

Cat control in a seabird colony has limited top-down effects on native and invasive mammalian mesopredators and prey but invasive rodents respond to seasonal pulse of productivity

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Abstract

Control of invasive predators is a priority to protect island biodiversity. Understanding the responses of other species in multi-species invaded food webs is important to avoid unintended consequences. We use an intensive two-year cat-trapping program in the vicinity of seabird colonies on Bruny Island, Tasmania, to estimate the change in densities of feral cats and investigate the effect of control on the behaviour and abundance of native and invasive mammal species. Cat density before control was extremely high then reduced by 5.4-fold consequent to control. We show a complex but subtle cascade of ecological effects among mesopredator and prey species, with a lagged response to a pulse of bottom-up productivity provided by breeding seabirds. Our study demonstrates that cat density on islands, particularly around seasonally rich food resources such as seabird colonies, can be very high, much higher than on mainland areas, and that control using trapping is effective reducing cat density in this focussed landscape context. Our results highlight the complexity of effects of control of an invasive predator on the broader ecosystem. The top-down effect of cats on the ecosystem was limited but the response of prey indicates a predator effect conditioned by temporal change in bottom-up productivity.

1. Introduction

The extreme threat to island biodiversity posed by invasive predators, demonstrated by the large number of species extinctions on islands (Bellard et al., 2017), highlights control of invasive predators as a priority for the protection of island biodiversity. Whether predator control is beneficial or not depends on the complexity of, and the relationship of the invasive predator to, the island food web of which it is part (Zavaleta et al., 2001). Eradicating a sole invasive predator from an island generally benefits biodiversity (Zavaleta et al., 2001) by reducing predation on native species, and has been documented to lead to increased breeding success and abundance of threatened seabirds (e.g. terns shearwaters and albatrosses; Ratcliffe et al., 2010). Island food webs are often complex, though, comprising multiple native and invasive predators and prey.

Control of an invasive predator can have unexpected adverse consequences where island ecosystems have several invasive species that have novel and complex interactions with native species (Bergstrom et al., 2009). Eradicating an invasive predator may remove top-down control on other invasive species, which can result in increased abundance of both herbivores and mesopredators with cascading effects on the ecosystem (Courchamp et al., 1999; Zavaleta et al., 2001). For example, the successful eradication of feral cats (*Felis silvestris catus*) on subantarctic Macquarie Island in 2001 removed predation pressure on the introduced European rabbit (*Oryctolagus cuniculus*) at the same time as releases of the *Myxoma* virus which suppress rabbit populations were reduced and favourable climatic conditions and vegetation recovery increased food supply (Dowding et al., 2009). These multiple factors resulted in high rabbit abundance and overgrazing which denuded the sensitive vegetation of the island (Bergstrom et al., 2009). In a second example, Rayner et al. (2007) demonstrated that reducing the number of domestic cats on Little Barrier Island, New Zealand, allowed rat populations to increase, which in turn caused population collapse of seabirds. Understanding top-down and bottom-up control mechanisms in food

webs is necessary for effective management of predator populations to protect biodiversity (Elmhagen and Rushton, 2007).

Feral cats are adaptable and opportunistic predators that can use a broad range of habitats (Doherty et al., 2014). Cats are recognised as among the most destructive alien predators for seabirds on islands (Medina et al., 2011), particularly for petrel and shearwater species, which are often naïve to mammalian predators and are clumsy when on the ground (Sih et al., 2010). Control or eradication of cats is a major priority for the conservation of colonially nesting seabirds (Holmes et al., 2019).

Unawanna-Allonah/Bruny Island is the fourth largest offshore island in LUTRUWITA/Tasmania, Australia. The island has an elongated shape with over 320 km of coastline, and supports numerous seabird colonies. Cat control was implemented in the vicinity of the largest seabird colony on 'The Neck', a narrow sand isthmus connecting the continental North and South Bruny, where migratory and colonially nesting short-tailed shearwaters (*Puffinus tenuirostris*) as well as little penguins (*Eudyptula minor*) breed over the summer months. The cat control undertaken in 2018 by the Bruny Island Cat Management Program (BICMP) is part of foundational work being used to assess the impacts of feral cats and the effectiveness of control, and to plan the long-term reduction of feral cat impacts on the island. Bruny Island supports a rich diversity of native terrestrial fauna. This includes the endangered native mesopredator, the eastern quoll (Family Dasyuridae, *Dasyurus viverrinus*; <https://www.iucnredlist.org/>) and native rodent, the swamp rat (*Rattus lutreolus velutinus*; Tasmanian subspecies known as the velvet-furred rat) that may be affected by predation and competition from feral cats. There are also two alien invasive rodent species on the island, the house mouse (*Mus musculus*) and black rat (*Rattus rattus*), that are both prey of feral cats and predators of birds, including colonially nesting seabirds (Dilley et al., 2016). Both these species are listed amongst the 100 most destructive invasive species (http://www.iucngisd.org/gisd/100_worst.php).

Our study focussed on identifying the potential cascading effects of the control of feral cats, implemented to protect seabirds, on these mammalian mesopredator and prey species. The aims of the project were: i) to estimate the densities of feral cats before and after the control program within and surrounding the seabird colony where the control activity was focussed, and ii) to investigate the effect of the cat control on the abundance and behaviour of native and invasive mammal species that cats might prey on or compete with. We monitored two sites, one within a seabird colony where the cat control was undertaken, and the other at a second smaller seabird colony on the southern part of the island that served as a control site for this study. Understanding this trophic network will guide cat control on Bruny Island and will have global implications for island conservation.

2. Materials And Methods

2.1. Study area

Bruny Island is located off the south-east coast of lutruwita/Tasmania, Australia (-43.27S, 147.34E). The island is 362 km² and is divided into two distinct continental land masses, North and South Bruny, which are connected by a narrow sand isthmus called “The Neck”. Cat control took place on the isthmus, where there is a seabird breeding colony, and adjacent areas to the north and south (which we refer to hereafter as North and South). Whalebone Point (WBP), located in far South Bruny, also supports a seabird colony but was not subject to cat control. We used it as a control site (Fig. 1). The vegetation at both sites is a mosaic of coastal heathland, dry coastal forest, saltmarsh and wetland (sourced TASVEG, the state government GIS vegetation layer (Department of Primary Industries, 2013)). The climate is classified as mild temperate, with four distinct seasons.

