

Restricted-area culls and red fox abundance: Are effects a matter of time and place?

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Abstract

Predators are often culled to benefit prey, but in many cases this conservation goal is not achieved or results remain unknown. The red fox (*Vulpes vulpes*) is a predator of global significance, and an invasive species in some regions. Red fox culls intended to benefit prey are often restricted to small areas, and effectiveness is rarely sufficiently evaluated. Given the economic, ecological, social, and welfare issues associated with lethal predator control, there is a strong need to assess the effects of spatiotemporal variation in culling intensity on red fox abundance. We surveyed red fox populations in fragmented forests of south-western Germany and related indices of local fox abundance to culling data, predicted landscape-scale fox abundance, and other covariates. We tested whether restricted-area culling was associated with local reductions in fox abundance, and examined how this relationship changed over time. Local fox abundance was temporarily reduced in spring, following winter culls. However, the effect was minor and fox populations had compensated for the reductions at the latest by autumn. Restricted-area culling therefore likely failed to sustain effects on fox abundance throughout the period most relevant for conservation (i.e., the reproductive period of the target prey species). To be effective as a conservation tool, culling will therefore require explicit spatiotemporal coordination matching the biology of predators and target prey.

KEYWORDS

camera trap, capercaillie, conservation hunting, grouse, mesopredator, population density, population regulation, predator control, wildlife management

1 | INTRODUCTION

The extirpation of apex predators and widespread habitat modification have altered predator communities in ecosystems across the globe (Estes et al., 2011; Prugh et al., 2009; Ripple et al., 2014). Major shifts in ecosystems are often expected following changes in apex predator abundance (Estes et al., 2011; Fretwell, 1987), including “mesopredator release” (Crooks & Soulé, 1999). Increased mesopredator abundance and activity may exert elevated

predation pressure on some prey (Brashares, Prugh, Stoner, & Epps, 2010; Prugh et al., 2009; Ritchie & Johnson, 2009), particularly specialist prey populations in productive fragmented landscapes (Brashares et al., 2010; Ryall & Fahrig, 2006). In response, managers often remove mesopredators in an attempt to benefit threatened prey species or increase the abundance of game species for hunting (Conner & Morris, 2015; Reynolds & Tapper, 1996), but the efficacy of such actions often remains poorly known (Doherty & Ritchie, 2017).

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The red fox (*Vulpes vulpes*) is a mammalian generalist mesopredator with one of the widest distributions of all carnivores (Hoffmann & Sillero-Zubiri, 2016), and is considered invasive in some regions, including Australia (Saunders, Gentle, & Dickman, 2010). Red foxes can reach high densities in fragmented anthropogenic landscapes in the absence of top down control (Güthlin, Storch, & Küchenhoff, 2013; Pasanen-Mortensen & Elmhagen, 2015; Pasanen-Mortensen, Pykönen, & Elmhagen, 2013), and due to resource subsidies (Bino et al., 2010; Hradsky et al., 2017). Accordingly, the red fox is a predator of global relevance for conservation and game management (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016; Lowe, Browne, Boudjelas, & De Poorter, 2000), and subject to lethal control efforts in many regions.

Predator control can benefit prey species where effectively implemented (Salo, Banks, Dickman, & Korpimäki, 2010), and this has been well demonstrated for birds in particular (Côté & Sutherland, 1997; Kämmerle & Storch, 2019; Smith, Pullin, Stewart, & Sutherland, 2010), but often control fails to achieve its conservation target (Lennox, Gallagher, Ritchie, & Cooke, 2018). Predator control efforts typically only have short-term impacts on predator populations (Conner & Morris, 2015; Lennox et al., 2018) and their effectiveness is, apart from in experimental studies, rarely quantified and evaluated in practice (Doherty & Ritchie, 2017; Walsh, Wilson, Benshemesh, & Possingham, 2012). Regardless of conservation targets, there are also ethical and economic issues to consider (Baker, Singleton, & Smith, 2007; Perry & Perry, 2008; van Eeden, Dickman, Ritchie, & Newsome, 2017; Wallach, Bekoff, Nelson, & Ramp, 2015). Given its controversial nature and limited resources in conservation, it is essential that any predator control has a strong evidence base of support (Doherty & Ritchie, 2017).

Fundamentally, the effectiveness of predator control depends on clear objectives and adequately intensive removal effort (Reynolds & Tapper, 1996; Salo et al., 2010). In addition, predator control must adequately match the ecological requirements of the respective target species (i.e., account for predator and prey biology) in both space and time to produce the desired conservation outcome (Conner & Morris, 2015; Lennox et al., 2018; Mahoney et al., 2018). In practice, however, the effectiveness of predator control may be limited by constraints such as the available person hours, the limits imposed by hunting legislation and/or the variation in property rights (access for control operations) across an area of interest, leading to potentially insufficient and spatially uncoordinated actions.

In Europe, the predominant method of red fox control is culls in spatially restricted areas such as hunting concessions or conservation reserves. Large variation in commitment

among individual hunters or property owners (e.g., in Germany: Langgemach & Bellebaum, 2005) may dilute an effect of predator control, creating a mosaic of culling intensity across the landscape. In such cases, culls become spatially structured harvests from continuously distributed predator populations (Conner & Morris, 2015) whose effects are rapidly challenged by immigration from surrounding source populations (Lieury et al., 2015; Newsome, Crowther, & Dickman, 2014; Porteus, Reynolds, & McAllister, 2018). Effects of such “restricted-area culling” on local red fox abundance are ambiguous (Baker & Harris, 2006; Heydon & Reynolds, 2000; Lieury et al., 2015; Newsome et al., 2014; Porteus, 2015) and it typically remains uncertain whether reductions in red fox abundance are adequate in both space (i.e., the area of interest) and time (i.e., the period of interest) to achieve conservation targets. This questions the application of predator control as a management tool (Lennox et al., 2018) and emphasizes the need for a more thorough evaluation of the relationship between spatial heterogeneity in culling intensity and spatiotemporal variation in red fox abundance.

In this study, we surveyed red fox populations in fragmented montane forests of south-western Germany using camera trap data and scat surveys across a network of study sites that differed in their culling strategy of red foxes (i.e., either targeted or no targeted removal of red foxes). We related indices of local variation in red fox abundance to culling data and predictions of landscape-scale red fox abundance to test whether restricted-area culling of red foxes was associated with local reductions in red fox abundance and how this relationship changed throughout the year. We predicted that red fox abundance would be locally reduced at the culled sites immediately following the cull, but that culling effects would be rapidly compensated later in the year.

