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ORIGINAL RESEARCH

An invasive-native mammalian species replacement process captured by camera trap survey random encounter models

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Abstract

Camera traps are used to estimate densities or abundances using capture-recapture and, more recently, random encounter models (REMs). We deploy REMs to describe an invasive-native species replacement process, and to demonstrate their wider application beyond abundance estimation. The Irish hare *Lepus timidus hibernicus* is a high priority endemic of conservation concern. It is threatened by an expanding population of nonnative, European hares *L. europaeus*, an invasive species of global importance. Camera traps were deployed in thirteen 1 km squares, wherein the ratio of invader to native densities were corroborated by night-driven line transect distance sampling throughout the study area of 1652 km^2. Spatial patterns of invasive and native densities between the invader's core and peripheral ranges, and native allopatry, were comparable between methods. Native densities in the peripheral range were comparable to those in native allopatry using REM, or marginally depressed using Distance Sampling. Numbers of the invader were substantially higher than the native in the core range, irrespective of method, with a 5:1 invader-to-native ratio indicating species replacement. We also describe a *post hoc* optimization protocol for REM which will inform subsequent (re-)surveys, allowing survey effort (camera hours) to be reduced by up to 57% without compromising the width of confidence intervals associated with density estimates. This approach will form the basis of a more cost-effective means of surveillance and monitoring for both the endemic and invasive species. The European hare undoubtedly represents a significant threat to the endemic Irish hare.

Introduction

Invasive species play a key role in the decline of native species (e.g., Miller et al. 1989; Atkinson 1996), the disruption of ecological communities (e.g., Sanders et al. 2003), and the degradation of ecosystems (e.g., Fritts and Rodda 1998). Thus, the establishment of ecologically competitive species outside their natural range is of considerable conservation concern (Usher et al. 1986; Wilcove et al. 1998; Harris and Yalden 2004). Early detection of an invasive species is considered to be essential in minimizing later management costs and effort, for example, in control of numbers or eradication (Myers et al. 2000; Mehta et al. 2007). Indeed, if an invader becomes established and expands its range rapidly, eradication becomes increasingly more impractical and economically

challenging. Thus, immediate action is often the only opportunity for cost-effective eradication (Stokes et al. 2006). Population conservation and management are dependent upon knowledge of the target species distribution and abundance (Mackenzie 2005). Monitoring the status and population processes of introduced, nonnative species, therefore, is crucial if potentially negative impacts are to be mitigated against.

Population enumeration of medium-sized mammals such as lagomorphs (pikas, rabbits, hares and jackrabbits) conventionally uses direct observation such as line-transect surveys (e.g., Smith and Nudegger 1985) and Distance Sampling (e.g., Reid et al. 2007), or indirect methods such as faecal sampling (e.g., Forys and Humphrey 1997). Distance Sampling (Buckland et al. 1993) is a popular method of surveying mammals, commonly used to estimate population densities in a wide variety of taxa, e.g., the red fox *Vulpes vulpes* (Ruette et al. 2003), rodents (Parmenter et al. 2003), primates (Marshall et al. 2008), and birds (Norvell et al. 2003). Distance Sampling relies on four assumptions: (1) all targets are detected with certainty at zero distance from transects; (2) targets are detected at their initial location; (3) distance measurements are exact (or at least not consistently biased); (4) transects are positioned randomly with respect to animal density; and (5) the area surveyed is representative of the entire area (Buckland et al. 1993). The estimation of densities and abundances rely on detection functions which model the probability of detection, given the distance of targets from transects. By fitting detection functions to the recorded distance of targets from transects, researchers are able to estimate the number of targets which were not detected during the survey. Distance Sampling is suitable for landscape- or population-scale abundance estimation as a minimum of 60–80 detections are required to obtain a smooth detection function (Buckland et al. 1993), thereby limiting its site-specific application for species that are detected infrequently, such as those that are cryptic, rare or occur at low-density (including recently introduced invaders). In contrast, remote sensing using modern camera traps provides a reliable means of detecting the presence of elusive, rare, cryptic, and nocturnal species with minimal disturbance (Cutler and Swann 1999; Silveira et al. 2003) as they can be left recording continuously *in situ*. Estimating density and abundance from camera trap data was restricted previously to adapted capture-recapture models for species with individually identifiable markings, for example, tigers *Panthera tigris* in India (Karanth 1995; Karanth and Nichols 1998), and ocelots *Leopardus pardalis* in Brazil (Trolle and Kery 2003). However, species which do not exhibit individual markings often account for a large proportion of a recorded assemblage (Carbone et al. 2001). Several species which lack unique markings have been subject to capture-recapture population estimation (e.g., Trolle et al. 2006; Kelly et al. 2008), but these studies fail to account for identification error (Oliveira-Santos et al. 2010). Thus, this approach is unsuitable for species without unique markings (for e.g., lagomorphs). Recently developed spatial capture-recapture (SCR) models provide a means of estimating population densities for unmarked populations from a variety of survey data (Chandler and Royle 2013). However, this method lacks precision at smaller sample sizes.

