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ORIGINAL PAPER

Impacts and management of unowned and owned cats at a seabird colony on Reunion Island (Western Indian Ocean)

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Abstract Cats (*Felis catus*) introduced on islands have strong impacts on biodiversity, and the main conservation actions to protect native fauna is cat eradication or control (i.e., regular culling). The situation is more complicated on inhabited islands because unowned cats coexist with owned cats. The social acceptance of cat control implies separating the impacts of unowned and owned cats. We investigated the spatial ecology and impacts of owned and unowned cats at a seabird colony in a periurban area on Reunion Island (Indian Ocean). We used multiple methodologies to investigate this question: GPS-tracking of cats, camera-traps at seabird nests, cat scat analysis and cat control. Owned cats had small home ranges and did not forage at the seabird colony. Unowned cats had larger home ranges and foraged at seabird colony. We identified two kinds of unowned cats, stray cats and semi-feral cats. Stray cats relied on food waste and rarely foraged at seabird colony. Semi-feral cats foraged mostly in natural habitats, including the seabird colony and rarely used food waste. Semi-feral cats were very active at the seabird colony and several preyed upon seabirds. Restaurants are an abundant source of food for cats and help sustain populations of unowned cats. Control of unowned cats during this study resulted in reduced cat activity at the seabird colony. To minimize negative impacts of cats on seabirds, our results suggest that the most effective strategy includes the permanent control of unowned cats, efficient management of food waste and sterilization of owned cats.

Keywords Biological invasion · Management plan · Owned cat · Spatial ecology · Seabird · Unowned cat

Introduction

Owned cats (*Felis catus*) have been introduced to most of the world's inhabited islands and have established unowned cat populations on most of them (Fitzgerald 1988; Atkinson 1989; Courchamp et al. 2003). Most native island animals have reduced behavioral, morphological, and life-history defenses against mammalian predators, thus cats have caused massive impacts, including extinctions of island endemic birds, reptiles, mammals and local extinctions of many seabirds (Medina and Nogales 2009; Hilton and Cuthbert 2010; Bonnaud et al. 2011, 2012; Doherty et al. 2016). Seabird population growth rate is very sensitive to additive adult mortality (Le Corre 2008), so these species are highly affected by introduced cats (Courchamp et al. 2003; Blackburn 2004; Donlan and Wilcox 2008). Eradication or control

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(i.e., regular culling) of cat populations is among the most important wildlife conservation priorities on many islands (Medina et al. 2011) and typically results in spectacular recoveries of threatened species (Cooper et al. 1995; Keitt and Tershy 2003; Ratcliffe et al. 2010; Jones et al. 2016).

On inhabited islands, free-roaming unowned and owned cats live in sympatry and both may impact local biodiversity (Duffy and Capece 2012; Nogales et al. 2013). This situation makes cat control difficult because owned cats can be culled accidentally and caused public consternation (Ratcliffe et al. 2010). Cat management in inhabited areas is a matter of contentious social debate and require strong arguments of the respective impacts of unowned and owned cats on native wildlife (Lilith et al. 2006; Kikillus et al. 2016; Mameno et al. 2017; Deak et al. 2019; Glen et al. 2020). Many studies have reported the negative effects of free-roaming unowned and owned cats on native species (Medina et al. 2011; Bonnaud et al. 2011; Ferreira and Genaro 2017; Palmas et al. 2017). However, very few have studied together these two categories of cats co-existing on islands in the same habitat, and potentially preying upon common native prey (see Hervías et al. 2014; Cove et al. 2018). Understanding the behavior and separating impacts of these different categories of cats is crucial to implement the best management plan in terms of cost effectiveness and social acceptance to protect threatened species (Dias et al. 2017; Piquet et al. 2019). Based on the impact of the different cat categories and on what is legal and feasible, a variety of lethal and non-lethal methods exist. For example, management efforts may include cat owner awareness actions and/or legislation (e.g., prohibition, regulation, confinement, sterilization); reduction of unowned cat abundance through the use of mechanical (e.g., culling, trap-neuter-return program), chemical or biological methods; deterrent devices (e.g., ultrasonic deterrent devices); and/or fences (Robertson 2008; Lohr et al. 2014; Commonwealth of Australia 2015; Crawford et al. 2018).

On Reunion Island, a tropical island in the Western Indian Ocean, several urban areas with free-roaming owned and unowned cats are located near sensitive wildlife areas. Most owned cats roam freely outside and this must be taken into account in cat management projects. The impact of unowned cats on native species has already been studied in remote areas of the island (Faulquier et al. 2009), but no study has been carried out in urban or periurban areas. In the south of the island, the coastal site of Grande Anse is a touristic area surrounded by a periurban area. The area hosts protected native species and several invasive mammals including owned cats and unowned cats. The cliffs of Grande Anse host a seabird colony and represent one of the last habitats for the endemic and critically endangered Manapany day gecko (*Phelsuma inexpectata*) (Sanchez and Probst 2011). Dead wedge-tailed shearwaters (*Ardenna pacifica*), likely killed by cats, are found each year at the breeding colony, especially during the beginning of the breeding season when adults are displaying on the ground. To implement an effective conservation strategy for native wildlife, especially for seabirds, we addressed the following questions: (*i*) do unowned and owned cats have an impact on seabirds? (*ii*) what is the influence of human activities on cat foraging behavior? (*iii*) what are the effects of cat removal on the activity of the remaining cats at seabird colony? and (*iv*) do any other invasive mammals threaten seabirds?

Materials and methods

Study area

Grande Anse (−21°37' S, 55°55' E) is located in the south of Reunion Island. The area includes a sandy coral beach surrounded by volcanic cliffs and by a semi-urban area (Fig. 1). The area around the sandy beach is covered by low coastal vegetation, patches of Australian pine tree (*Casuarina equisetifolia*), extensive rocky cliffs and some houses. The area is widely used by tourists and inhabitants as a recreational area. Three restaurants and a hotel (The Palm Hotel) are located near the beach and these infrastructures produce a large amount of food waste, which is partly accessible to cats.

