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1 **Running Head:** Cats, rats and birds in French Polynesian islands

2 **Introduced rat assemblage affects feral cat threat to biodiversity in French Polynesian**
3 **islands.**

4
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Code de champ modifié

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29 **Short summary**

30 Although invasive feral cats on islands worldwide strongly threaten the native fauna, there has
31 been little investigation of cat impacts in multi-invaded ecosystems. We assess feral cats'
32 abundance and predation on several French Polynesian islands harbouring differing
33 assemblages of rat species. We find high cat abundances indices and extensive predation on
34 endemic birds on islands free of black rats.

35 **Abstract**

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

39 **Aims.** This study assessed feral cats' impacts on island biodiversity in French Polynesian
40 islands harbouring differing assemblages of rat species by investigating their abundance and
41 trophic ecology.

42 **Methods.** We focused on six human-inhabited islands of three archipelagos in French Polynesia
43 (South Pacific) with differing rat species assemblages: Tahiti and Moorea, Ua Huka and
44 Tahuata, Rurutu and Rimatara.

45 We studied i) cat abundance, setting up camera traps during 15 consecutive days to provide an
46 abundance index, the General Index (GI) or mean number of virtual captures per camera per
47 occasion and ii) cat diet, performing macroscopic analyses of scat samples to determine the
48 Frequency of Occurrence (FO) of prey categories.

49 **Key results.** Our study reveals previously unreported patterns of cat abundance index for the
50 Society archipelago, with a GI of 0.30 ± 0.12 in Tahiti and 0.02 ± 0.02 in Moorea; for the
51 Marquesas, with a GI of 0.75 ± 0.20 in Ua Huka and 0.20 ± 0.06 in Tahuata; and for the Austral,
52 with a GI of 0.06 ± 0.04 in Rurutu and 0.19 ± 0.05 in Rimatara. Feral cats are shown to prey
53 strongly upon introduced rodents (FO = 91.33%), arthropods (37.84%), squamates (18.60%)

54 and birds (13.31%) in our study sites. FO of birds are particularly high in Rimatara (31.9%) and
55 Ua Huka (16.8%).

56 **Conclusions.** We demonstrate that feral cats represent a serious threat to biodiversity in French
57 Polynesia islands, with 15 species preyed upon including eight endemic birds, four of them
58 considered threatened by the IUCN Red List. Surprisingly, relative abundances of feral cats
59 were higher both on islands harbouring only one rat species (Ua Huka, with only *Rattus*
60 *exulans*) and on islands free of black rats. This finding raises questions regarding the
61 “hyperpredation” hypothesis for multi-invaded island ecosystems.

62 **Implications.** This study on islands with differing assemblages of introduced rodents
63 demonstrates the need for invasive predator studies in multi-invaded ecosystems, to improve
64 bird conservation and guide management strategies and site prioritisation.

65

66 **Keywords:** invasive predator; *Felis catus*; diet; camera trap monitoring; endemic bird
67 species; *Rattus* spp.

68

69 **Introduction**

70 Invasive populations of the feral cat *Felis catus* strongly threaten the native fauna on islands
71 worldwide (Doherty et al. 2016). In the Pacific region, where islands have high proportions of
72 endemic animal species, several studies have pointed out the urgent need to investigate cat
73 presence and predation pressure (Bonnaud et al. 2011, Nogales et al. 2013, Palmas et al. 2017).
74 French Polynesia, located in the South Pacific, is one of the geographical areas still lacking
75 reliable data on feral cat ecology and impacts (Bonnaud et al. 2010). The scientific community
76 has called for this gap to be filled rapidly because of the exceptional conservation stakes,
77 including a high extinction risk to endemic animal species (Medina et al. 2011, Palmas et al.
78 2017, Spatz et al. 2017). French Polynesia belongs to one of the world’s 36 biodiversity

79 hotspots, namely the “Polynesia-Micronesia Hotspot” (Myers et al. 2000, Harrison and Ness
80 2017). These diverse islands, ranging from high volcanic islands to atolls, harbour unique
81 biodiversity, particularly in terms of terrestrial avifauna. This includes 27 endemic bird species,
82 some now limited to small and localised populations and exhibiting strong decline during the
83 past decades (Monnet et al. 1993, Thibault and Meyer 2001, Thibault and Cibois 2017).

