NeoBiota 63: 177–200 (2020)
doi: 10.3897/neobiota.63.58005
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

# Rapid recolonisation of feral cats following intensive culling in a semi-isolated context

Pauline Palmas[1,2,3], Raphaël Gouyet[1], Malik Oedin[1,4], Alexandre Millon[5], Jean-Jérôme Cassan[6], Jenny Kowi[6], Elsa Bonnaud[2], Eric Vidal[1,7]

**1** *Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE), Aix Marseille Université, CNRS, IRD, Avignon Université, Centre IRD de Nouméa, BPA5, 98848, Nouméa cedex, New Caledonia, France* **2** *Ecologie Systématique Evolution, Univ. Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, 91400, Orsay, France* **3** *Univ. Polynesie Francaise, Ifremer, Ilm, Ird, Eio Umr 241, Tahiti, French Polynesia* **4** *Institut Agronomique Néo-Calédonien (IAC), Equipe ARBOREAL (AgricultuRe BiOdiveRsité Et vALorisation) BP73, Païta, New Caledonia, France* **5** *Institut Méditerranéen de Biodiversité et d'Écologie marine et continentale (IMBE), Aix Marseille Université, CNRS, IRD, Avignon Université, Europôle de l'Arbois, BP 80, 13545, Aix-en-Provence, France* **6** *Direction du Développement Economique et de l'Environnement (DDEE), Koohnê (Koné), Province Nord, New Caledonia, France* **7** *UMR ENTROPIE (IRD-Université de la Réunion-CNRS), Laboratoire d'Excellence Labex-CORAIL, Institut de Recherche pour le Développement, BP A5, 98848, Nouméa Cedex, New Caledonia, France*

Corresponding author: Pauline Palmas (pauline.palmas@ird.fr, palmas.pauline@gmail.com)

Academic editor: J. Jeschke | Received 26 August 2020 | Accepted 26 November 2020 | Published 29 December 2020

**Citation:** Palmas P, Gouyet R, Oedin M, Millon A, Cassan J-J, Kowi J, Bonnaud E, Vidal E (2020) Rapid recolonisation of feral cats following intensive culling in a semi-isolated context. NeoBiota 63: 177–200. https://doi.org/10.3897/neobiota.63.58005

## Abstract

Invasive feral cats threaten biodiversity at a global scale. Mitigating feral cat impacts and reducing their populations has therefore become a global conservation priority, especially on islands housing high endemic biodiversity. The New Caledonian archipelago is a biodiversity hotspot showing outstanding terrestrial species richness and endemism. Feral cats prey upon at least 44 of its native vertebrate species, 20 of which are IUCN Red-listed threatened species. To test the feasibility and efficiency of culling, intensive culling was conducted in a peninsula of New Caledonia (25.6 km²) identified as a priority site for feral cat management. Live-trapping over 38 days on a 10.6 km² area extirpated 36 adult cats, an estimated 44% of the population. However, three months after culling, all indicators derived from camera-trapping (e.g., abundance, minimum number of individuals and densities) suggest a return to pre-culling levels. Compensatory immigration appears to explain this unexpectedly rapid population recovery in a semi-isolated context. Since culling success does not guarantee a long-term effect, complementary methods like fencing and innovative automated traps need to be used, in accordance with predation thresholds identified through modelling, to preserve island biodiversity. Testing general assumptions on cat management, this article contributes important insights into a challenging conservation issue for islands and biodiversity hotspots worldwide.

**Keywords**
Camera trap monitoring, invasive predator, invasive species control, live-trapping, SECR analysis

## Introduction

Feral cats are among the most harmful invasive predators for insular native fauna (Bonnaud et al. 2011; Medina et al. 2011; Bellard et al. 2016; Doherty et al. 2016). They threaten more than 430 vertebrate species, including mammals, birds and reptiles, and are implicated in the recent extinction of 63 species (40 bird, 21 mammal and 2 reptile species), i.e. 26% of recent terrestrial vertebrate extinctions since AD 1500 (Doherty et al. 2016; Palmas et al. 2017). Mitigating feral cat impacts and reducing their populations has therefore become a global conservation priority (Doherty et al. 2017), especially on islands housing high endemic biodiversity (Nogales et al. 2013). Feral cat eradications have been successfully conducted on islands worldwide, generally resulting in clear conservation benefits for many island mammals, birds and reptiles (e.g. Campbell et al. 2011; Jones et al. 2016). However, although recent management actions succeeded in eradicating cats from small and medium-sized islands (up to 29,000 ha – Marion, Bester et al. 2002 and up to 63,000 ha – Dirk Hartog – Algar et al. 2020) including fenced enclosures, to date feral cat eradications remain largely unfeasible on the largest islands, particularly when inhabited (Nogales et al. 2004; Campbell et al. 2011; Oppel et al. 2011; DIISE 2020), and even harder to achieve in mainland areas.

If eradication is not feasible, population control – i.e. local limitation of predator abundance by culling or other measures – could constitute an alternative management strategy (Doherty et al. 2017). As for any "open" populations though, cats present a high risk of re-invasion since they can move rapidly and over long distances (Schmidt et al. 2007; Moseby and Hill 2011; Leo et al. 2016; McGregor et al. 2017): a typical response to spatially restricted culling is compensatory immigration from surrounding source populations (e.g. Lieury et al. 2015; Millon et al. 2019). Population control may thus entail a continuous removal of individuals (Lazenby et al. 2015). This is generally not a sustainable management strategy given the usually limited resources and time available for such conservation programmes (e.g. Doherty and Ritchie 2017; Venning et al. 2020). Most studies that found feral cat culling to be effective and with a lasting impact on the cat population were examining either intensive and sustained management efforts (Algar and Burrows 2004) or situations where populations are relatively closed (e.g. peninsulas and fenced areas, Short et al. 1997; Moseby and Read 2006). Our study area, a peninsula, was chosen for its potential to act as a population filter and limit immigration from surrounding populations (like Heirisson Prong in Short et al. 2002, and the Tasman Peninsula in Lazenby et al. 2015).

Camera trapping and a spatially explicit capture-recapture approach (hereafter, SECR) are novel and effective tools that are increasingly used to estimate occupancy rates, abundances and densities for feral cats in natural areas. They provide relevant information for conservation practitioners (such as recolonisation rate, spatial distribution of cats) and allow for testing the efficiency of culling as a management technique (Robley et al. 2010; Bengsen et al. 2012; Lazenby et al. 2015; McGregor et al. 2015). Surprisingly little is known about the speed with which a treated area is recolonised by cats. This is a crucial parameter for managers to estimate how long the positive effect of their control operations is lasting, so as to determine how frequently these have to be repeated in order to maintain invasive predators at a low density (Denny and Dickman 2010; Leo et al. 2018). The rate of re-invasion probably depends on the abundance of cats outside the treated area, the degree of connectivity of the treated area with the untreated peripheral areas and the intensity of removal of individuals during culling. Nor is there adequate data on the magnitude of control (i.e. the number of individuals or percentage of a population to remove) required to successfully reduce the invasive predators' population and impacts (e.g. Reddiex et al. 2006; Kapos et al. 2009; Denny and Dickman 2010; Walsh et al. 2012). Modelling studies can estimate optimal removal rates (e.g. Lohr et al. 2013), but proper modelling requires information on numerous parameters like the biology and distribution of both managed and sympatric species, or population sizes (Leo et al. 2018). This would enable to determine the viability of prey populations in the face of predation under different conditions and management programmes (e.g. King and Powell 2011).

We report herein a short but intensive feral cat culling operation conducted at Pindaï peninsula (New Caledonia), which is a priority conservation area for seabirds (it hosts a large colony of Wedge-tailed shearwaters, *Ardenna pacifica*) (Spaggiari et al. 2007). It is a case study of how efficient and durable the effects of such short intensive operations are, taking advantage of the peninsula's setting and simulating the typical resources currently available to local managers of natural areas (DDEE – Province Nord, New Caledonia).

Our specific aims were to (i) assess feral cat abundance and density, (ii) test a live-trapping protocol and its success in controlling feral cats, (iii) test the durability of the culling effect on feral cat abundance and densities, and (iv) derive guidance for adaptive and effective management.

While a compensatory effect from immigration was expected, we hypothesised that the lower connectivity between treated and untreated areas at this peninsular tip would limit cat re-colonisation as observed in different studies conducted in peninsulas or fenced areas (Short et al. 1997; Read and Bowen 2001).