Wedge-tailed shearwaters (around 200 pairs), white-tailed tropicbirds (*Phaethon lepturus,* around 20 pairs) and brown noddies (*Anous stolidus*, a few pairs) breed colonially on the cliffs of the area. Noddies breed on vertical cliffs and are out of reach of cats, whereas shearwaters and tropicbirds nest on sub-vertical cliffs, which are all accessible to cats. These two species breed in burrows or rock cavities. The three species are locally protected. On Reunion

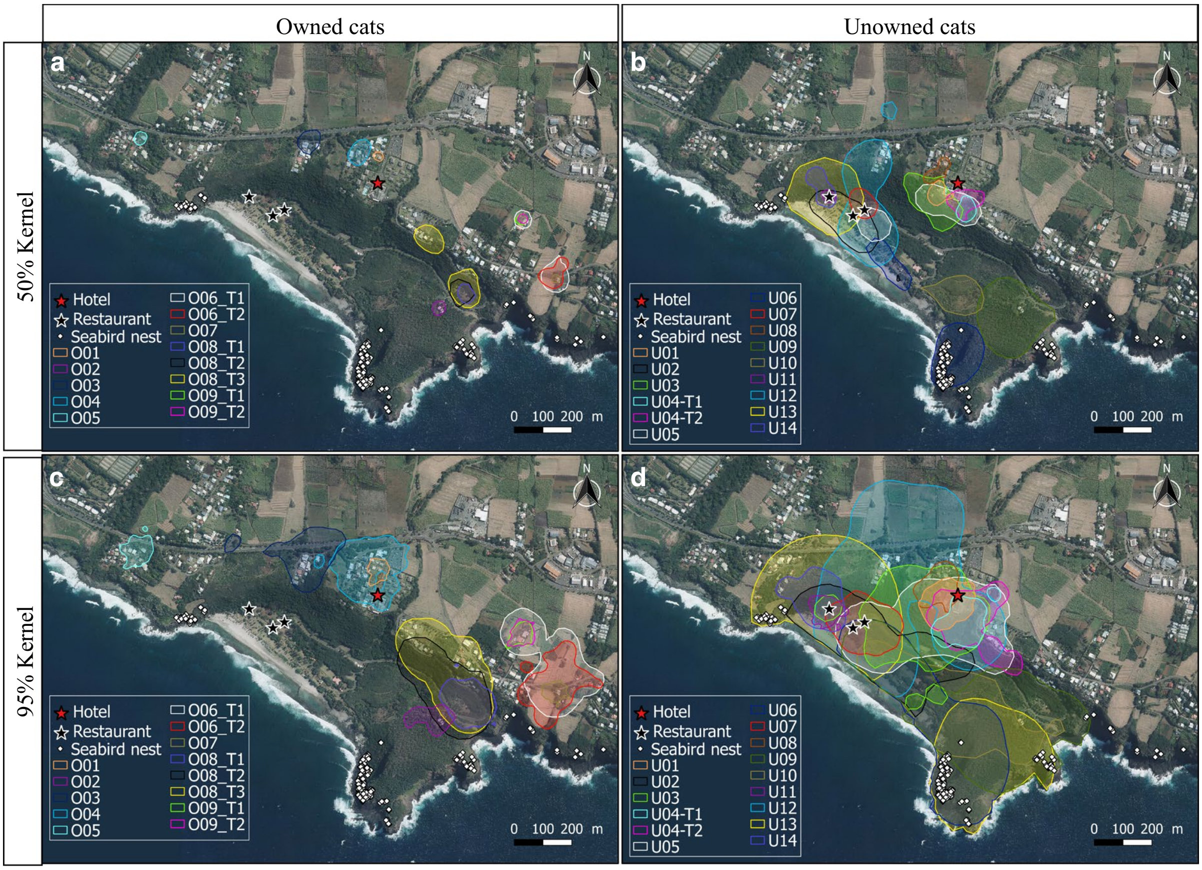

Fig. 1 Study area and results of GPS tracking of owned and unowned cats at Grande Anse, Reunion Island, between July 2015 and February 2016. **a** core home ranges of owned cats (50% kernel density estimator), **b** core home ranges of unowned cats, **c** home ranges of owned cats (95% kernel density estimator), and **d** home ranges of unowned cats. Owned cat ID number (e.g., O01), unowned cat ID number (e.g., U01), first cat tracking (T1), second cat tracking (T2), and third cat tracking (T3)

Island wedge-tailed shearwaters arrive from migration in August, they lay in November and incubate until late December. Chick-rearing occurs from late December to late April. White-tailed tropicbirds breed all year round. Cliffs near Grande Anse host one of the last populations of the Manapany day gecko. This endemic gecko lives in coastal vegetation. Several non-native mammals are present in the area: unowned and owned cats, rats (*Rattus rattus* and *Rattus norvegicus*), shrews (*Suncus murinus*), unowned and owned dogs (*Canis lupus familiaris*), house mice (*Mus musculus*) and tenrecs (*Tenrec ecaudatus*). All these non-native species take advantage of food waste left by people. We define "owned cats" as cats that live freely in the area and have owners who feed them and provide shelter in their houses. We define "unowned cats" as cats that live freely in the area and do not have owners. Among unowned cats, some feed mainly on human food waste (we refer to them as "stray cats") whereas others avoid human settlements and forage mostly on prey that they catch (referred to as "feral cats" when they have no contact with humans or "semi-feral cats" when they have casual contact with humans) (Kays and DeWan 2004; Commonwealth of Australia 2015). Several species of non-native geckos are also present: gold dust day gecko (*Phelsuma laticauda*), stump-toed gecko (*Gehyra mutilata*), common house gecko (*Hemidactylus frenatus*) and Indo-Pacific slender gecko (*Hemiphyllodactylus typus*).

Cat tracking and cat control

From July 2015 to February 2016, we tracked unowned and owned cats. We captured unowned cats with live-cage traps (Tomahawk 106 Live-Trap; Tomahawk, WI, USA) baited with fresh fish or meat, or commercial dry or wet cat food. We deployed between 3 and 15 traps simultaneously. We placed traps near the restaurants, the hotel and near the seabird colony. We baited traps in the evening and checked them every morning. When we captured a cat, a veterinarian sedated it with an intramuscular injection of ketamine (11 mg/kg) and determined its sex, age (≤ 6 months = juvenile, > 6 months = adult), weight and neutered status. The veterinarian checked if the cat was identified by a collar, a chip, or a tattoo. We then fitted the cats with a GPS transmitter (CatLog-S; Perthold Engineering LLC, Texas, USA) attached to a collar. The position accuracy of the GPS was between 5 and 10 m. The weight of the GPS and collar (68 g) was 2.40% of the average body weight of the unowned cats ($\bar{x} = 2.83 \pm 0.90$ [SD] kg, $n = 22$). We programmed the GPS to record one fix every 1, 5 or 10 min, starting at least 3 h after release. In total, we deployed 23 GPS on 22 different unowned cats (1 unowned cat was tracked twice). We released unowned cats at the same location where they had been captured. We recaptured 17 equipped unowned cats (recovery rate = 74%) 2 to 255 days after release. A veterinarian sedated the recaptured cats to recover the GPS and collar. We did not release the recaptured unowned cats into the wild, instead, we removed them from the area as part of a cat control operation to protect wildlife. The veterinarian checked if the cat was identified or not, assessed its health and decided its fate. Healthy and non-aggressive cats were given to local authorities in charge of stray animals to have them adopted. Unhealthy and aggressive cats were euthanized after the legal guard period of 4 days. Euthanasia was made by intravenous injection of pentobarbital. We also removed 13 unowned cats (not included in the GPS tracking protocol) from the area as part of the cat control operation.

