

Localised control of an introduced predator: creating problems for the future?

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Abstract Introduced mammalian predators have had significant impacts on many native prey species. Although control of such predators for conservation management is becoming increasingly commonplace, it is often undertaken at a relatively small scale in relation to the overall predator population. Processes such as immigration mean that it remains difficult to determine the effectiveness of control measures. We investigated the impacts of feral ferret *Mustela furo* removal on the entire feral ferret population on Rathlin Island, UK. Removal of ferrets prior to breeding led to a substantial increase in the post-dispersal population through the enhanced survival of juveniles. Despite increased numbers, overwinter survival remained high, potentially aided by the reduced territoriality shown by this feral species compared to wild carnivores. The response of this ferret population to control is a further illustration of the complex ecological processes and outcomes arising from the anthropogenic disruption of

wildlife populations. It highlights how partial or localised management may prove ineffective, and at worst might exacerbate the problems that management was designed to avert.

Keywords Ferret · Invasive species · *Mustela furo* · Mustelid · Population dynamics · Predator control · Territoriality

Introduction

Invasive non-native predators are a major threat to the survival of many native species (Veitch and Clout 2002); a situation which is often compounded by habitat loss and fragmentation, and other human activities (Vitousek et al. 1997). When such alterations in land use benefit exotic species, many of which are omnivores or generalist predators (Findlay and Houlihan 1997; McKinney and Lockwood 1999; Lockwood et al. 2007), then intensive management of predators may be necessary in order to conserve vulnerable native species (Veitch and Clout 2002).

The eradication of whole populations of an introduced predator may be the desirable option, and such attempts are becoming both more frequent and more ambitious (Veitch and Clout 2002; Towns and Broome 2003; Morrison et al. 2007; Parkes and Panetta 2009). This approach is not always suitable, however, whether because of the large ranges of

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well-established introduced species (Macdonald and Harrington 2003), a lack of adequate funds or because of political or public opposition (Bertolino and Genovesi 2003; Bremner and Park 2007). In such instances, targeted predator control that is limited to important sites, such as around colonies of breeding birds, is often a more acceptable option (Greenwood et al. 1990; Keedwell et al. 2002; Bolton et al. 2007). However, such an approach to management then creates a control zone within a wider landscape matrix that continues to support predators (Janzen 1986). Without a permanent barrier, immigration is inevitable and many predatory species are capable of dispersing over long distances (Byrom 2002; King and Powell 2006). This means that continuous monitoring and at least episodic control is typically required. In some cases this can result in little or no effect on overall predator populations, and so predator control under these circumstances can often appear a Sisyphean task (Greentree et al. 2000).

Nevertheless, because predation can have significant impacts on small prey populations (Sinclair et al. 1998), control of both invasive and native predators is regularly undertaken (Dowding and Murphy 2001; Kinnear et al. 2002; Macdonald and Harrington 2003). Thus an understanding of its effectiveness in controlling predator populations, and in generating conservation benefits, is essential (Smith et al. 2010). For example, limited control may not be appropriate with regards to the spatial scale at which the predator operates (Lahti 2001); and many predator populations have social and/or spatial structure, and culling can disrupt these systems with unpredictable results (Woodroffe et al. 2006; McDonald et al. 2008). The design and implementation of control programmes therefore needs to be carefully considered in order to avoid or mitigate against such outcomes. In addition, evidence about what contributes to a successful control operation is often lacking (Sutherland et al. 2004; King et al. 2009), so the examination of trial control programmes provides such an opportunity.

In this study, we examined the impact of predator control on an introduced non-native mustelid, the feral ferret *Mustela furo*. Members of the Mustelidae have been deliberately and accidentally introduced to a number of countries and islands (Long 2003; Clapperton and Byrom 2005; Bonesi and Palazon 2007), where they have usually adapted well and become major predators of native species (Macdonald

and Harrington 2003; King and Powell 2006). However, outside of New Zealand (Clapperton and Byrom 2005), the impact of introduced ferrets, although presumed to be negative, is essentially unknown. On our study island, for example, declines and changes in the distribution of ground and burrow nesting birds have been observed since the introduction of ferrets, despite positive habitat management for these species (Anonymous 2007, L. McFaul, unpublished data), but no contemporaneous assessment of ferret impact was conducted. When the impact of predation by ferrets has been detrimental, removing them has often been considered necessary (Clapperton and Byrom 2005), but the effect of such removal programmes on ferret populations is also unknown. We examined population level responses to control measures that were designed to represent predator control for the protection of key nesting areas for ground-nesting birds. We present a case whereby removal over such limited areas can make subsequent control efforts harder, and may give rise to a greater threat to prey populations that the management action was intended to protect.