The principal terrestrial predators on Bruny Island are the invasive alien feral cat (1.7-4.8 kg, unpublished data for Bruny cats) and the native eastern quoll (0.7-2.0 kg). Other native predators that occur on the adjacent Tasmanian mainland, the Tasmanian devil (*Sarcophilus harrisi*) and spotted-tailed quoll (*D. maculatus*), are absent from the island. Cats have been present on the island since the mid-1800s and occur across the entire island. There are two native and two invasive rodents present, which are prey of cats and may prey on seabirds. The rakali/water rat (*Hydromys chrysogaster*), at 0.8 kg (up to 1.3 kg) Australia’s largest native rodent, forages along the coast and may take some terrestrial prey, particularly seabirds in the breeding colonies. Swamp rats are an omnivorous native rodent, present mainly in denser vegetation and unlikely to prey on seabirds. Black rats and house mice are numerous, particularly in the seabird colonies and may prey on seabirds. At The Neck and WBP seabird colonies, adult shearwaters are present from September to late March. Chicks fledge in early May and leave the island soon after. Penguins are present at The Neck all year around.

2.2. Field study and study design

The field study was repeated in 2017 and 2019, with paired time periods in each year: during the short-tailed shearwater breeding season “BS” and after the shearwater breeding season “PBS”. We deployed a total of 113 camera stations in 2017 and 111 in 2019, for 24 to 87 consecutive days, respectively, in a grid array with cameras spaced on average 150 meters apart. We placed 93 and 91 camera stations across The Neck shearwater colony and the adjacent areas North and South in 2017 and 2019, respectively (Appendix S1). We placed 20 camera stations on Whalebone Point shearwater colony in 2017 and 2019 (Appendix S1).

Each camera station was set up with a fresh lure secured in a vented PVC canister, suspended 60 cm above the ground. We used lures to maximize the time that cats spent in front of the cameras to aid individual identification. The canister was filled with food attractants for predators (sardines, liver treats, and tuna oil), omnivores (truffle oil and walnut oil) and herbivores (peanut butter and rolled oats).

We monitored the lure stations using passive infrared-triggered cameras (Reconyx Hyperfire Professional PC600 and PC800) programmed to record three consecutive images each time the sensor was triggered, with one second interval between pictures, and no break between sets. Cameras were strapped to a tree or

post ~60 cm above ground and ~2.5 m from the lure. The cameras operated 24 hours a day, with most images obtained at night as all species were nocturnally active.

Following the first paired survey in 2017, BICMP undertook an intensive control program of cats at The Neck from July 2017 until July 2019 with the intention to reduce cat numbers around the shearwater colonies with a trapping effort of 4,185 cage trap-nights spread over two years. Cats were controlled on the isthmus and adjacent areas (North and South) as well as 7 km further north along the east coast at Cape Queen Elizabeth, which also has a shearwater colony. The combined area of cat control was much larger than the study area and allowed more effective reduction of cat numbers on and around The Neck. This program followed many years of opportunistic cage trapping and removal of feral cats at The Neck seabird colony during the shearwater breeding season but was much longer in duration, larger in geographic extent and more intensive in terms of the numbers and frequency of trapping. The intensive control program was undertaken using large wire cage traps (710 x 305 x 305 mm) baited with either tuna or chicken. Twenty two cats were trapped and removed (euthanized) during the study period on The Neck seabird colony, only one was removed from the South of The Neck, and none were removed from the site North of The Neck. An extra 20 cats were removed from Cape Queen Elizabeth during the same period.

2.3. Individual cat identification

Individual feral cats were uniquely identified from camera images through a combination of coat pattern and morphological characteristics (McGregor et al., 2015). All discrimination of individuals was done by one experienced observer (Author). We first grouped the images of feral cats as marked or unmarked (black) individuals. Although some black cats had small white patches on the neck or chest, these were not always visible depending on orientation of the image, and so all black cats were considered unmarked to avoid double-counting. The marked portion were tabby cats with naturally unique coat markings. We identified individual cats from this group based on matches in unique markings. Due to poor image quality, some images were considered as unidentifiable.

2.4. Statistical analysis

We estimated the effect of lethal control on the population density of feral cats over the two paired surveys using two different methods. First, we applied spatial mark-resight (SMR) models, a form of spatially explicit capture-recapture (SECR) that is used when only a part of the population is uniquely identifiable (McClintock et al., 2009; Efford and Hunter, 2018). Second, we used dynamic N-mixture models (Royle, 2004) for open populations (Dail and Madsen, 2011) to estimate relative abundance, detection probability and population dynamics of four species that may have been affected by the reduction in the cat population.

2.4.1. Population density estimates of feral cats – spatial mark-resight models

We estimated the density of cats for each of the eight deployments (two sites, two years, paired breeding/post-breeding season - BS/PBS) using a spatial mark-resight model, performed using the “secr” package (Borchers and Efford, 2008) in R version 4.0.2 (R Core Team, 2020). Such models have been used elsewhere in Australia to estimate abundance and density of feral cats (McGregor et al., 2015; Cunningham et al., 2020). To estimate the contribution of unmarked individuals to the overall population, the model assumes that marked and unmarked individuals have identical sighting probabilities (McClintock et al., 2009).

We constructed a set of capture histories for each of the eight deployments by dividing each 3-12 week survey period into a series of five-day intervals for each camera, in which each the number of separate individual cats detected was counted. This approach provided a sufficient number of days within each session to achieve high detection probabilities, while allowing a sufficient number of survey periods to construct encounter histories.

To aid estimation of model parameters, a ‘mask’ has to be chosen as the likely distance from an individual’s home-range centre at which its probability of detection is essentially zero (Balme et al., 2009). In our case, the mask serves several purposes: i) to distinguish habitat sites from non-habitat sites (i.e., the sea) within the outer limit, and ii) to define a region for which a post-hoc estimate of population size is required (i.e., North and South of The Neck). We chose a mask width of 2000 m around the cameras with a spacing of 100 m between the cells, as this is the estimated maximum width of home ranges of male cats in similar habitat type on the island (personal observation from GPS data), clipped to exclude the ocean. This resulted in an area of 20.14 and 7.92 km² in The Neck and Whalebone Point, respectively.

To estimate the detection function, we first assessed which functional form, half-normal HN or negative exponential EX, best fitted the observed data. The candidate forms differ primarily in the length of the distribution tail, that is, the probability they assign to very distant detections. Models were compared using information-theoretic multi-model inference (Burnham & Anderson 2002), and the detection function with the lowest AIC was used as the basis for further modelling. Next, we constructed biologically plausible models, influenced or not by the seabird breeding season, on the shoulder of the detection function (‘sigma’) and compared these with the null model. Finally, we constructed models to compare estimates of cat densities across: i) The Neck (treatment site where cat removal occurred) and Whalebone Point (control site), and ii) across the area to the North of The Neck seabird colony, The Neck colony, and the area to the South of The Neck colony. We divided The Neck area into three zones to nuance the cat densities of the seabird colony itself on The Neck isthmus compared to the adjacent land to the north and south of the isthmus (Appendix S2).