2 | METHODS

2.1 | Study area and species

The study area was located in the southern Black Forest mountain range in south-western Germany at elevations of 800 to approximately 1,300 m above sea level (Figure 1). The area is characterized by a land use mosaic dominated by mixed montane forests (approximately two-thirds forest cover, Braunisch & Suchant, 2007), fragmented by settlements, single farms, and agricultural land cover types (primarily livestock pastures; Figure 1). For more information on the study area, see Kämmerle, Coppes, Ciuti, Suchant, and Storch (2017) and Kämmerle, Corlatti, Harms, and Storch (2018). Red foxes occur in all parts of the study area and their relative abundance varies in relation to landscape

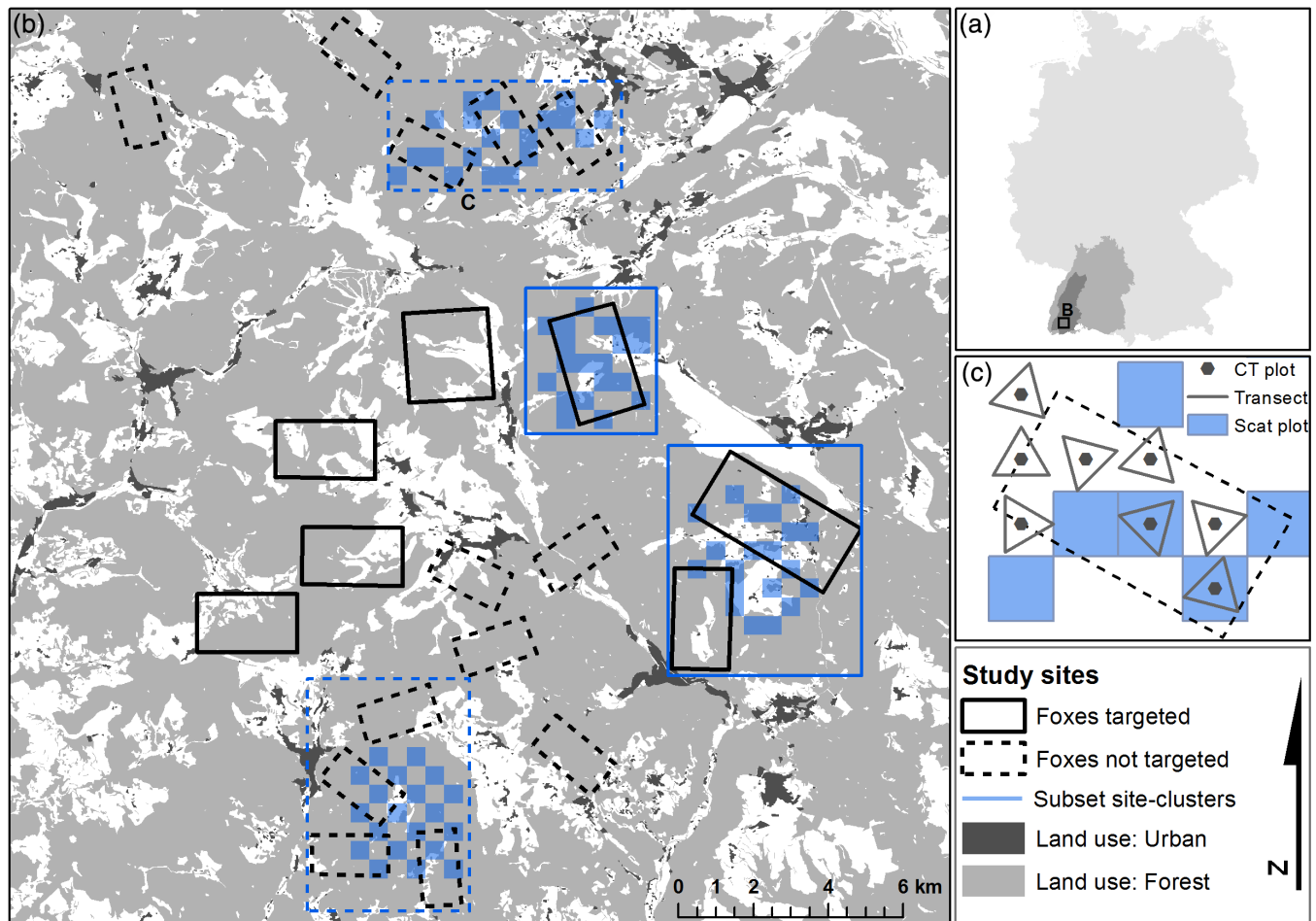


FIGURE 1 Overview of the study sites for estimating red fox abundance (B) in the southern Black Forest mountain range (dark grey) in the state of Baden-Württemberg, Germany (A). Camera traps were deployed at all study sites and during all sessions. The insert map (C) depicts the survey design within one study site within a site cluster for coinciding camera trap (CT) surveys and triangular scat transect counts or square scat plots, respectively

configuration (Güthlin et al., 2013). Red foxes are highly adaptable, medium-sized canids with a body size of 3–14 kg and a broad diet (Nowak, 2005; Soe et al., 2017), comparatively fast life-history and high dispersal ability (Devenish-Nelson, Harris, Soulsbury, Richards, & Stephens, 2013; Heydon & Reynolds, 2000; Walton, Samelius, Odden, & Willebrand, 2018). Fox populations are thus capable of compensating high culling-induced mortality. Home-range sizes obtained through VHF telemetry in parts of the study area (Kaphegyí, 2002) suggest low to intermediate red fox density (below five individuals km^{-2} ; Šálek, Drahníková, & Tkadlec, 2015). Management of red fox populations is incentivized in the study area, because red foxes are considered important predators of capercaillie (*Tetrao urogallus*), a locally threatened grouse species (Kämmerle et al., 2017). Grouse are ground nesting birds and thus vulnerable to predation of eggs and chicks as well as adult birds (Storch, 2007). The study area contains a remnant population of capercaillie that has experienced recent declines in abundance

and range extent (Coppes et al., 2016; Kämmerle et al., 2017). In the study area, capercaillie typically display at during April, lay and start nesting in May and subsequently raise chicks through July (Klaus, Andreev, Bergmann, Porkert, & Wiesner, 1989), making this the most relevant time for capercaillie conservation.