Materials and methods

Study site

Fieldwork was carried out on Rathlin Island (55°18'N 06°13'W; 1,525 ha), located off the north-east coast of Northern Ireland (Fig. 1). The vegetation is dominated by maritime heath and acid grassland, with small flushes, wetlands and ponds. Most land is grazed by cattle and sheep at low densities, and the island has a year round population of approximately 80 people. The island supports internationally important populations of breeding seabirds (Mitchell et al. 2004), and is designated for protection under a number of conservation instruments. Ferrets were intentionally released to Rathlin over several years in the 1980s in an attempt at biological control of introduced rabbits *Oryctolagus cuniculus* (L. McFaul pers comm.).

Population assessment

94 single entry mink cage traps (Solway Feeders Ltd.) were placed throughout the island on accessible land in an approximate grid system at 300–400 m spacing. Traps were placed in open-ended wooden

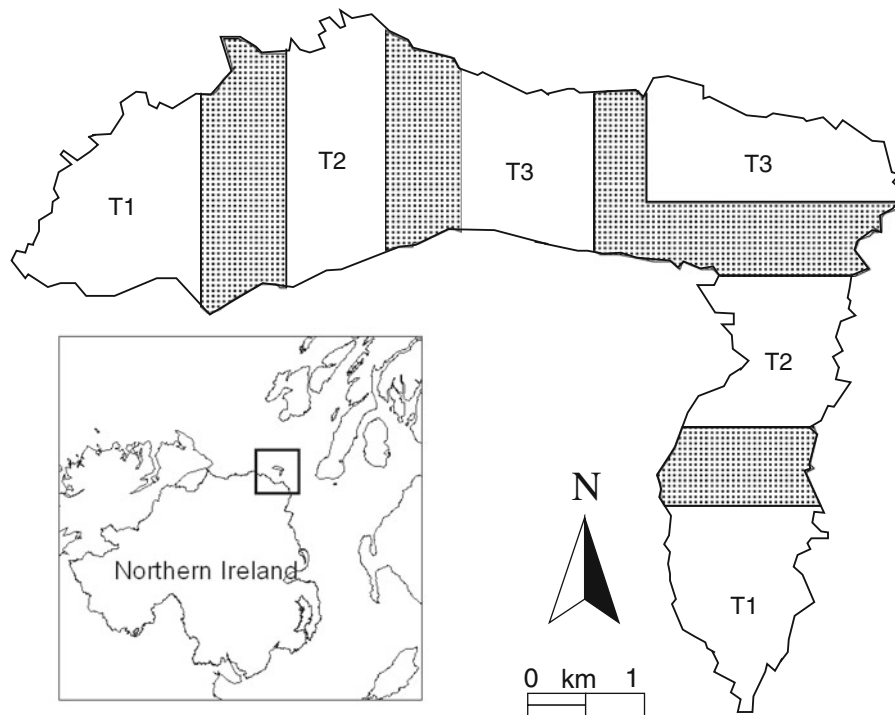


Fig. 1 Map of Rathlin Island study site showing randomly assigned ferret removal areas. Both T1 areas were trapped in 2006, both T2 areas were trapped in 2007, and neither T3 area

was trapped in either year. *Shaded areas* represent buffer zones between treatments. *Inset* shows Rathlin in relation to Ireland and the UK

tunnels to provide protection from the elements for trapped animals, as well as potentially making them more attractive to ferrets. They were baited with preserved fish, and were sited where animals were most likely to be moving naturally, such as alongside dry stone walls and other linear features. Trap sites remained the same between years. In 2005–2006 traps were operated in a rolling front of three groups of 32, 32 and 30 traps, effectively splitting the island into three sections. Traps were set for six consecutive nights, in November–December and again in February. In 2006–2007, with improved logistics and increased experience, all 94 traps were run for five successive nights per month from October–January inclusive. All traps were checked daily and rebaited if necessary. All captured ferrets were marked with individually numbered tags (1005–1003, National Band & Tag Co.) in both ears.

