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ORIGINAL PAPER

Using long-term population trends of an invasive herbivore to quantify the impact of management actions in the sub-Antarctic

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Abstract Accurate, long-term population estimates of invasive vertebrate pests are a key element of ecosystem management. Not only can they clarify the role of invasive species in changing ecosystem dynamics, they are also necessary to evaluate and assess management actions. Rabbits were first introduced to sub-Antarctic Macquarie Island in the 1870s, and since the 1960s have been targeted and influenced by a range of management programs. Here, for the first time, we model population trends of rabbits on Macquarie Island from the beginning of these management actions to the end of a recent, successful eradication attempt. We show that over a 38-year time frame, the population has undergone substantial fluctuations, peaking at over 350,000 individuals (27 indiv ha^{-1}) in the late 1970s, before declining to less than 30,000 individuals (2–3 indiv ha^{-1}) through the 1980s and early 1990s. From the late 1990s to 2005, the population increased relatively rapidly, this time peaking at approximately 221,000 individuals. After the commencement of eradication operations in 2010, the population dropped sharply, decreasing from 135,707 ± 25,995 to effectively zero in just over 12 months. This research contributes to our understanding of the complex population dynamics of sub-Antarctic invasive species and highlights the importance of monitoring in planning, understanding and assessing management actions. The development of models described here allowed population trends to be identified on Macquarie Island, despite 'noise' in the data from seasonality or sporadic observations. In consequence, the impacts of both long- and short-term management actions could be quantified. These techniques are applicable to other locations and species where long-term census data exist.

Keywords Biological invasion · Census techniques · Thermal imaging · Macquarie Island · Rabbits · Adaptively smoothed P-spline regression

Introduction

The impacts of invasive non-native mammals on islands are well documented, ranging from native species population declines to extinctions (Priddel et al. 2000; Courchamp et al. 2003). European rabbits *Oryctolagus cuniculus* (L.) are considered one of the world's most destructive invasive species (Bonnaud and Courchamp 2011), particularly on sub-Antarctic islands where vegetation has evolved with no grazing pressure (Courchamp et al. 1999; Chapuis et al. 2004; Brodier et al. 2011). Sub-Antarctic Macquarie Island, halfway between Australia and Antarctica (Fig. 1), is no exception. Rabbits were deliberately introduced as food by sealers in the late 1870s; however, little is known about their population trends or impacts prior to the mid 1900s when research on rabbit impacts on vegetation in the 1950s raised concerns about the effects of rabbits on the natural environment (Taylor 1955; Costin and Moore 1960).

A number of management actions have been undertaken since these observations in the 1950s. Trials using oat bait laced with 1,080 were initiated in the early 1960s, but met with limited success (Johnston 1966). The *Myxoma* virus

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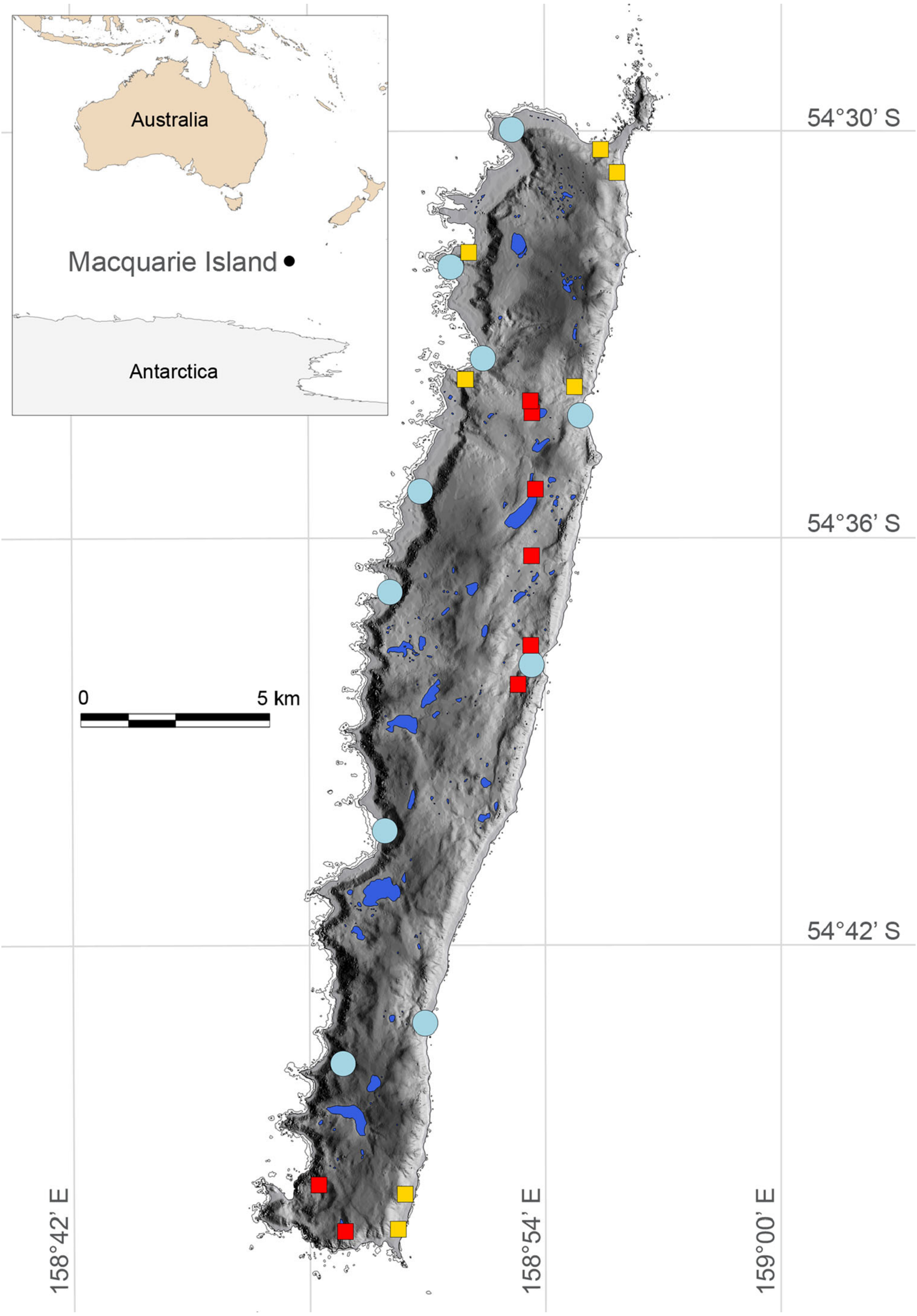

