

ARTICLE

Impact and control of feral cats preying on wandering albatrosses: Insights from a field experiment

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Abstract

Invasive alien species are a major threat to seabird species, and the number of impacted species is still increasing. A recent study revealed for the first time that feral cats preyed on a large albatross species and that without cat control, some albatross populations would markedly decline. We examined this new predator–prey system by individually monitoring known-age wandering albatross chicks with camera traps in a colony experimentally divided into zones with and without cat control. Our design allowed us to investigate how cat control influenced cat abundance and how this in turn influenced the probability for a chick to be preyed on by a cat. After cat controls, cat abundance was lower in controlled zones than in uncontrolled zones, while a survival analysis showed that the probability for a chick to die from cat predation depended on the zone but not on cat abundance. Our monitoring also provided a fine-scale investigation of the various sources of chick mortality. In addition to cat predation (24% of mortality overall), our data documented predation by giant petrels, for the first time in Kerguelen, and revealed a strong and unexpected effect of nest flooding on chick mortality. Overall, our results underline the need for future studies investigating interindividual variability in cat diet and spatial ecology.

KEYWORDS

Diomedea exulans, *Felis catus*, feral cats, field experimentation, giant petrels, invasive species, Kerguelen, management, nest flooding, predation, wandering albatrosses

INTRODUCTION

In 2022, a majority of seabird species (57%) were known to be in decline (Birdlife International, 2022). A quantitative review revealed that invasive alien species, bycatch in fisheries, and climate change were the top three drivers of this situation, affecting two-thirds of seabird species and hundreds of millions of individuals (Dias

et al., 2019). The major role played by invasive species is not surprising: they have colonized most islands (Ebenhard, 1988), seabirds nest mainly on islands (Spatz et al., 2014), and insular fauna is particularly sensitive to ecosystem disturbance (Courchamp et al., 2003). Among the invasive species directly threatening seabirds, mammals are the most detrimental group (Courchamp et al., 2003; Dias et al., 2019),

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and among mammals, rats (*Rattus* spp.) and cats (*Felis catus*) affect the highest number of seabird species worldwide (Dias et al., 2019).

Cats were mostly introduced on islands before the early 20th century and established feral populations on most major island groups, from subantarctic to arid regions (Courchamp et al., 2003). Their impact on native species is considerable (Doherty et al., 2016; Nogales et al., 2004). In seabirds, feral cats caused declines in the population abundance or in the geographical distribution of 45 endemic taxa (Medina et al., 2011). Besides indirect pathways such as competition for food or parasite transmission (Medina et al., 2014), feral cats mostly impact seabird populations through direct predation. In a review of feral cat diet studied on 40 islands, Bonnaud et al. (2011) showed that among 248 prey species identified, 46% were birds, 38% of which were seabirds. Several studies have assessed the actual number of individual seabirds consumed by cats. According to van Aarde (1980), over 450,000 seabirds, representing six species (*Pachyptila salvini*, *Pterodroma mollis*, *P. macroptera*, *Aphrodroma brevirostris*, *Procellaria aequinoctialis*, and *Halobaena caerulea*) were predated annually on Marion Island and 58,000 individuals (*Pachyptila desolata* and *Pterodroma lessonii*) on Macquarie Island according to Jones (1977). The ratio between the size of feral cat populations and the number of individual prey eaten can be extreme. An estimated population of 50 cats on Tasman Island (~120 ha) was expected to kill 54,000 seabirds annually (mostly *Pachyptila turtur*, Bryant & Shaw, 2006).

Assessing feral cat impact can also be inferred by comparing seabird population trends in nearby islands with and without cats or by documenting changes after cat removal (Brooke et al., 2018; Courchamp et al., 2003). Feral cats are the third most commonly eradicated taxa (Jones et al., 2016) and removal was achieved on at least 114 islands worldwide (DIISE, 2023). The consequences of feral cat eradication on seabird populations can be overwhelmingly positive. In Natividad Island, mortality of black-vented shearwaters (*Puffinus opisthomelas*) decreased by 90% following cat removal (Keitt & Tershy, 2003).

The important number of studies documenting the dramatic impact of feral cats on burrow nesting Procellariiform species contrasts with the paucity of reports concerning large, surface nesting, albatrosses (wandering albatross group: *Diomedea exulans*, *D. dabbenena*, *D. antipodensis*, and *D. amsterdamensis* and royal albatross group: *D. sanfordi* and *D. epomophora*) (Barbraud et al., 2021). Despite scarce and poorly documented evocations, decades ago, of predation (Dreux & Milon, 1967) or harassment (Smith, 1977) by cats on large albatross

chicks, their size, along with their ability to spit oil, was thought to preclude cats from preying on these species (Derenne, 1976; Jones, 1977). The belief that cats were not impacting large albatrosses was further corroborated by the absence of these species in feral cat diets (e.g., Bonnaud et al., 2011; Pontier et al., 2002).

In the case of wandering albatrosses, the absence of cat impact was further supported by the strong similarities in the demographic trajectories of colonies coexisting or not with feral cats throughout the southwestern Indian Ocean (Weimerskirch et al., 2018). Yet, Barbraud et al. (2021) recently provided several lines of evidence for a major role of feral cats in wandering albatross population demography at Kerguelen. Camera traps, deployed in 2014 in order to investigate the causes of a complete failure in wandering albatross breeding success at Pointe Morne colony (Figure 1), revealed several predation events of chicks by feral cats. The following year, a local control of feral cat population was initiated. Besides adding new evidence of cat predation in the nearby uncontrolled Cap Ratmanoff colony, Barbraud et al. (2021) reported that at Pointe Morne, the mean breeding success during the 3 years before the control was 26% and increased up to 80% during the three following years of control. In such a context, population modeling suggested that the albatross population would decline by 2.7%–4.5% per year without cat control (Barbraud et al., 2021). As the effect of cat control on wandering albatross breeding success in nearby colonies was more mitigated (authors, unpublished data) and as other populations of large albatrosses are potentially threatened by cats worldwide, there is an urgent need for a better comprehension of this new predator–prey system.

In this study, we provide a more in-depth investigation of feral cat impact on wandering albatross at Kerguelen. We individually monitored known-age wandering albatross chicks with camera traps from hatching (mid-March) to the end of July in a colony that showed a recent drastic decrease in post-hatching success (Barbraud & Delord, unpublished data). We set up an experimental design in which a single colony was divided into zones with and without feral cat control and monitored both cat abundance and chick mortality in these zones. Besides providing a fine-scale investigation of chicks' sources of mortality, our goal was to assess how cat control influenced cat abundance in controlled and uncontrolled zones and how this experimentally increased variability in cat abundance between zones influenced the probability for a chick to be predated by a feral cat. To our knowledge, this is the first study to question feral cat impact using fine-scale monitoring of known-age birds in the context of an experimental