For owned cats, we carried out a door-to-door survey within a radius of 800 m of the beach of Grande Anse and seabird nests, to identify cat owners willing to volunteer for tracking. We equipped 12 owned cats with the same GPS and collar as for unowned cats and with the same settings, and we determined the sex, age, and neutered status. Some owned cats being tracked several times and all of them roamed freely outside. The weight of the GPS and collar (68 g) was 1.86% of the average body weight of the owned cats ($\bar{x} = 3.66 \pm 0.62$ [SD] kg, $n = 12$). We recovered GPS, with the help of owners, after 2 to 14 days of tracking. There was no need to anaesthetize owned cats. Field protocols were approved by the CYROI institutional ethical committee, which is certified by the French Ministry of Higher Education and Research (NoAPAFIS#6916-20,151 00,213,267,087 v6).

GPS tracking data included the date, time, longitude, and latitude. We filtered the data by removing locations that implied a travel speed of more than 50 km/h (maximum speed for cats, Spies 1998) and by removing all locations at sea. We estimated home range (95% kernel) and core home range size (50% kernel) with the Kernel Density Estimate method (Worton 1989). Home range is defined as the area used by the cat during its normal activities of foraging, mating, and caring for young. Core home range is defined as the area used more frequently than any other areas and which probably contains the home site, shelter, and most dependable food sources (Burt 1943). The kernel density estimation is an efficient approach to quantify animals' home ranges. It is considered less biased than other methods, and can account for multiple centers of activity (Powell 2000; Börger et al. 2006; Lichti and Swihart 2011). To estimate kernel density, a smoothing parameter (h) must be defined to control the "width" of the kernel functions placed over each point (Worton 1989). We used the reference bandwidth method (href) to choose the smoothing parameter (Worton 1989). As cats were not tracked for the same duration and because we tested different GPS settings, all GPS tracks were not of the same duration, and they did not have the same number of fixes per unit of time. This may impact the estimate of home range size (Stickel 1954). To limit this bias we plotted, for each track, the home range size against the duration of the track and the number of fixes. Then, we visually checked the shape of the curve. In particular, we checked if the home range size reached an asymptotic value (i.e., above this value the home range did not increase with the duration of the track or the number of fixes). If there was an asymptote, we considered that the track accurately estimated home range and we kept this track in the dataset. Conversely, we removed all tracks for which the curve did not reach an asymptote. After visual analysis, we discarded 2 unowned cat tracks and 6 owned cat tracks. Also, two GPS fitted on owned cats encountered unknown problems and produced unusable data. In total, we kept 15 tracks of unowned cats (7 females and 8 males; 2 juveniles and 13 adults; 13 during the shearwater breeding season and 2 just before the breeding season) and 13 tracks of owned cats (8 females and 5 males; all adults; 10 during the shearwater breeding season and 3 before) (Table 1). We used the package "adehabitat" (Calenge 2006) in R software (R Core Team 2019) to calculate and plot home ranges. We mapped 50% kernel and 95% kernel contours of owned and unowned cats using QGIS software (QGIS Development Team 2019).

We compared the home range sizes between owned and unowned cats. Because several factors may influence cat movements (including sex, age, neutered status, food availability, and cat density) (Genovesi et al. 1995; Horn et al. 2011; Hervías et al. 2014; McGregor et al. 2015b; Palmas et al. 2017), we conducted multivariate analyzes to test the respective effect of each variable in our study area. We used linear mixed-effects models (LMM) to test the effects of cat category (owned or unowned), sex, tracking period (seabird breeding season or not), cat control (number of cats removed at the time of tracking), neutered status, age, and the interactions between cat category and sex, cat category and tracking period, cat category and cat control, on core home range size (50% kernel), and home range size (95% kernel) separately. We assessed multicollinearity among explanatory variables by calculating variance inflation factors (VIFs). VIFs were less than 1.9 for all variables suggesting no multicollinearity (Zuur et al. 2010). We included individual cats as a random effect (acting on the intercept of regressions) because some owned cats were tracked several times. First, for each variable, we calculated the difference of deviance between the full model and a model not including the target variable. Then, we built a complete model with all variables ordered from the variable that increased the deviance the most to the variable that increased the deviance the least when removed from the complete model. We used a stepwise backward elimination procedure of the least significant terms ($P > 0.05$) to determine the best adequate minimal model containing only significant terms (Crawley 2007). We used the package "lme4" (Bates et al. 2015) in R software for these analyses. We used an α value $= 0.05$ as the significance threshold for all statistical analyses.

Cat inventory and photo-ID database

During the door-to-door survey, we asked residents if they had cats and how many, to determine the number of owned cats using the area. For each owned cat, we asked owners if the cat was neutered and/or marked with a PIT tag (microchipped) or a tattoo. To determine which cat category (owned or unowned) frequented the seabird colony, we photo-identified each cat encountered during our study. We photographed owned cats on both sides from head to tail and we included all photographs in a photo-ID database. We also photographed unowned cats captured for GPS tracking or cat control on both sides from head to tail at the veterinary clinic. In addition, we photographed opportunistically the cats observed in the field. We carefully observed each cat photograph. If it did not match any cat in the database, we considered it as a new cat and we assigned a unique ID number. If it matched a known cat, we considered the photograph as a recapture of a known cat and added the new photograph to the database.

Camera-trap survey

From August 2015 to April 2016, we deployed 6 camera-traps (Stealth Cam G 42; Stealth Cam, Texas, USA) at the seabird colony. We deployed each camera in front of a seabird nest to monitor predator activities at the entrance of the nest. We deployed each camera for 5 to 99 consecutive days in front of a given nest. In total, we monitored 30 different nests. Camera-traps were active 24 h per day. Camera-traps automatically took a burst of five eight-megapixel pictures when a motion was detected with a delay of 5 s between successive bursts. Photographs were taken during the day (normal light) and at night (infrared sensors) with standard sensitivity for Stealth Cams.