Fig. 1 Macquarie Island. *Red squares* show rabbit count areas (RCAs) from 1974 to 2011; *yellow squares* show RCAs from 2005 to 2011; *blue circles* denote general areas of initial Rabbit Haemorrhagic Disease Virus release

(Glenfield strain) was introduced soon after in 1966, but proved unsuccessful, presumably due to a lack of vectors (Sobey et al. 1973). Consequently, the European rabbit flea *Spilopsyllus cuniculi* was introduced to the island in 1968 (Skira et al. 1983), and after 10 years of annual flea releases to achieve island-wide distribution, *Myxoma* virus (Lausanne strain) was successfully introduced in 1978 (Brothers et al. 1982). Although myxomatosis was extremely successful in initially reducing the rabbit population and maintaining it at relatively low numbers for around 20 years (Copson and Whinam 2001), rabbit number began to increase in the late 1990s (Terauds 2009). The timing of this increase coincided with an intensive and successful eradication operation targeting feral cats *Felis catus* on the island (Robinson and Copson 2014). Bergstrom et al. (2009a, b) presented evidence that this was the primary cause of the rapid population rise. Others have argued that the reasons behind the increase were more complex and suggested that it

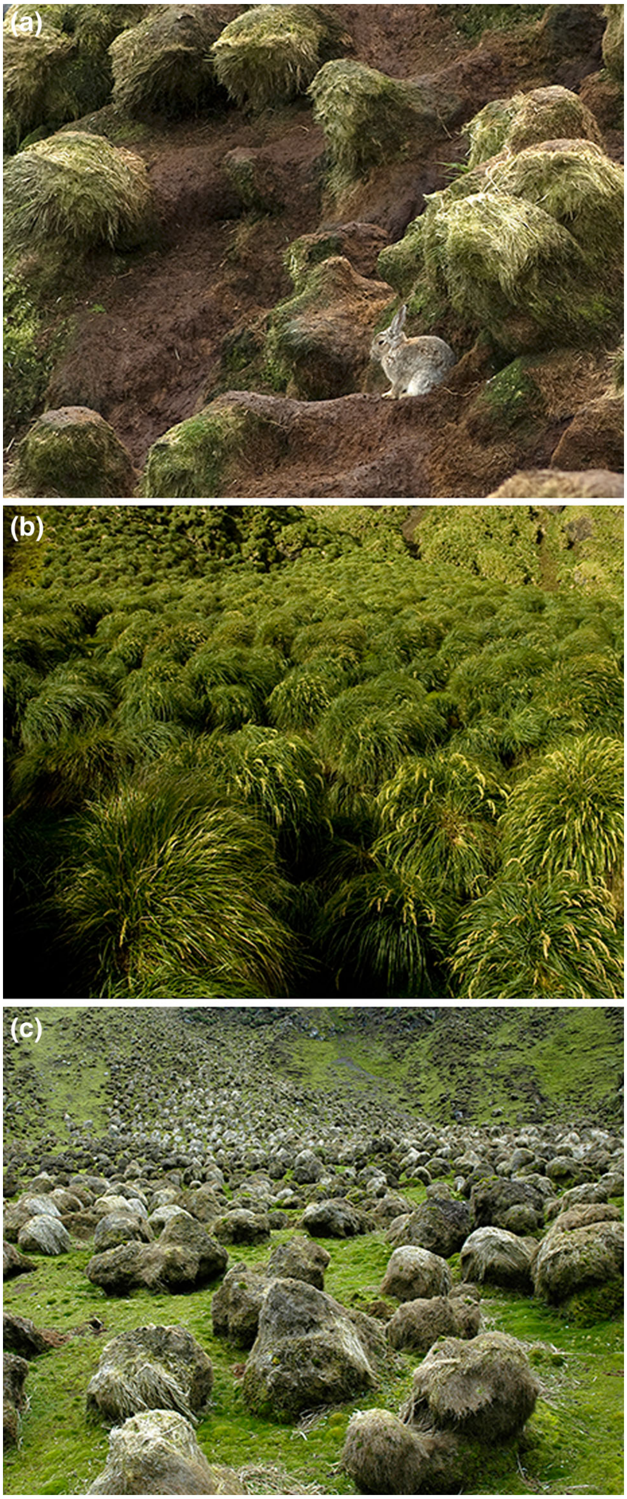

Fig. 2 Rabbits have caused massive vegetation changes on Macquarie Island, including (**a**) eating vegetation down to bare earth. The change has been rapid, with healthy tussock in the late 1990s (**b**) being destroyed across most of the islands coastal slopes and terraces by 2006 (**c**)

was due to a combination of several factors, including a reduction in the release of the *Myxoma* virus, attenuation of the virus, abundant food due to vegetation recovery and climate variability, together with the release from cat predation (Dowding et al. 2009; Whinam et al. 2014).