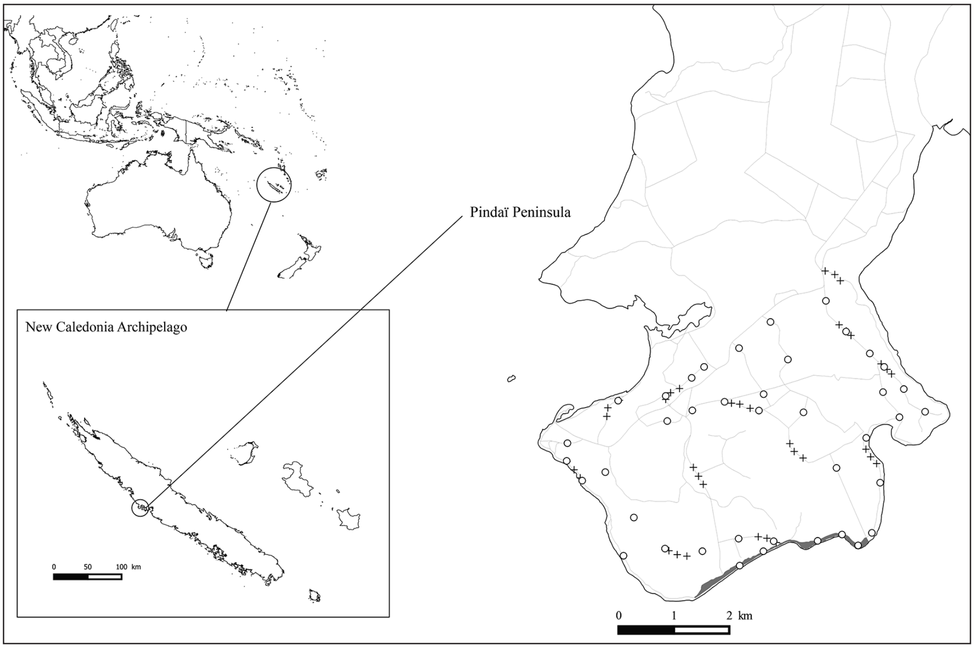


**Figure 1.** Location of the Pindaï Peninsula and sampling design; camera trap stations (cross, n = 77), live-trap positions (circle, n = 32), seabird colony (grey area), roads and trails (grey lines).

## Materials and methods

### Study site

The New Caledonia main island ("Grande Terre") is an old continental island located in the Pacific Ocean (Grandcolas et al. 2008). With an area of 16,372 km$^2$, it houses three main natural habitats: Dry forest, Humid forest and Maquis mosaic. The New Caledonian biodiversity hotspot shows outstanding terrestrial species richness and endemism rates (Myers et al. 2000; Mittermeier et al. 2011).

Since their introduction around 1860 (Beauvais et al. 2006), cats have invaded the New Caledonian archipelago, from seashore habitats to the highest altitude forest (1,628 m). A recent study showed that feral cats preyed upon at least 44 native vertebrate species, 20 of which are IUCN Red-listed threatened species (Palmas et al. 2017). As a result, the feral cat has been listed among the five priority invasive species for future management in New Caledonia. The Pindaï peninsula (Northern Province) has been identified as a priority site for feral cat management, part of a move to address conservation issues in natural areas through expert management.

The Pindaï Peninsula (21°19.40'S, 164°57.50'E; Fig. 1), with an area of 25.6 km$^2$, is between 2.45 km and 3.24 km wide and a maximum 7 km long. It has a low (<15 m) canopy and mean annual rainfall of less than 1,100 mm (Jaffré et al. 1993). It is covered in dry forest composed of a mosaic of sclerophyllous and mesic forests on

**Table 1.** Control schedule using live-traps and camera trapping according to Wedge-tailed shearwater breeding periods. Dash indicate inter-periods.

| | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Wedge-tailed shearwater presence (P.) and breeding periods | P. | P. Hatching | P. | | P. Juv. Fledging | – | | | | P. Adult arrival | P. | P. Laying |
| Camera trapping | – | | | 908 trap-days | – | | | | | 1181 trap-days | | – |
| Feral cat control by live-traps | – | | | | 1200 trap-days | | – | | | | | |

sedimentary and metamorphic rocks (Gillespie and Jaffre 2003; Isnard et al. 2016). Secondary successional sclerophyllous forests dominate this peninsula with *Acacia spirorbis* and *Leucana leucocephala* formations, and there is a large remnant of closed sclerophyllous forest to the East and South. To implement our culling campaign, we specifically chose the southern part of the peninsula because (i) it houses the largest Wedge-tailed shearwater colony of Grande Terre, the mainland of New Caledonia, with about 10,000–15,000 breeding pairs present from mid-October (adult arrival) to the end of May (juvenile fledging) (Table 1; Fig. 1) (Spaggiari and Barre 2003; BirdLife International 2016); (ii) the peninsula narrows (2.45 km) in the middle, providing lower connectivity between treated and untreated areas ; and (iii) it affords an area of 10.6 km$^2$ for intensive treatment, using the available human and material resources (i.e. local managers).

## Camera trapping design

40 camera traps (three were stolen during the study period) were deployed along paths and unsealed roads according to a systematic grid covering the study area (10.6 km$^2$). This grid was constructed on GIS (QGis 2.2.0), and was overlaid on an aerial photograph of the Peninsula to maximise homogeneity of camera trap distribution. Automated digital cameras with flash (7), infrared flash (2), black light (31) (CuddebackAmbush 1170, Cuddeback Attack IR 1156, Moultrie M1100i, respectively) were used. To ensure homogeneous detection probabilities throughout a camera trapping session, no baits or lures were used. Cameras were set up at a height of between 30 and 100 cm (to cover cat body height), directed towards the track preferentially used by cats (Turner and Bateson 2014; Recio et al. 2015), and were checked to confirm that the camera's shutter was triggered (Wang and Macdonald 2009; Nichols et al. 2017). There was an interval of ten seconds between trigger events, with three images captured in each of them, to maximise cat identification and to reduce the risk of fuzzy pictures.

Camera trapping was conducted for 30 successive days in both sessions (Table 2). A capture event was defined as all photographs of unique individuals within a 30-min time period (Di Bitetti et al. 2006; Farris et al. 2015). A sampling occasion was considered as one day (24 h) (Otis et al. 1978; Wang and MacDonald 2009). Camera traps were inspected at least once every two weeks to check battery system charge and

**Table 2.** Model selection results for density estimation (SECR) using four habitat masks (ZE; study area, ZE_AV; using MDMM pre-culling, ZE_AP; using MDMM post-culling and ZE_moy; using mean MDMM pre- and post-culling). Models are based on Akaike's information criterion corrected for small sample sizes (AICc). Delta AICc is the difference in AIC values between each model and the model with the lowest AIC. AICcwt is the model weight.

| Model N° | Model name | Model | Detection function | No. Par | LogLik | AICc | delta AICc | AICcwt |
|---|---|---|---|---|---|---|---|---|
| M1 | #secr_dfn15_ZE_Buffer_AP | λ(0)~1 σ~1 z~1 | hazard hazard rate | 3 | -1853.106 | 3712.798 | 0 | 0.5325 |
| M2 | #secr_dfn1_ZE_Buffer_AP | g0~1 σ ~1 z~1 | hazard rate | 3 | -1853.236 | 3713.058 | 0.26 | 0.4675 |
| M3 | #secr_dfn15_ZE_Buffer_Moy | λ(0)~1 σ ~1 z~1 | hazard hazard rate | 3 | -1864.527 | 3735.64 | 22.842 | 0 |
| M4 | #secr_dfn1_ZE_Buffer_Moy | g0~1 σ ~1 z~1 | hazard rate | 3 | -1864.62 | 3735.826 | 23.028 | 0 |
| M5 | #secr_dfn15_ZE_Buffer_AV | λ(0)~1 σ ~1 z~1 | hazard hazard rate | 3 | -1874.757 | 3756.1 | 43.302 | 0 |
| M6 | #secr_dfn1_ZE_Buffer_AV | g0~1 σ ~1 z~1 | hazard rate | 3 | -1874.792 | 3756.169 | 43.371 | 0 |
| M7 | #secr_dfn1_ZE | g0~1 σ ~1 z~1 | hazard rate | 3 | -1884.633 | 3775.851 | 63.053 | 0 |
| M8 | #secr_dfn15_ZE | λ(0)~1 σ ~1 z~1 | hazard hazard rate | 3 | -1884.694 | 3775.973 | 63.175 | 0 |
| M9 | #secr_dfn2_ZE_Buffer_AP | g0~1 σ ~1 | exponential | 2 | -1887.627 | 3779.54 | 66.742 | 0 |
| M10 | #secr_dfn16_ZE_Buffer_AP | λ(0)~1 σ ~1 | hazard exponential | 2 | -1889.41 | 3783.105 | 70.307 | 0 |
| M11 | #secr_dfn2_ZE_Buffer_Moy | g0~1 σ ~1 | exponential | 2 | -1897.213 | 3798.711 | 85.913 | 0 |
| M12 | #secr_dfn16_ZE_Buffer_Moy | λ(0)~1 σ ~1 | hazard exponential | 2 | -1898.902 | 3802.091 | 89.293 | 0 |
| M13 | #secr_dfn2_ZE_Buffer_AV | g0~1 σ ~1 | exponential | 2 | -1906.91 | 3818.106 | 105.308 | 0 |
| M14 | #secr_dfn16_ZE_Buffer_AV | λ(0)~1 σ ~1 | hazard exponential | 2 | -1908.556 | 3821.397 | 108.599 | 0 |
| M15 | #secr_dfn2_ZE | g0~1 σ ~1 | exponential | 2 | -1920.357 | 3844.999 | 132.201 | 0 |
| M16 | #secr_dfn16_ZE | λ(0)~1 σ ~1 | hazard exponential | 2 | -1921.938 | 3848.162 | 135.364 | 0 |
| M17 | #secr_dfn0_ZE_Buffer_AP | g0~1 σ ~1 | halfnormal | 2 | -1942.385 | 3889.055 | 176.257 | 0 |
| M18 | #secr_dfn14_ZE_Buffer_AP | λ(0)~1 σ ~1 | hazard halfnormal | 2 | -1942.945 | 3890.175 | 177.377 | 0 |
| M19 | #secr_dfn0_ZE_Buffer_Moy | g0~1 σ ~1 | halfnormal | 2 | -1946.147 | 3896.58 | 183.782 | 0 |
| M20 | #secr_dfn14_ZE_Buffer_Moy | λ(0)~1 σ ~1 | hazard halfnormal | 2 | -1946.684 | 3897.653 | 184.855 | 0 |
| M21 | #secr_dfn0_ZE_Buffer_AV | g0~1 σ ~1 | halfnormal | 2 | -1952.44 | 3909.165 | 196.367 | 0 |
| M22 | #secr_dfn14_ZE_Buffer_AV | λ(0)~1 σ ~1 | hazard halfnormal | 2 | -1952.966 | 3910.217 | 197.419 | 0 |
| M23 | #secr_dfn0_ZE | g0~1 σ ~1 | halfnormal | 2 | -1963.612 | 3931.509 | 218.711 | 0 |
| M24 | #secr_dfn14_ZE | λ(0)~1 σ ~1 | hazard halfnormal | 2 | -1964.072 | 3932.429 | 219.631 | 0 |