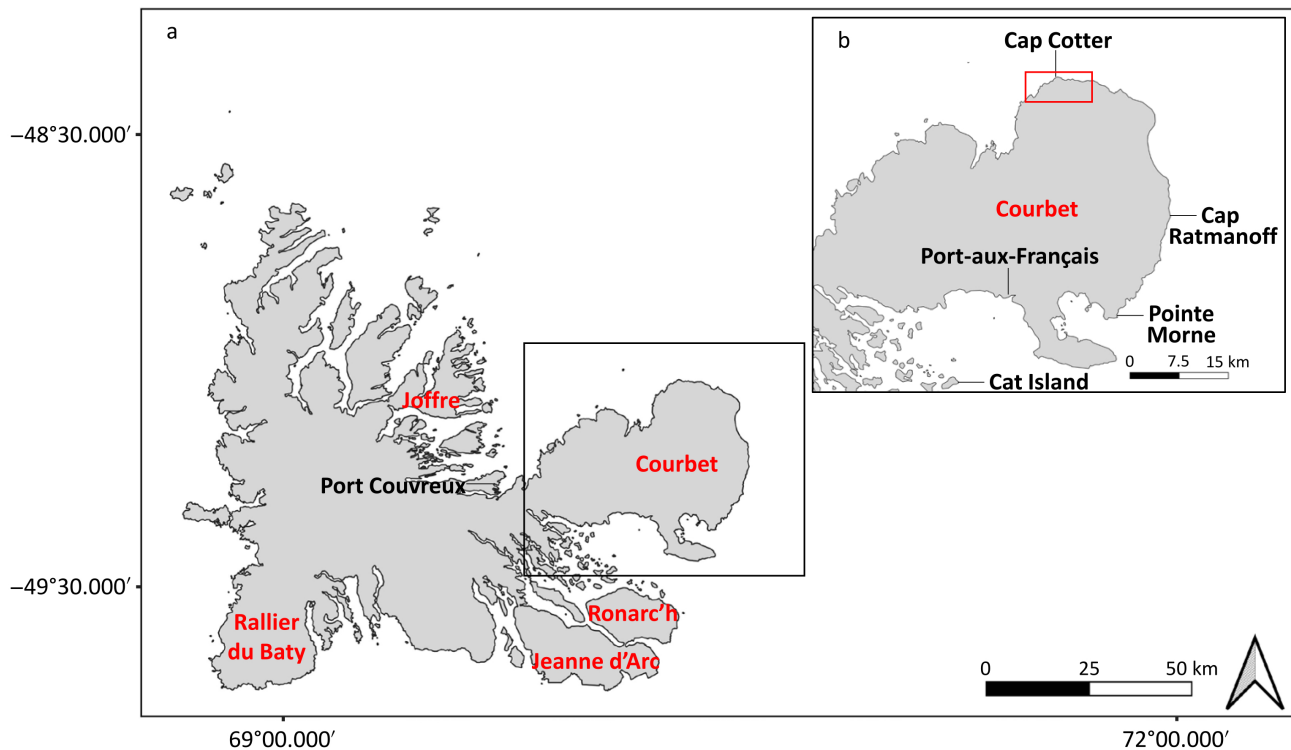


FIGURE 1 Overall map of Kerguelen (a) and of Courbet Peninsula (b) with the names referred to in the paper (red: peninsulas, black: localities). The red rectangle in b indicates the study area presented in Figure 2.

design, providing an in-depth investigation of this new predator–prey system.

MATERIALS AND METHODS

Study area

This study was carried out from December 2021 to July 2022 in the Kerguelen archipelago, southwestern Indian Ocean. Kerguelen includes a main island (“Grande Terre,” ~6700 km²) and hundreds of smaller islands (Figure 1a). Since 2006, Kerguelen, along with Crozet, Amsterdam, and Saint Paul islands, are a National Nature Reserve, and since 2019, it has been listed as a UNESCO world heritage site.

On Kerguelen, the average annual temperature is 4.5°C and the mean annual wind speed is 9.8 m/s. Precipitation occurs on an average of 285 days/year (Turner & Pendlebury, 2004).

Our study area was localized at Cap Cotter (49.057867° S, 70.304915° E), on the Courbet Peninsula (Figure 1b), and covers ~20 km² of meadows and small valleys with streams. This area is dominated by the native herbaceous perennial *Acaena magellanica*. Most of the marine mammals and large avifauna found in Kerguelen breed around Cap Cotter, and introduced mammals such

as feral cats, mice (*Mus musculus*), rabbits (*Oryctolagus cuniculus*), and reindeer (*Rangifer tarandus*) are frequent.

Study species

Wandering albatross

Adults arrive at the breeding sites in November and lay a single egg from late December to early January (Weimerskirch et al., 1993). Both parents incubate the egg alternately for about 80 days. After hatching (around mid-March), partners alternate chick brooding and short foraging trips at sea, for about 1 month (Weimerskirch & Lys, 2000). Thereafter, the chick is left alone, and parents mix short and long trips to regularly feed their chick throughout austral winter and spring. Fledging occurs around late November. The wandering albatross is a biennial breeder such that pairs successfully fledging a chick take a sabbatical year (Tickell, 1968).

In Kerguelen, wandering albatross monitoring started in 1971 on the Courbet Peninsula. The number of breeders sharply declined from the 1970s to the mid-1980s, followed by an increase and a stabilization at a lower level than reported at the beginning of the monitoring, leading to an overall decrease of 30%–35% (Weimerskirch et al., 2018). In the 2021–2022 breeding

season, 348 pairs reproduced on the Courbet Peninsula. The other colonies (frequent on the northern and southwestern parts of Kerguelen) are poorly documented (Weimerskirch et al., 1989).

When we started this study, feral cats were the only known predators of wandering albatross chicks in Kerguelen (Barbraud et al., 2021). Unlike on Marion Island for example, attacks by mice (Jones & Ryan, 2010) or giant petrels *Macronectes halli* (Dilley et al., 2013) had, to our knowledge, never been recorded.

Feral cat

Cat presence in Kerguelen has long been documented. As early as 1876, Kidder mentioned that on Cat Island (Figure 1b), “the domestic cat has, for many years, existed in a wild state.” Pascal (1984, 1994) relates its presence in 1920 on Jeanne d’Arc Peninsula (Figure 1a), and a picture from 1924 shows a black and white cat (i.e., the only two colors currently found in the feral cat population) with farmers in Port Couvreur (Figure 1a). Yet, the present population is thought to be the result of very few individuals introduced between 1951 and 1956 (Derenne, 1976; Pascal, 1984, 1994) by the first missions. The last estimation suggested a population of feral cats around 7000 individuals in the late 1990s (Say et al., 2002). A control program was started as early

as 1960 but was stopped in 1977 (Pascal, 1984). Cats have been occasionally hunted throughout Courbet Peninsula in the early 1970s (Derenne, 1976).

In Kerguelen, the diet of feral cats is mainly composed of rabbits, mice, and burrowing petrels, in proportions markedly differing across times and places, underlying their opportunistic predatory behavior (Derenne, 1976; Pontier et al., 2002). Field studies suggest that birds were consumed much more frequently in 1969–1970 (Derenne, 1976; Pascal, 1980) than in 1998–1999 (Pontier et al., 2002), suggesting that cats strongly impacted avifauna. This echoes with Pascal (1980), who assessed the annual consumption at 1.2 million birds in the 1970s.

