenous prey through the sudden population growth of a newly introduced predator (Courchamp et al. 2000). Some fieldwork-based studies have confirmed this theory (e.g. Veitch et al. 2004, Ringler et al. 2015, Russell and Lecorre 2009) but, with the exception of a recent study (Lamela-Lopez and Santos 2021), little attention has been paid to the effect of different rat species and their assemblages (combined presence of different rat species) on feral cat ecology.

This study investigated feral cat abundance index and diet on six inhabited islands in French Polynesia according to the presence or absence of three introduced rat species: Polynesian rats

Rattus exulans, black rats *Rattus rattus*, brown rats *Rattus norvegicus*. Our aims were to (i) detect the presence of feral cats on different study sites and estimate their relative abundances index, (ii) study feral cat trophic ecology and identify endemic species that are preyed on by cats and (iii) determine how the introduced rat assemblage affects feral cat abundance index and predation. We expected feral cat abundance index and predation pressure to be higher on islands harbouring more than one rat species because we expected the overall number of rats in multi-invaded islands to be higher.

Material and Methods

Study site

French Polynesia consists of about 120 main oceanic islands, including 33 high volcanic islands, 81 atolls and sandy islets and six raised atolls (Meyer and Salvat 2009), divided into five archipelagos (Austral, Gambier, Marquesas, Society, Tuamotu) and located between 7-28° S and 134-155° W in the South Pacific Ocean (Fig. 1). French Polynesia belongs to the biogeographic sub-region of Southeastern Polynesia, with Cook and Pitcairn islands (Mueller-Dombois and Fosberg 1998, Steadman 2006), and is one of the most isolated groups of islands in the world, lying between 5,000 and 6,000 km from the nearest continents (Americas, Asia, Australia). The climate of French Polynesia ranges from subtropical (Rapa in the Austral archipelago, with a minimum temperature of 8.5°C observed), to tropical (Society, Tuamotu) and subequatorial in the Marquesas (Laurent and Maamaatuaiahutapu 2019).

The rodent assemblage found in French Polynesia includes three rat species, the Polynesian or Pacific rat *Rattus exulans* introduced by the first Polynesian voyagers about 1,000 years ago (Matisoo-Smith et al. 1999), and the black or ship rat *Rattus rattus* and the brown rat *Rattus norvegicus* introduced during the 18th century by the first European sailors (Table 1). The mouse *Mus musculus* is also present. Six islands were studied: Tahiti and Moorea in Society archipelago, Ua Huka and Tahuata in Marquesas archipelago, and Rurutu and Rimatara in Austral archipelago. The following criteria were applied to select the six study sites: i) differing rat species assemblages: *R. exulans* only, *R. exulans* + *R. rattus*, *R. exulans* + *R. norvegicus*, *R. exulans* + *R. rattus* + *R. norvegicus* (Table 1), ii) no rodent or feral cat control programs in operation and iii) bird species conservation at stake. Moreover, given the climate diversity among these archipelagos, we chose to work on two islands per archipelago.

Feral cat abundance index

Camera trapping design

One site per island was selected based on accessibility on foot and the presence of birds in diverse habitats (Table A.1).Twenty camera traps were deployed along or near paths (30 metres from the paths) over 15 consecutive days in 2020-2021 (McGregor et al. 2015) (Table A.1). Automated digital cameras with black flash (Moultrie® MCG-12635, Browning® BTC-8A, Browning® BTC-8E and Bushnell® 119875) were used. Lure scent (1.25 mL of Salmon oil, ©Connovation) was sprayed above each camera trap to homogenise the detection probability of camera trap stations by attracting cats from surrounding areas (i.e. from paths to camera trap stations). The cameras were spaced by 100-200m, i.e. less than the reported radial distances of home ranges (Edwards et al. 2001, McGregor et al. 2015, Van der Ende et al. 2017) to ensure that a given cat was captured at multiple camera sites, thereby enhancing (i) the probability of capture of each feral cat and (ii) the robustness of abundance indicators (Lazenby et al. 2015). Cameras were set up at an optimal height of around 30 cm (cat body height) (Sparkes et al. 2021), and were checked to confirm that the camera's shutter was triggered (Wang and Macdonald 2009, Nichols et al. 2017). An interval of ten seconds between trigger events, with three images captured in each, was chosen to maximise cat identification and reduce the risk of fuzzy pictures (Palmas et al. 2020a, Sparkes et al. 2021). Vegetation was cleared around a perimeter of 1.5 metres in front of the camera to limit false triggers and to obtain better pictures of the animals (Stolked et al. 2015).