to download data from memory cards. At the end of each trapping period, the cameras were retrieved and the images downloaded. The trapping effort was obtained by multiplying the number of traps by the number of active capture days over the considered periods (Table 1). Capture per unit effort (camera trapping sampling occasion) was calculated by dividing the numbers of trapped cats per 100 trap-days.

## Feral cat trapping and culling

Cat trapping and culling were carried out for 38 days over 3.5 months (2–3 working days per week) during the dry cold season (between mid-May and July 2015, austral winter) in collaboration with wildlife rangers. In predator trapping, food availability in the targeted site may be decisive for control efficiency (i.e., baited traps may be more attractive when few alternative food resources are available) (Algar et al. 2013; Rocamora and Henriette 2015). Therefore, feral cat trapping and culling were carried out during the dry cold season, when resources are scarcer (i.e., before seabird arrival, a low activity period for squamates and invertebrates and probably the lowest rodent abundance).

Live traps (2 WIRETAINERS models, CatTrap and PossumTrap; 32 traps in total, 17 and 15 respectively of each model) were deployed across the 10.6 $km^2$ covered (Fig. 1). The trapping density rate (3 traps per $km^2$) was comparable to that of similar studies (e.g. Algar et al. 2010; Lazenby et al. 2015). Traps were deployed near paths and unsealed roads used by cats (Turner and Bateson 2014; Recio et al. 2015; Palmas et al. 2017). They were hidden in vegetation and out of direct public sight. Feral cats were live-trapped during both day and night, since our study site does not house non-target native species liable to be caught by this type of trap (Desmoulins and Barré 2005). Traps were checked and baited with oiled fish (tinned sardines) twice a day (Peters et al. 2011).

Trapped cats were euthanised by an accredited veterinarian using first a light anaesthetic via intramuscular injection of Tiletamine/Zolazepam (10 mg $kg^{-1}$ body-weight), followed by an intracardiac injection of Pentobarbital 500 mg/cat. The cats were handled in compliance with the directives of the Department of Conservation's Animal Ethics Committee, and the traps were used in accordance with New Caledonian regulations (Northern Province Environmental Code, New Caledonia).

## Data analyses

Camera trapping was used to calculate three complementary indicators of population abundance and density pre- and post-culling: (i) a general index of feral cat activity (GI), (ii) the minimum number of feral cats present in the study area (MKTBA), and (iii) feral cat absolute density (SECR).

The general index (GI) allowed us to estimate feral cat activity over the study area by measuring the mean of virtual camera capture events per station and per sampling occasion. This index follows 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 $j^{th}$.

To compare the GI calculated before and after culling, we used bilateral mean comparison: t-test with Welch approximation for unequal variance.

Camera-trapped cats were identified based on distinct natural markings (Karanth and Nichols 1998; Bengsen et al. 2012). First, adult cats were classified by coat colour and patterns on left or right flanks. Then morphological criteria were used: number, shape, dimension and position of stripes, bands and spots on the trunk and limbs; number and shape of rings on the tail; body signs such as scars or other distinctive traits; and sex (observation of the genital area or female with cubs). Pictures from each session were sorted into folders, one for each potential individual (McGregor et al.

2015). All identification folders were checked twice, by two different operators, for any inconsistencies requiring the pictures to be reassigned. The folders were then reviewed by another operator for validation.

Culled cats were identified using the same morphological criteria from the pictures of both flanks to (i) identify cats camera trapped during the pre-culling session and (ii) match right- and left-flank pictures of the same individual from the pre-culling pictures.

The minimum number of feral cats known to be alive (MKTBA, Lazenby et al. 2015) was calculated as the total number of individuals identified from one side (left or right side of all cat pictures). This ensured the identification of a maximum of individual cats. Since uniformly black cats are very difficult to identify individually, we assumed that our number of different black individuals was an underestimation.

Spatially explicit capture-recapture models were applied to capture-mark-recapture data to provide population density estimations (Efford et al. 2015). This allows not to use the study area calculation as a density reference (a major bias) and gives greater flexibility in study design (Efford et al. 2009). SECR models require that: (i) every animal has a non-zero probability of encountering a camera trap station during the sampling period (Karanth and Nichols 1998), (ii) the location and density of stations ensure that any feral cats (adult) can be photographed from at least two camera trap stations (Foster and Harmsen 2012; McGregor et al. 2015), and (iii) sampling design maximises capture probabilities (Burnham et al 1987). SECR estimations also require encounter histories for density calculations (Efford et al. 2015; McGregor et al. 2015). Here, such histories were built separately for pre- and post-culling sessions by dividing each of them into a series of 25 and 35 days, respectively (one sampling occasion corresponding to 24 h). This involved identifying each cat as observed or not, with the location of the camera trap. Cat density was estimated using the 'secr' library in R (Efford 2020). To avoid bias linked to low confidence in identification of black cats, the latter were excluded from the analyses (McGregor et al. 2015). Excluding black cats from SECR analyses reduced photo capture events by 13.05%, while black cats accounted for 11.1% of total culled cats.

The sampled population was assumed to be demographically closed during each camera trap session, based on the fact that (i) kittens were not considered in the analyses (Otis et al. 1978; McGregor et al. 2015 who used a 3–6 week survey period and SECR analysis for closed populations), (ii) there was a very low probability of mortality over the period considered, as this site houses no cat predators and is infrequently used by humans. The spatial-history capture matrix for camera trapping data was then constructed by linking each capture of each individual with the respective coordinates of the camera station and j-occasion, which covered 24 h. Trap detector type 'count' was chosen for the SECR analysis (allowing for multiple detections of the same individual within the same occasion, and including the two camera trapping sessions within the same analysis).

We evaluated six different spatial detection functions (half-normal, hazard half-normal, hazard rate, hazard hazardrate, hazard exponential, exponential), using two different functions for the distribution of home range centres: (i) a Poisson point process (Borchers and Efford 2008) and (ii) a binomial point process (Royle et al. 2009). We created four habitat masks using (i) the Mean Maximum Distance Moved (MDMM), the average maximum distance between detections of each individual (Otis et al. 1978), and (ii) the function *SECR* which excludes areas inaccessible to cats (open water) (Oppel et al. 2012). This yielded twenty-four different candidate models using all combinations of detection functions and masks. Root Pooled Spatial Variance (RPSV) was used to measure the dispersion of the sites where individual animals were detected, pooled over individuals (Calhoun and Casby 1958; Slade and Swihart 1983; Efford 2011). Mean home ranges pre- and post-culling were calculated using MDMM estimations (O'Connell et al. 2010).

SECR models were compared using delta-corrected Akaike Information Criterion (AICc) values and selected using the weighted AIC (AICwt) of each model (Burnham and Anderson 2002).

We then compared home range at individual level between the two sessions. Home range was calculated per individual using a Minimum Convex Polygon estimator (MCP 95%) and the "sf" package (Pebesma 2018), and compared using mean comparison analysis after checking that variance is homogeneous. Individuals with more than three dots from three different detectors out of alignment were kept. Generalized Linear Models (GLM) were run to test the effect of period on home range size. A Gaussian distribution and 'weights' option were used.

Residual homoscedasticity and normality were assessed via Q-Q plots and Shapiro-Wilk tests. All statistical analyses were conducted with R 3.0.3 software (R Core Team 2014), using "ade4" (Chessel et al. 2004), "pROC" (Fawcett 2006) "plyr" (Wickham 2011), "varComp" (Qu et al. 2013), "maptools" (Bivand and Lewin-Koh 2013) and "GISTools" (Brunsdon and Chen 2014) packages. For all analyses, significant relationships were inferred at $\alpha = 0.05$.