Defining controlled and uncontrolled zones

In order to set up our experimental design, we first exhaustively looked for incubating albatrosses over our ~20 km² study area. A total of 73 nests were identified, and their position was recorded (Garmin GPSMAP 65s; Figure 2).

In a second step, we designed controlled and uncontrolled zones. As a compromise between the minimal number of replicates and the minimum size of a zone given previous results on cat control efficiency (Barbraud et al., 2021),

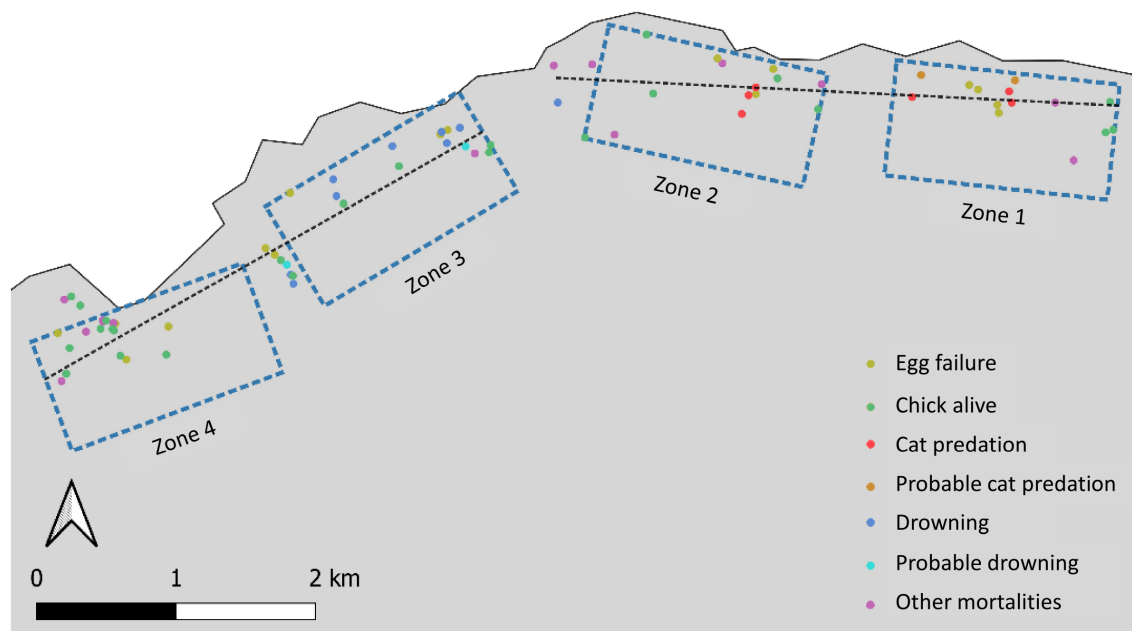


FIGURE 2 Experimental design showing the 73 monitored nests (colored dots), the four zones (dashed blue line) and the two transects (black dotted line). Cat removal was conducted in Zones 1 and 3 (i.e., “controlled” zones), not in Zones 2 and 4 (i.e., “uncontrolled” zones). The status of each nest at the end of the study (25 July 2022) is represented by different colors (see key on the map, and [Results](#) for details related to the sources of mortality).

we chose to consider four different zones, that is, two uncontrolled and two controlled rectangles of 2 km² (i.e., about the size of the controlled area in Pointe Morne), as shown in Figure 2. Hence, we expected two zones with high cat abundance (i.e., uncontrolled zones) and two zones with low cat abundance (i.e., controlled zones), allowing an investigation of the cat abundance–cat predation relationship.

We chose the location of the four zones according to the following criteria. First, we chose sectors with the same kind of habitat (see Appendix S1: Figure S1) and with a maximal and comparable number of wandering albatross nests. Second, we positioned zones in a way to insure an approximate equal abundance of cats among them before the cat controls started in order to avoid pre-laying maternal effects to interfere between experimentally increased cat abundance and chicks' physiological and behavioral stress proxies, which were part of another aspect of our experimental design (authors, unpublished manuscript). To do this, we chose two transects (“east” and “west” transects; Figure 2), as linear as possible according to the field constraints (e.g., lakes) and passing close by a maximum number of nests while avoiding bird disturbance. The east transect measured 4.04 km and the west transect 4.11 km. Third, we positioned two zones along each transect (Zones 1 and 2 along the east transect and Zones 3 and 4 along the west transect; Figure 2), in such a way that (1) the length of the segments of the east and west transects crossing each of the zones was identical (1.61 km) and (2) cat abundance did not statistically differ between the zones (see below). At the end, Zones 1, 2, 3, and 4 hosted respectively 14, 14, 15, and 17 nests. Thirteen extra nests were outside the zones (Figure 2) but were still monitored to document sources of chick mortality (see below).

The four zones were positioned relatively close to each other in respect to cat habitat use (Martin et al., 2013). This allowed us (1) to question, in a management context, whether cats may flee from controlled zones following human disturbance induced by control procedures (Fisher et al., 2015) and, if confirmed, (2) to expect a further increase in the variance in cat abundance between controlled and uncontrolled zones.

Finally, we attributed the controlled and uncontrolled treatments to each of the four zones. We chose to alternate controlled and uncontrolled treatments in order to reduce the probability for an environmental confounding factor to occur. Although initial cat abundance inside the four zones were not statistically different, Zones 1 and 3 nevertheless had lower cat abundance than Zones 2 and 4 (see below). Hence, alternating controlled and uncontrolled zones could have been achieved by controlling both areas with the higher (Zones 2 and 4) or with the

lower (Zones 1 and 3) abundance of cats. We chose to control zones where cats were initially less abundant in order to experimentally further increase the natural variability in potential predation pressure between zones, thereby allowing a more accurate investigation of the relationship between cat abundance and cat predation probability.

Assessing cat abundance

We used transects to assess cat abundance, as previously done for cats in Kerguelen (e.g., Say et al., 2002). A single observer walked the east and the west transects during daylight hours at a constant speed of ~4 km/h. For each observation of a cat, a GPS point was recorded and the corresponding zone was identified. Observations recorded while walking the parts of the transects localized outside the zones were not used in the analyses. We waited for at least 30 min before coming back when walking the same transect back and forth and considered cat observations to be independent. We performed this protocol during four sessions. The number of transects walked in each of the four sessions are presented in Table 1 and Figure 3 shows when the sessions occurred with respect to the cat controls (see below) and the phenology of the wandering albatross.

As zones were defined in similar habitats (Appendix S1: Figure S1), cat detection probability was considered to be the same in each zone. We compared cat abundance between zones and sessions using the statistical approach mentioned below and calculated a kilometric index (KI) as the number of observed cats/number of walked kilometers (Vincent et al., 1991), yielding an apparent density, to illustrate our results (Figure 3) and to investigate the cat abundance–cat predation relationship using the survival analysis described below.