2.2 | Red fox culling regime

In general, shooting and hunting of game species in the area is organized and concession-based according to German legislation. The study area contained privately allotted hunting concessions and hunting grounds managed by the state, both ranging between approximately 100 to 1,500 ha in size. Hunters in the study area typically focus on ungulate game species. Hunting of red foxes and several other mammalian mesopredators (e.g., *Martes* spp. *Meles meles*) is permitted without quota outside of the closed season. Incentives to cull foxes were provided during our study by local chapters of

the state hunters association aiming at capercaillie conservation, because state law requires conservation imperative to permit certain types of fox hunting. In addition, there was encouragement by the state hunters association to sell the fur through provision of infrastructure and awards for high shooting bags. The hunting season for the red fox in the area lasts from August to February, although the majority of the culling is performed during the winter months (i.e., December–February) by shooting. Accordingly, the culling intensity at a site is largely determined by the commitment of the concession owner, thus creating a mosaic of varying culling intensity across the landscape. Culling intensity ranged from 0 to 5 foxes per 100 ha⁻¹ shot annually at the study sites during the study period. In this study, we selected the participating hunting concessions based on their culling effort with regards to red foxes (i.e., no culling, occasional shooting, targeted removal). We established the culling strategy and average hunting bags in former years during stakeholder workshops.

2.3 | Survey design

We selected study sites within sets of several spatially adjoining groups of hunting concessions with a similar culling strategy. Sites were selected to be characterized by either targeted removal of red foxes or no fox removal (henceforth targeted and nontargeted sites; Figure 1). Rectangular study sites in targeted sites were designed to spatially match fox removal areas, while we assigned rectangular study sites of fixed size to nontargeted sites until equal field effort was achieved. We chose this approach to ensure that study sites in each of the two classes (i.e., targeted vs. nontargeted) were contained by areas of comparable culling strategy. Study sites in both classes were selected in areas of both similar landscape composition and similar predicted red fox abundance (using predicted relative abundance index [RAI] values as in GÜTHLIN, Storch, and Küchenhoff (2014); value range “targeted” sites: 1.25–2.58; “nontargeted” sites: 1.11–2.48; whole study area: 1.02–5.52), to minimize the potential bias of high hunting bags simply reflecting high fox abundance. We finally selected study sites from an area of approximately 30 × 60 km, comprising 26 concessions ranging in size between 140 and > 1,000 ha each (mean = 700 ha, *SD* = 400). The total surveyed concession area amounted to approximately 18,000 ha.

We surveyed populations of red foxes at the study sites at two spatial scales at a network of spatially coinciding plot locations. We assigned plots to all study sites using a systematic grid of 500 m spacing to assign plot centers. Grid orientation was moved in each study season by 250 m

(i.e., half the distance between plot centers) in a random direction, to avoid resampling at the same site.

For the first scale of analysis (henceforth “*landscape-scale*”), we assigned plots to all study sites in our study area. Due to differences in the size of study sites, six plots each were allocated to 13 nontargeted sites and 10–12 plots to seven targeted study sites that targeted foxes in order to achieve even distribution of effort (Figure 1). The selection of plots from the grid was stratified by the expected abundance of foxes using a proxy for fox abundance based on landscape composition and productivity (using predictions as in GÜTHLIN et al. (2013, 2014)).

For the second scale of analysis (“*site-clusters*”) we selected four separate sites or groups of sites (further called “clusters”), either targeting (two clusters) or not targeting (two clusters) foxes (Figure 1). These comprised 10 of the landscape-scale study sites (three sites targeting foxes; seven sites not targeting foxes).

Red fox populations were surveyed at three sampling occasions, henceforth referred to as winter, spring, and autumn abundance, respectively: between January and February (i.e., to coincide with the main culling period); from late March to mid-May (i.e., to represent breeding populations after the hunting season) and between late September and early November (i.e., postbreeding populations before the hunting season).

We surveyed red fox populations at plot locations using two complementary RAIs: camera traps and scat surveys. We performed camera surveys during all seasons at all sites using nonbaited, remotely triggered wildlife camera traps (Bushnell Trophy Cam Aggressor Low Glow). Camera trap surveys have previously been used to estimate landscape-scale red fox abundance and deliver estimates comparable with scat transects (GÜTHLIN et al., 2014). However, they outperform scat count methods when estimating small-scale variation in fox abundance and depicting relationships with environmental covariates of abundance (KÄMMERLE et al., 2018). To standardize detection probability across all sample plots and to maximize red fox detection rates, we placed cameras on logging tracks (i.e., similar to GÜTHLIN et al., 2014), always selecting the nearest track outwards from the plot center. All efforts were made to standardize camera deployment in the field. We strived to select similar tracks within each plot, but recorded trail width and trail class (Factor with four levels: 1 = game trail or almost completely overgrown logging track; 2 = nonmaintained logging track with young vegetation; 3 = maintained logging track; 4 = unpaved forest road) to correct for any differences between the probability of trail use by foxes among track types in the analysis. Cameras were placed as low as possible above the track (typically 0.5–1 m). Camera orientation was slightly angled sideways to ensure good coverage of the

track and detect fast-moving individuals. We set cameras to take sequences of three pictures with a 1-s delay between photo bursts. Cameras were placed in the field during two consecutive intervals per season, each spanning at least 14 (winter season) and 21 (spring and autumn) operational camera days before collection. Cameras were operational in the field between March 15, 2017 and March 12, 2017 as well as March 15, 2018 and May 15, 2018 for spring abundance (i.e., 2 years); between September 13, 2017 and November 10, 2017 for autumn abundance and between January 29, 2018 and March 9, 2018 for winter abundance. Images were sorted to species level. We then extracted the image metadata using the package *camtrapR* (Niedballa, Sollmann, Courtiol, & Wilting, 2016) in software R (R Core Team, 2019) and grouped image sequences into events using a break value of 5 min between images as a conservative value based on visual assessment of the images.