## Results

### Camera trapping

There were 908 camera trap-days in the pre-culling session and 1181 camera trap-days in the post-culling session. These yielded 473 feral cat detections from 51 of the 77 stations for pre-culling and 514 feral cat detections from 35 of the 40 stations for post-culling (Fig. 2). The camera trapping rates for the pre- and post-culling sessions were 50 and 43 detections/100 trap-days, respectively. Feral cat camera trapping rates varied spatially between pre- and post-culling sessions (Fig. 2).

Camera trapping yielded 416 feral cat pictures showing identifiable cats (209 left-flanked and 207 right-flanked). Pictures of cats' left flank, matched with the corresponding right flank, were used for the pre- and post-culling camera trap analyses MKTBA and SECR.

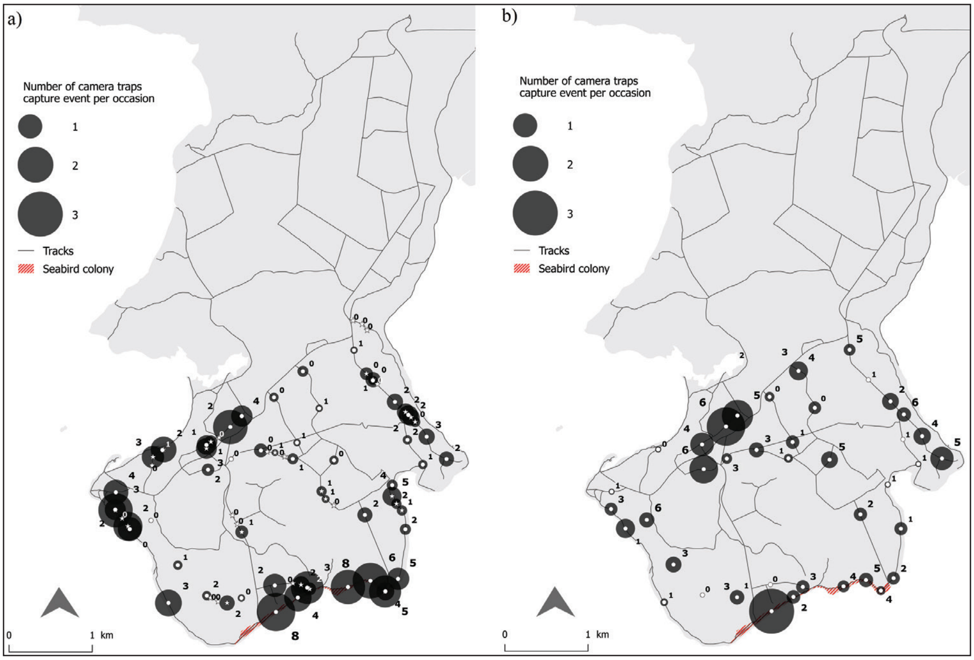


**Figure 2.** Variation in number of camera trapping events (black circles) and number of cats individually identified at camera trap stations pre- (**a**) and post- (**b**) culling. The sizes of black circles are proportional to the number of camera-trap capture events per sampling occasion. Camera trap stations; temporary locations (white stars), permanent locations (white points).

There was at least one uniformly black individual in the pre-culling session and two in the post-culling session, one of which was distinguished by distinctive damage to its tail. Uniformly coloured (here black) cats' pictures were not included in the SECR.

## Live-trapping

A total of 36 cats were trapped and culled during the campaign (26 females, 10 males), with a trapping effort of 1200 trap-days representing a capture per unit effort of 3 trapped cats / 100 trap-days. Females comprised 72.2% of all captured cats. The trapping campaign culled 44% of the feral cats previously identified by the pre-culling camera trap survey.

## Culling effect on cat indices and density

The General Index (GI ± S. E) did not differ significantly between pre- and post-culling sessions ($t = 1.28$, $df = 37$, p-value = 0.21), with respectively 0.50 ± 0.24 and 0.43 ± 0.15 virtual capture per sampling occasion per station (Suppl. material 3: Fig. S3).

A total of 40 different cats (MKTBA) were identified over the whole study period, with 25 and 23 different individuals from pre- and post-culling camera trap

**Table 3.** Mean Maximum Distance Moved (MDMM), the average maximum distance between detections of each individual (km$^2$) and feral cat density estimations (number of individuals per km$^2$) pre- and post-culling of feral cat populations. Results are given for the best SECR models; Model 1 (M1) and Model 2 (M2) according to AIC criteria.

| Model | Session | MDMM (km²) | Density ± S. E (cat. km$^{-2}$) | Inf. limit 95% | Sup. limit 95% |
|---|---|---|---|---|---|
| M1 | Pre-culling | 11.00 | 1.601 ± 0.327 | 1.077 | 2.380 |
| | Post-culling | 16.68 | 1.379 ± 0.301 | 0.903 | 2.105 |
| M2 | Pre-culling | 11.00 | 1.600 ± 0.327 | 1.077 | 2.379 |
| | Post-culling | 16.68 | 1.378 ± 0.300 | 0.903 | 2.104 |

sessions, respectively. Eight individuals (29%) were identified during both pre- and post-culling periods.

Of the twenty-four models tested (Table 2), model M1 (parameters: "hazard hazard rate" function, a probability function of λ(d) and mask « ZE+Buffer S2 ») and model M2 (parameters: "hazard rate" function, a probability function of g(d) and mask « ZE+Buffer S2 ») gave the best estimation of cat densities. Model M1 showed a ΔAICc = 0 and AICwt = 0.53, and Model M2 showed a ΔAICc = 0.26 and AICwt = 0.47 (Table 2). These two models yielded very similar parameter values (λ(0), g(0), σ, z) and densities (Table 3).

Estimated feral cat densities (D ± S. E.) were 1.60 ± 0.33 adult cats/ km$^2$ pre-culling and 1.38 ± 0.30 adult cats/ km$^2$ post-culling. The movements and home range of feral cat populations did change following culling. Root Pooled Spatial Variance (RPSV) was higher post-culling, with 752.2 m pre-culling and 878.9 m post-culling. The mean home range estimation using MDMM was more than twice as high post-culling (0.95 km² pre-culling and 2.21 km² post-culling). Mean home range (95% MCP) did not differ significantly between sessions, but appeared slightly higher post-culling (0.784 ± 0.338 km² pre-culling and 0.827 ± 0.351 km² post-culling). Before culling, the highest numbers both of detections and of identifications of individual cats were in the South of the Peninsula, around the seabird colony. After culling, the highest numbers of detections were in the North-West of the study area and the highest number of individually identified cats in the North-West and North-East (Fig. 2).

## Discussion and conclusion

The camera trapping method provided adequate cat detection, enabling us to estimate, for the first time, accurate cat densities in New Caledonia. It also provided an effective way to monitor variations in feral cat abundance, as in previous studies (e.g. Comer et al. 2018). Moreover, this trapping design enabled us to live-trap cats with a success rate within, or even slightly above, the range of other studies using wire cage traps (Algar et al. 2010; McGregor et al. 2015; Lazenby et al. 2015). This short but intense culling of resident feral cats proved to be effective in rapidly reducing the target population.

However, three months later, the different cat population indicators calculated post-culling showed little difference from those calculated pre-culling. Our culling campaign simulating the resource effort that might currently be expected from local natural site managers failed to reduce the feral cat population over the mid-term. Despite the favourable peninsula setting, this cat population recovered through recolonisation faster than expected. The natural geography of the site, a semi-isolated peninsula, did not limit connectivity between the treated and untreated feral cat sub-populations.

## Camera trap monitoring: advantages and consistency of the three indicators

Camera trapping at our study site resulted in a high level of feral cat detection, similar to or even higher than in studies using either un-baited or baited camera trapping methods. The high level of detection, and the high number of individual cats identified from at least two different stations, met the two requirements for accurate SECR calculations (Efford et al. 2015; McGregor et al. 2015). In addition, camera trap capture probabilities were optimised in this study by positioning camera trap stations close to open roads and tracks. Thus, we were able to almost systematically observe pictures of the stripe patterns on cat legs, which are considered to be suitable for individual identification (Bengsen et al. 2012). However, more pictures of cats' two flanks could be obtained by using paired cameras at each camera station (Karanth and Nichols 1998; McGregor et al. 2015), which would further improve cat identification. Moreover, all undistinguishable black cats were excluded from MKTBA and SECR analysis. Future studies could usefully attempt to incorporate uniformly coloured cats in analysis when they represent a significant proportion of the population, for example by using robust home range data based on a sample of GPS-tracked animals (e.g. Bengsen et al. 2011). Our camera trapping method provided an effective way to monitor variations in feral cat abundance, and the consistency of its estimation calculated with GI, MKTBA and densities via SECR should prove widely useful. The GI could be used to monitor changes in the feral cat population as an alternative to SECR estimations, which require more time and can be used to respond to more specific research questions (Bengsen et al. 2012; Legge et al. 2017). However, conclusions are often based on relative abundance indices, and this kind of index does not consider important parameters such as variable detection (Sollman et al. 2013). Since relative abundance indices do not systematically reflect differences in density (Sollman et al. 2013), a valuable avenue for future research would be to compare these different indices. In particular, we recommend that in areas of interest to managers, the first step should be to calculate all of the different indices (GI, MKTBA, densities). Second, the relationship between GI and the other indices should be determined; if GI is sufficiently reliable and in line with the densities estimated by SECR, only GI should be used. For this reason, we advocate hand-in-hand collaboration between researchers and managers from project set-up to evaluation of management results, especially in such remote areas (Meyer et al. 2018).