At the end of camera trapping periods, the cameras were retrieved and the pictures downloaded. Camera trap days were calculated by multiplying the number of camera traps by the number of active capture days over the deployment periods, to provide an accurate overview of the trapping effort. Days when cameras were not functioning because of technical problems were excluded from the calculations (Meek et al. 2014).

Camera trapping analysis

The general index (GI) of feral cat activity was calculated for this study. GI is easy to calculate and can be used to monitor variations in feral cat population as an alternative to harder-to-calculate indicators, such as estimated feral cat absolute density (Spatially Explicit Capture-Recapture: SECR, Efford 2015). It has been shown to be robust on relative abundance, leading to conclusions that are consistent with those based on other indices (Bengsen et al. 2012, Legge et al. 2017, Palmas et al. 2020a). The GI estimates feral cat activity (relative abundance approximation) by measuring mean camera capture events per camera and per occasion, following the equation of Engeman (2005).

$$GI = \frac{1}{d}\sum_{j=1}^{d}\frac{1}{sj}\sum_{i=1}^{sj}x_{ij}$$

with d = the day, s = the station, and x_{ij} the number of captures at the i^{th} station on occasion j^{th}.

Cat diet study

Sampling design and sampling effort

The feral cat diet was studied through scat analysis (e.g. Bonnaud et al., 2007), based on feral cat scats collected from the six islands between 2018 and 2021 with the same sampling effort (Fig. 1). Scats (n=491) were collected along paths and rural roads preferentially used by cats

(Turner and Bateson 2014, Recio et al. 2015) over the full range of habitat types: from sea level to 1,000 m asl; littoral/coastal and supra-littoral forests; from low-elevation dry to mesic forests; from mid-elevation mesic to wet ridge or plateau forests; from mid- to upper-elevation wet/rain valley forests; montane cloud forests; coconut plantations; low-elevation urbanised areas (Table A.1). The number of scats collected may varied according with environmental conditions (e.g. rainfall, car traffic, presence of coprophageous species (Ziadinov et al. 2008, Nijsse et al. 2014). Each cat scat was georeferenced, stored in an individual plastic bag and frozen until analysed.

Prey remains determination

Scats were washed under water over a 0.5-mm sieve to sort prey items (hair, bone fragments, teeth, squamate jaws and skink scales, bird feathers and arthropod chitin fragments). The prey items were examined under binocular microscope, compared to reference material and assigned to one of the five following prey categories: (1) introduced rodents, (2) squamates, (3) birds, (4) arthropods, (5) fish (Bonnaud et al., 2007). Samples containing no prey remains or only anthropogenic elements were excluded from the analysis (n=18, *i.e.* 3.67% of collected scats). Differential degradation of prey remains during the digestion process can cause the loss of some diagnostic characteristics (i.e. shape, size, colour), leading to uneven prey group identification (Zarzoso-Lacoste et al., 2016). To address identification issues, we systematically used a site-specific reference collection particularly relevant to identification of bird remains (feathers, claws, beaks).

Data analyses

For each type of cat prey, the Frequency of Occurrence (FO) per scat was calculated (Bonnaud et al. 2015). We used Levins' Standardised formula for trophic Niche Breadth (Levins' SNB) (Krebs 1999) $SNB=(B-1)/(n-1)$, where $B = 1/\Sigma p_i^2$ with p_i the fraction of prey item i in the diet

($\Sigma p_i = 1.0$) and n the number of prey categories in the predator's diet. SNB ranges from 0 to 1, with a value close to 0 indicating a narrow niche and a value close to 1 a broad niche.

