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Experimental evidence of competitive release in sympatric carnivores

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Changes in the relative abundance of sympatric carnivores can have far-reaching ecological consequences, including the precipitation of trophic cascades and species declines. While such observations are compelling, experimental evaluations of interactions among carnivores remain scarce and are both logistically and ethically challenging. Carnivores are nonetheless a particular focus of management practices owing to their roles as predators of livestock and as vectors and reservoirs of zoonotic diseases. Here, we provide evidence from a replicated and controlled experiment that culling Eurasian badgers *Meles meles* for disease control was associated with increases in red fox *Vulpes vulpes* densities of 1.6–2.3 foxes km^{-2}. This unique experiment demonstrates the importance of intraguild relations in determining species abundance and of assessing the wider consequences of intervention in predator populations.

Keywords: badger; culling; ecological processes; mesopredator release; predator removal; tuberculosis

1. INTRODUCTION

Predators may be linked by a variety of ecological processes, dependent upon whether they compete for resources, eat each other or have other regulatory effects within the community (Polis *et al.* 1989). Dynamic interactions among predators appear to have a profound influence on ecosystems often by precipitating trophic cascades involving mesopredator release and hyperpredation, with considerable economic or conservation impacts (Crooks & Soulé 1999; Johnson *et al.* 2007).

While observational studies are compelling, empirical investigation of interactions among carnivores requires replicated and controlled experiments and these are rare owing to considerable logistical and ethical problems (Sih *et al.* 1985). A recent exception was the randomised badger culling trial (RBCT; Donnelly *et al.* 2006) in England, which was set up to investigate the efficacy of culling badgers *Meles meles* in reducing the incidence of bovine tuberculosis in cattle herds. The trial also presented a unique opportunity to experimentally assess the effects of badger culling on sympatric red foxes *Vulpes vulpes*. Badgers have been shown to interact with a wide range of species as predator and competitor and they are implicated in the transmission of bovine tuberculosis to cattle (Neal & Cheeseman 1996; Macdonald *et al.* 2004). Red foxes are also of economic, conservation and epidemiological concern, as they kill and eat ground-nesting birds (Reynolds & Tapper 1995*a*), hares (Reynolds & Tapper 1995*b*) and livestock (Moberly *et al.* 2003) and are widely culled by farmers and gamekeepers. Additionally, in the event of a rabies outbreak in Britain, foxes are likely to be the principal wildlife vector (Smith & Wilkinson 2003). Since foxes use badger setts as breeding dens, share a similar diet and have been shown to interact directly with badgers (Macdonald *et al.* 2004), we hypothesized that culling badgers that are considered to be the dominant species (Macdonald *et al.* 2004), would result in mesopredator release and an increase in fox numbers.

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2. MATERIAL AND METHODS

(a) *Experimental design*

Full details of the design and implementation of the RBCT have been published previously (Independent Scientific Group 2007). Briefly, 10 triplets were established, each consisting of three matched trial areas of approximately 100 km^2 that were randomly assigned to proactive badger culling, localized reactive culling following the identification of TB in cattle or to experimental control with no badger culling. Reactive badger culling areas were treated as additional experimental controls because fox surveys in these areas were stopped after 2 years, before reactive badger culling was initiated. In all areas, the first fox surveys were carried out prior to badger culling. We studied four triplets: E (Wiltshire), G (Staffordshire/Derbyshire), H (Somerset) and I (Cotswolds). The study ran for 5 years (2002–2006) in triplet I, including 4 years of culling, and for 7 years (2000–2006) in the other three triplets, including 5 years of culling. Within triplets, trial areas were shown to hold similar densities of badgers prior to culling (Donnelly *et al.* 2006). The efficacy of badger culling in the RBCT has been estimated previously by using trapping data to calculate the estimated reduction in the badger population after the initial cull (Independent Scientific Group 2007; Smith & Cheeseman 2007).