2.4.2. Estimates of relative abundance of mesopredators – open N-mixture models

We employed the extended Dail-Madsen open population model, also called an open N-mixture model, (Dail and Madsen 2011; Hostetler and Chandler 2015) with a Poisson distribution to estimate variation in

demographic parameters of four native and invasive mesopredator and prey species: eastern quoll, swamp rat, black rat, and house mouse. The European rabbit and the water rat were not considered in our analysis because there were too few detections of these species. The Dail-Madsen model relies on temporally and spatially replicated detection histories, which are counts in the N-mixture model (counts of detections need to often exceed one). We defined a detection as independent if it was separated by at least 30 minutes from the next detection of that species at that camera site, as is commonly done in similar studies (e.g., Brook et al. 2012, Cunningham et al. 2019). We created species-specific detection histories for each camera, allowing us to assess factors that may affect species-specific detection. Missing data during a sampling occasion resulted from cameras malfunctioning and was accounted for in the detection histories. The Dail-Madsen model can be described as follow:

$$N_{it} \sim \text{Poisson}(\lambda)$$

$$G_{it} \sim \text{Poisson}(\gamma)$$

$$S_{it} \sim \text{Binomial}(N_{it-1}, \omega)$$

$$N_{it+1} \sim G_{it} + S_{it}$$

$$y_{it} \sim \text{Binomial}(N_{it}, p)$$

where N_{it} is the number of individuals at site i on survey occasion t , G_{it} is the number of gains (recruits) between seasons, S_{it} is the number of survivors that do not permanently emigrate, and y_{it} is the observed count at site i on survey occasion t . The four structural model parameters are initial abundance (lambda; λ), recruitment rate (gamma; γ), apparent survival (omega; ω) and detection probability (given presence; p), i.e., the probability of detecting N_{it} on a single survey. Apparent survival represents animals in site i at time t who survived in that site since time $t - 1$, and recruitment denotes gains at site i since time $t - 1$. Note that because individual animal identities are not recorded, no distinction is possible between either deaths and emigrants for the animals departing (apparent survival), or between births and immigrants for new arrivals (recruitment) (Dail and Madsen, 2011).

The four parameters (λ , γ , ω and p) can be modelled as functions of covariates. Due to the large number of covariate combinations possible among the four demographic parameters in the models, our approach was to do the modelling in four stages. In stage 1, we built a set of models to estimate p (see below for model selection). Using the model with the lowest AICc resulting from stage 1, we then built a set of stage 2 models to estimate λ . Using the same procedure, we then estimated γ and ω during stage 3 and 4 of the modelling stages, respectively.

In each of the four modelling stages, model candidates were compared using multi-model inference in an information theoretic framework (Anderson and Burnham, 2004), and all models with $\Delta\text{AICc} > 6$ were discarded as non-competitive fits to the data (Richards, 2015). Of the remaining competitive models, the more complex versions of models that had simpler, nested versions with smaller AICc values were also excluded to yield the final model set, and the top-ranked model was used to provide estimates and visualise fitted values (Richards, 2008, 2015). Although we used the top model with the lowest AICc in the

successive stages of the best model construction, we used the best model set to describe the relative contribution of each of the covariates for each parameter.

To fit the open N-mixture model, we used the unmarked package (Fiske and Chandler, 2011) in R (R Core Team, 2018), which provides a unified modelling framework for hierarchical models. Data were modelled using maximum likelihood methods with the function *pcountOpen*, specifically written to use the Dail and Madsen (2011) model in *unmarked* (Chandler and King, 2011). We estimated seasonal abundance for each species at each site using empirical Bayes methods, using the function *ranef* from *unmarked* and demographic parameters from the best-supported model.

3. Results

We recorded a total of 2,186 cat passes in front of the cameras from which individual cats were identifiable in 1,277 cases, across the four deployments of camera traps from 2017 to 2019 at two sites (The Neck and Whalebone Point), representing a total of 35 individually identifiable cats (Appendix S3). These detections were spread over 3,658 trap-nights, with an average of 457.25 per deployment (minimum = 140, maximum = 1012).

3.1 Changes in feral cat densities

Detection probability of cats declined exponentially with distance from the centre of the home-range, as indicated by the stronger support for the exponential detection function than the half-normal detection function (Appendix S4). The best-supported model describes the detection parameter sigma (shoulder of the detection function) varying with the breeding season (Appendix S4).

Cat densities at The Neck (including the control area at the seabird colony, and the areas immediately to the North and South) decreased from 1.4 to 0.56 cats/km² between the shearwater breeding seasons of 2017 and 2019, and from 1.9 to 0.45 cats/km² between the post-breeding season surveys of 2017 and 2019. For The Neck shearwater colony alone, cat densities decreased following cat control (between the 2017 and 2019 surveys) from 8.03 ± 0.72 cats/km² to 1.48 ± 0.28 cats/km² during the shearwater breeding season and from 15.51 ± 1.07 cats/km² to 3.20 ± 0.42 cats/km² after the shearwater breeding season (Figure 2b; Appendix S5b). In the adjacent areas, cat densities decreased from the 2017 to the 2019 survey, but to a lesser extent, from 0.93 ± 0.01 to 0.62 ± 0.09 cats/km² during the breeding season and from 0.70 ± 0.04 to 0.39 ± 0.01 cats/km² after the breeding season in the North of the Neck and from 1.52 ± 0.19 to 0.58 ± 0.09 cats/km² during the breeding season and from 0.61 ± 0.05 to 0.38 ± 0.06 cats/km² after the breeding season in the South of the Neck. The cat density within the Neck seabird colony was always higher than in the adjacent areas (Figure 2b).

Cat densities did not considerably change at the seabird colony at Whalebone Point (where there was no cat control) over the same time period. The mean density of cats at Whalebone Point was 0.39 ± 0.067

cat/km² (Figure 2a; Appendix S5a), lower than the lowest cat density recorded, following control, in the vicinity of The Neck.