## Effect of culling on cat abundance/density over time

Three months after the end of the culling campaign that eliminated 36 cats over 10.6 km$^2$, no meaningful differences in the relative abundance and density of feral cats were observed in response to culling, whatever the indicator of population size considered. The abundance index (GI) indicated a similar cat presence in the peninsula, the minimum number of individuals (MKTBA) decreased by only 8%, and estimated feral cat densities (SECR) were similar between the two sessions. No lasting effect of culling effort was therefore observed, despite the intensity of trapping and of traps deployed.

The recovery of the feral cat population is probably attributable to the immigration of new individuals rather than to a demographically-dependent process, as cat detections were mainly recorded in the North of the peninsula during the post-culling session. Culling operations could have removed dominant individuals whose extirpation enhanced the permeability of the population to young individuals. In fact, the abundance and distribution of feral cats are partly controlled by territorial behaviour and social interactions (Goltz et al. 2008). Removing dominant individuals could increase numbers, particularly of sub-adults (e.g. Lazenby et al. 2015) presenting lower home-range fidelity than adults and still seeking and delimiting their home ranges (McGregor et al. 2014). The probable attractiveness of the tip of this peninsula, with its large shearwater colony, could explain the rapid recolonisation of the culled area and the changes observed in activity patterns.

Post-culling, estimated home range and RPSV (Root Pooled Spatial Variance) increased by approximately 132% and 16.8% respectively. We also observed a trend towards a higher home-range Minimum Complex Polygon (MCP). Taken together, these findings may indicate that the cats recolonising the peninsula are largely young males travelling long distances in search of a territory (Algar et al. 2013; McGregor et al. 2014). These results could also support the hypothesis that the remaining cats may increase their range post-culling, having to move farther to access mates. Male territories are primarily determined by access to females, whereas female territories are primarily determined by prey availability and distribution of other females (Liberg et al. 2000; Turner and Bateson 2014). For this reason, the cats increasing their range in our study are more likely to be males, since we removed more females. The female-biased sex ratio of culled feral cats probably reflects a trapping bias due to differences between male and female behaviour (females may seek food resources more actively due to reproductive costs, "sex-bias" on trap attractiveness may also be linked to trapping method), rather than a disproportionate number of females (Molsher 2001; Short and Turner 2005; Algar et al. 2014). If future studies show a female-biased sex ratio, however, this would suggest faster population growth than with a non- or male-biased sex ratio (Short and Turner 2005). In any case, trapping more females could significantly contribute to controlling cat population dynamics, which suggests that trap attractiveness to females might be worth investigating.

Culling may provide a greater access to resources for the remaining local cats, thus promoting juvenile survival, although this would probably be more pronounced at a larger temporal scale. Since we only measured density across one season, we are unable to identify possible season-related or breeding-related changes in cat density.

While recovery or even increases in populations due to compensatory demographic response have been documented for numerous species, in contrast to our study, these were observed following low-level culling (Sinclair et al. 2006; Lazenby et al. 2015). Fortunately, most studies report a post-culling reduction in feral cat numbers, although often after an intensive and sustained control effort (Algar and Burrows 2004) or in situations where populations show limited population flows (e.g. peninsulas and fenced areas, Short et al. 1997; Moseby and Read 2006).

## Local and general implications for feral cat management

Camera trapping yields data on pre-culling population density, key information for scientists and managers who aim to control invasive predators. We provide here the first feral cat density estimates from New Caledonia. At our study site, feral cat density was estimated to be relatively high compared to many places in Australia (Bengsen et al. 2012; McGregor et al. 2015; Hohnen et al. 2020) and on two Salomon islands (Lavery et al. 2020). However, it is lower than at other locations: one Salomon island (Lavery et al. 2020), Great Britain (Langham and Porter 1991), Europe (Liberg 1980), New Zealand (Macdonald et al. 1987), United States (Warner 1985), and highly modified landscapes in Australia (Legge et al. 2017). According to the model by Legge et al. (2017), the feral cat density at Pindaï Peninsula (1.6 cats/ km²) is higher than expected (0.5–1 cat/ km²). This unexpected density illustrates the importance of specifically evaluating animal densities at each site before management actions start, especially given that New Caledonia tends to use base data from Australia. The higher density found here and the rapid return to initial densities argue for increasing the intensity and/or duration of trapping, which we calculated based on mean densities found in the literature.

As we co-conducted an intense but short culling effort, our trapping success is similar to that reported in comparable studies using wire cage traps (Algar et al. 2010; Lazenby et al. 2015; McGregor et al. 2015). The culling of 44% of camera-trapped feral cats is within or slightly below the range of other studies (e.g. 65% for Kangaroo Island in Bengsen et al. (2012), 44% and 56% for the Mount Field and Tasman Peninsula sites in Lazenby et al. (2015)). This culling effort can therefore be concluded to have been effective, but should be implemented longer (i.e. continuously) if possible, using more cage traps and at peninsula scale. Our findings support the view that lethal control in unfenced areas needs to be intense and continuous to reduce populations of resident animals, and immigration from the perimeter of core conservation areas needs to be limited (Veitch 1985; Norbury et al. 1998; Short et al. 1997; Edwards et al. 2001; Campbell et al. 2011; McCarthy et al. 2013). This applies even when recolonisation seems low due to the natural geography of the site, like a peninsula. Intense lethal control could be implemented during the presence of Wedge-tailed shearwaters in the

Pindaï peninsula colony, but their long breeding cycle (from October to May) makes this type of annual control costly and labour-intensive. Moreover, it is likely to result in large numbers of trap-shy feral cats (Parkes et al. 2014). We also recommend acting on a larger spatial scale, i.e. on the scale of the whole peninsula, which is rather wide and short compared to other peninsulas (e.g. Heirisson Prong in Short et al. 2002 and Tasman Peninsula in Lazenby et al. 2015).

For several years, innovative technical solutions have been sought to optimise the management of feral cats. These include both baiting and trapping strategies, as well as the development of efficient baits (e.g. Eradicat and Curiosity baits) and of automated traps that specifically recognise and poison feral cats (Algar et al. 2011; Johnston et al. 2011; Fisher et al. 2015; Fancourt et al. 2019; Read et al. 2019; Moseby et al. 2020). Other highly innovative genetic, cellular or behavioural methods are also being developed and offer promise for controlling feral cats in the future (Kinnear 2018; Moro et al. 2018). An interesting physiological and behavioural method called "Toxic Trojan prey", based on making the prey of feral cats specifically toxic to them, could be considered for feral cat control on our study site (Read et al. 2016).

Guard dogs could also be trained to protect wildlife and to prevent predation by feral cats on the Wedge-tailed shearwaters' breeding colony, as reported in two cases in South-West Victoria involving little penguins *Eudyptula minor* and gannets *Morus serrator* (van Bommel et al. 2010; Doherty et al. 2016). Exclusion fencing, widely used in Australia and New Zealand to protect biodiversity (Long and Robley 2004; Woinarski et al. 2014), might be another effective way to limit the recolonisation process that is particularly profitable and efficient in the peninsular context (Young et al. 2018; Tanentzap and Lloyd 2017). Last but not least, modelling approaches can provide numerical estimates of parameter values (e.g. predation rate) beyond which the prey population will decrease and/or cannot be sustained (Keitt et al. 2002; Peck et al. 2008; Bonnaud et al. 2009). Knowing such threshold values would support and greatly improve future management decisions.

## Acknowledgements

This study was funded by Province Nord (Contracts N°14C330, 15C331). We are very grateful to Corentin Chaillon, Agathe Gerard, Mathieu Mathivet, Edouard Bourguet and Province Nord landowners for providing support in fieldwork. We are also very grateful to the veterinary staff of Koné, particularly Henri Lamaignère and Yann Charpentier, for handling the feral cats. We thank Marjorie Sweetko for English language editing.

## References

Algar D, Burrows ND (2004) Feral cat control research: Western Shield review – February 2003. Conservation Science Western Australia 5: 131–163.

Algar D, Angus GJ, Brazell RI, Gilbert C, Withnell GB (2010) Eradication of feral cats on Faure Island, Western Australia. Journal of the Royal Society of Western Australia 93: 133–140.

Algar D, Hamilton N, Onus M, Hilmer S, Comer S, Tiller C, Bell L, Pinder J, Adams E, Butle S (2011) Field Trial to Compare Baiting Efficacy of Eradicat" and Curiosity" Baits. Unpublished report. Department of Environment and Conservation, Woodvale, 36 pp.

Algar D, Onus M, Hamilton N (2013) Feral cat control as part of rangelands restoration at Lorna Glen (Matuwa), Western Australia: the first seven years. Conservation Science Western Australia 8: 367–381.