Radio collaring and tracking

In both years, a sample of ferrets spread throughout the entire island were fitted with radio collars. Before

handling, ferrets were anaesthetised using isoflurane (Abbott Laboratories Ltd.). Mortality-sensing collars (11.5 g, TW-5, Biotrack Ltd.), representing a maximum of 2.5% of body mass, were fitted. All individuals were checked to ensure recovery was complete before being released within a few minutes of the initial procedure into a burrow or under thick vegetation close to the trapping site.

In 2005–2006, 18 individuals (nine male, nine female) were radio collared. One collar failed shortly after deployment, and two individuals died during the tracking period. In 2006–2007, 13 individuals (six males, seven females) were collared, with three individuals dying during this period. Animals were radiotracked on foot from the day after collaring through to early March to denning or activity spots, both during the day and night, using a 3 element Yagi antenna with either a TR-5 (Telonics) or a Mariner (Biotrack) receiver. Location co-ordinates were recorded using a handheld GPS unit (Garmin GPS72) with an accuracy of 5–10 m dependent on weather conditions, and checked on a topographic map. Intervals between tracking days were irregular,

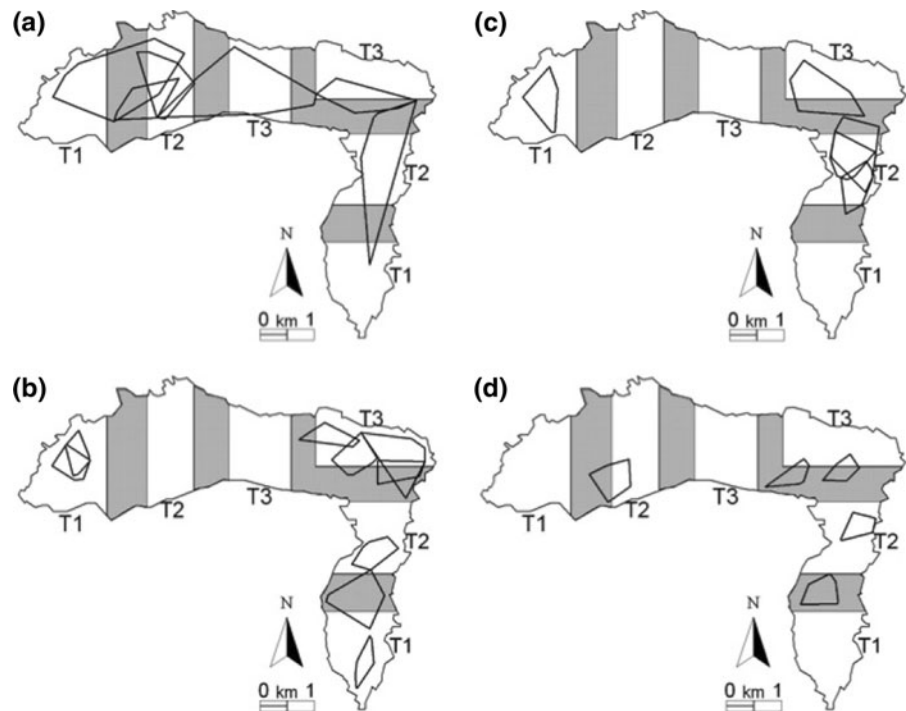
although they were typically less than 3 days and never more than seven.

Ferret control

The island was divided into six approximately equally sized treatment blocks (mean 151 ha, range 141–160 ha Fig. 1). The number of blocks was chosen as a balance between ensuring a degree of replication within the design while accommodating landowners and working with biologically meaningful space (Oksanen 2001). The size of a block was based on the results of the radio telemetry conducted over the winter of 2005–2006, and represents an area larger than the mean male ferret home range calculated from this study. Blocks were separated by buffer zones that were a minimum of 300 m across, a distance greater than the mean distance moved by male ferrets between consecutive fixes. Ferrets were removed from two randomly selected blocks in year 1 and from two different blocks in year 2, and were never removed from the final two blocks (Fig. 1). Thus both removal and non-removal treatments were replicated within each year, and the experimental removal treatment occurred as a crossover design between years. Clearly the confines of the island