We analyzed only detections of mammals because other animals (reptiles, birds, arthropods) in this area are not predators of seabirds. We defined a detection as an animal crossing the field view of a camera-trap, from the arrival to the departure of the animal. For each species detected, we calculated the number of detections, the percentage of detections (number of detections for that species/total number of detections)

Table 1 Core home range (ha; 50% kernel density estimator [50% kernel]) and home range (ha; 95% kernel density estimator [95% kernel]) for owned and unowned cats tracked using GPS collars at Grande Anse, Reunion Island, between July 2015 and February 2016

Track ID	Cat category	Neutered	Sex	Age	Fix rate	Day track	No. of fixes	Month	Cat control	Period	50% kernel	95% kernel
O01	Owned	Yes	F	Ad	5	4.31	436	Jul	0	No breeding	0.08	0.52
O02	Owned	No	F	Ad	5	3.49	99	Aug	1	Breeding	0.18	1.17
O03	Owned	No	M	Ad	5	4.00	237	Jul	0	No breeding	0.49	3.77
O04	Owned	No	M	Ad	5	3.69	321	Aug	1	Breeding	0.50	4.97
O05	Owned	No	F	Ad	10	5.71	207	Oct	9	Breeding	0.16	0.97
O06-T1	Owned	Yes	F	Ad	10	6.73	431	Sep	5	Breeding	1.14	7.19
O06-T2	Owned	Yes	F	Ad	10	6.07	236	Feb	35	Breeding	0.65	4.24
O07	Owned	No	F	Ad	5	4.69	530	Aug	1	Breeding	0.067	0.53
O08-T1	Owned	No	M	Ad	5	4.88	653	Jul	0	No breeding	0.30	2.58
O08-T2	Owned	No	M	Ad	10	9.34	550	Oct	9	Breeding	0.57	6.90
O08-T3	Owned	No	M	Ad	10	13.99	589	Feb	35	Breeding	1.87	8.48
O09-T1	Owned	Yes	F	Ad	5	3.89	96	Aug	1	Breeding	0.12	0.56
O09-T2	Owned	Yes	F	Ad	10	6.98	108	Sep	5	Breeding	0.079	0.65
U01	Unowned	No	F	Ad	10	15.66	754	Jan	17	Breeding	0.44	2.64
U02	Unowned	No	M	Ad	5	4.28	328	Jul	0	No breeding	3.06	12.69
U03	Unowned	No	M	Ad	5	4.87	542	Jul	0	No breeding	2.47	14.09
U04-T1	Unowned	No	M	Ju	5	3.73	217	Aug	1	Breeding	0.46	2.72
U04-T2	Unowned	No	M	Ju	5	5.07	809	Sep	5	Breeding	0.87	5.40
U05	Unowned	No	F	Ad	5	5.74	912	Aug	1	Breeding	3.11	15.10
U06	Unowned	No	F	Ad	10	6.96	354	Sep	5	Breeding	4.50	17.07
U07	Unowned	No	M	Ad	10	6.06	212	Sep	5	Breeding	0.78	4.33
U08	Unowned	No	F	Ad	10	6.68	237	Sep	5	Breeding	0.44	1.88
U09	Unowned	No	M	Ad	10	5.25	240	Sep	5	Breeding	5.17	23.24
U10	Unowned	No	F	Ad	10	8.15	344	Sep	5	Breeding	1.95	13.63
U11	Unowned	No	F	Ad	10	6.06	155	Oct	9	Breeding	0.16	1.09
U12	Unowned	No	M	Ad	10	6.05	247	Oct	9	Breeding	6.72	31.46
U13	Unowned	No	M	Ad	10	8.07	422	Oct	9	Breeding	5.27	30.95
U14	Unowned	No	F	Ad	10	5.02	143	Dec	15	Breeding	0.86	3.55

GPS fix intervals (minutes; [Fix rate]), number of days tracked (Day track), number of fix localizations (No. of fixes), number of cats removed (Cat control), breeding season (Period), first cat tracking (T1), second cat tracking (T2), third cat tracking (T3), female (F), male (M), adult (Ad), and juvenile (Ju) and the detection rate (number of detections per 100 trap nights, detections/100 TN). We grouped the behaviors of mammals into 3 categories: (*i*) unambiguous hunting behaviors (animal hunting a seabird), (*ii*) possible hunting behaviors (animal entering the nest or looking into it), and (*iii*) no interaction with nests, eggs, or seabirds. If a cat was detected, we compared it with the photo-ID database of owned and unowned cats to identify it. We calculated the cat detection rate (detections/100 TN) each month to quantify the effect of cat control on cat activity and abundance at the seabird colony.

Cat diet

From August 2015 to January 2016, we characterized cat diet by examining cat scats collected in the field, and by identifying prey remains in those samples (Nogales et al. 1988; Bonnaud et al. 2007; Palmas et al. 2017). We washed cat scats using a sieve (0.5-mm mesh) under a stream of water and we dissected them. We observed individual prey items under a binocular microscope and compared them to reference material from our own collection. We identified bird remains from feathers, beaks, bones and/or claws; mammal and lizard remains from bones, fur, skin and/or scales; and invertebrate remains by their shape and texture. We estimated the minimum number of prey individuals by jaws and teeth. We defined diet composition in terms of number of prey, the proportion of total prey (number of prey individuals for that species/total number of prey), and frequency of occurrence (number of scats containing items of prey individuals for that species/total number of scats).

Results

Cat tracking and cat control

We captured 44 different unowned cats during 633 trap nights (catch rate: 6.95 captures /100 TN). We removed 35 unowned cats from the area among which 32 were euthanized and 3 were adopted. Nine captured cats were not removed because we did not recapture 6 of them after GPS deployment and 3 cats escaped during handling.

Each track of unowned cats lasted 3.7 to 15.7 days and included between 143 and 912 fixes (Table 1).