In addition to camera trap surveys, we performed scat surveys at the study sites of the site-cluster scale sites (Figure 1). Scat abundance is thought to reflect fox abundance (Baker & Harris, 2006; G  thlin et al., 2014). We conducted randomly oriented triangular transects centered on each plot location of a total length of 1.3 km each (the maximum triangle size in a 250-m radius circular plot) during the spring and autumn season of 2017 and performed scat surveys in quadrat scat plots of 25 ha size (i.e., 500 × 500 m cells; henceforth “scat plots”; Figure 1) in the spring season of 2018 (Figure 1). We used randomly oriented transects, because G  thlin, Kr  schel, K  chenhoff, and Storch (2012) found random transect sampling to have higher precision than scat sampling along trails, which is the most common method to survey foxes (e.g., Baker & Harris, 2006; Carreras-Duro, Mole  n, Barea-Azc  n, Ballesteros-Duper  n, & Virg  s, 2016; Cavallini, 1994). For the spring season 2018, scat plots were randomly selected from the plot grid that was also used for camera placement within study sites of Scale 2. Trail-based scat sampling has been found to deliver data with low precision, while small scat plot cells (0.25 ha) produced a very small mean (i.e., large proportion of zeros; G  thlin et al., 2012). Accordingly, we designed larger scat plots to ensure a larger mean and higher precision by representatively sampling the whole plot (i.e., including tracks as well as all available habitat types). Scat plots were surveyed hap-hazardly aiming for representative plot coverage, but search effort was standardized by searching for three man hours on each plot. Scat was collected on both plots and transects at a walking speed of approximately 1 km/hr. We identified fox scats according to their size, shape, odor, and content (Olsen, 2013). Species with potentially similar scat in the study system are pine marten (*Martes martes*) and beech marten (*Martes foina*), which both typically produce scats that are much smaller, and dogs. We

applied multiobserver validation for scat identification (i.e., each scat was validated to be fox scat by at least one expert in addition to field volunteers). We randomly assigned observers to scat plots and transects (i.e., six observers each season). In addition, we scored scats along a gradient of scat quality (i.e., degree of decomposition) and identification certainty using three classes (A–C; A: highest; B: scats of intermediate quality; C: scats of low identification certainty). Spring surveys were conducted between March 29, 2017 and May 10, 2017 as well as April 2, 2018 and April 18, 2018 for spring abundance before ground vegetation interfered with search efficiency and between September 26, 2017 and October 25, 2017 for autumn abundance before snow cover prohibited field work. Snow cover prevented scat surveys during the winter season. Final sample sizes for each season and method are provided in Table 1.

2.4 | Environmental predictors

The set of environmental predictors used in this analysis comprised an index of landscape-scale variation in red fox abundance derived from a landscape model (G  thlin et al., 2013, 2014), a number of additional predictors of landscape configuration, as well as some site- and study-level covariates, which are described below in more detail (see Table 2 for a brief overview). In addition, we processed hunting bag data into a continuous predictor of culling intensity across the study area. For camera-based RAIs we extracted environmental data at the plot locations or from circular buffers as specified. For scat-based RAIs, environmental predictors were averaged within a 25-m circular buffer for random transects (i.e., minimum circular area around a triangular transect) or within square scat-plots.

TABLE 1 Sample sizes for the analysis of culling effects on red fox abundance during four sessions in three seasons and at two spatial scales

| Session 1: Spring 17 | Session 2: Autumn 18 | Session 3: Winter 17/18 | Session 4: Spring 18 |
|---|-------------------------|----------------------------|-------------------------|
| Landscape scale: Complete study area. | | | |
| Grid-based deployment of camera traps. | | | |
| N = 130 | N = 134 | N = 105 | N = 150 |
| Site clusters: Subset of the study area; Hunting strategy as: (High Low) | | | |
| Grid-based deployment of camera traps. | | | |
| N = 66 (28 38) | N = 66 (29 37) | N = 60 (26 34) | N = 83 (44 39) |
| Triangular scat transects (Sessions 1 and 2) and rectangular scat plots (Session 4) | | | |
| N = 59 (26 33) | N = 58 (27 31) | — | N = 82 (41 41) |

TABLE 2 List of predictors considered in the analysis of culling effects on red fox abundance in the Black Forest, south-western Germany. The abbreviations given are used throughout the text. Please see the method section for full details on all predictors

| Category | Description | Abbrev. | Unit | Source (resol.) | Resolution analysis |
|----------------|---|------------|---------------|---|--|
| Red fox | Predicted red fox abundance | FoxExp | Index (0–6) | Güthlin et al. (2013, 2014); (30 m) | Mean in buffer |
| | Normalized hunting bag as foxes culled km ⁻² | Hunting | Density (0–5) | Empirical | Mean in buffer (Landscape scale only) |
| | Fox culling strategy class as either high or low | HUNT | Factor | Empirical | Site location (Site clusters only) |
| Landscape | Distance to human settlement or town | HumDist | m | Geographical Information System (GIS; 50 m) | Site location (CT data) Mean in buffer (Scat) |
| | Distance to agricultural land use | AgriDist | m | GIS (50 m) | Site location (CT data) Mean in buffer (Scat) |
| | Distance to paved roads | RoadDist | m | GIS (50 m) | Site location (CT data) Mean in buffer (Scat) |
| Site controls | Slope of the terrain | Slope | Degree | GIS (50 m) | Site location (CT data) Mean in buffer (Scat) |
| | Variation in slope around plot location | SlopeSD | Degree | GIS (50 m) | Standard Deviation in buffer |
| | Proportion of ground covered by structures resisting fox movement | Resistance | Index (1–10) | Empirical | 20 m around camera (CT data only) |
| | Type of forest track as either track or trail. | Ctrail | Factor | Empirical | Site location (CT data only) |
| Study controls | Year of the study | Year | Factor | — | — |
| | Season of the study | Season | Factor | — | — |
| | Number of active camera trapnights | Trapnights | Days | Empirical | (CT data only) |

CT data: Data obtained using grid-based wildlife camera trap deployment at both spatial scales; Scat: data obtained by scat sampling along triangular linear transects or within rectangular scat plots at the scale of site clusters. Please see Figure 1 for the spatial scales.

2.5 | Predicted red fox abundance

We obtained an index of landscape-scale red fox abundance to correct for expected abundance when testing for culling effects on fox populations. Using the results of Güthlin et al. (2013, 2014), we predicted landscape-scale variation in the relative abundance of red foxes (hereafter “*predicted fox abundance*”) across the whole study area. The model associates increasing fox abundance with diverse and productive landscape types characterized by a mosaic of land cover types and is closely related to landscape-scale variation in absolute abundance of red foxes in the area (Güthlin et al., 2013, 2014). We predicted fox abundance following the protocol for data preparation described by Güthlin et al. (2014) and using the original predictors. The model is spatially but not temporally explicit, thus does not incorporate differences in fox abundance between seasons.