produce natural limitations to the degree to which treatment areas can be separated and replicated. However, ferrets held home ranges, and so while some of the male ranges crossed buffer zones (Fig. 2), the majority of animals were not found in multiple treatment areas. This was also found when marked individuals captured during population monitoring were captured in the same areas during removal treatments. This meant that we would be comparing removal areas (where ferrets were virtually absent) to non-removal areas (with a slightly reduced number of ferrets). In addition, we were not attempting to compare results from removal and non-removal areas; instead we were taking advantage of our understanding of the entire population to examine the effect of localised culling on population responses. Traps within removal areas were set using the same methods as for population monitoring, and were run immediately prior to and then throughout the bird nesting season (which commenced slightly earlier in 2007) from 10 April–15 July 2006, and 25 March–15 July 2007. Absence of ferrets from traps was corroborated with data from unbaited tracking tunnels (King et al. 1994) run monthly in all treatment blocks. No ferrets were detected in removal zones, but ferret tracks were found in non-removal zones in all months, including

Fig. 2 Overwinter home ranges of radiocollared ferrets as 95% minimum convex polygons in relation to treatment areas (T1, T2, T3) and buffer zones (shaded grey) (see materials and methods and Fig. 1 for details) for **a** males 2005–2006 ($n = 6$) **b** females 2005–2006 ($n = 9$) **c** males 2006–2007 ($n = 5$) **d** females 2006–2007 ($n = 5$)



the presence of juveniles at the expected time (T Bodey unpublished data). In removal areas, captured animals were first anaesthetised using iso-fluorane, and then euthanized with an intra-peritoneal injection of sodium pentobarbital (Euthatal, Merial Animal Health Ltd.).

Ageing methods

Skulls of euthanized individuals were prepared following the methodology of McDonald and Vaughan (1999). A lower canine was then extracted and sent for cementum aging (Matson's Laboratory LLC, USA), with all individuals ascribed a common birth date of 1 April.

Data analysis

For 2005–2006 with two trapping sweeps of the island, the Lincoln-Petersen unbiased estimator (Chapman 1951) was used to estimate population size, with an unbiased variance calculated as per Seber (1973). For 2006–2007, a comparative Lincoln-Peterson unbiased estimator was calculated using the information from the first and last trapping occasions only to replicate the 2005–2006 protocol. However, the four trapping sessions allowed calculation of a more robust estimate for this second study season using maximum likelihood methods in Program MARK version 5.0 (White and Burnham 1999) under the assumptions of a closed population. Prior analysis of the 2006–2007 recapture data as an open population with a standard Cormack-Jolly-Seber model and goodness of fit tests carried out in RELEASE suggested the assumptions were not violated, but also produced high monthly survival estimates, which supported known overwinter survival from telemetry data. Thus a closed population model was appropriate as demographic closure is all but complete, and the assumptions of geographic closure and no loss or misidentification of marks were met.

All measures of home range analysis have limitations, some of which vary with the behaviour of the study species. Minimum convex polygons (MCPs) are robust with smaller sample sizes, and are necessary for comparison with other studies of feral ferrets (Kenward 2001). As 100% MCPs are sensitive to outliers, 95% MCPs were also calculated, with results presented for the latter although patterns did not vary between metrics. All home ranges were plotted in

Arcview 3.2, and bootstrapping of 1,000 iterations of points plotted against increasing area was used to check whether asymptotes were approached. Animals with too few data points, whether through collar failure or lack of observations, were excluded from analyses. All locations were included for each individual as observations were made a minimum of 15 h apart, a time well in excess of that required for an individual to move to any point within its home range (Rooney et al. 1998). The influence of year and sex and their interaction term were examined for both measures of home range using generalised linear models with a Gaussian error structure. Values were natural log transformed prior to analysis in order to meet assumptions of normality. Home range percentage overlaps were calculated between collared ferrets for each home range measure as the geometric mean of the product of the ratios of the area of overlap ($area_{\alpha\beta}$) to home range size of each individual ($homerange_{\alpha}$ and $homerange_{\beta}$) in the pair (Minta 1993):

$$\begin{aligned} \% \text{ overlap} \\ = [(area_{\alpha\beta}/homerange_{\alpha})(area_{\alpha\beta}/homerange_{\beta})]^{0.5} \end{aligned}$$