Monitoring chick survival

In order to determine hatching dates (and so, chick age), as precisely as possible, we first checked nests around expected laying date (Weimerskirch et al., 1993). To reduce disturbance, we checked nests based on birds' behavior and shape of the nests. Excluding pairs that had already laid before we arrived in the study area, we managed to assess laying date with a precision of 1–11 days. Second, we determined hatching date by checking nests every 2 days around the expected date, based on the estimated laying date and on an incubation time of 80 days (Weimerskirch et al., 1993). Doing so, we managed to get the exact hatching date of all the birds except one late pair, whose egg hatched after the end of the field session.

TABLE 1 Periods and number of transects walked for each of the four sessions, with the corresponding walked distance in kilometers mentioned in parentheses.

Session	Period	No. transects walked (distance, km)	
		East	West
Session 1	4/1/2022–14/1/2022	29 (117.2)	30 (123.3)
Session 2	7/3/2022–26/3/2022	49 (198.0)	39 (160.3)
Session 3	29/5/2022–10/6/2022	32 (129.3)	28 (115.1)
Session 4	17/7/2022–24/7/2022	31 (125.2)	30 (123.3)

Note: Dates are presented as day/month/year.

To monitor chick survival, we used 47 Reconyx camera traps (HP2X and PC 900), set up to take one picture every 2 min, based on previous data on cat attack records (Barbraud et al., 2021). Cameras were mounted 8 m from the nest, 1 m above ground and fixed on aluminum poles with pieces of orange tape to facilitate detection by flying birds. As a preliminary test, we first deployed a camera in front of 39 nests (out of a total of 73) for 13 days (20 January 2022–3 February 2022) during incubation. This further allowed us to document the cause of some egg failures opportunistically (see [Results](#)). We then deployed a camera in front of nests where a chick hatched ($n = 57$), up to 25 July 2022. As we had

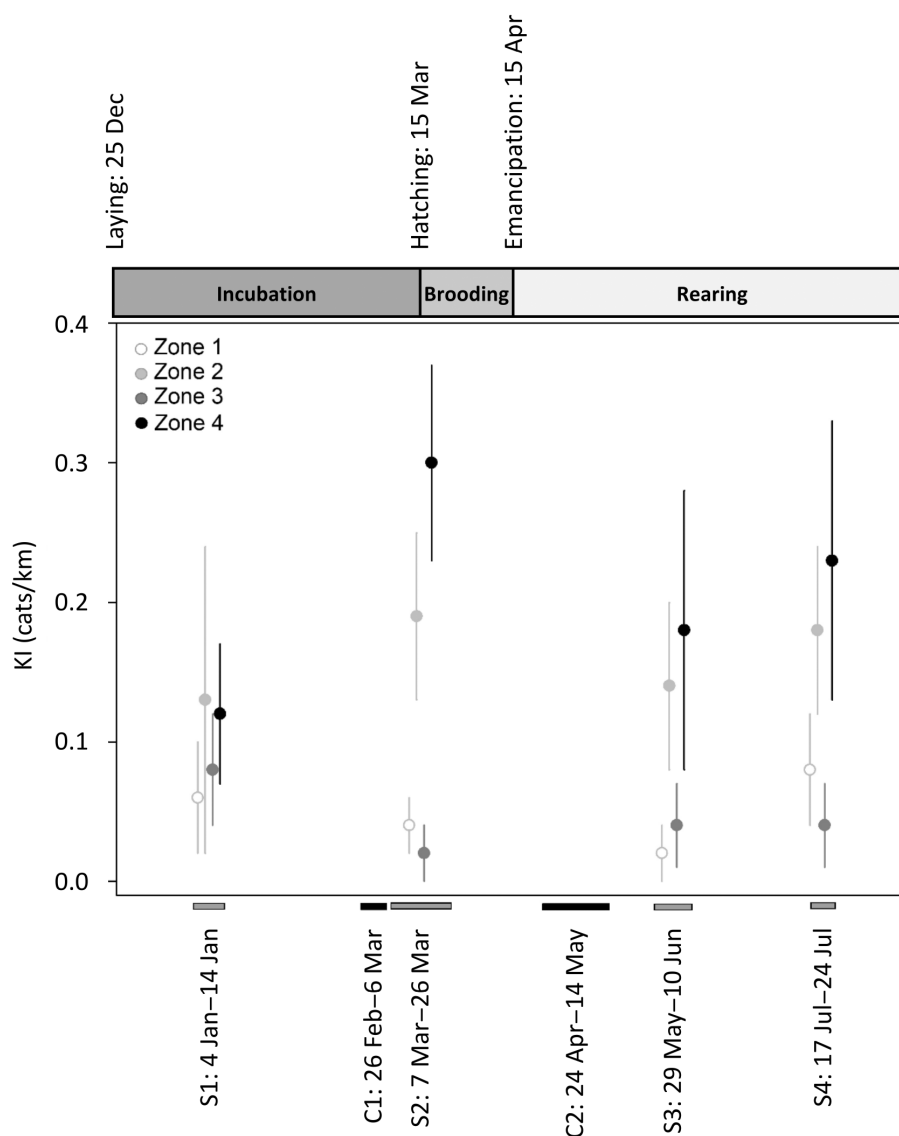


FIGURE 3 Number of cats observed by kilometer (i.e., kilometric index, KI) for the four zones and the four sessions (mean \pm SE). S1–S4 refer to Sessions 1–4 and C1 and C2 refer to cat Controls 1 and 2. The dates of sessions and the dates of controls are mentioned on the x axis. Hatching date is the average hatching date observed in our study area in 2022 and laying/emancipation dates are based on incubation and brooding length provided in Weimerskirch et al. (1993).

less cameras than the number of nests to be monitored, each time a monitored chick died, the camera was deployed in front of another nest. Using this approach, we managed to deploy a camera in front of all the nests at the moment of chick death, except two. However, the cause of death might be inferred when no camera was deployed (e.g., carcass found) and, alternatively, technical issues (e.g., snow on the lens) might challenge the identification of the cause of the death even when a camera was deployed. In fine, we could confidently assess the cause of death for all but one chick. While our camera trap monitoring stops at the end of July, fledging only occurs about 4 months later (see *Study species*). Overall chick mortality, induced or not by cats, is thus probably underestimated.

Finally, we questioned whether cats preferentially targeted light (expected to be easier to catch) or heavy (expected to be more profitable preys) chicks. We thus captured all the chicks of the colony between 30 and 33 days old and weighed them to the nearest 50 g with a Salter spring balance (Salter Weigh-tronix Ltd, West Bromwich, UK).

Controlling feral cats

To control the cat population, we principally used double door traps as reported in Barbraud et al. (2021). Additionally, in this study, we used leg-hold traps placed around inhabited burrows and shooting with riffle Tikka T3x 222. Shooting occurred opportunistically when checking traps, that is, daily.

We performed two cat controls (26 February 2022–6 March 2022 and 24 April 2022–14 May 2022) (Figure 3). For each control and each of the controlled zones, we used 10 double door traps, leading to approximately 0.2 km² per trap, as reported in Barbraud et al. (2021). During the first control, only double door traps and shooting were used. Excluding trap nights with nonfunctional traps (e.g., doors closed by the wind), hunting effort was 57 and 61 total trap nights in Zones 1 and 3, respectively. During the second control, we also used leg-hold traps. Hunting effort was 83 total trap nights for both Zones 1 and 3 for double door traps and 70 total trap nights for leg-hold traps, only in Zone 3. We determined sex, age (three age classes inferred from body size and teeth wear: 0–6 months, 6–12 months, and 1 year and older), and body weight for most of the cats.