The random encounter model (REM) provides a means of estimating population densities for species where individuals cannot be recognized reliably, by modeling animal movement processes and contact with cameras (Rowcliffe et al. 2008). The REM relies on three assumptions: (1) the movement of the targets is random; (2) detections represent independent contacts between cameras and animals; and, (3) the population is closed. Studies utilizing the REM will inherently violate one or more of these assumptions (e.g., the movement of animals in the landscape is never truly random). However, the model is considered to reasonably robust against certain violations of the assumptions (e.g., nonrandom movement due to interactions with the environment or other species; Rowcliffe et al. 2008; Manzo et al. 2011; Rowcliffe et al., 2012). The method does of course have inherent constraints, the most significant being estimations of group size and speed of movement, which may differ within species depending on habitat or prevailing environmental conditions. Furthermore, due to the requirement for random camera placement, rare species may be detected too infrequently for density estimates to be calculated (Rowcliffe et al. 2008). The REM has been used for a variety of medium-small mammals, including: captive mara *Dolichotis patagonium*, red-necked wallaby *Macropus rufogriseus*, Chinese water deer *Hydropotes inermis*, and Reeve's muntjac *Muntiacus reevesi* (Rowcliffe et al. 2008); wild lowland tapir *Tapirus terrestris* (Oliveira-Santos et al. 2010), pine marten *Martes martes* (Manzo et al. 2011), and Harvey's duiker *Cephalophus harveyi* (Rovero and Marshall 2009). Where cross-validation has been attempted, the REM produced similar density estimates of European wildcats *Felis silvestris silvestris* to those produced by capture-recapture models (Anile et al. 2014), and of Grévy's zebra *Equus grevyi*, using both camera trap capture-recapture and line transect Distance Sampling models (Zero et al. 2013).

Leporids (rabbits, hares, and jackrabbits) do not have individually identifiable markings (Angerbjörn and Flux 1995). Their pelage coloration tends to be uniformly dull, affording concealment from predators (Stoner et al. 2003). Camera trap studies focusing on leporids have generally described landscape and habitat utilization (McCarthy et al. 2012; Gantchoff and Belant 2014), or simply presence in particular mammalian communities

(Yasuda 2004; Rendall et al. 2014). The Irish hare *Lepus timidus hibernicus* is endemic to the island of Ireland, and a Priority Species (Anonymous 2005) listed on Annex V of the EU Habitats Directive (EEC 43/92 1992) requiring surveillance, monitoring, and reporting under Articles 11 and 17. The European brown hare *L. europaeus* is a native of the open grasslands of continental Europe and the Asian steppe (Flux and Angermann 1990). It was introduced to Ireland in the mid-to-late 1800s (Barrett-Hamilton 1898), is now established within the range of the Irish hare (Reid and Montgomery 2007; Caravaggi et al. 2015) and poses a significant threat to the ecological and genetic integrity of the native (Hughes et al. 2009; Reid 2011). Distance Sampling has been used to monitor numbers of Irish hare since the inception of the 'Northern Ireland hare Survey' in 2002 (Preston et al. 2003) and has also been used to determine the range and abundance of invasive European brown hares (Reid and Montgomery 2007; Caravaggi et al. 2015).