Results

Population size

In 2005–2006, 35 individuals were caught over 1,145 trap nights, with 66% recaptured at least once. This gave a catch per unit effort of 9.5 ferrets per 100 corrected trap nights. In 2006–2007, 62 individuals new for this trapping period were caught in 1907 trap nights, with 84% recaptured at least once. This produced a catch per unit effort of 11.6 ferrets per 100 corrected trap nights. For 2005–2006 the Chapman correction of the Lincoln-Peterson estimator \pm sd provided an estimate of abundance of 42 ± 4 . In 2006–2007 the same measure provided an estimate of abundance of 62 ± 7 . Applying maximum likelihood estimation to the data from 2006–2007, a model incorporating behavioural and individual responses to trapping (BH) was the most favoured, with twice as much support as for the model considering individual heterogeneity alone (H). Similar models incorporating an additional time component (BHT and HT) received much less support (Table 1). Population estimates from the first two models were almost

Table 1 Estimates of ferret population size on Rathlin Island

Model	AICc	Δ AICc	<i>W</i>	Model likelihood	Number of parameters	Deviance	Population estimate	Standard error
H, B	-72.42	0	0.58	1	4	13.03	63.7	2.15
H	-71.08	1.34	0.29	0.51	3	16.45	68.0	3.57
H, B, T	-68.57	3.85	0.08	0.15	7	10.59	63.4	2.14
H, T	-67.45	4.97	0.05	0.08	6	13.83	67.8	3.52

Estimates were generated from closed population models in program MARK. Models with Δ AICc > 7 are not shown. Model abbreviations are *H* individual heterogeneity of response, *B* behavioural response, *T* time response (Otis et al. 1978). Δ AICc is the difference between AICc values for each model and the baseline model with the lowest AICc, and *w* is the AICc weight

identical, and model averaging across all four models produced an abundance estimate of 65 ± 3 . Both methods thus suggest the island's total ferret population increased by approximately 50% following removal trapping across approximately one quarter of the island area.

Age structure

17 ferrets were removed in 2006 and 27 were removed in 2007 (Fig. 3), with ten more animals classed as young of the previous year in 2007. However there was no significant difference in capture rates between 1 year old and older ferrets between the 2 years (likelihood ratio 0.885, *df* = 1, *P* = 0.347). This was to be expected as different areas were trapped in the 2 years and so captured ferrets will not fully reflect any changes in population structure.

Home ranges

Fully explored home ranges were determined for 16 ferrets in 2005–2006 (six male, nine female) and for 10 individuals in 2006–2007 (five male, five female) (Fig. 2). Ferret home ranges were substantially greater for males (the larger sex) than females in both years, but the home ranges of both sexes were smaller in 2006–2007 than in 2005–2006 (Figs. 2, 4) (95% MCP mean \pm SD (ha) 2005–2006: males 136 ± 78 , females 35 ± 18 ; 2006–2007: males 54 ± 21 , females 22 ± 7). Both sex and year factors were significant (95% MCP: Year $F_{1,23} = 8.68$, *P* = 0.007; Sex $F_{1,23} = 33.96$, *P* < 0.001), but their interaction was not and was not included in the final model (Fig. 4). Where collared individuals were close enough together that range overlap was possible, substantial shared

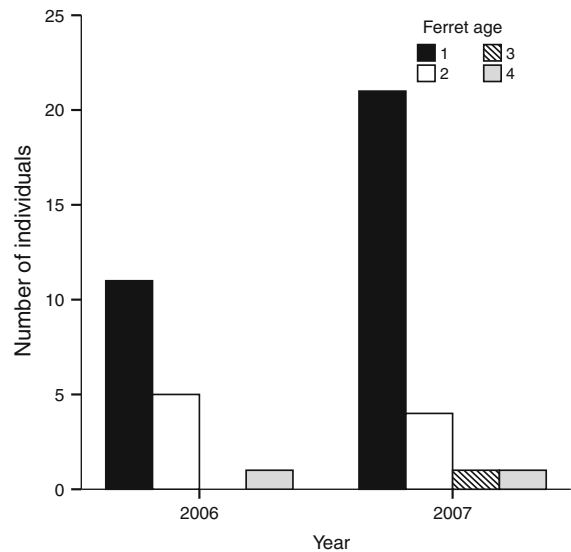


Fig. 3 Age of ferrets captured during predator control. Ferrets are all given the common birth date of April 1 so, for example, 1 year olds were all captured prior to April 1 the year after they were born and thus span the range from 0–1 years

areas were observed, with the extent of overlap being largely consistent between years and sex combinations (Table 2). Den sharing was observed through radio telemetry in both years (*n* = 23 occasions) and involved 20 different individuals.