Statistical analyses

All statistical analyses were conducted with the R statistical software (R version 4.0.1) using « dataset » (Giordani et al. 2020), « DescTools » (Signorell et al. 2021), « pROC » (Fawcett 2006), « car » (Fox and Weisberg 2019) packages with significant relationships inferred at $\alpha = 0.05$. Residual normality and homoscedasticity were assessed via Q-Q plots and Levene tests. One-way analyses of means (Welch One-way test - not assuming equal variances) were used to determine the effect of island on the GI. One-way ANOVA tests were used to determine the whether the number of native prey categories in the diet (i.e. all categories except rodents) differed among islands. All the islands had all the native species categories.

Results

Camera trapping and cat abundance (GI)

Camera trapping yielded a mean trapping effort per island of 422±64 camera trap days. This gave a total of 715 cat capture events with a mean of 133±67 capture events per island. (Table A.1). The General index (GI ± SE) varied significantly among the islands (F-value: 48.1, df : 5, p-value < 2.2e-16), showing the highest values in Ua Huka with a mean of cat capture events per camera per day that was double that of the other islands (Fig. 2). GI was relatively high in Tahiti, Tahuata and Rimatara, and lower in Rurutu and Moorea (Fig. 2). GI was higher on islands where fewer rat species were present (Ua Huka, Table A.1). Cats were more abundant on islands without *R. rattus* and *R. norvegicus* species.

Overall patterns of feral cat diet

The 473-scat analysis revealed that feral cats preyed most strongly upon introduced rodents (FO = 91.3%), followed by arthropods (37.8%, mainly insects) and squamates (18.6%, mainly lizards), then birds (13.3%) and fish (1.1%). A large part of scats (44.8%) were exclusively composed of introduced rodent remains, 46.5% contained remains of both introduced rodents and at least one of the four other prey categories, while 8.7% contained no introduced rodent remains but remains of at least one of the four other prey categories (Fig. 3).

In Tahiti (n = 52) and Moorea (n = 57), most scats contained only introduced rodent remains, one third contained both introduced rodent and other prey remains, and a few contained only other prey remains. In contrast, in Ua Huka (n = 226) and Tahuata (n = 82), most scats contained both introduced rodent and other prey remains, slightly more than one third contained only introduced rodent remains, and a few contained only other prey remains. In Rurutu (n = 9), all scats contained only introduced rodent remains, while in Rimatara (n = 47), almost half contained both introduced rodent and other prey remains, two fifths contained only introduced rodent remains and a few contained only other prey remains (Fig. 3).

Patterns of predation on different prey types

The number of native prey categories in cat scats significantly differed among the islands (F value: 8.581, df : 5, p-value < 0.001). Feral cats showed the greatest niche breadth (Levins' SNB) on islands without *R. rattus* and *R. norvegicus*, such as Ua Huka and Rimatara, a narrower niche in Tahuata, followed by Moorea and Tahiti, and no breadth in Rurutu (Fig. 4). In Rurutu only 9 scats were found and analyzed so results are unreliable.

Introduced rodents were the predominant prey category found in feral cat's diet for all the islands (Fig. 3, Fig. 4). Frequency of Occurrence (FO) of rodents in the cat diet did not vary across islands; the highest FO was found in Rurutu (100%), but FO was very high for the other islands too (ranging from 87.2% to 96.5%). Since the scats from Rurutu contained exclusively rodent remains, this island is not included in the following results on other prey consumption. Moreover, the Rurutu result is likely biased due to the low number of samples collected (9 cat scats). The FO of rodents in the cat diet was slightly higher on island harbouring *R. rattus*. The FO of arthropods and squamates in the cat diet was higher in the Marquesas islands, on islands free of *R. norvegicus* (Fig. 4). The FO of birds was higher on islands free of *R. rattus*: in Rimatara (31.9%), followed by Ua Huka (16.8%). Fish were consumed on three islands, with substantial consumption in Rimatara (4.3%) and Moorea (3.2%).