84 Domestic cats were first introduced into French Polynesia by Europeans around 1773 (Newell
85 2010). Feral individuals are currently present in most habitat types (low elevation coastal
86 forests, valley rainforests, dry to mesic ridge forests, montane cloud forest above 1,000 m asl,
87 Meyer and Palmas in press) of many inhabited atolls, even including high volcanic islands
88 (Legros 2011). However, little is known about their abundance and their impacts on native
89 fauna. Although it has been suggested that many bird species are threatened by feral cat
90 populations in French Polynesia (Holyoak and Thibault 1984, Thibault and Guyot 1988, Seitre
91 and Seitre 1992), there has so far been little tangible information or strong direct evidence of
92 predation pressure and impact. Feral cats are suspected of having contributed to the extinction
93 of at least five species of land birds belonging to the genus *Prosobonia* (sandpiper,
94 Scolopacidae), *Ptilinopus* (fruit dove, Columbidae), *Porphyrio* (swamphen, Rallidae) and
95 *Pomarea* (monarch flycatcher, Monarchidae) in French Polynesia (Thibault and Guyot 1988,
96 Doherty et al. 2016, Thibault and Cibois 2017).

97 The scarcity of published data on the impacts of feral cat populations on native and endemic
98 island fauna constitutes a major barrier to the development of appropriate conservation
99 strategies in French Polynesia (Meyer et al. 2018, Palmas et al. 2019). Preliminary data on the
100 diet of feral cats were collected between 2009 and 2018 in three high volcanic islands of the
101 Society archipelago, namely Moorea (Wilcox and Spotswood 2011), Tahiti (Zarzosso-Lacoste
102 2008) and Raiatea (Faulquier 2014), in Ua Huka in the Marquesas (*unpublished data*), and in
103 the raised atoll of Niau in the Tuamotu (Zarzosso-Lacoste et al. 2016, 2019). Except for Niau,

104 however, these data are not abundant and robust enough to allow scientists or land managers to
105 draw solid conclusions on the diversity and intensity of cat impacts. Nevertheless, these
106 preliminary studies revealed predation by feral cats on birds, notably on at least three native
107 seabird species: the Tahiti petrel *Pseudobulweria rostrata* in Moorea (Wilcox and Spotswood
108 2011) and in Raiatea (Faulquier 2014), the Baillon's or tropical shearwater *Puffinus bailloni*
109 (formerly called *P. lherminieri*, Audubon's shearwater) and the greater crested tern *Thalasseus*
110 *bergii* (syn. *Sterna bergii*) in Niau (Zarzos-Lacoste et al. 2019). The study in Niau also
111 highlighted feral cat predation on two terrestrial endemic species, the Atoll fruit-dove
112 *Ptilinopus coralensis* and the Tuamotu reed warbler *Acrocephalus atyphus* (Zarzos-Lacoste et
113 al. 2016).

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

126

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

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

136

137 **Material and Methods**

138 ***Study site***

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

149 The rodent assemblage found in French Polynesia includes three rat species, the Polynesian or
150 Pacific rat *Rattus exulans* introduced by the first Polynesian voyagers about 1,000 years ago
151 (Matisoo-Smith et al. 1999), and the black or ship rat *Rattus rattus* and the brown rat *Rattus*
152 *norvegicus* introduced during the 18th century by the first European sailors (Table 1). The mouse
153 *Mus musculus* is also present. Six islands were studied: Tahiti and Moorea in Society

154 archipelago, Ua Huka and Tahuata in Marquesas archipelago, and Rurutu and Rimatara in
155 Austral archipelago. The following criteria were applied to select the six study sites: i) differing
156 rat species assemblages: *R. exulans* only, *R. exulans* + *R. rattus*, *R. exulans* + *R. norvegicus*, *R.*
157 *exulans* + *R. rattus* + *R. norvegicus* (Table 1), ii) no rodent or feral cat control programs in
158 operation and iii) bird species conservation at stake. Moreover, given the climate diversity
159 among these archipelagos, we chose to work on two islands per archipelago.