3.2. Changes in abundance of mammalian mesopredators and prey

Sufficient data were obtained for four other species of mesopredators and prey to model the influence of cats and the environment on their abundance. The initial abundance of black rats, house mice, swamp rats and eastern quoll was strongly influenced by the site, with the null model more than 6 Δ AICc points above the model containing site (Table 1). Cat control and density reduction at The Neck colony and adjacent areas did not explain changes observed in the relative abundance of these four species. Cat presence on a given night, however, negatively influenced the probability of detecting black rats (estimate parameter for detection probability $p = -0.24$ [-0.37; -0.11] IC95%, s.e.= 0.07) and, to a lesser extent, swamp rats (estimate parameter for detection probability $p = -0.52$, [-1.28; 0.23] IC95%, s.e.= 0.39).

The final set of models that described the probability of detection and estimated abundance of black rats for each survey and each site had five parameters and included two interaction terms: between year and site, and between breeding season and site (Table 1, Appendix S6a). As well as detection probability being negatively affected by the presence of cats, there was evidence that rats were more detectable during the full moon, and during the shearwater breeding season. Recruitment of black rats was higher, and apparent survival lower, at both seabird colonies than in the areas adjacent to The Neck that did not have breeding seabirds, and recruitment and survival were both higher in 2019 than in 2017.

The candidate models describing the probability of detection and the estimated abundance of swamp rats for each survey and each site had six parameters (Table 1, Appendix S6b). The presence of cat on a given night on a given camera had only a weak negative effect on swamp rat detectability. Swamp rats were less detectable during full moon and after the seabird breeding season, and detection probability decreased with lure age. Recruitment of swamp rats was higher and apparent survival was lower in 2019 than in 2017. Recruitment was higher in the Whalebone Point shearwater colony than The Neck and adjacent areas. Recruitment was slightly higher (weak effect) and apparent survival lower after the seabird breeding season, relative to the breeding season.

The final model set that described the probability of detection and estimated abundance of house mice for each survey and each site had four parameters and included the interaction terms between year and site (Table 1, Appendix S6c). Mice were more detectable during the waning moon and less detectable during the waxing moon. Recruitment of house mice was higher, and apparent survival was lower, after the seabird breeding season. Recruitment was also higher in the Whalebone Point colony during year 2017, but not different among other sites.

Finally, the candidate model set describing the estimated abundance of eastern quoll for each survey and each site had three parameters (Table 1, Appendix S6d). Eastern quolls were more detectable during the waning moon than any other moon phase. Recruitment of quolls was lower on the site South of the Neck compared to all other sites. The apparent survival was not influenced by any variables we tested.

Table 1. Model selection results. Initial abundance and detection probability for black rat, house mouse, swamp rat and eastern quoll. Covariates considered: Cat detection per night per site (cat), Moon phase (moon), lure age (lure), Shearwater breeding season (breed), site of survey (site). Model selection based on Akaike's Information Criterion (AIC), number of parameters (nPar), the difference AICc from the best fit models (see methods for models selection), model weights (AICwt), and cumulative model weights (cltvWt).

	nPar	AICc	Δ AICc	AICwt	cltvWt
Black rat					
<i>Detection Probability (p)</i>					
λ (.) γ (.) ω (.) p (cat+breed+moon)	9	10036.41	0.00	0.60	0.60
λ (.) γ (.) ω (.) p (cat+moon)	8	10037.18	0.77	0.40	1.00
<i>Initial abundance (λ)</i>					
λ (site) γ (.) ω (.) p (cat+breed+moon)	12	10028.88	0.00	0.98	0.98
λ (.) γ (.) ω (.) p (cat+breed+moon)	9	10036.41	7.52	0.02	1.00
<i>Recruitment (γ)</i>					
λ (site) γ (breed+year+site+breed:site) ω (.) p (cat+breed+moon)	20	9790.69	0	1	1
<i>Apparent survival (ω)</i>					
λ (site) γ (breed+year+site+breed:site) ω (breed+year+site) p (cat+breed+moon)	25	9757.11	0.00	0.74	0.74
λ (site) γ (breed+year+site+breed:site) ω (breed+site) p (cat+breed+moon)	24	9759.18	2.07	0.26	1.00
Swamp rat					
<i>Detection Probability (p)</i>					
λ (.) γ (.) ω (.) p (cat+breed+moon+lure)	10	2207.42	0.00	0.55	0.55
λ (.) γ (.) ω (.) p (breed+moon+lure)	9	2208.67	1.24	0.29	0.84
λ (.) γ (.) ω (.) p (cat+moon+lure)	9	2210.70	3.28	0.11	0.94
λ (.) γ (.) ω (.) p (moon+lure)	8	2212.01	4.59	0.06	1.00
<i>Initial abundance (λ)</i>					
λ (site) γ (.) ω (.) p (cat+breed+moon+lure)	13	2161.41	0.00	1.00	1.00
λ (.) γ (.) ω (.) p (.)	10	2207.42	46.02	0.00	1.00
<i>Recruitment (γ)</i>					
λ (site) γ (breed+year+site) ω (.) p (cat+breed+moon+lure)	18	2069.99	0.00	1.00	1.00
<i>Apparent survival (ω)</i>					
λ (site) γ (breed+year+site) ω (breed+year) p (cat+breed+moon+lure)	20	2061.57	0.00	0.49	0.49
λ (site) γ (breed+year+site) ω (year) p	19	2061.77	0.20	0.44	0.94

(cat+breed+moon+lure)					
λ (site) γ (breed+year+site) ω (breed) p (cat+breed+moon+lure)	19	2065.62	4.05	0.06	1.00
House mouse					
<i>Detection Probability (p)</i>					
λ (.) γ (.) ω (.) p (moon)	7	6788.92	0.00	1.00	1.00
<i>Initial abundance (λ)</i>					
λ (site) γ (.) ω (.) p (moon)	10	6682.34	0.00	1.00	1.00
λ (.) γ (.) ω (.) p (moon)	7	6788.92	106.58	0.00	1.00
<i>Recruitment (γ)</i>					
λ (site) γ (year+breed+site+year:site) ω (.) p (moon)	18	6622.06	0.00	0.76	0.76
λ (site) γ (year+breed+site+breed:site) ω (.) p (moon)	18	6625.13	3.07	0.16	0.92
λ (site) γ (breed+site+breed:site) ω (.) p (moon)	17	6626.56	4.50	0.08	1.00
<i>Apparent survival (ω)</i>					
λ (site) γ (year+breed+site+year:site) ω (year+breed) p (moon)	20	6585.72	0.00	1.00	1.00
Eastern quoll					
<i>Detection Probability (p)</i>					
λ (.) γ (.) ω (.) p (moon+lure)	4	5216.29	3.92	0.11	0.91
λ (.) γ (.) ω (.) p (.)	5	5218.07	5.70	0.05	0.95
λ (.) γ (.) ω (.) p (lure)	5	5218.07	5.70	0.05	1.00
λ (.) γ (.) ω (.) p (cat)					
<i>Initial abundance (λ)</i>					
λ (site) γ (.) ω (.) p (moon+lure)	11	5181.66	0.00	1.00	1.00
λ (.) γ (.) ω (.) p (moon+lure)	8	5212.37	30.71	0.00	1.00
<i>Recruitment (γ)</i>					
λ (site) γ (site) ω (.) p (moon+lure)	14	5138.42	0.00	1.00	1.00
<i>Apparent survival (ω)</i>					
λ (site) γ (site) ω (.) p (moon+lure)	14	5138.42	0.00	1.00	1.00