We used remote-sensing camera trap REMs to estimate the density of two sympatric leporid species (one native, of conservation concern, and one invasive nonnative), and describe the invasive-native species replacement process. We discuss the spatial dynamics of replacement between native allopatry and shallow or deep sympatry (i.e., the outer 100%, or inner 50%, minimum convex polygons representing the range of the invasive species) in the invader's peripheral and core ranges. We used conventional line transect Distance Sampling to corroborate the spatial pattern of invasive-native replacement. We also describe a means by which future surveys could minimize survey effort in terms of the numbers of cameras used per unit area and the number of days during which they are deployed. Consequently, we provide explicit guidelines for the future monitoring of this particular species replacement process. Such data will provide a greater understanding of the invasive-native species dynamic and inform population management measures.

Materials and Methods

Study area

The study area (1652 km^2) was located in Mid-Ulster, Northern Ireland (centroid coordinates 54°45′21.1″N, 6°39′29.6″W). This region was previously surveyed for European hares in 2006 (Reid et al. 2007), though the current study area was 1027 km^2 larger than that used in the previous study to account for range expansion. The landscape had an undulating topography, and was comprised of agricultural fields, the majority of which were improved or rough grassland (EEA 2010). The climate was temperate, characterized by frequent rainfall of 950 mm per year (MetOffice 2015). Human activity was high, due to the agricultural (pastoral) nature of the landscape. However, overall human population density was low with ≤100 people per km^2 (ONS 2012).

Camera trapping

Camera trap surveys were carried out between April and November 2013. The study area was split into three geographical strata using invasive species sightings collected during nocturnal line transect surveys (Caravaggi et al. 2015), delineated using minimum convex polygons (MCPs): a zone of (1) deep sympatry in the European hare's core range (inner 50% MCP); (2) shallow sympatry in the invasive European hare's peripheral range (outer 50% MCP); and, (3) native Irish hare allopatry (outside the invasive species range). Details of how these zones were delineated followed Caravaggi et al. (2015). Thirteen 1 km^2 squares were selected randomly: four in native allopatry, five in shallow sympatry and four in deep sympatry (Fig. 1). Within each 1 km square, twenty points were generated randomly and located in the field using a Garmin eTrex 30 GPS unit. A Bushnell Trophy Cam HD (model 119477) camera trap was positioned on the nearest vertical feature (e.g., fence, gate post, or tree) to each randomly selected point, facing into the field. Cameras were erected at a height of approximately 30 cm from the ground, with a 10–15° downward tilt, and configured to record video clips, each of 60 s in duration, when triggered. Cameras used a passive infrared (PIR) sensor; recordings were triggered by movement. Diurnal footage was captured in the visual spectrum; nocturnal footage was captured in the infrared spectrum. Video footage allowed the detection of closely associated conspecifics, with a 60 s delay between triggering events minimizing the potential for immediate re-detection of the same animal. Successive triggers, therefore, were defined as separate independent events, unless there was evidence to the contrary (e.g., a hare remaining in the same spot for several minutes, and, hence, several successive triggers), in which case re-detections were removed in an effort to avoid false inflation of final density estimates. Cameras were left *in situ* for 7 × 24 h periods (hereafter referred to as days).