Table 2 Results of the best adequate minimal model explaining core home range size (50% kernel density estimator) of cats tracked with GPS collars for a minimum of 3 days at Grande Anse, Reunion Island, between July 2015 and February 2016 (adjusted $r2 = 0.90$)

Parameter	Estimate	SE	df	*t*-value	*P* value
Intercept	3834.08	5580.71	21	0.69	0.500
Cat category (unowned cat)	21,511.75	7180.95	21	3.00	0.007

Standard error of parameter (SE), degrees of freedom (df), and *t* statistic (*t*-value) issued from linear mixed-effects models

Table 3 Results of the best adequate minimal model explaining home range size (95% kernel density estimator) of cats tracked with GPS collars for a minimum of 3 days at Grande Anse, Reunion Island, between July 2015 and February 2016 (adjusted $r2 = 0.92$)

Parameter	Estimate	SE	df	*t*-value	*P* value
Intercept	3459.22	27,154.04	20	0.13	0.900
Cat category (unowned cat)	86,092.63	32,518.88	20	2.65	0.016
Sex (male)	71,043.59	32,061.87	20	2.22	0.039

Standard error of parameter (SE), degrees of freedom (df), and *t* statistic (*t*-value) issued from linear mixed-effects models

Each track of owned cats lasted 3.5 to 14 days and included between 96 and 653 fixes. None of the tracked unowned cats were neutered and among 13 tracked owned cats, 5 were neutered. Core home range (50% kernel) were influenced by cat category (Table 2) and home range (95% kernel) were influenced by cat category and sex (Table 3). Tracking period, age, cat control and neutered status did not influence home range and core home range size. There were no significant interactions between the different factors tested. Core home range and home range of unowned cats (respectively $\bar{x} = 2.42 \pm 0.55$ [SE] ha with a median size of 1.96 ha and $\bar{x} = 11.99 \pm 2.65$ ha with a median size of 12.69 ha) were 5.1 times and 3.7 times larger than those of owned cats (respectively $\bar{x} = 0.48 \pm 0.14$ ha with a median size of 0.30 ha and $\bar{x} = 3.27 \pm 0.80$ ha with a median size of 2.58 ha) ($P = 0.007$ and $P = 0.016$). Home range of males ($\bar{x} = 11.66 \pm 2.69$ ha, median size = 6.90 ha) were 2.5 times larger than those of females ($\bar{x} = 4.72 \pm 1.60$ ha, median size = 1.88 ha) ($P = 0.039$). There was large variability of home range size among unowned cats (min. 1.09 ha; max. 31.46 ha). Ten unowned cats were present only near the restaurants or the hotel and they had a smaller home range (Fig. 1). Four unowned cats (U06, U09, U10, U13) visited the restaurants, the hotel and the seabird colony and consequently had a larger home range. One female (U06) had its core home range at the seabird colony. Owned cats stayed near the house of their owners and never visited the seabird colony, restaurant, or beach. The home ranges of owned and unowned cats only overlapped near the hotel.

Cat inventory

We visited 112 houses during the door-to-door survey, which represents 93% of the houses identified within a radius of 800 m of the beach of Grande Anse. Thirty percent of these houses had at least one cat. We identified 69 different owned cats among which 15 were neutered (22%) and 11 were marked with a PIT tag (microchipped, 16%). We also identified 55 different unowned cats in the study area (44 during captures and 11 opportunistically in the field by photo ID). We regularly observed groups of unowned cats (max. 9 cats in a group) near the restaurants.

Camera-trap survey

We obtained 1106 days of camera-trapping, totaling 80,286 photographs. Monitoring effort per month was approximately the same from September to January with an average of 172 monthly trap nights (min. 156; max. 187) (Fig. 2). Monitoring effort was lower in August and between February and April with an average of 62 trap nights (min. 30; max. 107). We obtained 339 mammal detections (Table 4). The most frequently detected mammal species was the shrew (55% of the detections). Cats were the second most detected mammal species with 62 detections (18%). Among these 62 detections, we identified 8 unowned cats from our photo-ID database. These 8 unowned cats represented 34 detections (55% of all cat detections). None of the owned cats included in our photo-ID database were camera-trapped at the seabird colony. We detected two unowned cats fitted with GPS collars at the seabird colony with camera-traps (U06 and U13). Other mammals detected were black rats (8% of the detections), tenrecs (6%), dogs (5%), humans (4%) and house mice (1%). For cats, we observed 1 unambiguous hunting behavior targeting a shearwater, which represents 2% of cat detections, and 15 possible hunting behaviors, which represent 24% of cat detections. Also, 25 detections of shrews (13% of total detections) showed possible hunting behaviors (an animal entering the burrow), 11 detections (58%) for tenrecs, 9 detections (32%) for black rats, and 3 detections (18%) for dogs.

The cat detection rate was high before the cat control operation, with 16.67 detections/100 TN in August, despite a relatively low monitoring effort (Fig. 2). These detections decreased with the removal of 9 cats between August and October (4.81 detections/100 TN in October). In November, there was no cat removal and detections increased to 7.39

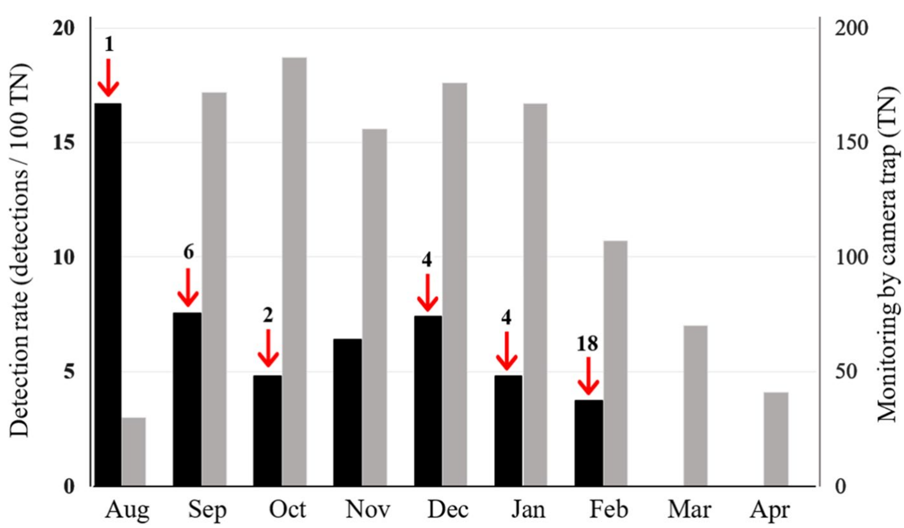

Fig. 2 Effect of cat control on cat activity (detections/100 trap nights) at the Grande Anse seabird colony, Reunion Island, between August 2015 and April 2016. Black bars represent detection rate (detections/100 trap nights) per month at the seabird colony, gray bars represent the camera-trap monitoring effort per month (number of trap nights, TN), and red arrows represent the number of cats removed each month