160

161 ***Feral cat abundance index***

162 *Camera trapping design*

163 One site per island was selected based on accessibility on foot and the presence of birds in
164 diverse habitats (Table A.1). Twenty camera traps were deployed along or near paths (30 metres
165 from the paths) over 15 consecutive days in 2020-2021 (McGregor et al. 2015) (Table A.1).
166 Automated digital cameras with black flash (Moultrie® MCG-12635, Browning® BTC-8A,
167 Browning® BTC-8E and Bushnell® 119875) were used. Lure scent (1.25 mL of Salmon oil,
168 ©Connovation) was sprayed above each camera trap to homogenise the detection probability
169 of camera trap stations by attracting cats from surrounding areas (i.e. from paths to camera trap
170 stations). The cameras were spaced by 100-200m, i.e. less than the reported radial distances of
171 home ranges (Edwards et al. 2001, McGregor et al. 2015, Van der Ende et al. 2017) to ensure
172 that a given cat was captured at multiple camera sites, thereby enhancing (i) the probability of
173 capture of each feral cat and (ii) the robustness of abundance indicators (Lazenby et al. 2015).
174 Cameras were set up at an optimal height of around 30 cm (cat body height) (Sparkes et al.
175 2021), and were checked to confirm that the camera's shutter was triggered (Wang and
176 Macdonald 2009, Nichols et al. 2017). An interval of ten seconds between trigger events, with
177 three images captured in each, was chosen to maximise cat identification and reduce the risk of
178 fuzzy pictures (Palmas et al. 2020a, Sparkes et al. 2021). Vegetation was cleared around a

179 perimeter of 1.5 metres in front of the camera to limit false triggers and to obtain better pictures
180 of the animals (Stolcked et al. 2015).

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

186

187 *Camera trapping analysis*

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

$$196 \quad GI = \frac{1}{d} \sum_{j=1}^d \frac{1}{s_j} \sum_{i=1}^{s_j} x_{ij} ;$$

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

198

199 *Cat diet study*

200 *Sampling design and sampling effort*

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

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

211

212 *Prey remains determination*

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

224

225 *Data analyses*

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

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

231

232 *Statistical analyses*

233 All statistical analyses were conducted with the R statistical software (R version 4.0.1) using «
234 dataset » (Giordani et al. 2020), « DescTools » (Signorell et al. 2021), « pROC » (Fawcett
235 2006), « car » (Fox and Weisberg 2019) packages with significant relationships inferred at $\alpha =$
236 0.05. Residual normality and homoscedasticity were assessed via Q-Q plots and Levene tests.
237 One-way analyses of means (Welch One-way test - not assuming equal variances) were used
238 to determine the effect of island on the GI. One-way ANOVA tests were used to determine the
239 whether the number of native prey categories in the diet (i.e. all categories except rodents)
240 differed among islands. All the islands had all the native species categories.

241

242 **Results**

243 *Camera trapping and cat abundance (GI)*

244 Camera trapping yielded a mean trapping effort per island of 422 ± 64 camera trap days. This
245 gave a total of 715 cat capture events with a mean of 133 ± 67 capture events per island. (Table
246 A.1). The General index ($GI \pm SE$) varied significantly among the islands (F-value: 48.1, df :
247 5, p-value $< 2.2e-16$), showing the highest values in Ua Huka with a mean of cat capture events
248 per camera per day that was double that of the other islands (Fig. 2). GI was relatively high in
249 Tahiti, Tahuata and Rimatara, and lower in Rurutu and Moorea (Fig. 2). GI was higher on
250 islands where fewer rat species were present (Ua Huka, Table A.1). Cats were more abundant
251 on islands without *R. rattus* and *R. norvegicus* species.

252

253 *Overall patterns of feral cat diet*

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

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

268

269 *Patterns of predation on different prey types*

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

275 Introduced rodents were the predominant prey category found in feral cat's diet for all the
276 islands (Fig. 3, Fig. 4). Frequency of Occurrence (FO) of rodents in the cat diet did not vary
277 across islands; the highest FO was found in Rurutu (100%), but FO was very high for the other
278 islands too (ranging from 87.2% to 96.5%). Since the scats from Rurutu contained exclusively

279 rodent remains, this island is not included in the following results on other prey consumption.
280 Moreover, the Rurutu result is likely biased due to the low number of samples collected (9 cat
281 scats). The FO of rodents in the cat diet was slightly higher on island harbouring *R. rattus*. The
282 FO of arthropods and squamates in the cat diet was higher in the Marquesas islands, on islands
283 free of *R. norvegicus* (Fig. 4). The FO of birds was higher on islands free of *R. rattus*: in
284 Rimatara (31.9%), followed by Ua Huka (16.8%). Fish were consumed on three islands, with
285 substantial consumption in Rimatara (4.3%) and Moorea (3.2%).