(b) *Data collection and density estimation*

Nocturnal spotlight counts of foxes (Heydon *et al.* 2000; Ruette *et al.* 2003) were carried out once a year from 57 to 64 fixed points in each trial area. Points were located along tracks and minor roads at least 500 m apart. Points were surveyed from the roof of stationary Land Rovers, and radial distances to foxes were measured using laser rangefinders.

Multi-covariate distance sampling (Buckland *et al.* 2001) was used to estimate fox density. To derive detection function models, sightings were pooled (Heydon *et al.* 2000) across areas, but separate models were derived for each year and treatment. This method provided density estimates that were fully independent between years, as the primary aim of our study was to monitor changes in fox density between years and assess responses to treatments (see electronic supplementary material for full details of field methods and additional distance analyses).

(c) *Statistical analysis*

Variance in fox densities was analysed by fitting a REML model to density estimates for each area in each year (Quinn & Keough 2002). Annual observations were treated as repeated measures of each area by modelling errors from sequential observations with a first order autoregressive structure. The main effects, treatment, triplet, trial area and year and the interactions between treatment, triplet and year were entered as fixed, categorical terms. Treatment had two levels: culled (a proactive treatment area after the initiation of badger culling) or not culled (treatment areas before the initiation of badger culling and control areas with no culling). The significance of explanatory terms was assessed by their Wald statistics, tested against a chi-squared distribution. Only significant interactions were included in the final model (table 2).

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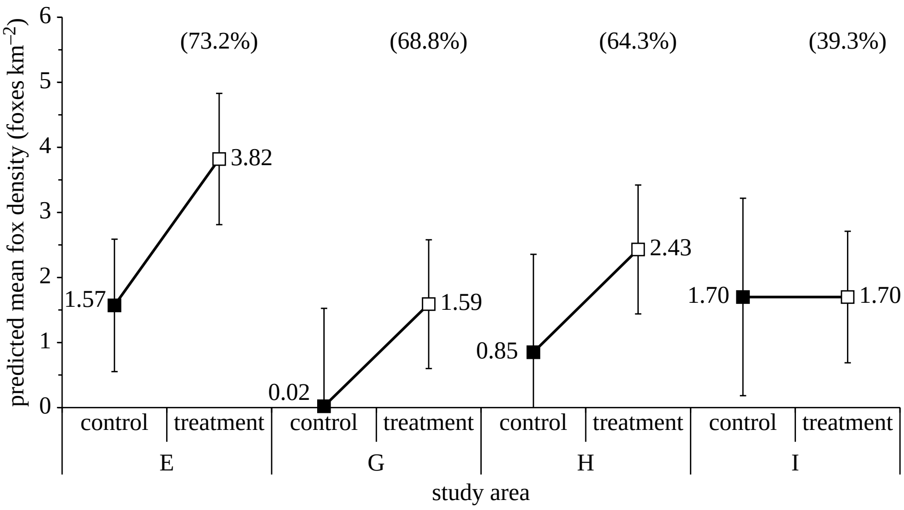

Figure 1. Predicted mean fox densities and standard errors in response to experimental badger culling. Densities are reported for four triplets (E, Wiltshire; G, Staffordshire/Derbyshire; H, Somerset and I, Cotswolds), each consisting of matched treatment and control conditions. The average effects and the constant were used to calculate the predicted means for each triplet for treatment and control conditions. The estimated efficiency of badger removal at the initial cull in each treatment area, calculated by Smith & Cheeseman (2007), is shown in parentheses.

3. RESULTS

There was a substantial reduction in the badger population in all triplets, though the efficacy of the initial cull in triplet I was lower than that of others included in this study (table 1; Smith & Cheeseman 2007). Fox densities ranged from 0.25 foxes km^{-2} in area G3 in 2005 to 5.15 foxes km^{-2} in area E2 in 2000. Estimates of fox densities in all experimental treatment and control areas are given in the electronic supplementary material, table S1. Densities were significantly affected by badger culling, and this effect varied between triplets (figure 1 and table 2). The effect of the interaction between treatment and triplet on fox density is shown graphically using the average effects and the constant to calculate the predicted means for each triplet with culling and with no culling (figure 1). Controlling for patterns of background temporal and spatial variation, predicted mean fox densities under treatment conditions were 1.6–2.3 foxes km^{-2} higher than under control conditions in three triplets, while in triplet I, where there was a less effective initial badger cull (table 1), fox densities were unchanged.