During the first control, six cats were killed: three in Zone 1 (two in TomaHawk traps, one shot) and three in Zone 3 (all in TomaHawk traps). Among the sexed and aged individuals, two were males, two were females, one was aged 0–6 months, and four were older than

1 year. During the second control, 24 cats were killed: seven in Zone 1 (six in TomaHawk traps, one in leg-hold trap) and 17 in Zone 3 (13 in TomaHawk traps, two in leg-hold traps, and two shot). Among the sexed and aged individuals, 15 were males, seven were females, nine were aged 0–6 months, two were aged 3–12 months, and 12 were older than 1 year.

Statistical analyses

Cat abundance according to zones and sessions

We fitted generalized linear mixed models with the number of cats observed by transect (i.e., counts data) as the response variable using a Poisson distribution. The number of cats observed ranged 0–5. “Zone identity” was the explanatory variable, with four levels. Transect identity was included as a random term to account for the nonindependence of the observations recorded in both zones crossed by a given transect (i.e., Zones 1 and 2 when walking the east transect or Zones 3 and 4 when walking the west transect). The observer identity and the date were also included as random terms. We ran a separate model for each session to allow models to converge and to meet the model assumptions. We compared the deviance between models with and without “zone identity” using a χ^2 test with the appropriate number degrees of freedom. We used the glmmTMB, DHARMA, and emmeans packages in R 2022.07.2 (R Core Team, 2022).

Chick survival analysis

The observations of live and dead chicks formed a set of observable events from which we estimated the proportion of chicks that died by specific causes. This was performed using a probabilistic capture–recapture multi-event model that linked the observed events to transitions between possible alternative individual states (Schaub & Pradel, 2004). We considered chicks can move across six states: alive (A, $n = 24$), death from predation by cats (DC, $n = 8$), death from predation by giant petrels (DP, $n = 2$), death by drowning (DD, $n = 11$), death from inadequate parental care (DA, $n = 6$), and death from other causes (DU, $n = 6$) (i.e., weather conditions other than drowning [$n = 3$], unknown predation [$n = 2$], and unknown cause [$n = 1$]) (see below). We also included an additional state that corresponds to an unobservable dead state (Tavecchia et al., 2012).

Chicks were observed in seven mutually exclusive events. The first event (coded 0) is a non-encounter and indicated that the chick was not observed.

This corresponded to the observation period before the chick was born and after its death. Events 1, 2, 3, 4, 5, and 6 refer to observations of chicks in the A, DC, DP, DD, DA, and DU states, respectively. Details of the model parameterization can be found in Appendix S2.

RESULTS

Cat control and cat abundance

The differences in the KI between the four zones varied according to the sessions (Figure 3). In Session 1, despite more cats being observed per kilometer in Zones 2 and 4 (KI = 0.13 and 0.12 cats/km, respectively) than in Zones 1 and 3 (KI = 0.06 and 0.08 cats/km, respectively), cat abundance did not significantly relate to zone identity ($\chi^2 = 1.74$, $df = 3$, $p = 0.63$). In Sessions 2 and 3, that is, following the first and second controls, respectively, cat abundance differed according to zone identity (Session 2: $\chi^2 = 29.01$, $df = 3$, $p < 0.001$; KI = 0.04, KI = 0.19, KI = 0.02, KI = 0.30 for Zones 1, 2, 3, and 4 respectively; Session 3: $\chi^2 = 8.00$, $df = 3$, $p = 0.03$; KI = 0.02, KI = 0.14, KI = 0.04, KI = 0.18 for Zones 1, 2, 3, and 4, respectively). In Session 2, post hoc comparisons revealed that both controlled zones (i.e., 1 and 3) had significantly lower cat abundance than both uncontrolled zones (i.e., 2 and 4), while there was no difference within controlled and uncontrolled zones. In Session 3, post hoc comparisons revealed no difference. Finally, in Session 4, cat abundance also differed according to zone identity ($\chi^2 = 8.83$, $df = 3$, $p = 0.03$, KI = 0.08, KI = 0.18, KI = 0.04, KI = 0.23 for Zones 1, 2, 3, and 4 respectively). Post hoc tests did not reveal significant difference between zones.

Causes of egg and chick failure

Camera survey or opportunistic observations allowed us to document most of the causes of egg or chick failure.

Eggs

Of 73 active nests (with an egg), 14 failed before hatching. Among them, eight eggs were found unattended (including three broken and one rotten), one hatching chick was found dead with half of the body still in the egg, and five nests were empty. A camera trap was deployed in front of three of these 14 nests. On two occasions, surveys revealed that the incubating parent just left the nest and on one occasion, the

egg fell from the nest when the parent turned around. Finally, two more nests failed just before or just after hatching. They were considered as “egg failure”.

Chicks

Among the 57 hatched chicks, 33 died before 25 July 2022. For one chick, we had no cues about the cause of death. For the 32 other chicks, we identified three main causes of chick mortality, detailed below (see also Figure 2).

First, 14 chicks died from meteorological causes. They were aged 5–105 days. Nine chicks died following the flooding of their nest, in four different rainy events (26 March, 9 April, 3 May, and 22 June; Video S1). Given the presence of a stream right beside their nest, we are confident that two more chicks died because of nest flooding, during two of the same four occasions, although their deaths were not documented by a camera trap. Three more chicks died because of meteorological causes. One of them died buried by snow (23 June; Video S2). The two last nests were not flooded but both chicks probably died due to thermic stress, again during one of the four same above occasions (3–4 May). Besides the heavy rain mentioned above, temperatures were particularly low on this occasion: the hourly temperature records provided by a weather station situated in the center of the study area revealed that between 3 April and 3 June, only 60 records were below 1°C and that among these 60 measures, 25 were recorded between 3 May 7:00 AM and 4 May 07:00 AM.

Second, 12 chicks died because of predation. Six chicks died because of cat predation (Videos S3 and S4). All attacks occurred at night (8:00 PM–6:00 AM), and in all occasions, a single cat was involved. Chicks were always alone in the nest when the attack occurred but on three occasions, a parent was nearby. Two parents saw the cat attacking but did not interfere. One parent joined the nest but too late. The six chicks that died from cat predation were 29–50 days old. We believe two more chicks died because of cat predation, although the attacks were not recorded by camera traps. In both cases, the carcass had puncture wounds under the bill or around the neck (Appendix S1: Figure S3), as also documented in Barbraud et al. (2021) following cat attacks. This strongly suggests a premortem cat attack. Yet, one of these two chicks was only 2 days old. Hence, the parent may have deserted the nest (as recorded for another nest, see below) before the attack occurred. The second chick was 61 days old. Overall, cats contributed to 24% of chick mortality. Besides cat predation, two chicks were predated by giant petrels (Video S5). They were aged 55 and 71 days. No parent was present. Predation

occurred at 8:30 PM and 6:00 AM, by a single or several individual giant petrel(s). Finally, two camera traps showed pictures of a chick who disappeared in the next picture. We do not think about other explanation than predation. Attacks can be very fast. In one record of cat predation in our study, the cat was visible on only one picture. Nevertheless, we cannot attribute these deaths to either cats or giant petrels. One of these chicks was 41 days old and the other was 27–41 days. No parent was present. Attacks occurred at 5:00 AM and 8:00 AM.