2.6 | Landscape predictors

In addition to predicted fox abundance, we obtained the distance of a camera site to the closest agricultural land cover

type (i.e., mainly montane pastures). We used mean distance for each scat-plot or transect for this and all other landscape predictors (Table 2). We also obtained the distance to paved roads and the distance to the closest human settlement. We considered towns, villages, and individual farms and assigned values based on whichever type of settlement was located closest to the plot location (camera) or plot center (scat). Finally, we obtained the slope at the plot site as well as the variation in slope within a 250-m circular buffer as an index for terrain ruggedness around plot locations (camera) or plot centers (scat), because we expected fox movement on tracks (i.e., high RAIs) to be more likely in steep or rugged terrain.

2.7 | Site and study covariates

We recorded a number of plot site covariates at each camera trap location. We estimated the proportion of ground in a 20 m buffer around each camera location covered by vegetation or coarse woody debris that could hinder red fox movement as an index of movement resistance. During winter, we estimated the depth of snow cover at the site. To combine

both measurements, we standardized both types of values by dividing values by the respective maximum value (i.e., to obtain a range of 0–1) and multiplied final values by the factor 10 to obtain an index of movement resistance during all seasons. We expected red fox movement to be channeled onto forest tracks at plots with high index values. We also processed the type of forest track at each camera site into a factor variable with two levels, “trail” for original track types 1 and 2 and “track” for original types 3 and 4.

2.8 | Red fox culling

We processed raw hunting bag data into a continuous predictor of culling intensity across the study area. We obtained governmental hunting bag data at the concession level for both years of the study (i.e., hunting season 2016/2017 and 2017/2018) and assigned red fox hunting bags for each study year to the centroid of each hunting concession in our study area. We repeated this for all surrounding hunting concessions up to a distance of more than one mean fox home-range diameter distance to the study area. Raw hunting bags of each study year were normalized by the area of each concession to obtain the number of foxes culled km^{-2} . We then processed the normalized bag data to obtain a continuous estimate of variation in culling intensity across the landscape by interpolating values using a two-dimensional minimum-curvature tension spline that exactly passed through the input points in software ArcMap 10.5.1 (ESRI, 2018). For the analysis at the landscape scale, we extracted the mean culling intensity value within a 250 m buffer around the plot location. At the scale of site clusters, the factorial predictor of culling intensity “HUNT” was determined by the study design (“high” vs. “low”; i.e., as sites either targeting foxes or not). Normalized hunting bags were significantly larger at “high” sites than at “low” sites in both years and for both camera and scat data (Wilcoxon-Mann-Whitney test, camera: $U = 6,791, p < .001$; scat: $U = 312, p < .001$).

3 | STATISTICAL ANALYSIS

All analyses were carried out using free software R (version 3.5.2; R Core Team, 2019). We assessed environmental predictors for collinearity by calculating pairwise Pearson correlations and we only retained predictors with a correlation coefficient $|r| < .6$. We analyzed RAIs by fitting generalized linear models (GLMs) with negative binomial distribution of errors and the abundance index as a response. We used negative binomial regression, because GLMs with a Poisson error distribution indicated very strong overdispersion and a bad fit to the data. We verified that parametric assumptions regarding model fit were met.

For camera-based RAIs at both spatial scales, GLMs were fitted using the MASS library (Venables & Ripley, 2002) using the number of active trap nights at each camera station as a model offset to correct for sampling periods of different length. Prior to fitting GLMs, we calculated the intraclass correlation coefficients of the study sites in all seasons (library ICC; Wolak, Fairbairn, & Paulsen, 2012) to ensure that there was no bias from within-site clustering of RAI data. This was not the case. Full models of camera-based RAIs for Scale 1 and Scale 2 included distance to human settlements (“HumDist”), distance to agricultural land use (“AgriDist”), distance to paved roads (“RoadDist”), the slope, and the variation in slope (“SlopeSD”; see Table 2). A number of control variables were included to account for differences in detection probability between plots: the type of track at the camera site (“Ctrail”) and the movement resistance index (“Resistance”) as well as the year of the study (“Year”). At the landscape scale, we included the interaction of the continuous normalized hunting bag size (“Hunting”) and the “Season.” The model at the scale of site clusters differed by the inclusion of the categorical culling strategy (“HUNT”) interacted with “Season.”

For the scat-based RAIs at the scale of site clusters, we fitted negative binomial generalized mixed-effect models (GLMMs) with a random intercept term for observer ID in R package glmmADMB (Fournier et al., 2012; Skaug, Fournier, Bolker, Magnusson, & Nielsen, 2016) to account for differences in detection probability between observers. We built two models: (a) including counts of all scats as a response and (b) only including scats of high identification certainty (i.e., classes A and B). Due to convergence issues with the full models, we were forced to fit a reduced model on the scat count data (see Kämmerle et al., 2018) and we selected the reduced set of predictors based on our hypotheses. Accordingly, the full model only included the predicted red fox abundance, a factor variable correcting for the type of scat sampling conducted (i.e., transect vs. plot; i.e., equivalent to “Year”; Table 2) and an interaction of “Season” with the hunting strategy class (“HUNT”). We assessed whether fitting a zero-inflated model improved model fit by means of Akaike information criterion (AIC), but proceeded without as this was not the case.

Continuous predictors were standardized by subtracting the mean and dividing by the standard deviation in all models to allow for comparison of effect sizes and to ease model convergence. We assessed by means of AIC whether inclusion of a quadratic term for predicted fox abundance improved model fit for all models and retained it if this was the case. We otherwise present full model results. All data supporting the results are included in the supplements (Appendix S1).

4 | RESULTS

In total, we analyzed camera-based RAI data comprising 2,977 red fox events from 11,675 active trap nights at the scale of the whole study area (landscape scale) and 1,380 red fox events from 6,437 active trap nights at a subset of sites (site clusters) across three seasons in 2 years. In addition, scat-based RAI data comprised 477 fecal samples collected on 199 occasions at Scale 2, of which 255 samples were classified as being red fox scat with high certainty and 222 as low certainty.