Bird species found in feral cat diet

We identified a total of 15 bird species in the feral cats' diet, 12 of them being native species (Table A.2). There was evidence of predation on eight species endemic to the archipelagos or islands, including four IUCN Red-listed threatened species (three listed as "CR" and one as "EN"). The number of endemic species and IUCN Red-listed threatened species preyed on by feral cats varied between islands, with five endemic species (including two listed as "CR") for Ua Huka, two endemic species (one "EN" and one "CR") for Rimatara and one endemic species each for Tahiti and Tahuata (Table A.2).

Discussion

This study described some aspects the ecology of feral cats in several islands of French Polynesia. It sought to (i) explore how the rat species assemblage affects cat abundance and diet on islands in the South Pacific region where numerous endemic species are threatened, and (ii) fill a knowledge gap highlighted by previous studies on feral cat data in this geographic area (Bonnaud et al. 2011, Nogales et al. 2013, Palmas et al. 2017).

Feral cat abundance in multi-invaded islands: effect of rat assemblages

This study revealed marked inter-island differences in cat abundances that are mainly differentiated by rat species presence and assemblages. Higher cat abundance was expected on islands with multiple rat species that could constitute a stable resource for feral cat populations. The two Marquesas islands studied (Ua Huka and Tahuata) are similar in land area, altitude, climate conditions and human population, but have different numbers of rat species (only *R. exulans* in Ua Huka, *R. exulans* and *R. rattus* in Tahuata). Counter-intuitively, the island harbouring only one species of rat (Ua Huka) showed the highest feral cat abundance. In the Austral archipelago, cat abundance was three times higher in Rimatara (where *R. exulans* and *R. norvegicus* are present) than in Rurutu (with *R. exulans* and *R. rattus*). The absence of *R. rattus* and *R. norvegicus* seems to be conducive to higher cat abundance index. These three rat species are known to occupy different trophic niches (Sugihara 1997, Harper et al. 2005, Shiels et al. 2013, Zarzoso-Lacoste et al. 2019), and habitat partitioning has been demonstrated for *R. rattus* and *R. exulans* when sympatric (Strecker and Jackson 1962, Shiels 2010). *R. norvegicus* is larger than the two other species (Russell et al. 2005, Innes 2005b, King et al. 2011), more commensal and therefore more restricted to disturbed and urban areas (Nicholson and Warner, 1953; Twibell, 1973), could indirectly reinforce the feral cat population through reproduction between feral and roaming cat populations. Despite the known sympatric co-existence of these rat species (Harper et al. 2005, Shiels et al. 2013, Zarzoso-Lacoste et al. 2019), competition in these particular ecosystems could affect rat accessibility for cats (abundance, diurnal activity, arboreal habits Harper and Bunbury 2015, Harper et al. 2015). We assume here that the co-occurrence of rat species in these systems could eventually lead to lower absolute rat biomass (through strong competition for trophic resources and habitat, King et al. 2011). Previous studies showed substantial diet overlap between *R. rattus* and *R. exulans*, suggesting exploitative and resource competition (Harper et al. 2005, Zarzoso-Lacoste et al. 2019); studies also found an effect from commensalism on these species' distribution throughout segregated spatial niches, increased diurnal activity and reduced skull sizes related to the number of other rodent species (Yom-Tov et al. 1999, Russell and Clout 2004, Harper et al. 2015)).

Feral cat diet

The 473 analysed feral cat scats represent a robust and significant sampling effort even for rarer prey (Bonnaud et al. 2011). However, wide differences in scat sampling appeared between islands, with reliable results obtained here for all the islands except Rurutu (n=9). In Rurutu, scats were collected from tracks extensively used by cars, and heavy rainfalls occurred in the weeks prior to our sampling. Dogs, which are particularly common on this island, could consume the cat scats (Ziadinov et al. 2008, Nijsse et al. 2014).