Table 4 Detections and behavior for each mammal species during the camera-trap survey at the Grande Anse seabird colony, Reunion Island, between August 2015 and April 2016 (1106 trap nights)

	No. of det	Ind	% Detections	Detection rate	% Unambiguous hunting	% Possible hunting
S. murinus	187	–	55.16	16.91	0.00	13.37
F. catus	62	8	18.29	5.61	1.61	24.20
R. rattus	28	–	8.26	2.53	0.00	32.14
T. ecaudatus	19	–	5.60	1.72	0.00	57.89
C. lupus familiaris	17	3	5.01	1.54	0.00	17.65
H. sapiens	12	1	3.54	1.08	0.00	8.33
Undetermined rodent	12	–	3.54	1.08	0.00	0.00
M. musculus	2	–	0.59	0.18	0.00	0.00

Number of detections (No. of det.), number of individuals identified (Ind.), percentage of detections (% Detections), detection rate/100 trap nights (Detection rate), percentage of unambiguous hunting behaviors (% Unambiguous hunting), and percentage of possible hunting behaviors (% Possible hunting)

Table 5 Cat scat composition at Grande Anse, Reunion Island, between August 2015 and January 2016

	N	% Total prey	% Occurrence
Mammals	34	53.97	29.79
R. rattus	18	28.57	12.77
M. musculus	3	4.76	3.19
S. murinus	1	1.59	1.06
Undetermined Mammals	12	19.05	12.77
Seabirds	4	6.35	4.26
A. pacifica	4	6.35	4.26
Land birds	16	25.40	17.02
Reptiles	3	4.76	3.19
Insects	6	9.52	3.19
Food garbage	–	–	67.08

Number of prey items found (N), proportion of total prey (% Total prey), and frequency of occurrence (% Occurrence). Number of cat scats analyzed = 94

detections/100 TN in December. Between December and late February, we removed 26 cats, and detections decreased to 3.74 detections/100 TN in February and 0/100 TN in March and April, suggesting that the control operation significantly reduced the abundance of unowned cats at the seabird colony.

Cat diet

We analyzed 94 cat scats, which contained 63 prey items. We found food waste in 67% of the scats (Table 5). Mammals were the most frequent prey, followed by land birds, insects, seabirds, and reptiles. Among mammals, the black rat was the most important prey. Four scats (4% of occurrence) contained remains of wedge-tailed shearwaters and 3 scats (3% of occurrence) contained remains of unidentified reptiles. We failed to confirm the predation by cats on Manapany day geckos because we could not distinguish the remains of this species from that of other geckos.

Discussion

Spatial ecology of owned and unowned cats and influence of human activities

Owned and unowned cats had different spatial ecology leading to different impact on native wildlife. Although GPS collar devices may have slightly reduced home range sizes, devices used was light (2% of body mass for owned and unowned cats) and we may reasonably assume that our tracking study reflected adequately spatial ecology of cats (Coughlin and van Heezik 2014). Owned cats had smaller home ranges and they never reached the seabird breeding sites. Both GPS tracking and the camera-trap survey showed that only unowned cats foraged at the seabird colony. None of the owned cats tracked with GPS descended the cliffs and reached the beach of Grande Anse. All of them remained near the houses of their owners and in surrounding urban and agricultural areas. As shown in other studies, home range size decreased with ownership (Schmidt et al. 2007; Horn et al. 2011). As owned cats are fed, they do not need to search for food away from their home (Tennent and Downs 2008). Unowned cats had larger home ranges than owned cats, as reported in previous studies (Biró et al. 2004; Schmidt et al. 2007; Horn et al. 2011). These cats are not fed and they are sexually active. Thus, they have to search for food and mates, and their movements and distribution depend on both food availability and sexual behavior (Barratt 1997; Schmidt et al. 2007).

All tracked unowned cats foraged at the restaurants, the hotel or the beach, taking advantage of food waste. Some were also directly fed by customers and owners of the restaurants (A. Choeur, personal observation). Food waste availability was the primary determinant of unowned cat distribution (and probably abundance) at Grande Anse. We observed a high abundance of cats at the restaurants and the hotel (up to 9 cats observed together at one restaurant). The core home range of most unowned cats overlapped largely at these restaurants and the hotel. Food waste represents a predictable source of easily available food for cats and this probably increases their foraging efficiency, body condition and thus breeding parameters and survival. Food waste is known to artificially increase the carrying capacity of cat populations in urbanized and semi-urbanized areas (Liberg and Sandell 1988; Mirmovitch 1995; Genovesi et al. 1995; Algar et al. 2003; Schmidt et al. 2007; Piquet et al. 2019). Thus, poor management of food waste and supplemental feeding at restaurants contributed to maintaining a large unowned cat population near the seabird colony.

For both owned and unowned cats, males had larger home ranges than females. The scale of movements is influenced by differences in reproductive behavior between the sexes. Males are more solitary and disperse more widely than females to defend their territory against other males and to look for breeding partners (Liberg 1980). We expected that neutered cats would have a smaller home range than non-neutered cats (Hervías et al. 2014; Ferreira et al. 2020) but differences were not significant. This may be due to the small sample size ($n=5$ neutered cats tracked) and/or to intrinsic behavior variation of some cats that have the "personality" to roam widely, regardless of their neutered status (Mendl and Harcourt 2000; Litchfield et al. 2017).

The home range, distribution and behavior of unowned cats were extremely variable among individuals. We identified two kinds of unowned cats, semi-feral cats and stray cats. Semi-feral cats were cats that foraged mostly in natural habitats (rocky cliffs, forest, coastal vegetation, and the seabird colony) and rarely had contact with humans. These cats rarely foraged at the beach, the restaurants, or the hotel. Semi-feral cats represented the minority of the tracked unowned cats (4 cats out of 14). This result is also confirmed by the fact that we identified only 8 cats out of the 55 unowned cats by photo ID at the seabird colony. Their home ranges and core home ranges were mostly in natural habitats. They had larger home ranges and were aggressive during capture. We did not classify these cats as true "feral cats" because they fed on food waste occasionally, so they were not completely independent of humans.