Algar D, Hamilton N, Pink C (2014) Progress in eradicating cats (*Felis catus*) on Christmas Island to conserve biodiversity. Raffles Bulletin of Zoology 30: 45–53

Algar D, Johnston M, Tiller C, Onus M, Fletcher J, Desmond G, Hamilton N, Speldewinde P (2020) Feral cat eradication on Dirk Hartog Island, Western Australia. Biological Invasions 22: 1037–1054. https://doi.org/10.1007/s10530-019-02154-y

Beauvais ML, Coléno A, Jourdan H (2006) Invasive Species in the New caledonian archipelago: A major economic and environmental hazard. Collection Expertise Collégiale, IRD Editions. Paris, France, 259 pp.

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biology Letters 12: e20150623. https://doi.org/10.1098/rsbl.2015.0623

Bengsen A, Butler J, Masters P (2012) Applying home-range and landscape-use data to design effective feral-cat control programs. Wildlife Research 39: 258–265. https://doi.org/10.1071/WR11097

Bester MN, Bloomer JP, van Aarde RJ, Erasmus BH, van Rensburg PJJ, Skinner JD, Howell PG, Naude TW (2002) A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. South Africa Journal of Wildlife Research 32: 65–73.

BirdLife International (2016) IUCN Red List for birds. http://www.birdlife.org [Downloaded from march 2017]

Bivand R, Lewin-Koh N (2013) Maptools: Tools for reading and handling spatial objects. R package version 0.8, 23.

Bonnaud E, Bourgeois K, Vidal E, Legrand J, Le Corre M (2009) How can the Yelkouan shearwater survive feral cat predation? A meta- population structure as a solution? Population Ecology 11: 261–270. https://doi.org/10.1007/s10144-008-0134-0

Bonnaud E, Medina FM, Vidal E, Nogales M, Tershy B, Zavaleta E, Donlan CJ, Keitt B (2011) The diet of feral cats on islands: a review and a call for more studies. Biological Invasions 13: 581–603. https://doi.org/10.1007/s10530-010-9851-3

Borchers DL, Efford MG (2008) Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64: 377–385. https://doi.org/10.1111/j.1541-0420.2007.00927.x

Brunsdon C, Chen H (2014) GISTools: some further GIS capabilities for R. R package version 0.7-4. https://CRAN.R-project.org/package=GISTools

Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society, Monograph 5: 1–437.

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: a Practical Information-theoretic Approach (2nd edn.). Springer-Verlag, Berlin.

Calhoun JB, Casby JU (1958) Calculating home range and density of small mammals. Public Health Reports 73: 1143–1145.

Campbell KJ, Harper G, Algar D, Hanson CC, Keitt BS, Robinson S (2011) Review of feral cat eradications on islands. In: Veitch CR, Clout MN, Towns DR (Eds) Island Invasives: Eradication and Management. Gland, Switzerland: IUCN and Auckland, New Zealand: CBB, 37–46.

Chessel D, Dufour AB, Thioulouse J (2004) The ade4 package-I-One-table methods. R News 4: 5–10.

Comer S, Speldewinde P, Tiller C, Clausen L, Pinder J, Cowen S, Algar D (2018) Evaluating the efficacy of a landscape scale feral cat control program using camera traps and occupancy models. Scientific Reports 8: e5335. https://doi.org/10.1038/s41598-018-23495-z

Denny EA, Dickman CR (2010) Review of cat ecology and management strategies in Australia. Invasive Animals Cooperative Research Centre, Canberra.

Desmoulins F, Barré N (2005) Oiseaux des Forêts Sèches de Nouvelle-Calédonie. Programme Forêt Sèche and Société Calédonienne d'Ornithologie, Nouméa, 105 pp.

Di Bitetti MS, Paviolo A, De Angelo C (2006) Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. Journal of Zoology 270: 153–163. https://doi.org/10.1111/j.1469-7998.2006.00102.x

DIISE (2020) Database of island invasive species eradications. Island conservation. http://diise.islandconservation.org

Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences 113: 11261–11265. https://doi.org/10.1073/pnas.1602480113

Doherty TS, Dickman CR, Johnson CN, Legge SM, Ritchie EG, Woinarski JCZ (2017) Impacts and management of feral cats *Felis catus* in Australia. Mammal Review 47: 83–97. https://doi.org/10.1111/mam.12080

Doherty TS, Ritchie EG (2017) Stop jumping the gun: a call for evidence-based invasive predator management. Conservation Letters 10: 15–22. https://doi.org/10.1111/conl.12251

Edwards GP, De Preu N, Shakeshaft BJ, Crealy IV, Paltridge RM (2001) Home range and movements of male feral cats (*Felis catus*) in a semiarid woodland environment in central Australia. Austral Ecology 26: 93–101. https://doi.org/10.1111/j.1442-9993.2001.01091.pp.x

Efford MG, Borchers DL, Byrom AE (2009) Density estimation by spatially explicit capture-recapture: likelihood-based methods. In: Thomson DL, Cooch EG, Conroy MJ (Eds) Modeling Demographic Processes in Marked Populations. Springer, New York, 255–269. https://doi.org/10.1007/978-0-387-78151-8_11

Efford MG (2011) Estimation of population density by spatially explicit capture-recapture analysis of data from area searches. Ecology 92: 2202–2207. https://doi.org/10.1890/11-0332.1

Efford MG (2015) secr: Spatially explicit capture-recapture models. R package version 2.9.4. http://CRAN.R-project.org/package=secr

Efford M (2020) secr: Spatially explicit capture-recapture models. R package version 4.3.1. https://CRAN.R-project.org/package=secr

Fawcett T (2006) An introduction to ROC analysis. Pattern Recognition Letters 27(8): 861–874. https://doi.org/10.1016/j.patrec.2005.10.010

Engeman RM (2005) Indexing principles and a widely applicable paradigm for indexing animal populations. Wildlife Research 32: 203–210. https://doi.org/10.1071/WR03120

Fancourt BA, Cremasco P, Harry G, Speed J, Wilson C, Gentle M (2019) Evaluation of different baiting strategies for the control of feral cats in eastern Australia. 1st Queensland Pest Animal & Weed Symposium, 151–155.

Farris ZJ, Kelly MJ, Karpanty S, Ratelolahy F (2015) Patterns of spatial co-occurrence among native and exotic carnivores in north-eastern Madagascar. Animal Conservation 19: 189–198. https://doi.org/10.1111/acv.12233

Fisher P, Algar D, Murphy E, Johnston M, Eason C (2015) How does cat behaviour influence the development and implementation of monitoring techniques and lethal control methods for feral cats? Applied Animal Behaviour. Science 173: 88–96. https://doi.org/10.1016/j.applanim.2014.09.010

Foster R J, Harmsen BJ (2012) A critique of density estimation from camera-trap data. Journal of Wildlife Management 76: 224–236. https://doi.org/10.1002/jwmg.275

Gillespie TW, Jaffré T (2003) Tropical dry forests in New Caledonia. Biodiversity and Conservation 12: 1687–1697. https://doi.org/10.1023/A:1023649831355

Goltz DM, Hess SC, Brinck KW, Banko PC, Danner RM (2008) Home range and movements of feral cats on Mauna Kea, Hawai'i. Pacific Conservation Biology 14: 177–184. https://doi.org/10.1071/PC080177

Grandcolas P, Murienne J, Robillard T, Desutter-Grandcolas L, Jourdan H, Guilbert E, Deharveng L (2008) New Caledonia: a very old Darwinian island? Philosophical transactions of the Royal Society of London – Series B, Biological sciences 363: 3309–3317. https://doi.org/10.1098/rstb.2008.0122

Hohnen R, Berris K, Hodgens P, Mulvaney J, Florence B, Murphy BP, Legge SM, Dickman CR, Woinarski JCZ (2020) Pre-eradication assessment of feral cat density and population size across Kangaroo Island, South Australia. Wildlife Research 47(7–8): 669–676. https://doi.org/10.1071/WR19137

Isnard S, L'huillier L, Rigault F, Jaffré T (2016) How did the ultramafic soils shape the flora of the New Caledonian hotspot? Plant and Soil 403: 53–76. https://doi.org/10.1007/s11104-016-2910-5

Jaffré T, Morat P, Veillon JM (1993) Etude floristique et phytogéographique de la forêt sclérophylle de Nouvelle-Calédonie. Bulletin du Museum National d'Histoire Naturelle, Botanique Series 15: 107–147.

Johnston M, Algar D, O'Donoghue M, Morris J (2011) Field efficacy of the Curiosity feral cat bait on three Australian islands. In: Veitch CR, Clout MN, Towns DR (Eds) Island Invasives: Eradication and Management. IUCN, Gland, 182–187.