4. Discussion

We show a complex but subtle cascade of ecological effects amongst mesopredator and prey species in response to an intensive two-year program of cat control in an island ecosystem. Understanding the responses of other species to invasive predator control in multi-species invaded food webs is important to avoid unintended consequences of control (Bergstrom et al., 2009), particularly in island ecosystems which are characterised by high rates of extinction (Bellard et al., 2017). Key results are that while trapping in the vicinity of the shearwater colonies around The Neck isthmus on Bruny Island reduced the cat density by 5.4-fold, there was no direct measured effect on the abundance or behaviour of native and invasive mammal species that cats might prey on or compete with. There is, however, evidence of avoidance by swamp rats and black rats of cats and of lower survivorship of these species at times of year when cat densities are highest. Importantly, recruitment of both invasive and native rodents and density of cats increased after the seabird breeding season, indicating a lagged response to bottom-up productivity from the breeding seabirds. We reiterate that in these N-mixture models, recruitment and survival refer to the number of camera sites that gained or lost detections of the species over the survey periods. The ecological system around the shearwater colony is driven more by bottom-up resourcing than the ability of cats to control rodent densities, particularly of invasive rodents. We discuss the implications of these results for reducing damaging collateral effects in cat control programs.

Feral cat densities are exceptionally high (1.7–0.5 cat/km² pre–post-control) at the shearwater colony at The Neck on Bruny Island, greater than the average density of cats on mainland Tasmania and Australia (0.27 [IC95% 0.18-0.45] cats/km²) (Legge et al., 2017), although density at the smaller Whalebone Point shearwater colony (0.39 cat/km²) was similar to mainland densities. While cat densities are often higher on islands than on mainlands due to abundant food resources, including colonially-nesting seabirds and ongoing inputs of food from washed-up marine life (Legge 2017), two features specific to Bruny Island may explain the very high densities of cats at The Neck. First, Bruny Island lacks larger mammalian predators, in particular the Tasmanian devil, that are able to limit the abundance of feral cats elsewhere (Hollings et al., 2016; Cunningham et al., 2020). Second, the geographical particularity of The Neck, an isthmus creating a bottleneck between two land masses, may concentrate the movements of feral cats travelling between the northern and southern areas, giving an apparent elevated local density. It is unlikely that the densities recorded on The Neck isthmus are found elsewhere on Bruny Island, as indicated by the lower densities in the areas adjacent to The Neck and at the control site.

Feral cat control through targeted trapping across a large area around The Neck seabird colony on Bruny Island was effective in reducing cat density. A total control effort of 4,185 trap nights over two years was effective at reducing cat density by an average of 3.3-fold (22 cats removed), a control efficiency of 54%, with ~81% of cats removed for a ~44% reduction of the population. The control efficiency on Bruny Island was better than that modelled by McCarthy et al. (2013), in which population dynamic simulations found that to achieve a 44% cat control efficiency would require the removal of at least 57% of cats

annually to sustain a 25% decrease in population size. To achieve close to or zero cats on the Neck of Bruny Island would require 3,500 trap-nights, given the capture rate of one cat per 190 trap-nights and assuming the control efficiency would stay constant. This seems feasible and the result is encouraging, although it does not consider issues such as declining capture success as cat density decreases, learned aversion of traps by cats through time, and immigration from adjacent regions, all of which would likely increase the number of trap-nights. For the eradication to be useful to protect the seabird colony in the long term, an ongoing cat control in this area or consideration for eradicated cat across the entire island would be required.

The presence of the shearwater breeding colony at The Neck provides a seasonal nutrient and productivity pulse which triggers a lagged bottom-up response in recruitment of rodents and local movement and density of cats, independent of the cat control. Prior to the control operations, cat density on The Neck seabird colony in 2017 increased between the shearwater breeding and post-breeding seasons, and correspondingly decreased, albeit to a lesser extent, in the areas adjacent to the colony. This increase in the local density of cats on the colony, after the shearwaters have left on migration, may be explained by the apparent population dynamic response of rodents to the productivity pulse from the shearwater breeding. Recruitment of both black rats and swamp rats was higher after than before the breeding season (seasonal pulse of productivity) and at the two seabird colonies relative to surrounding areas (general habitat productivity), with black rat recruitment showing an overall stronger increase at both seabird breeding sites than in surrounding areas (breeding season by site interaction term) than did swamp rats (additive model). Overall, there were more detections of black rats than swamp rats, which could be due to habitat suitability. Recruitment of house mice was more variable, with an overall decrease in response following seabird breeding. The amplitude and direction of response in recruitment varies across years and sites (interaction effect), with high abundance but only in 2017 at Whalebone Point, where cat density is low and unchanging, possibly masking effects. Seabird colonies are areas of high productivity, contributing pulses of nutrients to islands from live prey for predators, guano, fish scraps, feathers, unhatched eggs and dead chicks and adults (Polis and Hurd, 1996). These pulses of nutrients delivered during the breeding season cascade upwards through the trophic network, with strong positive effects on soil nutrient levels and increased plant productivity (Anderson et al., 2008), which provides a rich food source for invasive and native rodents in addition to the direct predatory and scavenging benefits of the seabird breeding season.

All three rodent species are omnivorous and obtain part of their diet by predation (Dilley et al., 2016). House mice are reported to be a significant cause of mortality for Atlantic petrel chicks and consume a considerable amount of avian carrion during the early spring seabird breeding season in lowland areas of the temperate South Atlantic Gough Island, which is an important haven for breeding sea birds (Jones et al., 2003). A lagged response in rodent recruitment to the pulse of nutrients in seabird colonies, after the breeding season, has been reported from both island and continental systems (Russell and Ruffino, 2012). The spring pulse of food from breeding seabirds on Gough Island boosts the body condition of house mice to an annual peak, just prior to their single annual breeding season (Jones et al., 2003). Productivity pulses, cascading through increased recruitment of consumers such as rodents, could

indirectly facilitate high densities of predators, and could be the factor that attracts feral cats to move into the seabird colonies after the birds have left on migration (Kittle et al., 2016). By providing energy and nutrients to fuel a diverse array of consumer populations, seabirds are central to the dynamics of islands ecosystems (Russell and Ruffino, 2012).