286

287 *Bird species found in feral cat diet*

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

295

296 **Discussion**

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

302

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

304 This study revealed marked inter-island differences in cat abundances that are mainly
305 differentiated by rat species presence and assemblages. Higher cat abundance was expected on
306 islands with multiple rat species that could constitute a stable resource for feral cat populations.
307 The two Marquesas islands studied (Ua Huka and Tahuata) are similar in land area, altitude,
308 climate conditions and human population, but have different numbers of rat species (only *R.*
309 *exulans* in Ua Huka, *R. exulans* and *R. rattus* in Tahuata). Counter-intuitively, the island
310 harbouring only one species of rat (Ua Huka) showed the highest feral cat abundance. In the
311 Austral archipelago, cat abundance was three times higher in Rimatara (where *R. exulans* and
312 *R. norvegicus* are present) than in Rurutu (with *R. exulans* and *R. rattus*). The absence of *R.*
313 *rattus* and *R. norvegicus* seems to be conducive to higher cat abundance index. These three rat
314 species are known to occupy different trophic niches (Sugihara 1997, Harper et al. 2005, Shiels
315 et al. 2013, Zarzoso-Lacoste et al. 2019), and habitat partitioning has been demonstrated for *R.*
316 *rattus* and *R. exulans* when sympatric (Strecker and Jackson 1962, Shiels 2010). *R. norvegicus*
317 is larger than the two other species (Russell et al. 2005, Innes 2005b, King et al. 2011), more
318 commensal and therefore more restricted to disturbed and urban areas (Nicholson and Warner,
319 1953; Twibell, 1973), could indirectly reinforce the feral cat population through reproduction
320 between feral and roaming cat populations. Despite the known sympatric co-existence of these
321 rat species (Harper et al. 2005, Shiels et al. 2013, Zarzoso-Lacoste et al. 2019), competition in
322 these particular ecosystems could affect rat accessibility for cats (abundance, diurnal activity,
323 arboreal habits Harper and Bunbury 2015, Harper et al. 2015). We assume here that the co-
324 occurrence of rat species in these systems could eventually lead to lower absolute rat biomass
325 (through strong competition for trophic resources and habitat, King et al. 2011). Previous
326 studies showed substantial diet overlap between *R. rattus* and *R. exulans*, suggesting
327 exploitative and resource competition (Harper et al. 2005, Zarzoso-Lacoste et al. 2019); studies
328 also found an effect from commensalism on these species' distribution throughout segregated

329 spatial niches, increased diurnal activity and reduced skull sizes related to the number of other
330 rodent species (Yom-Tov et al. 1999, Russell and Clout 2004, Harper et al. 2015)).

331 *Feral cat diet*

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

338 Rodents were the cats' food staple in French Polynesia, with 91.33% of feral cat scat samples
339 containing rodent remains, which is consistent with the literature (e.g.; Bonnaud et al. 2011)
340 (44.05 ± 28.3 , 55 studies). Rodents thus provide feral cats with a stable and abundant food
341 resource that helps to maintain cat populations (Courchamp et al. 1999). Apart from rodents,
342 feral cats also preyed on a wide range of prey, from arthropods to birds. Interestingly, they
343 exhibited a broader trophic niche in Rimatara and Ua Huka (the two islands free of *R. rattus*),
344 with higher FOs for secondary prey (birds, arthropods, squamates and fishes). Since cats in the
345 natural areas of these two islands only have access to *R. exulans*, which have a lower biomass
346 (smaller in size and mass) than *R. rattus* (Atkinson 1985, Atkinson and Towns 2005, Shiels et
347 al. 2014), they may need to secure additional food resources by hunting more alternative prey
348 (Turner and Bateson 2014, Palmas et al. 2020b). *R. exulans* might be less accessible to cats on
349 Ua Huka and Rimatara, since *R. exulans* appear to be more arboreal in native forests when black
350 rats are absent (Marples, 1955; McCartney, 1970; Twibell, 1973). Furthermore, *R. rattus*-free
351 islands are more likely to offer richer diversity and availability of native naïve species
352 (especially birds) that constitute very easy prey for opportunistic cats (Seitre and Seitre 1992,
353 Turner and Bateson 2014, Palmas et al. 2020b). Indeed, this study listed 15 bird species preyed