4.1 | Fox abundance

Camera-based red fox RAIs had a significant positive relationship with the predicted landscape-scale fox abundance at both scales (Table 3; Figure 2). In addition, camera-based

RAIs decreased significantly with increasing distance to agricultural land uses and sealed roads, but were significantly positively related to the distance to human settlements (Table 3). With regards to plot-level controls, fox RAIs increased significantly with the movement resistance index and there were more events on tracks than on smaller trails. There was no significant effect of slope or terrain ruggedness on camera-based RAIs. There were significantly more fox events in spring than in autumn, but the pattern differed between the scales of analysis for the winter season, indicating strong variation across study sites (Table 3). There was no significant effect of slope or terrain ruggedness on camera-based RAIs.

Reduced scat-based RAI models included a significant linear positive effect of predicted fox abundance for both the all-scats model and the model with a reduced sample of scats of high fox certainty (Table 3; Figure 2). There were fewer

TABLE 3 Model results of the negative binomial generalized linear models (GLMs) for camera-based relative abundance index (RAI) at both spatial scales (top row) and scat-based RAI (bottom row), either including all scats or only scats with high identification certainty. Estimates of model coefficients, standard errors, and *p* values are provided. For variable abbreviations see Table 2

| Camera RAI (landscape scale) | | | | Camera RAI (site clusters) | | | |
|-------------------------------------|---------|-------|----------------|--|---------|-------|----------------|
| Predictor | β | SE | <i>p</i> value | Predictor | β | SE | <i>p</i> value |
| Intercept | 1.494 | 0.060 | <0.001 | Intercept | 1.318 | 0.123 | <0.001 |
| FoxExp | 0.049 | 0.049 | 0.317 | FoxExp | 0.063 | 0.075 | 0.382 |
| FoxExp ² | 0.124 | 0.022 | <0.001 | FoxExp ² | 0.140 | 0.032 | <0.001 |
| AgriDist | −0.100 | 0.035 | 0.005 | AgriDist | −0.160 | 0.051 | 0.001 |
| HumDist | 0.121 | 0.035 | <0.001 | HumDist | 0.030 | 0.047 | 0.545 |
| RoadDist | −0.177 | 0.030 | <0.001 | RoadDist | −0.103 | 0.041 | 0.011 |
| SlopeSD | 0.051 | 0.030 | 0.088 | SlopeSD | −0.043 | 0.040 | 0.282 |
| SlopeS | −0.008 | 0.031 | 0.793 | SlopeS | −0.035 | 0.040 | 0.384 |
| Resistance | 0.167 | 0.027 | <0.001 | Resistance | 0.147 | 0.039 | <0.001 |
| Ctrail-trail | −0.580 | 0.059 | <0.001 | Ctrail-trail | −0.530 | 0.082 | <0.001 |
| Year-2018 | −0.364 | 0.075 | <0.001 | Year-2018 | −0.334 | 0.103 | 0.001 |
| Hunting | 0.007 | 0.068 | 0.916 | HUNT-Low | 0.250 | 0.161 | 0.122 |
| Season-Spring | 0.545 | 0.076 | <0.001 | Season-Spring | 0.364 | 0.152 | 0.016 |
| Season-Winter | 0.280 | 0.112 | 0.012 | Season-Winter | −0.503 | 0.215 | 0.019 |
| Hunting*Spring | −0.144 | 0.073 | 0.049 | HUNT-Low*Spring | 0.100 | 0.182 | 0.583 |
| Hunting*Winter | 0.037 | 0.085 | 0.661 | HUNT-Low*Winter | 0.550 | 0.238 | 0.021 |
| Scat RAI: All scats (site clusters) | | | | Scat RAI: High certainty (site clusters) | | | |
| Predictor | β | SE | <i>p</i> value | Predictor | β | SE | <i>p</i> value |
| Intercept | 0.044 | 0.220 | 0.840 | Intercept | −0.185 | 0.243 | 0.448 |
| Fox | 0.282 | 0.055 | <0.001 | Fox | 0.180 | 0.077 | 0.020 |
| Year-2018 | 1.083 | 0.151 | <0.001 | Year-2018 | 0.657 | 0.182 | <0.001 |
| HUNT-Low | 0.551 | 0.275 | 0.321 | HUNT-Low | −0.114 | 0.349 | 0.247 |
| Season-Spring | −0.270 | 0.272 | 0.045 | Season-Spring | −0.361 | 0.312 | 0.744 |
| HUNT-Low*Spring | 0.253 | 0.304 | 0.404 | HUNT-Low*Spring | 0.957 | 0.390 | 0.014 |

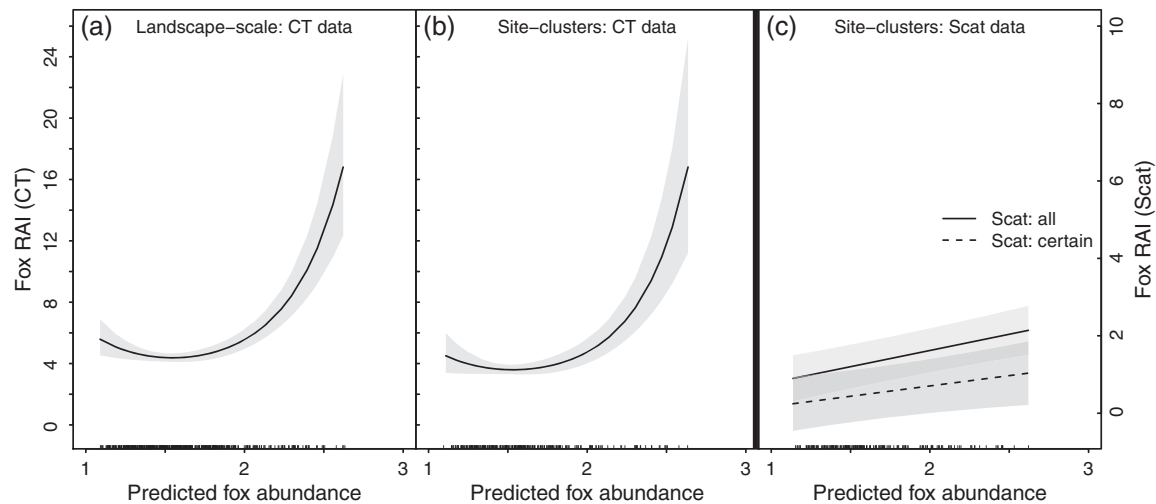


FIGURE 2 Conditional effect plots of the relationship of predicted relative red fox abundance at the landscape scale and small-scale variation in red fox relative abundance indices (RAIs) for camera data at the landscape (a) and site-cluster scale (b) and scat data (c). All other covariates were set to the mean. Point estimates are provided with their 95% confidence intervals

scats found in spring than in autumn, but confidence intervals of this effect overlapped zero for scats of high fox certainty. More scats were detected on scat plots than on random transects (Table 3).