Regardless of the mechanism behind it, the impacts of the rapidly increasing population were dramatic and devastating. They included direct impacts on vegetation with concomitant effects on the geomorphology (Scott and Kirkpatrick 2008, 2013) and indirect impacts on the island's fauna (e.g. seabirds—Brothers and Bone 2008; stream invertebrates—Marchant et al. 2011). The increase in rabbits and the dramatic escalation in vegetation damage (Bergstrom et al. 2009a; Scott and Kirkpatrick 2013; Fig. 2), combined with the associated indirect effects, resulted in considerable pressure on Australian government agencies to address these impacts on Macquarie Island ecosystems. Once the importance of such a program was recognized, the Macquarie Island Rabbit and Rodent Eradication Plan was initiated in 2004, finalised in 2006 (Tasmania Parks and Wildlife 2007), with full funding secured in 2007 (AUD24.7 million over 8 years).

After a lengthy planning and consultation process, the first phase of the operation (aerial baiting with brodifacoum cereal pellets, targeting both rabbits and rodents) began in June 2010. Obtaining representative estimates of rabbit numbers was an important aspect of the logistical planning, particularly in informing the amount of bait required, which in turn influenced the number of helicopters, quantity of fuel and staff resources required to undertake the operation. Population monitoring is typically a key component of any major management action, including eradications (Courchamp et al. 2003). It not only allows more efficient logistical planning (as described above; see also Priddel et al. 2000) but also reduces the likelihood of unintended consequences (Chapuis et al. 2011). Furthermore, long-term monitoring can play an important role in understanding the efficacy of management actions, as well as flow on effects (Brodier et al. 2011; Chapuis et al. 2011).

Ongoing inclement weather resulted in early abandonment of the initial baiting program, with less than 10 % of the island baited. An independent committee assessed the impact of non-target species mortality from baiting, and based on advice from the New Zealand Department of Conservation Island Eradication Advisory Group, it recommended that to minimise the number of poisoned pest carcasses (and thereby reduce the extent of secondary poisoning of non-target bird species), the next baiting attempt should be preceded by the release of Rabbit Haemorrhagic Disease Virus (RHDV). RHDV is specific to rabbits, and therefore, there are no secondary poisoning issues that are associated with the use of baits containing the poison brodifacoum. In February 2011, RHDV-laced carrots were spread by hand at 10 selected locations (Fig. 1), and the virus moved rapidly through the population. In May 2011, the aerial baiting phase recommenced.

It was successfully completed in July 2011 and immediately followed by the deployment of hunters and trained rabbit dogs. At completion of the baiting operations, it represented the largest operation of its kind attempted anywhere in the world.

Only a few studies have attempted to document long-term trends in the Macquarie Island rabbit population and the associated impacts on the ecosystem of this World Heritage Area (Copson et al. 1981; Copson and Whinam 1998, 2001). The latter provided some whole island estimates between the early 1970s and early 1990s, but the first contemporary, comprehensive long-term rabbit population estimates were provided in an unpublished report to the managing authority (Tasmania Parks and Wildlife Service—Terauds 2009). These results have since been used by a number of studies to examine the mechanisms underlying population fluctuations and the associated ecosystem impacts (Bergstrom et al. 2009a, b; Dowding et al. 2009; Scott and Kirkpatrick 2013; Whinam et al. 2014). Here, we present new methods of extrapolating spot counts that more accurately represent the whole island landscape compared to earlier studies. We also incorporate new data provided by emerging technologies, together with non-parametric regression models to estimate the most representative population numbers and trends to date, providing new quantitative insights into the effects of island management actions. The results presented here represent the first account of rabbit population estimates and trends from the inception of monitoring in 1974 to the completion of the successful eradication project in 2011.

Materials and methods

Study site

Macquarie Island (54°30′S, 158° 57′E) is a 12 785 ha sub-Antarctic island approximately 1,500 km south-east of Tasmania, lying almost midway between Australia and Antarctica (Fig. 1). It is 34 km long and 5 km wide at its widest point, with generally steep coastal slopes rising to an upland plateau that undulates between 200 m and just over 400 m above sea level. The cool, moist and windy maritime climate is typically sub-Antarctic, with a mean annual temperature range of 3.8–6.6 °C, limited seasonal and diurnal ranges and annual precipitation of approximately 950 mm (Pendlebury and Barnes-Keoghan 2007; Adams 2009). Megaherbs and tussock grass dominate the tall coastal and slope vegetation, with short grasses, small herbs and sedges predominant in the mid-altitude vegetated plateau. These communities are widespread and cover over 60 % of the island. Feldmark communities are more common at higher altitudes with cushion plants (*Azorella macquariensis*) and bryophytes dominating the vegetation. While there is evidence that the island has suffered periods of extensive vegetation loss through rabbit grazing in the past (Taylor 1955; Costin and Moore 1960), the lack of quantitative data on rabbits prior to the 1970s mean that it is difficult to put more contemporary changes in a true historical context. Nevertheless, there is little doubt that the terrestrial ecosystem of the island has undergone significant change in the last decade from rabbit grazing, with considerable vegetation loss over much of the island, particularly the coastal slopes (Terauds and Stewart 2008; Bergstrom et al. 2009a; Scott and Kirkpatrick 2013).