Rodents were the cats' food staple in French Polynesia, with 91.33% of feral cat scat samples containing rodent remains, which is consistent with the literature (e.g.; Bonnaud et al. 2011) (44.05 ± 28.3, 55 studies). Rodents thus provide feral cats with a stable and abundant food resource that helps to maintain cat populations (Courchamp et al. 1999). Apart from rodents, feral cats also preyed on a wide range of prey, from arthropods to birds. Interestingly, they exhibited a broader trophic niche in Rimatara and Ua Huka (the two islands free of *R. rattus*), with higher FOs for secondary prey (birds, arthropods, squamates and fishes). Since cats in the natural areas of these two islands only have access to *R. exulans*, which have a lower biomass (smaller in size and mass) than *R. rattus* (Atkinson 1985, Atkinson and Towns 2005, Shiels et al. 2014), they may need to secure additional food resources by hunting more alternative prey (Turner and Bateson 2014, Palmas et al. 2020b). *R. exulans* might be less accessible to cats on Ua Huka and Rimatara, since *R. exulans* appear to be more arboreal in native forests when black rats are absent (Marples, 1955; McCartney, 1970; Twibell, 1973). Furthermore, *R. rattus*-free islands are more likely to offer richer diversity and availability of native naïve species (especially birds) that constitute very easy prey for opportunistic cats (Seitre and Seitre 1992, Turner and Bateson 2014, Palmas et al. 2020b). Indeed, this study listed 15 bird species preyed on by cats in French Polynesia, among which 6 are endemics. Feral cats seem to represent a strong threat for birds particularly on islands where *R. rattus* is absent, feeding intensively on this prey group in Rimatara (FO = 31.9%) and in Ua Huka (16.8%). The birds preyed upon included six endemic species, four of which are critically endangered (Table A.2): the Kühl's lorikeet (*Vini kuhlii*, CR) (Birdlife 2016) and the Rimatara reed-warbler (*Acrocephalus rimitarae*, CR) (Birdlife 2021) in Rimatara; the ultramarine lorikeet (*Vini ultramarina*, CR) (Birdlife 2018) and the Iphis monarch (*Pomarea iphis*, CR) (Birdlife 2017) in Ua Huka. These species are strictly respectively endemic to the two islands and the latest census revealed population decreases for Rimatara's species. Finally, *R. exulans* may be a prime resource and an energetically profitable prey for cats on our study sites due to its potential naivety towards this predator. Indeed, while the sympatry of cats and *R. rattus* in Europe has a history at least 1000 years long (Zeuner 1963, Rackham 1979), the sympatry of cats and *R. exulans* probably only dates back 250 years. It was only in the 18th century that feral cats were introduced into French Polynesia (Newell et al. 2010), whereas *R. exulans* were introduced 1200 years ago (Wilmshurst et al. 2011). Moreover, the two species originated from two distinct areas, despite the recent demonstration of cohabitation in China around 5000 BP (Roberts 1991, Hu et al. 2014). Their distinct origins or limited or discontinuous cohabitation period may thus have reduced anti-predator behaviour (Blumstein et al. 2002, Cliff et al. 2022) in *R. exulans*.

Hyperpredation is recognised within the scientific community as an ecological process particularly relevant to cat predation in multi-invaded ecosystems (Smith and Quin 1996, Courchamp et al. 1999, 2000, Zhang et al. 2006). The theory was confirmed through fieldwork-based studies on different islands (e.g. Raoul Island in New Zealand, Veitch et al. 2004, Ringler et al. 2015; Europa and Juan de Nova islands in the Indian Ocean, Russell and Lecorre 2009, Ringler et al. 2015) showing higher cat population abundance when rat present on islands. However, these studies generally failed to consider rodent species assemblage, with only very recent studies examining correlations between cat and rat species abundances (Lavery et al. 2020, Lamela-Lopez and Santos 2021). By assessing both cat abundance index and diet on six multi-invaded inhabited islands in French Polynesia differing in introduced rat species assemblage: *R. rattus, R. norvegicus, R. exulans,* our study has raised new questions about rat ecology and the hyperpredation hypothesis in multi-invaded inhabited islands which seems not reliable in all island and intraguild predation systems (e.g. Russell et al. 2009 showed a similar effect on long-lived native preys when rat are presents or absents). More bio-ecological studies of introduced rat species in multi-invaded island ecosystems are crucial to disentangle prey-predator relations and to plan efficient management strategies.