4.2 | Culling effects

After accounting for differences in fox abundance, landscape composition, and plot characteristics between sites, there was a significant negative effect of hunting bag size on local red fox abundance during spring (landscape scale; Table 3; Figure 3), but confidence intervals for winter and autumn clearly overlapped zero.

This pattern was reflected by the results obtained from clusters of sites: Camera-based RAIs were significantly lower at clusters where foxes were targeted than at clusters where they were not in the winter season, with the size of the effect decreasing through the year (Table 3; Figure 3). Effects were thus largest in winter, reduced in spring, and had been largely compensated in autumn (compare Figure 1; predicted mean differences in RAI values: 1.97 in winter, and 1.59 in spring and 0.74 in autumn; Figure 3). Scat-based RAIs in targeted and nontargeted sites were not different in autumn, but were lower at targeted sites in spring. This difference was significant for scats of high fox certainty (Table 3; Figure 3), but not for scats of lower identification certainty.

5 | DISCUSSION

Lethal predator control remains a contentious issue, and a strong evidence base is therefore essential. Using

complementary RAIs covering three seasonal periods, we showed that—after accounting for the expected variation in landscape-scale red fox abundance—restricted-area culling was capable of reducing local fox abundance. We found a significant negative, albeit small, effect of increasing hunting bags on fox abundance at the landscape scale (entire study area) immediately following the culls, and this pattern was reflected using both scat and camera data at smaller scales (site clusters). However, our results show that culling effects were short lived and had been compensated by fox populations in autumn (i.e., September–November), most likely by compensatory immigration from surrounding areas (Lieury et al., 2015). In addition, an experiment conducted in the study area using artificial nest experiments as an index of predation risk in summer (i.e., May – July; the reproductive period of the target prey species) found no effects of fox culling on predation risk or fox occurrence probability (Kämmerle, Niekrenz, & Storch, 2019). This indicates that culling effects had already been compensated by fox populations immediately after our spring study session, rather than with the onset of dispersal in autumn.

Our results are in line with previous work on restricted-area culls of foxes that suggest that culling can temporarily reduce their local abundance, but this is rarely sustained even where removal effort is large, as culling effects are quickly compensated by fox immigration and/or reproduction (Baker & Harris, 2006; Lieury et al., 2015; Newsome et al., 2014; Porteus, 2015). Some previous work also suggests that networks of estates with active fox control may suppress regional fox abundance to a certain degree (Heydon & Reynolds, 2000; Heydon, Reynolds, & Short, 2000), but most highlighted the strong potential of compensatory immigration to offset the effects of isolated culls

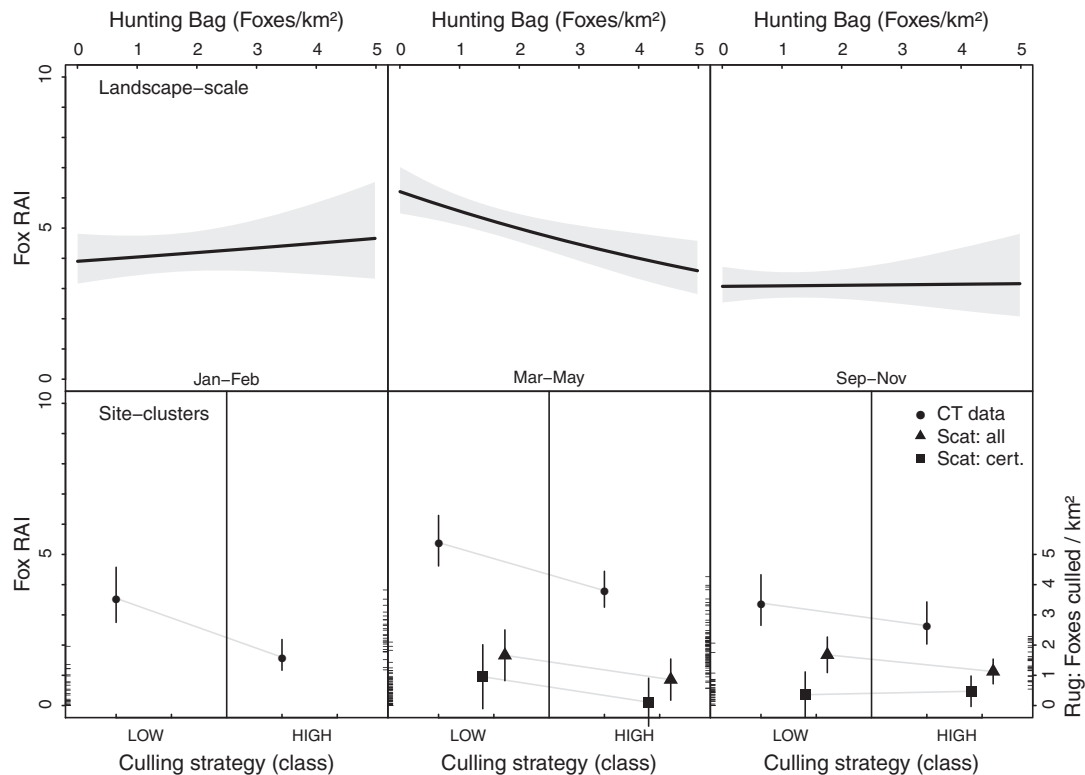


FIGURE 3 Conditional effect plots of red fox abundance indices as a function of culling intensity in three seasons for both spatial scales. The majority of culling was conducted in January and February. All other covariates were set to the mean. Point estimates are provided with their 95% confidence intervals

(Lieury et al., 2015; McLeod, Saunders, & Miners, 2011; Newsome et al., 2014; Porteus et al., 2018). In our study, comparatively few areas with large culls sizes were imbedded in a mosaic of sites without fox control, rendering an effect on the reproducing population unlikely. This is also supported by extremely male-biased sex ratios in the culled foxes of as much as five to one animals culled in the study area (unpublished data) and the accessibility of cull sites for foxes from the wider landscape considering the potential dispersal distances of red foxes (Nowak, 2005; Walton et al., 2018). Finally, previous work highlights the importance of seasonal timing for the effectiveness of culls, but recommendations vary. While some recommend to concentrate effort in spring and summer before dispersal (Porteus, 2015), others found winter culls to be most effective (Lieury et al., 2015; Rushton, Shirley, Macdonald, & Reynolds, 2006). In our study, hunters achieved the majority of the cull during the winter months. Given that red fox populations are limited by winter severity in areas with harsh winters (Bartoń & Zalewski, 2007; Elmhagen & Rushton, 2007; Pasanen-Mortensen et al., 2013) and juvenile mortality is typically high (Devenish-Nelson et al., 2013; Gosselink, Van Deelen, Warner, & Mankin, 2007), concentrated culls during the winter season should theoretically be capable of introducing additional mortality. This is supported by our finding of

significantly lower fox abundance following winter culls in our study area, which is characterized by comparatively high winter severity (up to 160 days $<0^{\circ}\text{C}$ / year; period 1961–1990; German Weather Service DWD).