Spot counts

Rabbit count areas were established in 1974 in an attempt to assess the efficacy of the impending release of *Myxoma* virus. They were set-up at randomly selected sites to cover a geographic spread of the island and include all of the major rabbit habitats (Copson et al. 1981, Fig. 3). The methodology has remained consistent since their inception. Each rabbit count area (RCA) is 2 hectares in area (20,000 m^2) and approximately rectangular in shape (within topographical constraints), with boundaries marked by 2-m orange PVC poles. The observation posts are on elevated positions, with most approximately 100–200 m away from the closest boundary of the RCA. Observers use 7–12× magnification binoculars to count rabbits within RCAs once in each month, in daylight, on days with winds generally <30 knots and without heavy precipitation. An RCA is closely examined in a methodical manner over a period of approximately 15 min and the number of individual live rabbits recorded. Eight RCAs were monitored regularly between 1974 and 2004. Field observations from 2000 to 2004 suggested that these spot count areas were not providing representative estimates of the whole population, with rabbit numbers appearing to increase disproportionately on coastal slopes and terraces compared to plateau areas. In response, an additional seven fixed rabbit count areas were set up in 2005, primarily in these coastal areas, bringing the total to 15 RCAs (Table 1; Fig. 3). Thermal imaging was intermittently trialled in conjunction with spot counts since 2007, but only since 2010 in a way that allowed robust comparisons with standard counts.

Thermal imaging counts

For thermal imaging counts, a custom thermal imager based on a ULIS 384 × 288 focal plane array (25-µm pitch) fitted with a 50-mm lens was used, providing sufficient resolution to readily detect a rabbit sized target at distances up to 200 m while maintaining a reasonable field of view. Visual counts (VC) of an RCA were first made using the standard method with binoculars, and then, the thermal imager was used to scan the same region and rabbits again counted. A higher