Implications for management

This study increased the list of birds known to be hunted by cats in French Polynesia to 19 species. They include 8 endemic birds, four of which are considered threatened (IUCN Red List) and all of which are legally declared protected species in French Polynesia under the "Code de l'Environnement". This assessment of the feral cat threat in French Polynesia suggests that the overall feral cat impact remains underestimated and points to a need for more studies addressing Pacific islands (Bonnaud et al. 2011, Nogales et al. 2013, Palmas et al. 2017). Based on our results, we strongly recommend that feral cats be legally classified as pest species in French Polynesia (or a "threat to biodiversity" under the "Code de l'Environnement", like 52 other invasive alien plant and animal species), and that management strategies be initiated if endemic bird populations continue to decline.

However, since feral and domestic cats belong to the same species (*Felis catus*), drafting a regulatory text specifically concerning feral cats in French Polynesia is challenging (C. Brocherieux, DIREN/French Polynesian Department of the Environment, pers. com.). Indeed, on these small islands, the proximity of human dwellings to areas of conservation concern precludes using the notion of "distance from dwellings" applied as a criterion to distinguish feral cats from domestic cats in other French Pacific territories (e.g. New Caledonia, Code de l'Environnement de la Province Nord, 2018). Although New Zealand lacks national legislation for cat management, it has a legislated territorial mandate to control feral cats on public conservation land (Walker et al. 2017, Department of Conservation, New Zealand Government). One solution in French Polynesia could be to set up feral cat control strategies in natural areas ("zones naturelles") only, excluding urban areas and areas dedicated to human activities as defined by the official Land Use Plans ("plans general d'aménagement") set up for most of the island counties ("communes") in French Polynesia. Given the diversity of French Polynesian islands (e.g. size, topography, remoteness, presence of domestic cats) and the multi-invasion context, feral cat management plans should be adapted to each island.

Given the limited resources available for conservation programs and the high costs associated with lethal control of invasive predators, we recommend that future actions be prioritised according to the urgency of conservation situations (most affected and threatened native species, e.g. Rimatara and Ua Huka here) and management and support facilities (e.g. Rimatara, with strong involvement of the mayor and the island population in environmental issues).

Data availability

The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of Interest

The authors declare no conflicts of interest.

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Figure 1. Location of French Polynesia in the South Pacific, and of the six studied islands: Tahiti and Moorea (Society archipelago), Ua Huka and Tahuata (Marquesas), Rurutu and Rimatara (Austral)

Figure 2. Boxplot of the GI (cat capture events per camera per day) by island, with mean and median GI (red dot and black line respectively) and 95% Confidence Interval (vertical line)

Figure 3. Percentage of scats by island containing i) only rodent remains (black), ii) remains of both rodents and at least one other prey (squamates, birds, arthropods, fish) (grey), iii) no rodent remains but remains of at least one other prey (white)

Figure 4. Cat diet according to Frequency of occurrence (FO) of feral cat prey categories (rodents, squamates, birds, arthropods, fish) in the six study sites (n=473 scats), and Levin's SNB for each site

Table 1. Characteristics of the studied islands with their rat species assemblage (according to Fourdrigniez et al. 2014, TIB 2022). Number of inhabitants according to most recent population census in 2017 (www.ispf.pf).

Archipelago	Island	Land area (km²)	Highest summit (m)	Population (inhabitants)	Rats (*Rattus* spp.)
Society	Tahiti	1,045	2,241	192,760	*R. exulans*, *R norvegicus*, *R. rattus*
	Moorea	140	1,207	17,718	*R. exulans*, *R norvegicus*, *R. rattus*
Marquesas	Ua Huka	83	884	678	*R. exulans*
	Tahuata	61	1,050	671	*R. exulans*, *R. rattus*
Austral	Rurutu	32	389	2,574	*R. exulans*, *R. rattus*
	Rimatara	8	83	885	*R. exulans, R norvegicus*