Excluding the chick who was predated at 29 days, not weighed, the other chicks predated by feral cats (aged 32–50 days), weighed from 1.2 to 2.9 kg when captured in the age of 30–33 days. Their body mass did not differ from the body mass of unpredated chicks at the same age ($t = -0.03$, $df = 4.63$, $p = 0.98$). Hatching dates were also similar between both predated and unpredated chicks ($t = -0.07$, $df = 5.21$, $p = 0.95$).

Finally, the remaining six chicks died following interactions, or the lack of interactions, with parents. One chick (aged 7 days) left the nest during a shift in brooding period and probably died of thermic stress before being eaten by a brown skua (*Catharacta skua lönnbergi*) 2 days later. Four chicks (aged 3–42 days) died in the nest, under the parent ($n = 3$) or alone ($n = 1$), with no apparent explanation. Finally, one chick died following nest desertion by parents. This chick was aged 33 days but had a body weight close to a just-hatched chick (i.e., 275 g).

Survival analysis

Model selection indicated that chick survival probability varied between weeks (Table 2). Weekly survival ranged from 0.732 ± 0.069 to 1 (Figure 4), and mean weekly survival probability was 0.940 ± 0.010 . Among the sources of mortality (Figure 5a), the most important was drowning (0.333 ± 0.082), followed by predation by cats (0.242 ± 0.075), inadequate parental care and other causes (both 0.182 ± 0.067), and predation by giant petrels (0.061 ± 0.042).

There was no effect of KI on the proportion of deaths due to cat predation, considered either as a covariate or as a group (Table 2). However, the proportion of deaths because of cat predation varied between zones, being high in Zones 1 and 2 where cat abundances were 0.047 and 0.170 cats/km, respectively, while no cat predation occurred in Zones 3 and 4 where cat abundances were 0.033 and 0.237 cats/km, respectively (Figure 5b). There was no effect of the age of the parents on the proportion of death by drowning (Table 2).

DISCUSSION

We designed a field experiment aimed at investigating how cat control influenced cat abundance in controlled and uncontrolled zones and how the experimentally increased variance in cat abundance between zones related to the probability for a chick to be predated by a

TABLE 2 Modeling the effects of time on wandering albatross chick survival, of cat abundance on the proportion of death by cats, and of age of the parents on the proportion of death by drowning.

Model	Survival	Transition	Dev	rk	AIC _c	Slope
Modeling s						
M1	s(.)		348.5	5	358.6	
M2	s(w)		309.3	16	342.3	
Modeling α						
M3		$\alpha(.)$	271.2	5	281.4	
M4		$\alpha(g)$	255.8	8	272.1	
M5		$\alpha(KI)$	272.1	6	284.3	-3.18 (-13.71 to 7.35)
M6		$\alpha(KI \text{ low/high})$	271.2	6	283.3	
Modeling γ						
M7		$\gamma(.)$	168.0	5	178.0	
M8		$\gamma(\text{father age})$	167.0	6	179.2	-0.16 (-0.48 to 0.17)
M9		$\gamma(.)$	190.9	5	201.0	
M10		$\gamma(\text{mother age})$	190.7	6	202.9	0.04 (-0.13 to 0.21)

Note: s, weekly survival probability; α , proportion of death by cats; γ , proportion of death by drowning; g, zone effect; KI, cat abundance as a covariate; KI low/high, cat abundance as a group covariate.

Abbreviations: AIC_c, corrected Akaike information criterion; Dev, deviance; KI, kilometric index; rk, model rank.

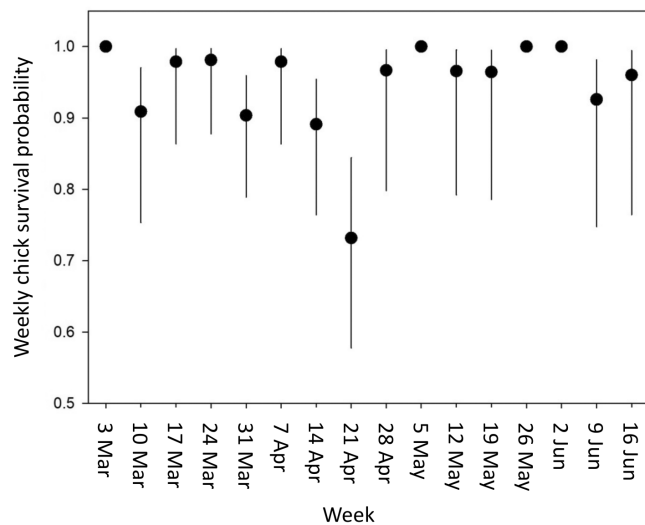


FIGURE 4 Weekly survival of wandering albatross chicks at Cap Cotter, Kerguelen, in 2022. Errors bars are 95% CIs. Estimates are from model M2 (Table 2).

feral cat. After cat-removal sessions, the abundance of cats was lower in controlled zones as compared with uncontrolled zones while the probability for a chick to die from cat predation depended on the zone but not on cat abundance. Our fine-scale monitoring of known-age chicks further allowed us to examine the sources of mortality in this colony experiencing a recent drastic decline in breeding success. Camera traps surveys not only showed feral cat predation, as documented recently in another colony in Kerguelen (Barbraud et al., 2021), but also revealed predation by giant petrels, for the first time in Kerguelen. Our data further revealed a strong and unexpected effect of nest flooding on chick mortality. These results are discussed below.

Predation on wandering albatross chicks

Although previously mentioned (Dreux & Milon, 1967), no attack of feral cats on any large albatross species had been firmly established before Barbraud et al. (2021) documented this behavior in Kerguelen. Our data add new evidence of feral cat predation on wandering albatrosses, in another colony. The predation we report all occurred at night. This contrasts with Barbraud et al. (2021) who found higher attack rates during daytime. Given the probable low proportion of individual cats involved in chick predation (Barbraud et al., 2021), the discrepancy between Barbraud et al. (2021) and the present study probably simply echoes with the natural heterogeneity in activity patterns between individual cats, as previously underlined in this feral cat