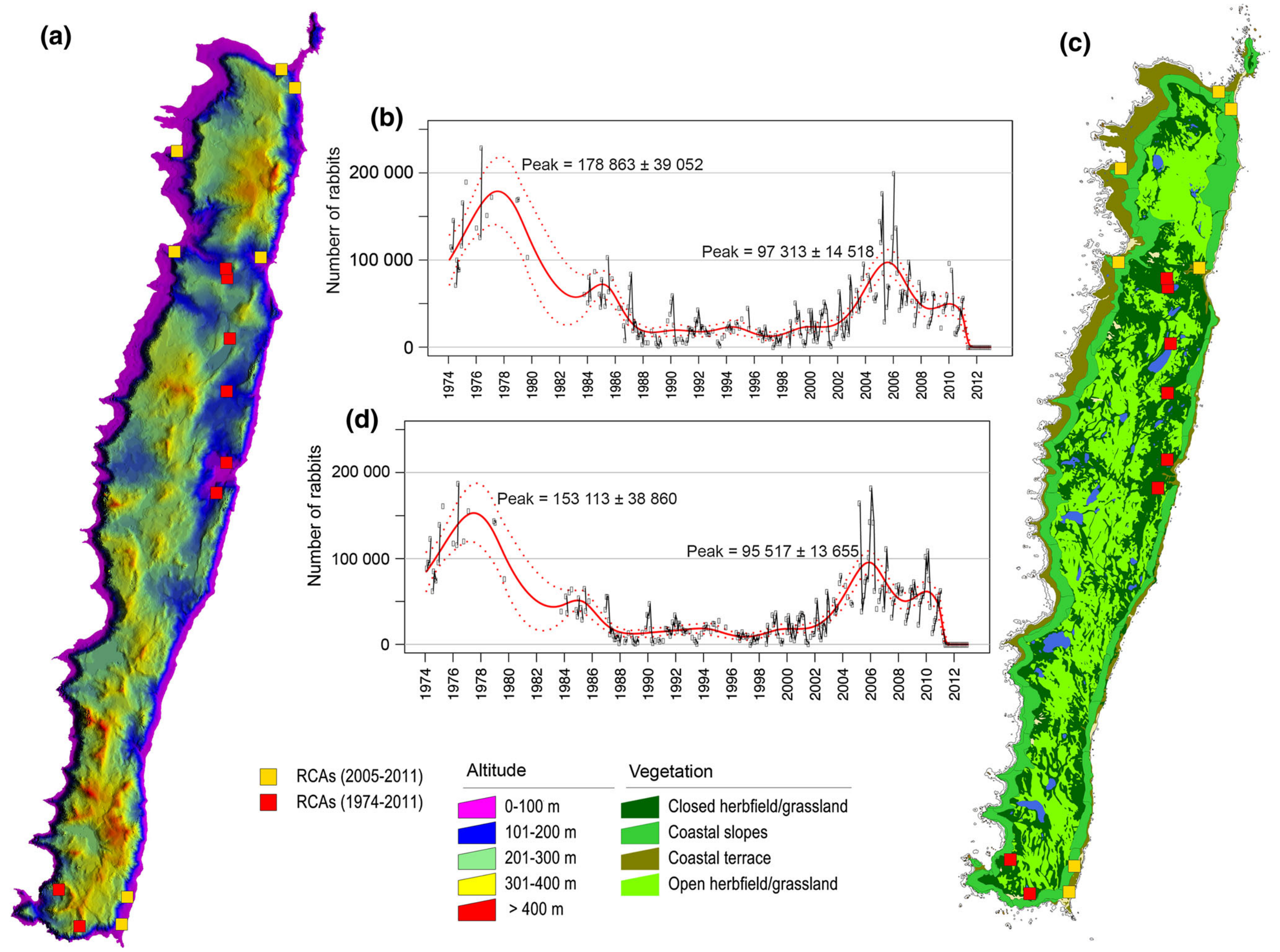

Fig. 3 (**a**) Map of Macquarie Island showing 100 m altitudinal strata and rabbit count areas. Based on the Macquarie Island Digital Elevation Model supplied by the Australian Antarctic Data Centre (http://data.aad.gov.au). (**b**) Population trends of rabbits on Macquarie Island extrapolated from area in altitudinal strata. Points (*o*) indicate monthly island-wide estimates, with non-missing adjacent months joined with *solid black lines*. The *solid red line* is the smoothed estimate and *red dotted lines* indicate the 95 % confidence interval (**c**) Map of Macquarie Island showing four main vegetation classes and rabbit count areas. (**d**) Population trends of rabbits on Macquarie Island extrapolated from areas in vegetation classes. Points (*o*) indicate monthly island-wide estimates, with non-missing adjacent months joined with *solid black lines*. The *solid red line* is the smoothed estimate and *red dotted lines* indicate the 95 % confidence interval

magnification optical scope (US Optics SN-3 3.8–22 × 58 mm) was used to inspect any inconclusive thermal signs. Thermal imaging counts used in these analyses ($n = 51$) were made in 2010 and 2011, across a range of months and at different rabbit count areas. The ratio of thermal counts (TC) to VC was used in nonparametric tests to test for any effects of location, month or year. Corrected VC were estimated from the model that best described the linear relationship between the visual and TC.

Extrapolating spot counts to whole island estimates

Model 1: Altitude

Macquarie Island was divided into 100-m altitudinal strata, using Manifold® Systems (V8) GIS with data from the Macquarie Island Digital Elevation Model (Fig. 3a), and the area of each section was calculated using a Lambert equal-area projection of the island (Table 2). Each RCA was assigned to an altitudinal stratum (Table 1). The highest stratum (>400 m) covered a very small area (<0.1 km^2) and was very unlikely to contain rabbits due to lack of appropriate vegetation or habitat and was therefore not considered in the models further. The second highest stratum (300–400 m) also covered a relatively small area (9.7 km^2), and given there were no RCAs in this stratum, a single stratum was created from 200 to 400 m. Each rabbit count was converted to count m^{-2} and, using the area of the strata, extrapolated to estimate rabbit numbers (Eq. 1). The mean (±SD) of these estimates was calculated for each band (Eq. 1.), and the three estimates (and SDs) from each band were summed to provide a whole island estimate in

Table 1 Locations of rabbit count areas, the year they were set-up, the height above sea level and vegetation class to which they were allocated

Name	Latitude	Longitude	Year set-up	Height (m)	Vegetation class
South Square Lake	−54.5693	158.8946	1974	154	Closed herbfield
Red River	−54.6044	158.8943	1974	110	Closed herbfield
Prion Lake	−54.588	158.896	1974	177	Closed herbfield
North Square Lake	−54.5664	158.894	1974	157	Open herbfield
Hurd Point	−54.7703	158.8149	1974	256	Open herbfield
Green Gorge South	−54.6359	158.8887	1974	83	Closed herbfield
Green Gorge North	−54.6265	158.894	1974	40	Coastal slope
Caroline Cove	−54.7589	158.8038	1974	216	Coastal slope
Hurd North	−54.7612	158.8405	2005	80	Coastal slopes
Hasselborough Bay	−54.5046	158.9238	2005	61	Coastal terrace
Hurd Royal	−54.7697	158.8374	2005	12	Coastal terrace
Gadgets Gully	−54.5103	158.9308	2005	80	Coastal slopes
Finch Creek	−54.5629	158.9126	2005	45	Coastal slopes
Mawson Point	−54.5611	158.8665	2005	38	Coastal terrace
Langdon Point	−54.5299	158.8679	2005	10	Coastal terrace

Table 2 Areas of each altitudinal strata and vegetation class used in the spot count extrapolations. Based on areas calculated using a Lambert equal-area projection

Height	0–100	100–200	200–300	300–400	Total
Area (km^2)	25.79	40.74	44.08	9.76	120.37
Veg class	Closed herbfield	Open herbfield	Coastal slopes	Coastal terrace	
Area (km^2)	36.63	25.65	12.23	44.56	119.08

each month (Eq. 2.). Overall island estimates [total rabbit numbers (TRN)] and associated standard errors were only calculated for any given month if there was a mean and SD for each altitudinal strata.

$$B_x = \sum\left(\frac{RC_y}{20000} \times A_{B_x}\right)/n \tag{1}$$

$$TRN = \sum B_x \tag{2}$$

where B_x = the mean count in altitudinal band x (0–100, 100–200, 200–400 m strata); RC_y = monthly rabbit count in RCA y; A_{Bx} = area of strata x in metres; n = number of RCA counts; and 20,000 represents the conversion factor from hectare to m^2.

Model 2: Vegetation

In the second method, the vegetation of Macquarie Island was classified into four main habitats based on the map of Selkirk et al. (2009) and unpublished local knowledge (Fig. 3c). These habitats were closed herb vegetation (including grasses, graminoids, forbs and ferns, ranging in height but generally lower than 0.5 m), open herb vegetation (alternating strips of closed herb and bare ground), coastal slopes (generally dominated by tall tussock *Poa foliosa* and/or megaherbs) and coastal terraces (mix of closed herb and mires). The area of each habitat was calculated on a Lambert equal-area projection of the island using GIS software (Manifold® Systems V8), and RCAs were allocated to a habitat based on their location (Tables 1, 2). As the RCAs prior to 2005 did not include any coastal terrace sites, three habitats were used for these estimates, with coastal slopes and coastal terraces grouped. The same extrapolation techniques to those described above were used to derive estimates of island-wide rabbit numbers from the raw counts, and also from the corrected raw counts using the thermal imaging data.