354 on by cats in French Polynesia, among which 6 are endemics. Feral cats seem to represent a
355 strong threat for birds particularly on islands where *R. rattus* is absent, feeding intensively on
356 this prey group in Rimatara (FO = 31.9%) and in Ua Huka (16.8%). The birds preyed upon
357 included six endemic species, four of which are critically endangered (Table A.2): the Kūhl's
358 lorikeet (*Vini kuhlii*, CR) (Birdlife 2016) and the Rimatara reed-warbler (*Acrocephalus*
359 *rimatarae*, CR) (Birdlife 2021) in Rimatara; the ultramarine lorikeet (*Vini ultramarina*, CR)
360 (Birdlife 2018) and the Iphis monarch (*Pomarea iphis*, CR) (Birdlife 2017) in Ua Huka. These
361 species are strictly respectively endemic to the two islands and the latest census revealed
362 population decreases for Rimatara's species. Finally, *R. exulans* may be a prime resource and
363 an energetically profitable prey for cats on our study sites due to its potential naivety towards
364 this predator. Indeed, while the sympatry of cats and *R. rattus* in Europe has a history at least
365 1000 years long (Zeuner 1963, Rackham 1979), the sympatry of cats and *R. exulans* probably
366 only dates back 250 years. It was only in the 18th century that feral cats were introduced into
367 French Polynesia (Newell et al. 2010), whereas *R. exulans* were introduced 1200 years ago
368 (Wilmshurst et al. 2011). Moreover, the two species originated from two distinct areas, despite
369 the recent demonstration of cohabitation in China around 5000 BP (Roberts 1991, Hu et al.
370 2014). Their distinct origins or limited or discontinuous cohabitation period may thus have
371 reduced anti-predator behaviour (Blumstein et al. 2002, Cliff et al. 2022) in *R. exulans*.
372 Hyperpredation is recognised within the scientific community as an ecological process
373 particularly relevant to cat predation in multi-invaded ecosystems (Smith and Quin 1996,
374 Courchamp et al. 1999, 2000, Zhang et al. 2006). The theory was confirmed through fieldwork-
375 based studies on different islands (e.g. Raoul Island in New Zealand, Veitch et al. 2004, Ringler
376 et al. 2015; Europa and Juan de Nova islands in the Indian Ocean, Russell and Lecorre 2009,
377 Ringler et al. 2015) showing higher cat population abundance when rat present on islands.
378 However, these studies generally failed to consider rodent species assemblage, with only very

379 recent studies examining correlations between cat and rat species abundances (Lavery et al.
380 2020, Lamela-Lopez and Santos 2021). By assessing both cat abundance index and diet on six
381 multi-invaded inhabited islands in French Polynesia differing in introduced rat species
382 assemblage: *R. rattus*, *R. norvegicus*, *R. exulans*, our study has raised new questions about rat
383 ecology and the hyperpredation hypothesis in multi-invaded inhabited islands which seems not
384 reliable in all island and intraguild predation systems (e.g. Russell et al. 2009 showed a similar
385 effect on long-lived native preys when rat are presents or absents). More bio-ecological studies
386 of introduced rat species in multi-invaded island ecosystems are crucial to disentangle prey-
387 predator relations and to plan efficient management strategies.

388

389 *Implications for management*

390 This study increased the list of birds known to be hunted by cats in French Polynesia to 19
391 species. They include 8 endemic birds, four of which are considered threatened (IUCN Red
392 List) and all of which are legally declared protected species in French Polynesia under the
393 “Code de l’Environnement”. This assessment of the feral cat threat in French Polynesia
394 suggests that the overall feral cat impact remains underestimated and points to a need for more
395 studies addressing Pacific islands (Bonnaud et al. 2011, Nogales et al. 2013, Palmas et al. 2017).
396 Based on our results, we strongly recommend that feral cats be legally classified as pest species
397 in French Polynesia (or a “threat to biodiversity” under the “Code de l’Environnement”, like
398 52 other invasive alien plant and animal species), and that management strategies be initiated
399 if endemic bird populations continue to decline.

400 However, since feral and domestic cats belong to the same species (*Felis catus*), drafting a
401 regulatory text specifically concerning feral cats in French Polynesia is challenging (C.
402 Brocherieux, DIREN/French Polynesian Department of the Environment, pers. com.). Indeed,
403 on these small islands, the proximity of human dwellings to areas of conservation concern

404 precludes using the notion of “distance from dwellings” applied as a criterion to distinguish
405 feral cats from domestic cats in other French Pacific territories (e.g. New Caledonia, Code de
406 l'Environnement de la Province Nord, 2018). Although New Zealand lacks national legislation
407 for cat management, it has a legislated territorial mandate to control feral cats on public
408 conservation land (Walker et al. 2017, Department of Conservation, New Zealand
409 Government). One solution in French Polynesia could be to set up feral cat control strategies in
410 natural areas (“zones naturelles”) only, excluding urban areas and areas dedicated to human
411 activities as defined by the official Land Use Plans (“plans general d'aménagement”) set up for
412 most of the island counties (“communes”) in French Polynesia. Given the diversity of French
413 Polynesian islands (e.g. size, topography, remoteness, presence of domestic cats) and the multi-
414 invasion context, feral cat management plans should be adapted to each island.

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

420 **Data availability**

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

423

424 **Conflicts of Interest**

425 The authors declare no conflicts of interest.

426

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447

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

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

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

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

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

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

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