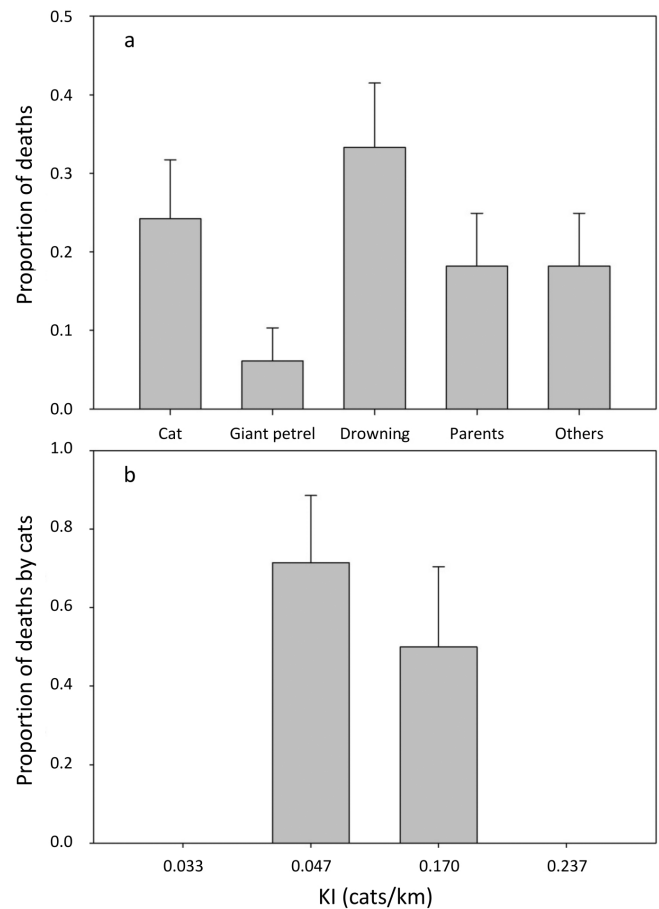


FIGURE 5 Causes of mortality of wandering albatross chicks at Cap Cotter, Kerguelen, from March to June 2022. (a) Proportion of deaths as a function of mortality causes. Estimates are from model M2 (Table 2). (b) Proportion of deaths by cats as a function of cat abundance. Estimates are from model M4 (Table 2). KI, kilometeric index.

population (Blanchard et al., 2018; Martin et al., 2013) and others (Recio & Seddon, 2013). A non-mutually exclusive explanation is that our presence in the colony, more pronounced than in Barbraud et al. (2021) and restricted to daily hours, may have discouraged diurnal predation.

Our camera traps revealed that giant petrels preyed on wandering albatross chicks. Although Barbraud et al. (2021) reported that giant petrels approached albatross chicks, no predation had been previously reported in Kerguelen to our knowledge, unlike in Marion Island (Dilley et al., 2013). Barbraud et al. (2021) suggested that giant petrels were attracted by cues (e.g., down or blood) following cat attacks. Under this hypothesis, given that attacks by cats (re)started only recently in Kerguelen, an increase in attacks by giant petrels on chicks might be expected in the coming years if giant petrels start considering chicks as attractive and, accordingly, increase

albatross nest survey (see Dilley et al., 2013 for similar reasoning). Our surveys confirmed a role for remains of attacks, and probably of parental feeding, in triggering approaches by predators, that is, both cats and giant petrels (see also Video S5). A camera trap showed a cat waiting for the parent to leave the nest after food delivery to approach and feed on the ground. During the following 2 days, cats and giant petrels alternatively visited the nest's immediate surroundings and fed on the ground, sometimes briefly threatening the chick. At some occasions, the chick erected, in a posture compatible with regurgitation/oil spitting. Finally, a giant petrel killed the chick. We noticed the presence of oil and small remains of food all around the nest. Smith (1977) noted that wandering albatross chicks responded to cat harassment by "regurgitating proventricular fluid and some stomach contents," suggesting that "continuous harassment by cats could lead to starvation of the chick." Food remains, coming from dropping during parental feeding or from chick regurgitation triggered by predators (or not, i.e., spontaneous regurgitation of indigestible food), probably attract predators. Scavenging might have triggered harassment to induce food regurgitation, which may in turn have triggered predatory behavior.

Feral cat control and abundance

Cat controls succeeded in increasing the initial nonsignificant difference in cat abundance between controlled and uncontrolled zones. This pattern was triggered by both decreased and increased cat abundance in controlled and uncontrolled zones, respectively (Figure 3). The decrease probably reflects the numerical response of cat removal (see e.g., Bloomer & Bester, 1992; Leo et al., 2018). Nonexclusively, it may also result from an avoidance of humans following disturbance induced by hunting and trapping (Fisher et al., 2015). This may particularly be expected for cat observations performed during the second session as it immediately followed the first control (Figure 3), and such an extensive human pressure was new in this study area. Our proxy may thus underestimate cat abundance in controlled zones if some individuals displayed increased shyness. Nevertheless, some individuals may have responded to disturbance by fleeing to uncontrolled zones, thereby also explaining the increased cat abundance in uncontrolled zones following the first control. This increase might also have been triggered by new individuals moving toward the colony from outside the study area for reasons unrelated to cat control (e.g., reproduction, foraging, and dispersion) and subsequently selecting undisturbed habitats.

More data on feral cat habitat use (e.g., Nottingham et al., 2022; Rodriguez-Recio et al., 2022), particularly following controls, are needed to better understand our results. In particular, to which extent the pattern of cat abundance reported in controlled and uncontrolled zones in Sessions 2 and 3 may have been triggered by a recolonization of controlled zones from uncontrolled zones following an important amount of cats removed during the second control deserves further investigation.

Interindividual variability in diets: A need of real facts in feral cats

The probability for a chick to die because of cat predation did not relate to cat abundance. Although basic assumptions may lead to the prediction of a linear increase in prey mortality with increasing predator abundance (e.g., Lotka–Volterra equations), experimental and modeling approaches have shown that predator–prey relationships are usually more complex (Abrams, 1993; DeRoy et al., 2020; Kratina et al., 2009). For instance, killing rate by predators can be a function not only of prey (Holling, 1959) but also of predator density when, for example, interference competition or cooperation between individual predators occurs (e.g., Abrams & Ginzburg, 2000). Variability in prey selection among individual predators adds further complications (Pettorelli et al., 2015). As expected for generalist species (Bolnick et al., 2007) such as feral cats (Bonnaud et al., 2011; Medina et al., 2011), some studies revealed that the large dietary niches reported for feral cat populations were the result of a heterogeneous cluster of individual narrower niches (Moseby et al., 2015, 2021; Ringle et al., 2015; see also Dickman & Newsome, 2015 for house cats). Such individual preferences are widespread among predators (Pettorelli et al., 2011, 2015), including felids (Dickman & Newsome, 2015 and references therein). In this context, for a given predator population size, the overall impact on a given prey is expected to depend on the proportion of individual predators feeding on that prey, thereby introducing stochasticity in the predator abundance–prey mortality relationship. Moseby et al. (2021) reported that in South Australia, prey over 500 g (the size of many mammal species known to be threatened by feral cats in their study area) were more likely to be predated by cats over 4.2 kg, whose proportion in the population ranged from 7% to 45% over the 30-year study period.

Several lines of evidence suggest that in Kerguelen, only a fraction of cats prey upon chicks. Based on color patterns and other individual characteristics identified on camera traps, Barbraud et al. (2021) reported that only

five individuals were involved in chick attacks among the 19 identified. In the present study, the cat(s) observed in all predation events was a (were) large black cat(s) with no apparent distinguishable characteristics. Importantly, while our study area covered $\sim 20 \text{ km}^2$, all predation events occurred in an area of $\sim 0.39 \text{ km}^2$ (Figure 2), encompassing a part of both Zones 1 and 2. Given previous data published on home range size of feral cats in Kerguelen (i.e., average size of 0.58 km^2 , Martin et al., 2013), this is compatible with the hypothesis that a single individual was involved in all predation events. In a management context, this raises the question of including a buffer around a controlled zone (e.g., Cruz et al., 2015).