The R package ‘survey’ (Lumley 2012) was also used to derive estimates for each altitude band or vegetation area and provided the same results.

Smoothed regression

Given the gaps in the data, high variance around estimates and difficulties in delineating clear trends, we fitted a smooth regression to the mean monthly estimates to describe the changes in rabbit population over time. Three data sets were used. The first two were based on the raw counts and extrapolated using both the altitude and vegetation strata. For the third data set, all raw counts were multiplied by the thermal imaging correction factor and then extrapolated using the vegetation strata. Several regression methods were considered, including multivariate adaptive regression splines (MARS) (Friedman 1991), a variable span running line smoother (Friedman 1984), penalised thin-plate regression splines (Wood 2003, 2006), and an adaptive smoother based on P-splines where the strength of penalty was allowed to vary over the covariate (time) (Wood 2006 as implemented in R package mgcv 1.7–22). In each instance, cross-validation or generalised cross-validation (GCV, Craven and Wahba 1979) was used to select the degree of smoothness.

While all methods recovered the same general 'shape' of the time-series, considerable differences were apparent in their treatment of small-scale variation and in estimates of uncertainty in those parts of the time-series with few data. We therefore favoured an adaptively smoothed P-spline as this method effectively captured changes in uncertainty of the smoothed function through time, as well as providing the flexibility required to approximate changes in mean function on a scale of 1–5 years (depending on frequency of observations). Total island estimates were derived from the sum of scaled strata counts, so to account for this scaling, and increasing variance with population size, the error distribution was modelled as quasi-Poisson using a log link. Fitting routines for adaptive smooths cannot at the present time accommodate autocorrelation terms, and this was reflected in models by a small degree of over-fitting. To alleviate this problem, and to help fit through sparse data in the early 1980s, we restricted the dimension of the smoothing basis to 20 and imposed a penalty basis of dimension five. All analyses were conducted in R version 2.15 (R Core Development Team 2012).

Results

Thermal imaging correction

Overall, TC were significantly higher than VC ($n = 51$, Wilcoxon $Z = -6.2$, $p < 0.001$). Nonparametric tests provided no evidence that the ratio of TC to VC (TC/VC) was significantly influenced by location (Kruskall–Wallis $\chi^2 = 3.9$, $df = 5$, $p = 0.57$), month (K–W $\chi^2 = 3.0$, $df = 2$, $p = 0.86$) or year (Mann–Whitney $Z = -0.76$, $p = 0.44$). Linear regression showed the two variables were highly correlated ($R^2 = 0.97$) and, as the underlying assumptions of the regression were met, VC were adjusted using the VC–TC relationship to obtain:

$$\mathrm{VC}_{\mathrm{TC}} = \mathrm{VC} * 2.32 + 0.63$$

Amended counts $\mathrm{VC}_{\mathrm{TC}}$ were then used as the basis for extrapolations using vegetation class areas, and these were in turn modelled using the suite of time-series models described earlier.

Population trends

Our choice of final model to describe population trends was an adaptively smoothed P-spline of 16.9 effective degrees of freedom, with model smoothness estimated using generalised cross-validation. This model accounted for 74 % of the total deviance and was sufficiently adaptive to capture much of the small-scale variation at scales of 1–5 years. Using the model described above, island population estimates derived from altitudinal strata and vegetation class showed similar broad patterns although there were differences in peaks numbers in both the 1970s and 2000s (Fig. 3). While both altitudinal strata and vegetation class extrapolation models produced similar results, we hereafter report only the vegetation class model corrected for thermal imaging counts. The vegetation class model was considered the best for reporting final, corrected estimates because it seemed slightly more conservative than the altitudinal model. Furthermore, since rabbits are known to prefer some different vegetation classes on the island to others (Copson et al. 1981), these analyses are likely to provide the most representative estimates of whole island numbers.

Amended counts ($\mathrm{VC}_{\mathrm{TC}}$) extrapolated by vegetation class were used to describe rabbit population trends on Macquarie Island and relate them to a suite of management actions (Fig. 4). Over the 38 years that records have been kept, estimates of rabbit numbers peaked at 355,222 ± 78,556 (22–34 indiv ha^{-1}) in June 1977. Following the introduction of myxomatosis in December 1978, numbers declined rapidly to approximately 20,000–30,000 individuals (<3 indiv ha^{-1}) in less than 10 years, and this population level was maintained until the late 1990s through effective use of *Myxoma* virus. Numbers began to rise slowly in the mid-late 1990s, and then increased rapidly through the early 2000s at approximately 20 % per annum between 2000 and 2005, peaking at 221,600 ± 31,680 individuals or 17 indiv ha^{-1}. Numbers then declined before plateauing again, then rising marginally through 2008–2010. The next decline immediately followed the first (unsuccessful) baiting attempt in 2010 when approximately 10 % of the island was baited. The decline continued after the release of RHDV in February 2011 and an aerial bait drop that covered the whole island from May to July 2011. From the first, aborted bait drop in 2010, the eradication project reduced the entire rabbit population from 135,707 ± 25,995 individuals to effectively zero in the space of around 12 months. Only 13 rabbits were found and killed by the hunters between 4 July 2011 and 19 November 2011. From mid-2011, no rabbits were observed in rabbit count areas, and no rabbits or fresh sign has been seen since late November 2011. In April 2014, the Parks and Wildlife service declared the Macquarie Island Rabbit and Rodent Eradication Operation a success, with all three introduced species successfully eradicated.