Discussion

Our results indicate a substantial between-year increase in ferret population size following control efforts; an effect that was likely to have been driven by an increase in juvenile survival and recruitment to

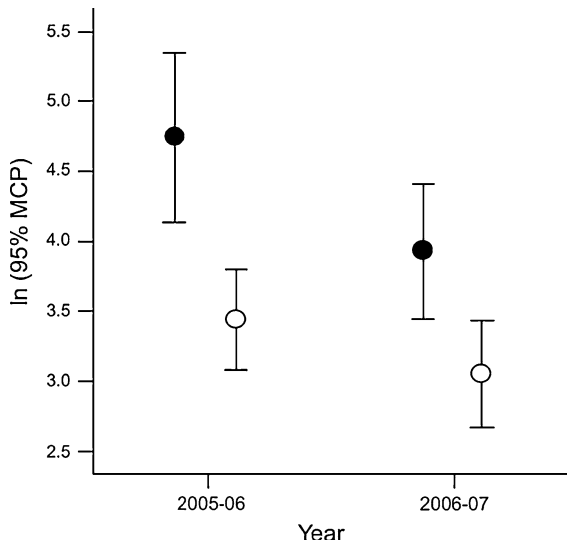


Fig. 4 Ferret home range size (ha) in different study years. Home ranges are plotted as natural log transformed 95% minimum convex polygons (MCPs) of male (black circles) and female (white circles) ferrets. 100% MCPs presented the same pattern

the adult population in individuals born outside trapped blocks which were then able to move into this unoccupied space. While a small number of individuals were removed even though their home ranges only partly spanned a removal area, this effect was limited to a few male ferrets in 2005–2006 only (Fig. 2), and does not alter this main conclusion. A population increase has an obvious significance for the prey species that predator control is designed to protect, and demonstrates that the development of predator management strategies should not ignore factors linked to the surrounding areas and the ecology of the species being controlled.

Population changes and survival

Prior to manipulation, ferret numbers on Rathlin were not high, with a density of approximately 3 ferrets per km². Models of ferret population dynamics from New Zealand, have demonstrated the importance of density dependent limitation in population growth, principally through low juvenile recruitment (Barlow and Norbury 2001; Caley et al. 2002). Barlow and Norbury (2001) suggested a 50% reduction in population size would be required to ensure a significant decrease in ferret numbers the following year. In our study, natural mortality over winter was low, and most individuals caught over winter were recaptured in the spring. Removal trapping over only part of the island was successful in substantially reducing the population in 2006, with at least 43% of the total population removed prior to the emergence of young of the year. Thus, adult densities were reduced in the period immediately prior to juvenile recruitment, reducing any potential impact of this constraint. However, while the total removed was close to the value suggested by Barlow and Norbury (2001) to be necessary for sustained population reduction, the opposite effect was observed.

Removal trapping in the second year was not implemented until after any density dependent recruitment effects could have operated (King et al. 1994; Byrom 2002), so the observed increase clearly represents enhanced juvenile survival, particularly where adults have been removed (Byrom 2002). In our study, removal blocks can only have been fully repopulated through immigration of juveniles from non-removal blocks, resulting in substantial overcompensation in recruitment levels across the entire population (Sinclair 1996). Although mortality (through decreased

Table 2 Overlap in the home ranges of male and female feral ferrets on Rathlin Island

Year	Home range measure	Mean % overlap (range)		
		Between females and males	Between males	Between females
2005–2006	100%MCP	23.7 (5.3–41.7)	34.8 (13.8–73.4)	34.3 (5.8–52.1)
	95%MCP	23.7 (2.3–51.7)	26.2 (6.0–73.9)	34.7 (5.8–52.1)
2006–2007	100%MCP	34.1 (16.4–49.9)	33.2 (15.7–52.8)	– ^a
	95%MCP	33.6 (5.1–56.6)	33.7 (11.0–63.3)	– ^a