While cats seem to track increasing rodent recruitment, an important question is whether cats have a predatory impact on rodent behaviour or populations. Black rats and swamp rats both recognise feral cats as a predator. Both species reduced their visitation to camera stations (becoming less detectable) on nights when cats were present, indicating risk-sensitive behaviour in response to cats (Bedoya-Pérez et al., 2021). House mice did not behaviourally avoid cats at the camera stations (no influence of cats on nightly detectability). Anderson and Polis (1999) found that house mice will ignore the risk of predation to maximise foraging at high population density and low food supply. The patterns of survival of the three rodent species across the two years, the breeding and post-breeding seasons and the different geographic areas may reflect changes and differences in cat density, although the results are complex and there is no direct statistical association between the numerical density of cats and the population dynamics of these rodent species. Survival of all three species was lower post-breeding, when cat densities were higher in the seabird colonies than during seabird breeding, although this effect was seen at all sites. For black rats, survival was lower in the seabird colonies than the areas away from the colonies. That this effect was evident at both The Neck which had high cat density and at Whalebone Point which had low cat density suggests a change in cat diet or behaviour that we didn't measure. As a result of the relationship between recruitment and survival, the estimated abundance of black rats is higher post-breeding season of the seabirds in both colonies, but this increase seems higher in the Neck colony, which could be a consequence of the reduction of cat predation (Fig. 5).

Eastern quolls, a marsupial mesopredator of invertebrate and vertebrate prey, smaller than and at risk of predation by cats, did not respond to changes in cat density, despite their populations declining on mainland Tasmania where cat densities are high (Fancourt et al., 2015). Despite experimental confirmation of anti-predator responses to cats (Jones et al., 2004), the nightly detection probabilities of eastern quolls, which can reflect risk-sensitive behavioural avoidance, were not influenced by the same-night presence of cats at camera stations. Nor were population parameters responsive to cat density or to site. The values for initial abundance reflected the distribution of eastern quolls on Bruny Island, where they are abundant in the drier north and uncommon in the south (Parker, 2016). Quolls do not seem to focus on seabirds as a primary prey resource, although quolls are present in the seabird colony and have been observed killing shearwaters (Author personal observation). In this prey-rich environment, top-down influences from cats of intraguild predation or interference or exploitation competition may not be important drivers of quoll behaviour or population dynamics, as suggested by Fancourt et al. (2015).

A holistic approach to invasive species management is an important pre-requisite to implementing successful wildlife management (Lurgi et al., 2018). This includes understanding the functional roles of predators in a whole of ecosystem context, and integrated control of multiple species, applying several methods and including control or eradication of invasive prey (Marlow and Croft, 2016). Invasive

predators are frequently co-introduced with invasive prey, species of rodents and European rabbits, which have amongst the highest intrinsic rates of increase of any mammals (Ballari et al., 2016). Control of feral cats has had unexpected outcomes in complex, multispecies food webs, due to predatory or competitive release of invasive mesopredators and prey species with further cascading effects on ecosystems (Rayner et al., 2007; Bergstrom et al., 2009; Brook et al., 2012). Control measures not only reduce predator density and predatory impact but can lead to behavioural changes in mesopredators and prey in response to relaxed top-down pressure (Sih et al., 2010). Responses can be rapid (Peckarsky et al., 2008), with mesopredators or prey shifting to more optimal foraging areas or time periods, with fitness benefits translating to increases in abundance (Lima, 1998).

The ecological implications of the demographic responses of invasive and native rodents to seasonal changes in seabird presence, the consequent nutrient pulses, and the subsequent focus of cats on The Neck isthmus are not known and need further investigation. Simultaneous control of populations of invasive prey species, in this case black rats and house mice, could increase the success of the current cat control by reducing overall food availability and the potential for prey switching, especially when the seabirds are not breeding. Also important is investigating the predatory and competitive relationships between these invasive prey species because control or eradication of only one might increase the number of another (Zavaleta et al., 2001; Courchamp et al., 2003; Ballari et al., 2016). As mesopredators and aggressive competitors, rats can regulate mouse populations on islands where both alien mammals have been introduced (Caut et al., 2007). Rat eradication can result in the release of mouse populations, if mice are not eradicated in the same time, which can lead to increased mouse damage to seabirds, plants or insects (Caut et al., 2007; Ruscoe et al., 2011). The predatory impact of black rat and house mouse on seabirds or other species on Bruny Island is not known.

Seabird life histories are characterised by high longevity and low fecundity (Weimerskirch 2002), which means that responses to cat control will be slow but also probably strongly positive, and will require long-term monitoring to detect. Although we did not measure the impact of cat predation on shearwaters in this study, the shearwater colony at The Neck is being monitored (Eric Woehler and Mary-Ann Lea, personal communication). Cats prey on both adults and chicks in shearwater colonies on Tasmanian islands (Scoleri et al., 2020) but population growth in long-lived seabirds is more sensitive to changes in adult survival than to changes in breeding success (Bonnaud et al., 2010).

Conclusions

Our study demonstrates that cat density on islands, particularly around seasonally rich food resources such as seabird colonies can be very high, much higher than on mainland areas, and that control using trapping is effective in this focussed landscape context at reducing cat density. The rate of reduction was encouraging and suggests that eradication might be possible under sustained control. The control of cats did not have a direct measurable impact on the abundance of prey or other mesopredator species. The

substantial reduction in cat density may have impacted the invasive rodent populations, though, mediated through complex trophic cascades, with lagged effects of nutrient pulses working through primary productivity to support recruitment in rodents, which also subsequently attracted cats to the site of the colony after the seabirds had left on migration. The complexity of this system indicates the need for further research into ecological dynamics between cats, native mesopredators, and invasive and native rodents. Integrated control of multiple invasive predator and prey species is indicated, particularly as invasive rodents are known to prey on seabird eggs and chicks. Eradication or control programs for invasive predators need to be based on research that provides an understanding of community dynamics to reduce unexpected adverse consequences in complex communities with multiple species of native and invasive predators and prey.