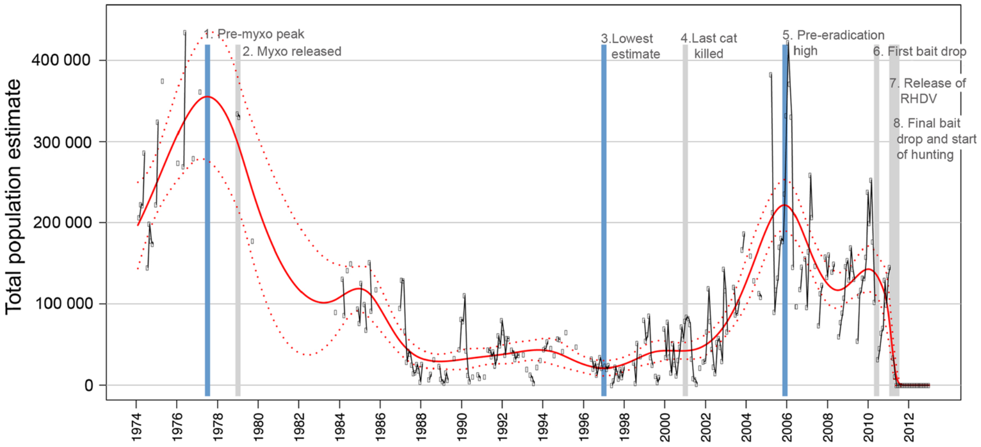

Fig. 4 Population trends of whole island rabbit numbers on Macquarie Island based on thermal imaging correction and extrapolated from vegetation class areas. Points (*o*) indicate monthly island-wide estimates, with non-missing adjacent months joined with *solid black lines*. The *solid red line* is the smoothed estimate and *red dotted lines* indicate the 95 % confidence interval

Corrected veg	Approximate date	Population estimate from model	Notes
1. Pre-myxo peak	June 1977	355 222 ± 78 556	Date from model
2. Myxo introduced	Dec 1978	297 287 ± 81 095	Copson (1981)
3. Trough after myxo	Dec 1996	20 669 ± 9211	Date from model
4. Last cat killed	Dec 2000	41 996 ± 10 319	TASPAWS
5. Pre-eradication high	Nov 2005	221 600 ± 31 680	Date from model
6. Preliminary bait drop	May 2010	135 707 ± 25 995	10% of island baited
7. RHDV released	February 2011	50 653 ± 23 879	Hand baited
8. Successful bait drop	May 2011	7825 ± 11 090	Whole island baited

Discussion

One of the primary goals of this study was to quantify and describe the long-term population change of rabbits on Macquarie Island. We showed that the effective introduction and ongoing use of the *Myxoma* virus successfully reduced the whole island rabbit population by hundreds of thousands of individuals, to less than 10 % of its peak in the late 1970s, and its continued use maintained the population at these levels until the mid 1990s. After a gradual increase through the late 1990s, from 2001 to 2006, the population increased fivefold, again rising to a total island population numbering in the hundreds of thousands. The population peaked in late 2005 at over 200,000 individuals, but these high numbers were relatively short-lived. Finally, the island-wide eradication operation, beginning with the first, aborted baiting operation in 2010 reduced the population from over 100,000 individuals, to effectively zero in less than 12 months.

While there are few data to explain the first 1977 peak (where cats were present in the absence of *Myxoma*), it seems clear that the *Myxoma* virus was responsible for the decline and maintenance of low rabbit numbers for almost 20 years following its introduction in late 1978. However, there has been considerable debate regarding the mechanisms driving the population increase that peaked in 2005. Bergstrom et al. (2009a, b) considered predation by cats, the amount of *Myxoma* distributed and climate variability, and concluded that removal of the cats was the primary reason for this increase. Dowding et al. (2009) took a different view and suggested that while top-down control of rabbits by cats was likely to be a factor, it was one of several, including changes in the distribution and efficacy of the *Myxoma* virus, climate variability and vegetation recovery. Others have suggested that changes in rabbit numbers are likely to be driven by a range of factors (Brothers and Bone 2008; Robinson and Copson 2014; Whinam et al. 2014). The mechanisms behind the rabbit population decline from 2005 onwards do not appear related to any management actions; however, in light of the dramatic vegetation loss on the coastal slopes (Scott and Kirkpatrick 2008; Bergstrom et al. 2009a; Scott and Kirkpatrick 2013; Fig 2), it seems likely that this was a response to a severe reduction in food resources, in a typical 'boom and bust' scenario. Recent work on the long-term interactions of rabbits with vegetation on the island suggests that vegetation–rabbit dynamics are complex, species specific and spatially variable (Scott and Kirkpatrick 2013; Whinam et al. 2014).