Jones HP, Holmes ND, Butchart SH, Tershy BR, Kappes PJ, Corkery I, Aguirre-Muñoz A, Armstrong DP, Bonnaud E, Burbidge AA, Campbell K (2016) Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113: 4033–4038. https://doi.org/10.1073/pnas.1521179113

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79: 2852–2862. https://doi.org/10.1890/0012-9658(1998)079[2852:EOTDII]2.0.CO;2

Kapos V, Balmford A, Aveling R, Bubb P, Carey P, Entwistle A, Hopkins J, Mulliken T, Safford R, Stattersfield A, Walpole M, Manica A (2009) Outcomes, not implementation, predict conservation success. Oryx 43: 336–342. https://doi.org/10.1017/S0030605309990275

Keitt BS, Wilcox C, Tershy BR, Croll DA, Donlan CJ (2002) The effect of feral cats on the population viability of black-vented shearwaters (*Puffinus opisthomelas*) on Natividad Island, Mexico. In: Animal Conservation forum. Vol. 5, No. 3. Cambridge University Press, 217–223 pp. https://doi.org/10.1017/S1367943002002263

King CM, Powell RA (2011) Managing an invasive predator pre-adapted to a pulsed resource: a model of stoat (*Mustela erminea*) irruptions in New Zealand beech forests. Biological Invasions 13: 3039–3055. https://doi.org/10.1007/s10530-011-9993-y

Kinnear JE (2018) Mammal conservation and invasive species control in Australia: harnessing a potential extinction machine. Australian Mammalogy 40: 131–135. https://doi.org/10.1071/AM17022

Langham NPE, Porter RE (1991) Feral cats (*Felis catus* L.) on New Zealand farmland. I. Home range. Wildlife Research 18: 741–760. https://doi.org/10.1071/WR9910741

Lavery TH, Alabai M, Holland P, Qaqara C, Vatohi N (2020) Feral cat abundance, density and activity in tropical island rainforests. Wildlife Research 47(7–8): 660–668. https://doi.org/10.1071/WR19205

Lazenby BT, Mooney NJ, Dickman CR (2015) Effects of low-level culling of feral cats in open populations: a case study from the forests of southern Tasmania. Wildlife Research 41: 407–420. https://doi.org/10.1071/WR14030

Legge S, Murphy BP, McGregor H, Woinarski JCZ, Augusteyn J, Ballard G, Baseler M, Buckmaster T, Dickman CR, Doherty T, Edwards G, Eyre T, Fancourt B, Ferguson D, Forsyth DM, Geary WL, Gentle M, Gillespie G, Greenwood L, Hohnen R, Hume S, Johnson CN, Maxwell N, McDonald P, Morris K, Moseby K, Newsome T, Nimmo D, Paltridge R, Ramsey D, Read J, Rendall A, Rich M, Ritchie E, Rowland J, Short J, Stokeld D, Sutherland DR, Wayne AF, Woodford L, Zewe F (2017) Enumerating a continental-scale threat: how many feral cats are in Australia? Biological Conservation 206: 293–303. https://doi.org/10.1016/j.biocon.2016.11.032

Leo BT, Anderson JJ, Phillips RB, Ha RR (2016) Home Range Estimates of Feral Cats (*Felis catus*) on Rota Island and Determining Asymptotic Convergence. Pacific Science 70: 323–331. https://doi.org/10.2984/70.3.4

Leo BT, Anderson JJ, Ha J, Phillips RB, Ha RR (2018) Modeling Impacts of Hunting on Control of an Insular Feral Cat Population1. Pacific Science 72: 57–67. https://doi.org/10.2984/72.1.4

Liberg O (1980) Spacing patterns in a population of rural free roaming domestic cats. Oikos 35: 336–349. https://doi.org/10.2307/3544649

Liberg O, Sandell M, Pontier D, Natoli E (2000) Density, spatial organisation and reproductive tactics in the domestic cat and other felids. In: Turner DC, Bateson P (Eds) The domestic cat: the biology of its behavior. Cambridge University Press, Cambridge, 119–147.

Lieury N, Ruette S, Devillard S, Albaret M, Drouyer F, Baudoux B, Millon A (2015) Compensatory immigration challenges predator control: an experimental evidence-based approach improves management. Journal of Wildlife Management 79: 425–434. https://doi.org/10.1002/jwmg.850

Lohr CA, Cox LJ, Lepczyk CA (2013) Costs and benefits of trap-neuter-release and euthanasia for removal of urban cats in Oahu, Hawaii. Conservation Biology 27: 64–73. https://doi.org/10.1111/j.1523-1739.2012.01935.x

Long K, Robley A (2004) Cost Effective Feral Animal Exclusion Fencing for Areas of High Conservation Value in Australia. Arthur Rylah Institute for Environmental Research, Heidelberg, 61 pp.

Macdonald DW, Apps PJ, Carr GM, Kerby G (1987) Social dynamics, nursing coalitions and infanticide among farm cats, *Felis catus*. Ethology 28: 1–64.

McCarthy RJ, Levine SH, Reed JM (2013) Estimation of effectiveness of three methods of feral cat population control by use of a simulation model. Journal of the American Veterinary Medical Association 243: 502–511. https://doi.org/10.2460/javma.243.4.502

McGregor HW, Legge S, Jones ME, Johnson CN (2014) Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. PLoS ONE 9: e109097. https://doi.org/10.1371/journal.pone.0109097

McGregor HW, Legge S, Potts J, Jones ME, Johnson CN (2015) Density and home range of feral cats in north-western Australia. Wildlife Research 42: 223–231. https://doi.org/10.1071/WR14180

McGregor HW, Cliff HB, Kanowski J (2017) Habitat preference for fire scars by feral cats in Cape York Peninsula, Australia. Wildlife Research 43: 623–633. https://doi.org/10.1071/WR16058

Medina FM, Bonnaud E, Vidal E, Tershy BR, Zavaleta ES, Donlan JC, Keitt BS, Le Corre M, Horwath SV, Nogales M (2011) A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biology 17: 3503–3510. https://doi.org/10.1111/j.1365-2486.2011.02464.x

Meyer JY, Strasberg D, Vidal E, Jourdan H, Delnatte C, Muller S (2018) Quelle stratégie de recherche pour une meilleure conservation de la biodiversité terrestre dans les îles tropicales ultramarines françaises? Naturae 2018 2: 15–26.

Millon A, Lambin X, Devillard S, Schaub M (2019) Quantifying the contribution of immigration to population dynamics: a review of methods, evidence and perspectives in birds and mammals. Biological Reviews 94: 2049–2067. https://doi.org/10.1111/brv.12549

Mittermeier RA, Turner W, Larsen F, Brooks T, Gascon C (2011) Global Biodiversity Conservation: The Critical Role of Hotspots. In: Zachos FE, Habel JC (Eds) Biodiversity Hotspots. Berlin, 3–22. https://doi.org/10.1007/978-3-642-20992-5_1

Molsher RL (2001) Trapping and demographics of feral cats (*Felis catus*) in central New South Wales. Wildlife Research 28: 631–636. https://doi.org/10.1071/WR00027

Moro D, Byrne M, Kennedy M, Campbell S, Tizard M (2018) Identifying knowledge gaps for gene drive research to control invasive animal species: the next CRISPR step. Global Ecology and Conservation 13: e00363. https://doi.org/10.1016/j.gecco.2017.e00363

Moseby KE, Read JL (2006) The efficacy of feral cat, fox and rabbit exclusion fence designs for threatened species protection. Biological Conservation 127: 429–437. https://doi.org/10.1016/j.biocon.2005.09.002

Moseby KE, Hill BM (2011) The use of poison baits to control feral cats and red foxes in arid South Australia I. Aerial baiting trials. Wildlife Research 38: 338–349. https://doi.org/10.1071/WR10235

Moseby KE, McGregor H, Read JL (2020) Effectiveness of the Felixer grooming trap for the control of feral cats: a field trial in arid South Australia. Wildlife Research 47(8): 599–609.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. https://doi.org/10.1071/WR19132

Nichols M, Glen AS, Garvey P, Ross J (2017) A comparison of horizontal versus vertical camera placement to detect feral cats and mustelids. New Zealand Journal of Ecology 41: 145–150. https://doi.org/10.20417/nzjecol.41.11.

Nogales M, Martín A, Tershy BR, Donlan CJ, Veitch D, Puerta N, Wood B, Alonso J (2004) A review of feral cat eradication on islands. Conservation Biology 18: 310–319. https://doi.org/10.1111/j.1523-1739.2004.00442.x

Nogales M, Vidal E, Medina FM, Bonnaud E, Tershy BR, Campbell KJ, Zavaleta ES (2013) Feral cats and biodiversity conservation: the urgent prioritization of island management. Bioscience 63: 804–810. https://doi.org/10.1525/bio.2013.63.10.7

Norbury GL, Norbury DC, Heyward RP (1998) Space use and denning behaviour of wild ferrets (*Mustela furo*) and cats (*Felis catus*). New Zealand Journal of Ecology 22: 149–159.

Northern Province Environmental Code (2018) Northern Province Environmental Code. 219 pp. https://www.province-nord.nc/sites/default/files/parutions/code_de_lenvironnement_mis_a_jour_le_16-02-18_.pdf

O'Connell AF, Nichols JD, Karanth KU (2010) Camera Traps in Animal Ecology: Methods and Analyses. Springer Science & Business Media, 271 pp.

Oppel S, Beaven B, Bolton M, Vickery JA, Bodey TW (2011) Eradication of invasive mammals on islands inhabited by humans and domestic animals. Conservation Biology 25: 232–240. https://doi.org/10.1111/j.1523-1739.2010.01601.x

Oppel S, Hervías S, Oliveira N, Pipa T, Cowen H, Silva C, Geraldes P (2012) Estimating feral cat density on Corvo Island, Azores, to assess the feasibility of feral cat eradication. Airo 22: 3–11.