5.1 | Conservation implications

In order to achieve conservation targets, culls must reduce predator abundance and their effects be of sufficient magnitude to align spatially and temporally with the goals and timeframes of conservation actions. Predator control efforts therefore require explicit spatiotemporal coordination and, ideally, should be accompanied by rigorous monitoring of their effectiveness. Although we found significant reductions in fox abundance indices in spring, culling practices in our case seemed to fall short of sustaining effects during the timeframe that was most relevant for conservation (i.e., reproductive period of the target prey species), given that culling effects had already been compensated shortly after the spring surveys (Kämmerle et al., 2019). With regards to spatial scale, our results at the scale of site clusters indicate that red fox abundance can be significantly reduced following the cull, despite variation in culling intensity within the site cluster (Figure 3). This suggests that, given appropriate timing and effort, culls are theoretically capable

of reducing abundance within a target area during a short period of conservation concern. Comparison of effect sizes in the final camera-based models at both scales indicates, however, that the achieved reduction in red fox abundance in our study was marginal in comparison to the effect of differences in landscape-scale red fox abundance on local RAI values (i.e., change in index value approximately five times smaller for culling effects, compare Figure 2 and Figure 3). This may suggest that the culling effects were small in comparison to the carrying capacity of the landscape, although cull sizes exceeded the expected red fox density in the area. However, the range of culls sizes achieved in our study inherently limits our evaluation of cull intensity. While effects may have been stronger if cull sizes had been larger, our findings are nonetheless in line with previous work reporting effects of small magnitude (Lieury et al., 2015; Newsome et al., 2014). In addition, experiments with artificial nests in our study area indicate that landscape-scale red fox abundance rather than culling influences predation risk at culled sites (Kämmerle et al., 2019).

Small effect sizes and rapid compensation question the ability of restricted-area culls (as practiced in our study area) to achieve conservation targets, unless cull intensity is sufficiently high and culls have appropriate timing. Removal effort needs to be high and cover the complete area of conservation concern in order to avoid rapid compensation of culling effects. In our case, it is likely that—to be effective—removal intensity would need to be equal to (or higher than) the values achieved in this study. In addition, effort should be concentrated to coincide with the most relevant time for conservation. However, culling is illegal during this time under local hunting law (hunting season closed from March to July), and culls may thus need to be focused toward the end of the hunting season.

Our findings emphasize the importance of quantifying the effectiveness of predator control efforts when the goal is prey species conservation. Whether effective removal planning can be achieved given the requirements of local hunting legislation, the available effort and variation in property rights is a context specific decision. Accordingly, despite the evidence for reduced red fox abundance following restricted-area culling in this study, our data does not support incentives for uncoordinated recreational red fox culls as a conservation measure, unless culls appropriately reflect the requirements imposed by biology of predator and prey in space and time.

5.2 | Technical considerations

In this study, we used interpolated normalized hunting bags (i.e., foxes culled km^{-2}) as an index of culling intensity at our study plots. There is, however, the potential risk that

high hunting bags are a reflection of high fox density (i.e., more foxes are culled in areas of high density with equal effort), because the data are not corrected for effort. In order to overcome this issue, we first selected hunting concessions based on their culling strategy (i.e., targeted fox removal vs. no fox removal) rather than based on hunting bag data and, secondly, placed study sites within areas of comparable expected red fox abundance (range of predicted relative fox abundance: “targeted” sites: 1.25–2.58; “non-targeted” sites: 1.11–2.48; whole study area: 1.02–5.52). Accordingly, we are confident that differences in culling data reflect differences in culling intensity among our study sites.

There were some issues with model fit for the final scat-based GLMMs. However, due to the lack of variability in scat data, more complex models did not converge and negative binomial GLMMs had much better fit than Poisson models. Nonetheless, results of these models should only be interpreted with caution due to issues with model fit and scat identification certainty. The difference in significance for the effect of culling on scat RAIs in spring between the model containing all scats and only scats of high identification certainty most likely reflects the influence of misidentified scats on the results (i.e., confidence intervals are inflated by inclusion of uncertain scats). This is supported by the presence of a trend toward higher values in low-culling sites in both models. Although scat misidentification rates were low in a previous study in the area (i.e., < 5%; Güthlin et al., 2012), we were unable to quantify their influence on our results. In addition, despite comparatively short survey periods for scat sampling, differences in scat detectability within sessions, for instance owing to precipitation, cannot be fully excluded. Scat data should thus be used only to complement findings of the camera-based models at both scales.

6 | CONCLUSIONS

In summary, restricted-area culling was associated with reduced red fox abundance in target areas immediately after the cull, but effects were short lived and small in magnitude. Despite achieving a temporal reduction in red fox abundance, restricted-area culling likely fell short of reducing red fox abundance throughout the period most relevant for conservation due to rapid compensation of culling effects. Accordingly, red fox culls as a conservation tool require explicit spatiotemporal planning suited to the biology of foxes and their prey, but whether this can be achieved is a context-specific decision. Currently, there is little evidence to support incentives for uncoordinated fox culls as a conservation measure.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

J.L.K. is responsible for conceptual design, data collection, statistical analysis, interpretation, and manuscript writing. E.G.R. is responsible for data analysis, interpretation, and manuscript writing. I.S. is responsible for conceptual design, interpretation, and manuscript writing.

DATA ACCESSIBILITY STATEMENT

All data used in the manuscript are included in the supplements (Appendix S1).

ETHICS STATEMENT

Field data collection was carried out in accordance with local legislation. No animals were handled or harmed.

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SUPPORTING INFORMATION

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

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