Declarations

AUTHOR CONTRIBUTIONS

Cyril Scomparin: Conceptualization, Methodology, Formal analysis, Investigation, Writing – Original Draft, Visualization. **Caitlan Geale:** Conceptualization, Methodology, Formal analysis, Investigation. **Christopher N. Johnson:** Conceptualization, Methodology, Writing – Review & Editing, Supervision. **Menna E. Jones:** Conceptualization, Methodology, Writing – Review & Editing, Supervision, Funding acquisition.

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ETHICS STATEMENTS

This work was carried out under the University of Tasmania Animal Ethics Permits: A0016370 & A0017365, Department of Primary Industries, Parks, Water and Environment Permits: FA17040 & FA18156 and with authority to undertake research on Forest, Crown and Park lands.

STATEMENTS & DECLARATION

Financial interests:

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involvement in study design, collection, analysis and interpretation of data, in writing of the report, or in the decision to submit the article for publication.

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Figures

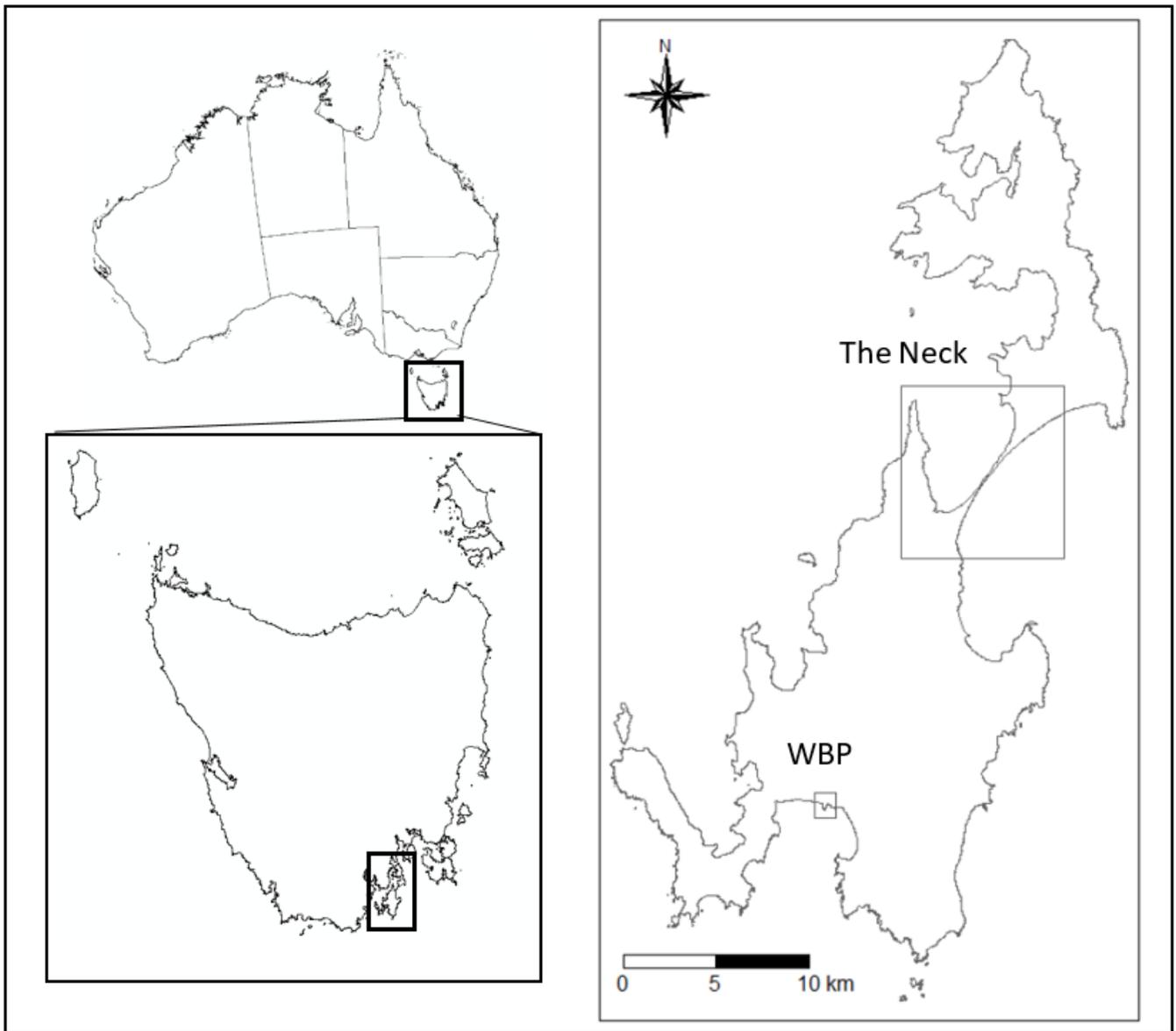


Figure 1

Map of lunawanna-allonah/Bruny Island, located off the south-east coast of lutruwita/Tasmania, Australia, showing the two field sites: The Neck, including North and South, and Whalebone Point (WBP).