Otis DL, Burnham KP, White C, Anderson DR (1978) Statistical inference from capture data on closed animal populations. Wildlife Monographs 62: 1–135.

Palmas P, Jourdan H, Rigault F, Debar L, De Meringo H, Bourguet E, Mathivet M, Lee M, Adjouhgniope R, Papillon Y, Bonnaud E, Vidal E (2017) Feral cats threaten the outstanding endemic fauna of the New Caledonia biodiversity hotspot. Biological Conservation 214: 250–259. https://doi.org/10.1016/j.biocon.2017.08.003

Parkes J, Fisher P, Robinson S, Aguirre-Muñoz A (2014) Eradication of feral cats from large islands: an assessment of the effort required for success. New Zealand Journal of Ecology 38: 307–314.

Pebesma E (2018) Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10: 439–446. https://doi.org/10.32614/RJ-2018-009

Peck DR, Faulquier L, Pinet P, Jaquemet S, Le Corre M (2008) Feral cat diet and impact on sooty terns at Juan de Nova Island, Mozambique Channel. Animal Conservation 11: 65–74. https://doi.org/10.1111/j.1469-1795.2007.00153.x

Peters D, Wilson L, Mosher S, Rohrer J, Hanley J, Nadig A, Silbernagle M, Nishimoto M, Jeffrey J (2011) Small Indian Mongoose – management and eradication using DOC 250 kill traps, first lessons from Hawaii. In: Veitch CR, Clout MN, Towns DR (Eds) Island Invasives: Eradication and Management. Gland, 225–227.

Qu L, Guennel T, Marshall SL (2013) Linear Score Tests for Variance Components in Linear Mixed Models and Applications to Genetic Association Studies. Biometrics 69: 883–892. https://doi.org/10.1111/biom.12095

R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Read J, Bowen Z (2001) Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. Wildlife Research 28: 195–203. https://doi.org/10.1071/WR99065

Read JL, Peacock D, Wayne AF, Moseby KE (2016) Toxic Trojans: can feral cat predation be mitigated by making their prey poisonous? Wildlife research 42: 689–696. https://doi.org/10.1071/WR15125

Read JL, Bowden T, Hodgens P, Hess M, McGregor H, Moseby K (2019) Target specificity of the Felixer grooming "trap". Wildlife Society Bulletin 43: 112–120. https://doi.org/10.1002/wsb.942

Recio MR, Seddon PJ, Moore AB (2015) Niche and movement models identify corridors of introduced feral cats infringing ecologically sensitive areas in New Zealand. Biological Conservation 192: 48–56. https://doi.org/10.1016/j.biocon.2015.09.004

Reddiex B, Forsyth DM, McDonald-Madden E, Einoder LD, Griffioen PA, Chick RR, Robley AJ (2006) Control of pest mammals for biodiversity protection in Australia. I. Patterns of control and monitoring. Wildlife Research 33: 691–709. https://doi.org/10.1071/WR05102

Rocamora G, Henriette E (2015) Invasive Alien Species in Seychelles. Biotope – Muséum national d'Histoire naturelle, Paris, 384 pp.

Royle JA, Karanth KU, Gopalaswamy AM, Kumar NS (2009) Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. Ecology 90: 3233–3244. https://doi.org/10.1890/08-1481.1

Schmidt PM, Lopez RR, Collier BA (2007) Survival, fecundity, and movements of free-roaming cats. Journal of Wildlife Management 71: 915–919. https://doi.org/10.2193/2006-066

Short J, Turner B, Risbey DA, Carnamah R (1997) Control of feral cats for nature conservation. II. Population reduction by poisoning. Wildlife Research 24: 703–714. https://doi.org/10.1071/WR96071

Short JB, Turner B, Risbey DA (2002) Control of feral cats for nature conservation III. Trapping. Wildlife Research 29: 475–487. https://doi.org/10.1071/WR02015

Short J, Turner B (2005) Control of feral cats for nature conservation. IV. Population dynamics and morphological attributes of feral cats at Shark Bay, Western Australia. Wildlife Research 32: 489–501. https://doi.org/10.1071/WR04102

Sinclair ARE, Fryxell JM, Caughley G (2006) Wildlife Ecology, Conservation, and Management (2nd edn.). Blackwell Publishing, Oxford.

Slade NA, Swihart RK (1983) Home Range Indices for the Hispid Cotton Rat (Sigmodon hispidus) in Northeastern Kansas. Journal of Mammalogy 64: 580–590. https://doi.org/10.2307/1380513

Sollmann R, Mohamed A, Samejima H, Wilting A (2013) Risky business or simple solution – relative abundance indices from camera-trapping. Biological Conservation 159: 405–412. https://doi.org/10.1016/j.biocon.2012.12.025

Spaggiari J, Barré N (2003) Dénombrement des puffins du Pacifique (*Puffinus pacificus chlororynchus*) nichant dans la colonie de la presqu'île de Pindaï. Société calédonienne d'ornithologie, Nouméa, Nouvelle-Calédonie.

Spaggiari J, Chartendrault V, Barré N (2007) Zones importantes pour la conservation des oiseaux de Nouvelle-Calédonie. Société calédonienne d'ornithologie – SCO et BirdLife International. Nouméa, Nouvelle-Calédonie, 216 pp.

Stokeld D, Frank AS, Hill B, Choy JL, Mahney T, Stevens A, Young S, Rangers D, Rangers W, Gillepsie GR (2015) Multiple cameras required to reliably detect feral cats in northern Australian tropical savanna: an evaluation of sampling design when using camera traps. Wildlife Research 42: 642–649. https://doi.org/10.1071/WR15083

Tanentzap AJ, Lloyd KM (2017) Fencing in nature? Predator exclusion restores habitat for native fauna and leads biodiversity to spill over into the wider landscape. Biological Conservation 214: 119–126. https://doi.org/10.1016/j.biocon.2017.08.001

Turner DC, Bateson PPG (2014) The domestic cat: the biology of its behaviour (3rd edn.). Cambridge University Press, Cambridge, 279 pp. https://doi.org/10.1017/CBO9781139177177

van Bommel L (2010) Guardian Dogs: Best Practice Manual for the Use of Livestock Guardian Dogs. Invasive Animals Cooperative Research Centre, Canberra, 127 pp.

Veitch CR (1985) Methods of eradicating feral cats from offshore islands in New Zealand. In: Moors PJ (Ed.) Conservation of island birds. International Council for Bird Preservation technical publication no. 3: 125–141.

Venning KRW, Saltré F, Bradshaw CJ (2020) Predicting feral cat-reduction targets and costs on large islands using stochastic population models. bioRxiv e149393. https://doi.org/10.1101/2020.06.12.149393

Walsh JC, Wilson KA, Benshemesh J, Possingham HP (2012) Unexpected outcomes of invasive predator control: the importance of evaluating conservation management actions. Animal Conservation 15: 319–328. https://doi.org/10.1111/j.1469-1795.2012.00537.x

Wang SW, Macdonald DW (2009) The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. Biological Conservation 142: 606–613. https://doi.org/10.1016/j.biocon.2008.11.023

Warner RE (1985) Demography and movements of free-ranging domestic cats in rural Illinois. Journal of Wildlife Management 49: 340–346. https://doi.org/10.2307/3801527

Wickham H (2011) The Split-Apply-Combine Strategy for Data Analysis. Journal of Statistical Software 40: 1–29. https://doi.org/10.18637/jss.v040.i01

Woinarski JCZ, Burbidge AA, Harrison P (2014) The Action Plan for Australian Mammals 2012. CSIRO Publishing, Melbourne. https://doi.org/10.1071/9780643108745

Young LC, Behnke JH, Vanderwerf EA, Raine AF, Mitchell C, Kohley CR, Dalton M, Mitchell M, Tonneson H, DeMotta M, Wallace G, Nevins H, Hall CS, Uyehara K (2018) The Nihoku Ecosystem Restoration Project: A case study in predator exclusion fencing, ecosystem restoration, and seabird translocation. Pacific Cooperative Studies Unit Technical Report 198. University of Hawai'i at Mänoa, Department of Botany. Honolulu, HI., 83 pp.

## Supplementary material 1

**Figure S1**

Authors: Pauline Palmas, Raphaël Gouyet, Malik Oedin, Alexandre Millon, Jean-Jérôme Cassan, Jenny Kowi, Elsa Bonnaud, Eric Vidal

Data type: figure

Explanation note: Box plot home range MCP pre post.



Link: https://doi.org/10.3897/neobiota.63.58005.suppl1

## Supplementary material 2

**Figure S2**

Authors: Pauline Palmas, Raphaël Gouyet, Malik Oedin, Alexandre Millon, Jean-Jérôme Cassan, Jenny Kowi, Elsa Bonnaud, Eric Vidal

Data type: figure

Explanation note: Accu curve preculling.



Link: https://doi.org/10.3897/neobiota.63.58005.suppl2

## Supplementary material 3

**Figure S3**

Authors: Pauline Palmas, Raphaël Gouyet, Malik Oedin, Alexandre Millon, Jean-Jérôme Cassan, Jenny Kowi, Elsa Bonnaud, Eric Vidal

Data type: figure

Explanation note: Accu curve livetrapping.



Link: https://doi.org/10.3897/neobiota.63.58005.suppl3