Table 1. Estimated reduction of the badger population after the initial cull in proactive culling treatment areas. (After Smith & Cheeseman 2007.)

area	total number of badgers culled	number of badgers caught in initial cull	pre-culling population estimate	estimated reduction at initial cull (%)
E	1463	605	827	73.2
G	996	427	621	68.8
H	593	162	252	64.3
I	661	219	556	39.3

4. DISCUSSION

The randomized treatment and control design of the study provide robust experimental evidence that increases in fox density were a result of reducing badger density and were not due to background variation in fox density. Further, there was unlikely to have been any systematic, sustained bias in factors affecting fox density between the matched treatment and control areas in this study, since the random allocation to treatments was central to the design of the RBCT, and owing to the long duration of treatment and observation periods.

It was beyond the scope of our study to determine the specific mechanism responsible for the increase in fox density in areas with reduced badger numbers. However, foxes and badgers share similar diets in the UK in terms of the range of food types eaten, and female foxes are known to use unoccupied badger setts to rear cubs (Neal & Cheeseman 1996). Therefore, given the dominance of the badger in aggressive interactions (Macdonald *et al.* 2004), the reasons for badgers appearing to limit fox density could include exploitative competition for key resources. A reduction in such competition due to badger culling could potentially cause increased adult fox survival and immigration, or increased cub production and survival.

In the wider ecological context, controlled experimental manipulations of predator populations have frequently been advocated in order to better understand carnivore communities and their role in ecosystem functioning (Polis *et al.* 1989; Glen & Dickman 2005). However, such manipulations are scarce, despite the profound importance of carnivore interactions on community structure. Observational studies of interactions between carnivore species have provided compelling evidence for their importance in determining carnivore abundance and distribution (Berger & Gese 2007), and hence the impact on their prey (Johnson *et al.* 2007). For example, the hypothesis that competition with wolves *Canis lupus* influences the distribution and abundance of coyotes *Canis latrans* (Petersen 1995) in much of North America was supported by research showing a strong negative correlation between the density of wolves and that of coyotes (Berger & Gese 2007). In Australia, introduced red foxes and cats

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Table 2. Summarized results of REML model explaining variance in fox densities with respect to experimental badger culling.

fixed term	Wald statistic	d.f.	*p*-value
triplet	6.77	3	0.08
trial area	3.01	7	0.88
treatment	5.30	1	0.02
year	23.29	5	<0.001
triplet × treatment	8.29	3	0.04

Felis catus are thought to have been responsible for the declines and extinctions of a wide range of native mammalian prey (Dickman 1996). However, their impacts on marsupials appear less severe in areas where dingos *Canis familiaris dingo* remain abundant and cats and foxes are killed by the larger predator (Johnson *et al.* 2007). Dingo numbers are controlled owing to their role in the predation of livestock, but this is likely to be detrimental to maintaining native biodiversity.

Controlled experiments produce stronger inferences than observational studies, being less open to alternative explanations (Sih *et al.* 1985). For example, experimental removal of coyotes precipitated an increase in mesopredators including badgers *Taxidea taxus* and grey foxes *Urocyon cinereoargenteus*, and a concurrent decline in rodent species richness and diversity (Henke & Bryant 1999). However, such experiments on mammalian carnivore communities are likely to remain rare. This study provides valuable experimental support for previous observations of the significance of competition among sympatric carnivores in ecosystem processes.

From an applied perspective, badger culling, undertaken at least at the temporal and spatial scales applied in the RBCT, is likely to result in markedly higher fox densities. This raises issues relating to the costs of predation on livestock and game, the ecological impact of foxes in conservation terms as predators of ground-nesting birds and hares, and risks to public health as potential vectors of rabies. Therefore, this finding also demonstrates the practical importance of assessing the wider ecological consequences of manipulating wildlife populations.

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