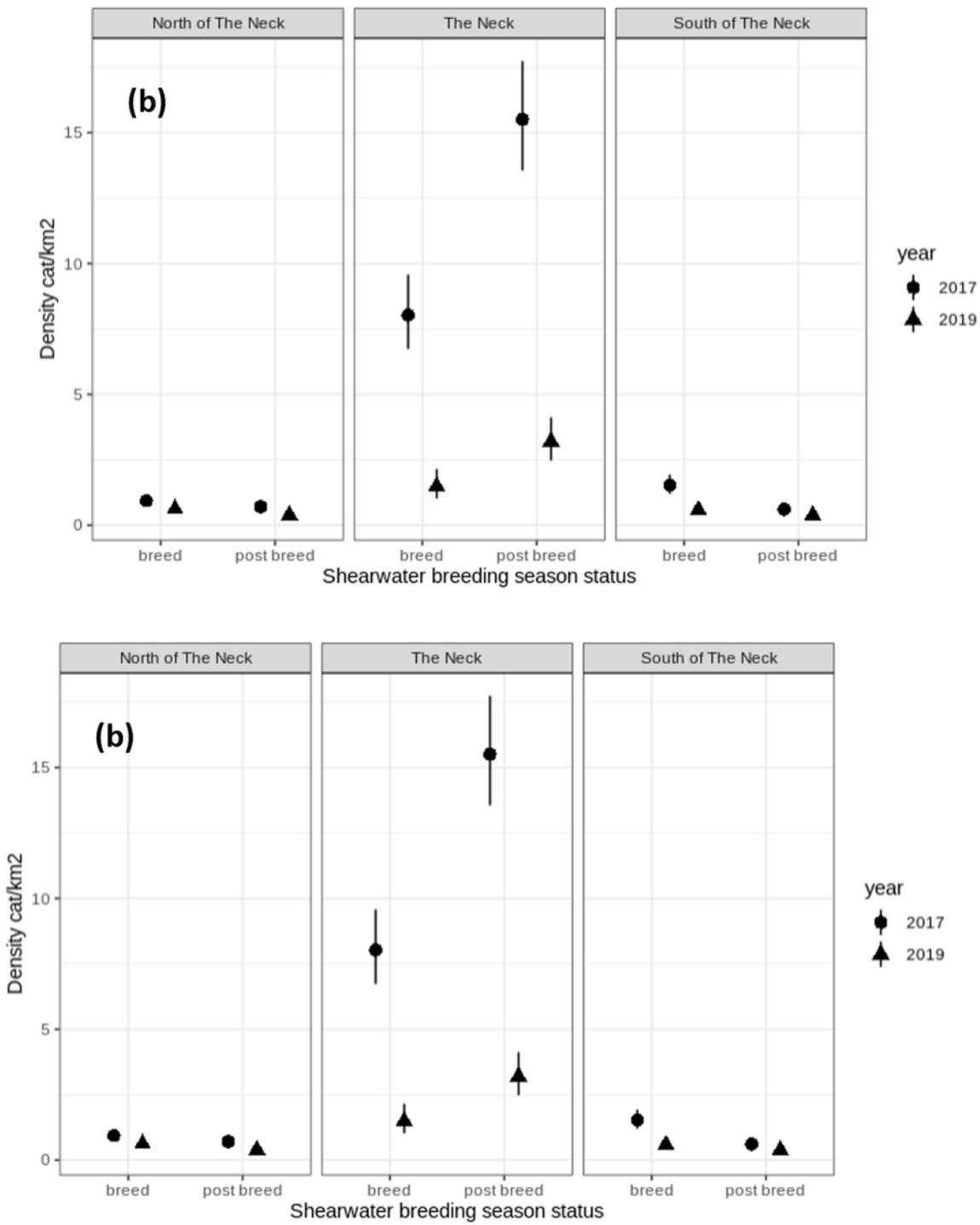


Figure 2

Feral cat densities across a) The Neck (treatment site) and Whalebone Point (control site) and b) the North, South and the colony sites of the Neck, on lunawanna-allonah/Bruny Island, lutruwita/Tasmania, Australia, during the shearwater breeding season (breed) and post-breeding season (post breed), in 2017 and 2019.

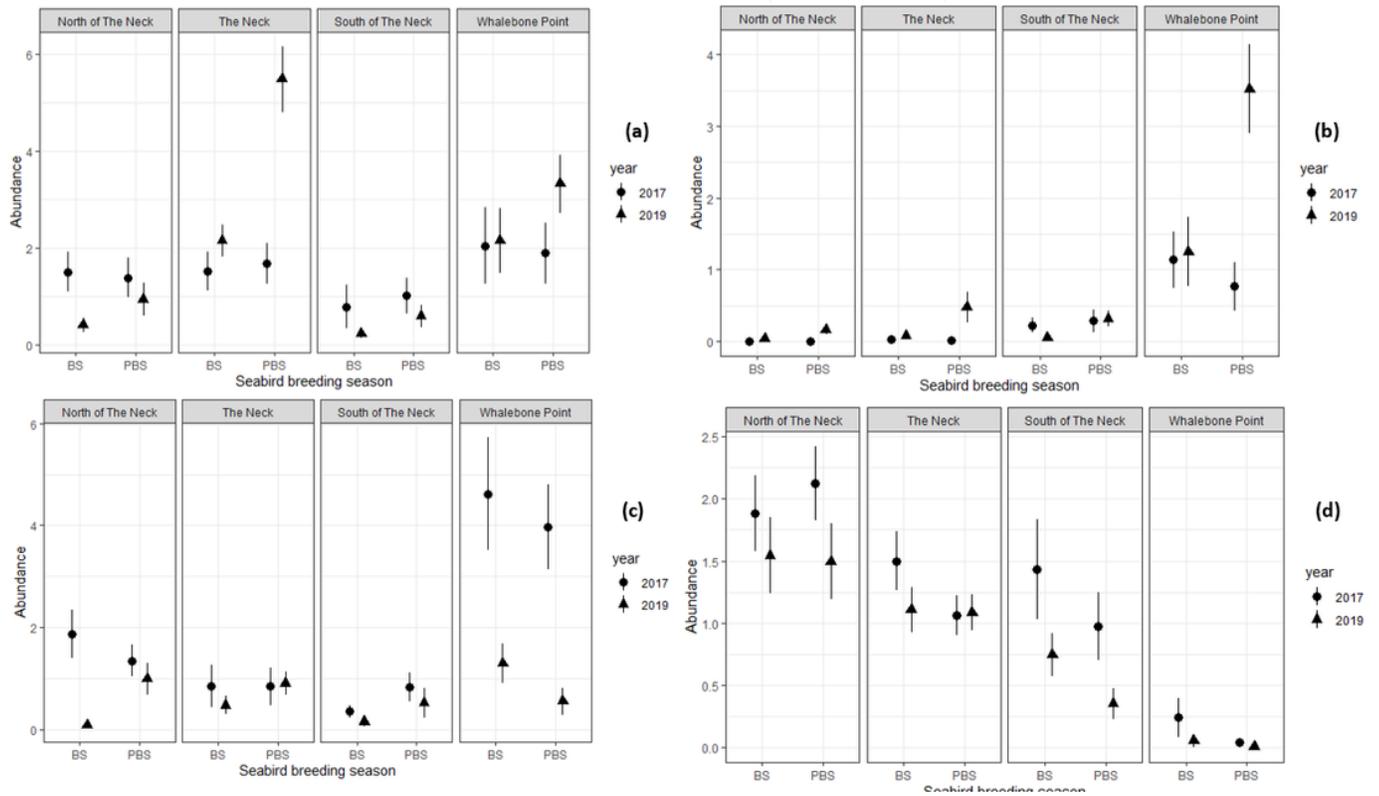


Figure 3

Relative abundance estimated by the best N-mixture model selected for black rat (a), swamp rat (b), house mouse (c) and eastern quoll (d) populations. The abundances are estimated per camera on four sites on lunawanna-allonah/Bruny Island -Iutruwita/Tasmania, Australia during the shearwater breeding season (BS) and post-breeding season (PBS), in 2017 and 2019.

Supplementary Files

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