Stray cats were unowned cats that relied on food waste originating from humans, especially at the restaurants and the hotel. These cats represented the majority of tracked unowned cats (10 cats out of 14). They foraged at the rocky cliffs only occasionally and did not feed at the seabird colony. They had smaller home ranges and stayed near the restaurants or the hotel. Some of these cats were not aggressive during capture, begged for food in groups from restaurant clients and were easily approached. These movement patterns and behaviors are explained by the presence of predictable and abundant food resources but also by the strong interaction between cats and humans (Liberg and Sandell 1988; Mirmovitch 1995; Genovesi et al. 1995; Schmidt et al. 2007).

Such behavioral differences between cat categories have already been reported (Schmidt et al. 2007; Moseby et al. 2015; Dickman and Newsome 2015; Cove et al. 2018). Schmidt et al. (2007) reported that some unowned cats exploited food resources in anthropogenically modified areas while others did not. We hypothesize that semi-feral cats are cats that have rarely been in contact with humans during their lives, and tend to avoid contact. On the other hand, stray cats are cats that may have been born near restaurants or were abandoned as kittens and have frequently interacted with humans since birth, and they probably search for such contacts.

Impacts of cats

Cats in our study area had three very different behavioral profiles, and these were related to their status (owned cats, stray cats, and semi-feral cats). These greatly influenced their impact on seabirds. This result has strong implications for cat management and seabird conservation. Indeed, profiling specialized predators can lead to a more efficient targeted rather than generic control strategy. By reducing the number of cats that have to be removed, such targeted control generally has a higher social acceptability than non-targeted control (Burrows et al. 2003; Priddel and Wheeler 2004; Moseby et al. 2015).

Semi-feral cats have a direct impact on seabirds. The four semi-feral cats that were tracked, foraged at the seabird colony. We detected 6 other cats with camera-traps at the seabird colony, which brought to at least 10 the number of semi-feral cats that visited the seabird colony during our study. The camera-trap survey showed that semi-feral cats were very active at the seabird colony and some of them had hunting behaviors targeting seabirds. Although the remains of shearwaters in cat scats could be explained by scavenging, cat behaviors at the seabird colony suggest that they do prey upon shearwaters. It is impossible to distinguish scats belonging to owned cats, semi-feral cats and stray cats. However, both our tracking data and camera-trap data suggest that semi-feral cats were the only cats to visit the seabird colony. Each year, between 5 to as many as 40 shearwaters are found dead at the breeding colony, most of them with distinctive signs of predation. Our results strongly suggest that semi-feral cats killed them. It is possible that among semi-feral cats, not all prey upon seabirds and only some may be specialized in this way. Indeed, we observed only one hunting behavior targeting shearwaters and three-quarters of the detections were without any interaction with nests or seabirds. In addition, we only found four percent of scats with the remains of seabirds. Some studies have shown that in a population of cats, some cats specialize in a particular type of prey, causing higher impacts (Mendl and Harcourt 2000; Dickman 2009; Moseby et al. 2015; Bradshaw 2016). However, even if only some semi-feral cats prey on seabirds, this does not mean that their impact may be regarded as insignificant. The population growth rate of seabirds, particularly petrels and shearwaters, is very sensitive to any change in adult survival (Le Corre 2008) and even low predation rates each year can lead to significant additive mortality that could threaten the colony. Furthermore, the death of one adult of a breeding pair invariably leads to the failure of the current breeding attempt because both parents share parental duties equally. Predation pressure also affects behavior and may cause separation of mates and nest abandonment (O'Donnell and Sedgeley 2010; Greenwell et al. 2019). This could explain the poor breeding success (40%) observed at this colony (A. Choeur, unpublished data). Also, wedge-tailed shearwaters, like other shearwater species, are known to display and call for long periods on the ground in front of burrow entrances, especially at the beginning of the breeding season. This behavior makes pre-breeding prospectors particularly vulnerable to cat predation (Bonnaud et al. 2009). Thus, long-term cat predation at Grand Anse and probably at other shearwater colonies may also threaten populations by reducing the number of future breeders. Ultimately, the small shearwater colony on Grande Anse could be a relic of old larger colony decimated by cats. Reducing cat impact may lead to an expansion of the distribution and abundances of seabirds (see: Ratcliffe et al. 2010; VanderWerf et al. 2014).

Semi-feral cat predation on native species is probably underestimated in our study. Indeed, cats are known to kill prey without eating them, a behavior referred to as "surplus killing" (Biben 1979; Peck et al. 2008; Loyd et al. 2013; McGregor et al. 2015a). Surplus killing is not detectable through scat analysis because cats do not eat these preys. Scat analyses alone may lead to an underestimation of the predation rate. Surplus killing may be important in our context as we regularly observed dead shearwaters, presumably killed but not consumed by cats. The four semi-feral cats identified in our study were removed from the area at the beginning of the study (September and October). This may explain why we did not observe any direct evidence of predation with camera-traps after October. We did not detect predation by cats on white-tailed tropicbirds but this cannot be ruled out because they live in the same habitats and are as vulnerable as shearwaters. Finally, even if we failed to identify species of geckos in scats, semi-feral cats are a putative predator of the Manapany day gecko that lives on the coastal vegetation on the cliffs.

Stray cats did not forage at the seabird colony during our study so they do not seem to represent a direct risk for seabirds. However, these cats may represent an indirect risk because they may become semi-feral and change their diet if food waste becomes unavailable (which is a management requirement, see below and also Shionosaki et al. 2016). Indeed, cat categories (stray and semi-feral) are not permanent (Newsome 1991; Moodie 1995) and cats may change from stray to semi-feral depending on the amount of food available at human settlements. Other studies reported that cats fed by people or feeding on food waste can also have an important impact on local fauna (Grant and Longnecker 1999; Hawkins et al. 2004; Loss et al. 2013; Maeda et al. 2019). In our case study, direct or indirect food provisioning by humans may cause "hyper-predation" on seabirds. Permanent food availability induces population growth of unowned cats, some of which (semi-feral cats) may then hunt native species, thereby enhancing the predation pressure (Maeda et al. 2019).

Owned cats had reduced home ranges and did not forage at the seabird colony. Owned cats did not represent a direct risk to seabirds but they may threaten seabirds indirectly by maintaining the unowned cat population (through breeding or abandonment by their owners). Indeed, owned cats were numerous in the area (minimum 69 owned cats identified less than 800 m from the seabird colony), very few were neutered and we found an overlap of the home ranges of unowned and owned cats. Uncontrolled and unwanted breeding of owned cats often leads to the abandonment of cats or kittens in the area and this greatly reduces the benefit of unowned cat removal. We often observed young cats near the beach, probably abandoned recently by their owners (A. Choeur, personal observation). These abandonments are extremely damaging both to the local fauna but also to the cats themselves whose sanitary condition and body condition decline rapidly once in the wild. Moreover, cats that survive these abandonments join the unowned cat population.