Ideally, a comprehensive population model would take into account all potentially important covariates that could influence rabbits numbers, such as predation, food availability, vegetation dynamics, temperature, precipitation and anthropogenic control measures. While work to develop a population dynamics model to incorporate these measures is currently under way, we here restrict ourselves to a simple nonparametric smooth function to describe the main features of the data. We do this because even in a relatively simple model setting, the time-series of rabbit numbers on Macquarie Island presents complex issues to overcome in developing a model describing the monthly population trend over time. Inconsistency in sampling effort, combined with the difficulties of operating in a harsh environment, has meant that monthly counts may be absent for several months at a time, and this issue has confounded earlier attempts to estimate and quantify continuous trends (e.g. Copson and Whinam 2001; Terauds 2009). Furthermore, while the timing of management actions are known, the time-lag between intervention and their impact, which may itself attenuate over time, are not well understood on Macquarie Island. For these reasons, in the current study, we adopted a pragmatic approach that largely ignored (or more accurately smoothed) seasonal variation and missing data in favour of describing broad continuous trends.

We fitted several regression models to describe long-term rabbit population numbers, favouring those methods that could adapt to the way the structure of the data changed over time. Our choice of final model consisted of an adaptively smoothed P-spline with model smoothness estimated using generalised cross-validation. One particular advantage of this model was the fact that sampling intensity and estimated population variability affected the estimation of uncertainty about the mean trend. While the model was sufficiently adaptive to capture much of the small-scale variation, it failed to capture several unusually high estimates occurring in 2006. It is possible that these unusually high estimates were attributable to some extremely high and temporally unstable localised rabbit numbers in areas around some of the rabbit count areas.

The extrapolation techniques used allowed whole island estimates to be obtained from relatively few (but representative) spot count areas. Furthermore, our results suggested both altitude and vegetation were effective ways of partitioning the island and using as a basis for the extrapolations. Our analytical techniques required the assumption that rabbit numbers in rabbit count areas adequately represented the altitudinal and vegetation strata that they were in and that they remained representative over the time frame that monitoring was undertaken. We tested the validity of the latter assumption by using both altitude (which will not change over the time frame) and vegetation (which possibly could) in our calculations and found that both methods provided similar results. Furthermore, our estimates based on altitude and uncorrected vegetation show similar patterns and magnitudes to that shown by Copson and Whinam (2001) who used quite different extrapolation techniques. We suggest that by using broad strata, such as altitude or major vegetation types, which are unlikely to change significantly over time, extrapolating from spot counts can be an effective method for estimating population numbers and assessing trends over time.

Regardless of the efficacy of the extrapolations, there are several factors that potentially influence or bias counts The most important of these is likely to be rabbit detectability. On any counting occasion, an unknown proportion of the population is underground (Kolb 1991; Moseby et al. 2005) or missed (Parer and Price 1987; Fletcher et al. 1999; Poole et al. 2003), so that estimates presented here represent, at best, an index of abundance. However, by using data from thermal imaging technology (where significantly fewer rabbits were missed) and the associated correction factor, we significantly improved overall estimates (and therefore delineation of trends) of rabbit numbers. Previous estimates of rabbit numbers were substantially lower (e.g. Copson and Whinam 2001; Terauds 2009) and may have underestimated population numbers by more than a factor of two. We estimate that the number of individual rabbits may have reached over 350,000 individuals at its peak in the 1970s and over 200,000 rabbits in the last decade. Our new estimates are likely realistic in light of the massive vegetation impacts seen on the island in the last 15 years (e.g. Fig. 2; Scott and Kirkpatrick 2008, 2013; Bergstrom et al. 2009a), and reinforce the usefulness of thermal imaging as a tool in undertaking counts of cryptic vertebrate species in different habitats.

Despite the limitations brought about by detectability, the counts and associated monthly estimates have proved useful in not only understanding population dynamics, but also in assessing the efficacy of management actions. For example, they not only quantified the effectiveness of the myxomatosis control operation, but also highlighted when it was failing. The value of long-term monitoring has been shown for a range of threatened native species (e.g. Holland et al. 2012), and here, we highlight its usefulness in managing invasive species. The collection and collation of this long-term (38 years) data set required ongoing commitment from the Tasmania Parks and Wildlife Service, and the value of this long-term strategy is evident when compared to other studies, which have clearly shown that sporadic spot counts will always underestimate rabbit population numbers (Parer and Price 1987; Fletcher et al. 1999; Poole et al. 2003; Moseby et al. 2005). Our results also underestimate whole island rabbit numbers for the same reasons; however, the issues are mitigated by the long-term nature of the monitoring program and the demonstrated capacity to detect change. They represent the best estimates of the whole island population to date and clearly highlight how it has changed over time.

A decrease in density or abundance of a vertebrate pest species is one measure of the management activity's efficacy. However, the success and/or efficacy of management must be ultimately measured by a reduction of the impact caused by the managed population, or an increase in the density or condition of the values the management action aims to protect. While positive signs of habitat change have already been documented on Macquarie Island (Shaw et al. 2011; Scott and Kirkpatrick 2013), other studies in the sub-Antarctic have shown that the removal of rabbits does not always result in predictable effects (Chapuis et al. 2011).

In the French sub-Antarctic, long-term monitoring of seabirds and vegetation on Ile Verte (almost twice the size of Macquarie Island at ~22,000 ha) allowed the complex and interrelated consequences of that rabbit eradication to be identified and tracked over time. The Tasmanian Parks and Wildlife Service recently confirmed that the eradication attempt has been successful and that all rabbits, rats and mice have been eradicated from Macquarie Island. The consequences of such a huge reduction in vertebrate pest numbers in such a short space of time are only just becoming evident; however, the complexities highlighted by other sub-Antarctic studies (e.g. Brodier et al. 2011; Chapuis et al. 2011) reinforce the need for the continuation of ongoing monitoring on Macquarie Island to clarify these responses and their interactions.

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