Overlap is calculated as the geometric mean of the product of the ratios of the area of overlap to home range size of each individual in the pair, and expressed as a percentage

^a No female-female overlaps were found for collared females in 2006–2007 as animals were too geographically separated

prey availability and colder temperatures over winter for example) might then be anticipated to reduce the population, this was not apparent. Concurrent work on ferret diet (Bodey et al. 2010) revealed the potential for anthropogenic resources in the form of livestock carrion to sustain the ferret population even following decreases in their main lagomorph prey. However, it also demonstrated that the larger ferret population did not proportionately increase its consumption of this resource, indicating live prey levels were sufficient to support the great majority of new recruits. Thus the island was able to support a larger ferret population and, while this could be maintained as a result of current land management practices even if favoured lagomorph prey were depleted (Bodey et al. 2010), for how long remains unknown. However, clearly such fluctuations in predator numbers can have important ramifications for protective management of prey species in subsequent seasons (Courchamp et al. 2000). Even if predation of a species is only incidental, more animals will inevitably lead to more predation incidents, and for small populations of rare species, particularly those limited to topographical or habitat islands, the presence of such a predator can then be the difference between survival and extinction (Sinclair et al. 1998). In a mainland situation, such an increase in predator populations may not have greater deleterious impacts on localised prey though, as young animals are more likely to disperse in an attempt to find suitable underpopulated areas (e.g. Byrom 2002).

Territoriality

Small carnivorous mustelids typically display intrasexual territoriality (Johnson et al. 2000). Although Powell (1994) suggested that either high or low densities of food can lead to territorial breakdown in mustelids, studies of several exclusively carnivorous mustelid species demonstrate the maintenance of intrasexual territories even in these situations (Balharry 1993; Murphy and Dowding 1994; Herr et al. 2009). Our results clearly demonstrate a lack of either spatial or temporal territoriality between individuals, with both substantial range overlaps and frequent sharing of den sites; especially as these observations are restricted to collared individuals and so represent the minimum of shared occupancy. Field studies in New Zealand (Norbury et al. 1998; Ragg 1998) concur with this conclusion. Home ranges reported here are within the range of values from

studies in New Zealand, all of which are based on MCPs or trapping grid captures (summarised in Clapperton and Byrom 2005). However, both the mean and maximum MCP values for female home ranges are lower than those found in previous studies (Clapperton and Byrom 2005). Female home ranges did not shrink to the same extent as those of males, and so they may be closer to their lower limit on Rathlin.

Not only is the lack of territoriality in a carnivorous mustelid unusual, but so is the reduction in range size of both sexes between study years. While such an effect has been demonstrated in the red fox *Vulpes vulpes* even though ranges then fell below the optimum for resource acquisition (Sargeant 1972), ferret survival known from recapture rates, the observed body condition of animals (T Bodey unpubl. data), and prey consumption (Bodey et al. 2010) does not suggest resources were limiting here. However, even in cases where anthropogenic subsidies allow animals to reduce their home ranges (e.g. small Indian mongoose *Herpestes javanicus*, Quinn and Whisson 2005), spatial segregation was shown to be maintained. It is likely that the domesticated history of the feral ferret (Blandford 1987) is an important explanatory factor contributing to this increased tolerance of conspecifics and apparent lack of territoriality. This may be particularly relevant in relatively 'new' populations such as Rathlin's (present for approximately 25 years) compared to the more established populations in areas such as New Zealand (>100 years). However, such behaviour reduces the effectiveness of several management options. For example, reducing the number of denning sites, which has been recommended as a non-lethal control option (Frey and Conover 2007), will have a reduced impact in animals that are prepared to share dens. Similarly, ferrets are known to share even small carcasses simultaneously (Ragg et al. 2000, T Bodey pers. obs), and so the availability of anthropogenic dietary subsidies such as edible waste or fallen livestock (Quinn and Whisson 2005; Bino et al. 2010; Bodey et al. 2010) may also be an important consideration as these can sustain higher densities of predators than would otherwise be anticipated.