Effects of cat control

The removal of 35 cats in the area greatly reduced cat activity and abundance at the seabird colony, as shown by camera-trap monitoring. The problem for cat control on large islands is that the area may be reinvaded rapidly (Moseby and Hill 2011; Palmas et al. 2020). Cat density may increase after cat removal because new individuals may move into the area after dominant cats are removed (Lazenby et al. 2015). We did not observe rapid recolonization during the two months after the control. As cats were concentrated near food areas, intense control at these places in our study probably reduced the density of cats over a large area, thereby preventing rapid reinvasion. In addition, the distribution of cats was mainly determined by the distribution of food rather than territoriality, which can also explain why cats did not re-invade the seabird colony after cat control. It is also for this reason that cat control did not influence the home range size of tracked cats. However, recolonization in the longer term seems inevitable and future studies will be required to determine the cat-control-frequency necessary to maintain low abundance throughout the year.

Our diet analysis showed that cats prey upon black rats and house mice, so rat and mouse densities may increase after cat removal, the so-called mesopredator-release effect (Courchamp et al. 1999). As rats (and to a lesser extent mice) are seabird predators, this may result in more rat predation of seabirds. On islands with multiple invasions, with both introduced predators and local prey, it is commonly suggested that the best solution is to simultaneously eradicate apex predators and mesopredators (Zavaleta et al. 2001; Courchamp et al. 2003). When multiple eradications are not feasible, actions on cats should be done first because the impact of mesopredators (rats and mice) on seabirds is known to be lower than that of cats (Hughes et al. 2008; Le Corre 2008; Russell and Le Corre 2009; Russell et al. 2009; Dumont et al. 2010). Furthermore, the removal of apex predators does not always lead to the release of their prey (Cooper et al. 1995; Girardet et al. 2001; Ratcliffe et al. 2010), especially on tropical islands where populations of mesopredators like rats are regulated by bottom-up processes and not by top-down processes (Russell et al. 2009; Ringler et al. 2015; Russell and Kaiser-Bunbury 2019).

Impacts of other mammal species

We observed several species of introduced mammals at the seabird colony: black rats, house mice, shrews, dogs and tenrecs. No predation has been directly observed but this does not mean that it does not take place.

The impact of rats and mice on the eggs and chicks of seabirds is well known (Towns et al. 2006; Rayner et al. 2007; Jones et al. 2008; Angel et al. 2009; Ringler et al. 2015). This may explain the high breeding failure during the incubation period (47%; A. Choeur, unpublished data), although this could also be the result of cat predation on incubating adults. The presence of dogs at the seabird colony is problematic because they are known to predate both chicks and adults (Lunney et al. 1990; Hodges and Nagata 2001; Del Viejo et al. 2004). Shrews are small and probably cannot attack an egg or a chick, although they are very abundant in the area and were frequently observed entering the burrows.

The tenrec is large and omnivorous and may attack seabird chicks or eggs, although predation of seabirds by tenrecs is not documented. More than 50% of the tenrec detections consisted of tenrecs that were looking into the nests or were entering them. Further studies should be conducted locally to better quantify the impacts of this species on seabirds.

Management implications

At places where predator eradication is impossible, predator-proof fences may be a good solution to protect native wildlife from invasive predators (Long and Robley 2004; Burns et al. 2012; Young et al. 2013). However, in our context, building a fence to prevent cat reinvasion after a removal operation seems unrealistic because the area is used by thousands of people and the acceptability of such a project would probably be extremely low. Furthermore, building and maintaining a cat and rodent-proof fence is extremely expensive (Clapperton and Day 2001; Burns et al. 2012). A cost-benefit analysis could be undertaking to accurately compare the different management options (Lohr et al. 2013).

According to our results, we have three management recommendations for any place where owned and unowned cats coexist and may impact the native fauna, and where complete eradication and fencing are unfeasible. (*i*) Removal of unowned cats. The unowned cats have large home ranges and feed on native species. At Grande Anse, we recommend an intense cat removal operation each year before the shearwater breeding season begins in August. Our data suggest that cat control at the seabird colony and on the beach is unlikely to cause harm to owned cats. Camera monitoring should then be implemented throughout the breeding season to rapidly detect any cats that forage at the seabird colony and carry out targeted controls. In addition to culling operations, other methods to reduce impact of cats (e.g., ultrasonic deterrents devices, guard dogs) could be tested locally before recommending their use (Nelson et al. 2006; van Bommel et al. 2010; Crawford et al. 2018). (*ii*) Investigate the impact of owned cats to implement management strategies adapted to the local context. Owned cats do not necessarily have an impact on native wildlife. Hard decisions about owned cats (ownership prohibition, confinement), often contested, are not always necessary. In our study area, although owned cats do not threaten seabirds, they may indirectly impact them by supplementing the unowned cat population through reproduction or abandonment. We recommend a large-scale public awareness campaign to encourage people to neuter their pets, tag them and continue to feed them regularly (with no access to food for unowned cats). (*iii*) Food waste management. Food waste and public bins are important and predictable food sources for cats. We recommend using only cat-proof public bins and to prohibit cat feeding in the area. This should be accompanied by a public awareness campaign and public communication to inform users of the area of the impact of cats on wildlife and on the need to avoid feeding them. A sudden decrease in resource availability may cause a temporary increase in predation pressure on the native prey (Yirga et al. 2012; Shionosaki et al. 2016). It is thus important that cat removal and food waste reduction are done simultaneously. On the other hand, because the other introduced mammals present in the area (rodents, dogs, tenrecs) probably feed on food waste (Pocock et al. 2004; McKinney 2006), reducing this food source may contribute to reduce their abundance (Piquet et al. 2019) and also mitigate a potential mesopredator-release effect due to cat removal operations.

Ultimately, management of owned and unowned cats in urban and tourist areas requires a concerted effort of all users (tourists, residents, cat owners, restaurant, and hotel managers). These users can be encouraged by awareness campaigns based on scientific studies, such as our own, which are essential for better acceptability and sustainable management in the long term (Dias et al. 2017; Russell et al. 2018).

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Data availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Code availability R scripts used are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Field protocols were approved by the CYROI institutional ethical committee, which is certified by the French Ministry of Higher Education and Research (NoAPAFIS#6916-20151 00213267087 v6).

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