Additional studies are needed to confirm and characterize diet diversification among individual cats in Kerguelen. Isotopic (Araújo et al., 2011; Ringler et al., 2015) and morphological/molecular (e.g., Dawson et al., 2020) approaches might be straightforward in this context. These would allow to assess the proportion of individual cats preying upon chicks in the population. Then, the proportion of chicks in the diet of those individuals could be investigated as a “specialization” does not exclude preying upon other preys. In our system, chicks are available to

cats only a fraction of the year, unlike rabbits. Hence, individuals preying upon chicks may actually be the true “generalists” at the scale of the year as their diet will change in summer, that is, when no chick is available. Conversely, individuals preying upon rabbits during the chick period could be “specialists,” possibly preying upon rabbits all year round. Future studies should investigate the role of rabbits in our system as they may allow cats, including those feeding on wandering albatross chicks in autumn/winter, to persist all year round (see Bonnaud et al., 2011; Medina et al., 2011 for reviews; Santin-Janin, 2010; Weimerskirch et al., 1989 for Kerguelen and Courchamp et al., 2000 for theoretical aspects of this so-called “hyperpredation” process).

Finally, the question of which individual cats predate chicks arises, both in a fundamental perspective and for designing relevant management plans (see below and Appendix S3). Genetic samples of cats preying upon chicks would allow to test previous suggestions of heritability of this behavior (Barbraud et al., 2021), as shown in some predator species (Estes et al., 2003; Guinet & Bouvier, 1995) including cats (Bradshaw, 1992). Recent advances, such as DNA analysis of samples taken

TABLE 3 Possible management options in the context of the feral cat–albatross system in Kerguelen (see Appendix S3 for further details).

Options	Approaches	Comments	References
No action		Expected outcomes are albatross population extinction, emergence of an antipredator tactic in albatrosses, or disappearance of chick-predation behavior in cats.	Barbraud et al. (2021); Dilley et al. (2013); Ibáñez-Álamo et al. (2015); Medina et al. (2014)
Local control	Control of “specialized” individuals, as long as the problem persists.	Achievable by focusing on the diet (e.g., aversive conditioning) or on the phenotypic trait associated with diet preference (e.g., sex or size).	Dickman and Newsome (2015); Jaeger et al. (2001); Moseby et al. (2015, 2021); Nogales et al. (2004); Pettorelli et al. (2011); Read et al. (2016, 2019); Smith et al. (2000)
	Nonselective control, as long as the problem persists.	Easier to perform than selective control proposed above. May create a “vacuum effect.”	Barbraud et al. (2021); Devillard et al. (2011); Minnie et al. (2018); Palmas et al. (2020); Robinson et al. (2008); Santin-Janin (2010); Short and Turner (2005); van Rensburg and Bester (1988)
Local eradication	Eradication at the scale of an ecologically valuable area.	High feasibility given the topography of Kerguelen. Opportunity for <i>in natura</i> experiments. Possibility of local “ecological kickbacks.”	Caut et al. (2007); Cleeland et al. (2020); Courchamp et al. (1999, 2000); Cox et al. (2022); Kinnear (2018); Krajick (2005); Moro et al. (2018); Parkes et al. (2014); Phillips et al. (2016); Soulé et al. (1988); Zavaleta et al. (2001)
Total eradication	Eradication at the scale of Kerguelen.	Technically challenging. Possibility of “ecological kickbacks” at large scale.	
Preventing further colonization	Fencing between territories with and without cats.	Technically feasible and expected higher social acceptability than other options. Risk of avian collision.	Barbraud et al. (2021); Doherty et al. (2017); Roberts et al. (2018); Weimerskirch et al. (1989)

from wounds on carcasses or survival chicks (Moseby et al., 2015), could be promising approaches in this context. This could further allow to investigate a potential link between some phenotypic traits (e.g., sex) and chick-predation behavior (see Appendix S3).

Meteorological aspects

Altogether, almost 25% of the chicks died from meteorological factors. This is an unexpected result that deserves further investigation. While large-scale climatic effects on seabird populations are well studied (review in e.g., Barbraud et al., 2012), including for wandering albatrosses (e.g., Rolland et al., 2010), fine-scale aspects are seldom documented (see e.g., Cleeland et al., 2020; Deeming & Reynolds, 2015). In seabirds, Lefebvre (1977) reported a mortality of 12% in Laysan albatross chicks following the flooding and the subsequent cold exposure after a single storm.

At the Cap Cotter colony, nests were sometimes localized nearby small streams inside small valleys (see aligned nests in Figure 2). In case of heavy rain events, these nests were particularly at risk because the stream overflowed. Breeders may select these habitats because they provide protection from the wind, which is of particular importance for the chick, both for thermoregulation aspects and to prevent being blown from the nest (Momberg et al., 2022). Moreover, nest mounds may be easier to build on more humid substrates. These ecologically attractive habitats could be selected by first and less-experienced breeders, but our results do not support this hypothesis. Accurate chick survival monitoring in relation to fine-scale weather and habitat characteristics (in particular flooding risk and wind exposure) is required to further explore this pattern.

We then questioned whether the critical period for chicks regarding nest-flooding probability (i.e., March–June) experienced more heavy rain events in 2022 than in previous years, starting 2007. The number of days with total amount of precipitation greater than 5, 10, and 15 mm at the Port-aux-Français meteorological station, at ~33 km from the study area, were 9–23 (16 for 2022), 4–13 (7 for 2022), and 1–8 (2 for 2022), respectively, suggesting that 2022 experienced average precipitation patterns. However, more complex patterns may be involved. If, as suggested above, nest sites less exposed to wind are more exposed to flooding, breeders may face a trade-off in nest site selection. Because, over the period 1985–2018, mean wind speed increased across the Southern Ocean (by approximately $2 \text{ cm s}^{-1} \text{ year}^{-1}$; Young & Ribal, 2019), the attractiveness of nest sites less exposed to wind may have increased, thereby also

leading to an increased risk of flooding. In parallel, the potential increased frequency/magnitude of rainfall events (e.g., Cleeland et al., 2021) should also be considered. While surveys suggest that mean annual precipitation is decreasing in Kerguelen (Lebouvier et al., 2011), potential changes in within-year patterns remain poorly known (Le Roux & McGeoch, 2008).

CONCLUSION

Several aspects discussed above may be of interest in the context of management. In particular, whether or not some individual cats “specialized” on chicks should be considered when choosing the management approach to be performed (Dickman & Newsome, 2015; Jaeger et al., 2001; Moseby et al., 2015; Pettorelli et al., 2011). Several management options exist (summarized in Table 3 and detailed in Appendix S3), keeping in mind that besides technical feasibility, the risk of “ecological kickbacks” (Krajick, 2005) and social acceptability should also be closely examined.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Blanchard, 2023) are available from <https://doi.org/10.6084/m9.figshare.24559894.v2>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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