Implications for predator control programmes

King et al. (2009) recently highlighted a number of the difficulties encountered in eradicating small

mustelids. The key problems noted were a lack of accessible traps and latent individual variability, in particular wariness to trapping devices. A time component was not supported in our models, reflecting the high density and ease of access to traps for individuals in our study. Our best supported model did suggest individual variation in response to traps, which may be a result of an increase in young animals, but the behavioural response of the population suggested a general trend towards 'trap happy' rather than wary individuals. Although studies with other mustelid species have reported trap-shy behaviour after trapping for radio tracking studies (e.g. Zubergoitia et al. 2006), previous control of the ferret population on Rathlin has been irregular and very limited in extent, and so individuals may not have had an opportunity to learn or become wary (King et al. 2009). Ragg (1997) also found no difference in trappability between adult and juvenile ferrets, suggesting there may not be predictable differences between 'experienced' and 'naïve' individuals.

The restrictions inevitably imposed on the ferret population by virtue of our island study site are likely to contribute to reductions in home range size as juveniles are unable to disperse as, for example, occurs in mainland populations in New Zealand (Byrom 2002), so these results may be less applicable to a mainland situation. However, self-sustaining feral ferret populations in the UK are all found on relatively small islands such as on the Outer Hebrides and the Isle of Man (Kitchener and Birks 2008), probably because of their inability, again as a result of their domestic past, to successfully compete with wild carnivores (Kitchener and Birks 2008). These islands also frequently support internationally important breeding bird populations (e.g. Mitchell et al. 2004), and similar situations are found on several other European islands where feral ferrets have established such as the Azores, Madeira and Canary Islands (documented in Medina and Martin 2009). Thus our results are likely to have relevance to a number of other island situations in which ferrets are capable of threatening native fauna.

Clearly, where ferrets are introduced to an island, complete eradication is the obvious solution. However, on inhabited islands, this is only feasible if both local and wider-scale public support is obtained, particularly if this will necessitate lifestyle changes perceived as inconvenient, unnecessary or costly to

islanders (Opper et al. in press). In the meantime, it might seem sensible to protect important and/or rare populations through localised control, but control operations will only be effective if reductions in predator density exceed any potential density-dependent response in the population (Barlow et al. 1997). On a small island, it is feasible to examine the impacts of control on the overall population of an introduced vertebrate predator (Russell et al. 2009), a situation we were able to exploit here to examine population responses to the effect of localised culling. However, control over limited areas effectively represents a haphazard harvest of the predator population, and may well be irrelevant to its long-term size, particularly with highly fecund species such as mustelids (McDonald and Harris 2002). It can also, as our study suggests, be counter-productive if it results in an overall increase in predator numbers.

While complete eradication of invasive predators in a mainland context, as opposed to ongoing control, is difficult, advances are being made (e.g. Zabala et al. 2010). Such an approach is to be encouraged, particularly if it can be implemented prior to small scale control that may only serve to 'educate' intelligent species (King et al. 2009). Such control is also, in many instances, ultimately a continuous drain on resources, with repeated reinvasion from surrounding unmanaged areas (Parkes and Panetta 2009). In addition, while conditions on a protected area may be known and held constant, this is unlikely to apply to the surrounding environment, and so monitoring is necessary on a wider scale if any meaningful understanding of population-level dynamics, and thus the likely effectiveness of control, is to emerge (Wolff et al. 2002; King et al. 2007).

Consideration of the ecology of the species involved is also essential in order to properly assess levels of threat and determine how management options can most effectively deliver conservation benefits. In territorial species, removal of individuals may lead to increased territory size and decreased predator density (Gese 1998; Baker et al. 2000). Alternatively it may lead to higher rates of dispersal (McDonald and Harris 2002; Woodroffe et al. 2006), and so habitat management may be a more suitable option (Jiménez and Conover 2001). The non-territorial structure of feral ferret populations found both in this study and in New Zealand (Norbury et al. 1998; Ragg 1998) reduces the effectiveness of such

management options. The presence of individuals does not preclude the presence of additional animals, and therefore control may seem the best option. But removal can result in enhanced juvenile survival and reinvasion from surrounding areas, leading to the rapid recovery and, particularly within an island context, even increases in the total population. This paradox merits further consideration as it may also act for other flexible species, particularly if defining resources such as shelter or food are not limiting (Frey and Conover 2007).

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