Positive species identification of detected hares was not possible with 100% accuracy due to the prevalence of hybrids in the area (Hughes et al. 2009). Identification was based on the presence of contrasting black ear-tips (present in the invasive), ear length relative to the head (longer in the invasive), pelage color and texture (mixed blacks and browns in invasive, uniform browns/reds in the native), the head shape in profile (flat or convex in the invasive), the presence of white stripes on the muzzle (present in the invasive), and the color of the dorsal tail surface (black in the invasive). Hybrids between mountain

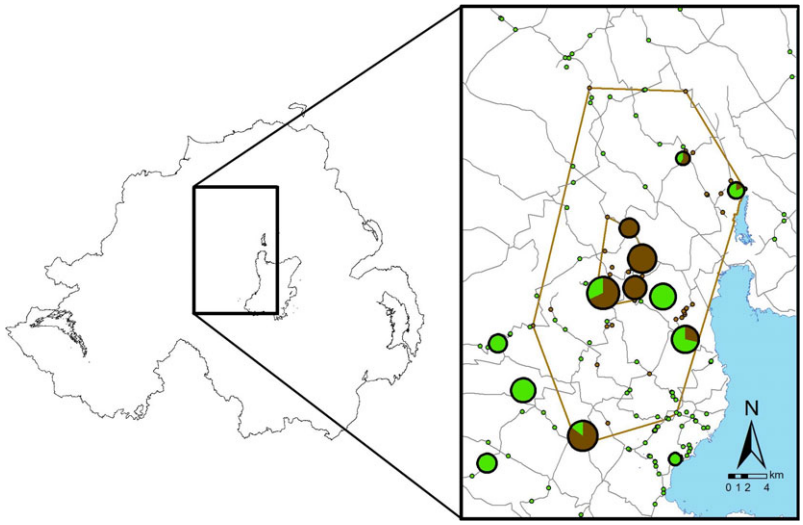

Figure 1. Hare surveys in Mid-Ulster, Northern Ireland during 2012–13 showing nocturnal spotlight transects (grey lines) and European and Irish hare sightings (brown and green dots, respectively) used to delineate the range of the invasive species (outer 100% minimum convex polygons [MCP] and core range (inner 50% MCP). Camera trapping arrays were deployed in 13 randomly selected 1 km^2 squares (bold pie charts) showing the proportion of detections that were European and Irish hares (brown and green, respectively) with the size of each pie chart scaled for the total number of detections.

hares *L. timidus* and European hares have been described as exhibiting considerable phenotypic plasticity, making identification difficult (Lönnberg 1905; Gureev 1964; cited in Thulin et al. 2006). Thus, the phenotypes of animals were categorized as either Irish hare-like or European hare-like; hereafter referred to simply as Irish or European hares (Fig. 2). In a capture-recapture study of puma *Puma concolor* in South America, Kelly et al. (2008) noted that density estimates can be substantially affected by variation between observers, and suggested that at least two independent observers view each capture. As such, several observers independently viewed all captured footage to ensure consistency of identification. There were no disagreements in assigned species identities.

Random encounter model

The REM (Rowcliffe et al. 2008) requires three parameters and two data inputs to calculate population density estimates (D): y = number of detections, t = survey effort in hours, v = speed of movement (distance travelled in 24 h), r = radial distance to the animal (in metres), and θ = zone of detection ($2a$, where a is the angle of detection, in radians):

$$D = \frac{y}{t}\frac{\pi}{(vr(2+\theta))} \quad (1)$$

The estimation of r and θ followed the methodology of Rowcliffe et al. (2011) wherein both measures were dependant on the location of individual animals in each detection. Mean values were calculated and subsequently utilized in the REMs. In order to establish r and θ, a reference photograph was taken at the end of each survey period and prior to camera trap collection, using a handheld digital camera with a wider field of view than that of the camera trap, thereby mitigating against incidental trap movement during the survey, and, hence, potential issues with subsequent image alignment. In the field of view, bamboo canes were placed at 1 m intervals directly in front of the camera out to 5 m, forming a central line bisecting the camera's field of view. On each side, left and right of the central line, additional bamboo canes were placed at 1 m intervals, out to 5 m, thereby forming two lines parallel to the central line. Each square delineated by a set of four nearest-neighboring canes was orthogonal (Fig. 3A). This was used to calibrate an overlaid grid which was superimposed on each detection image using Adobe Photoshop®. The 1 × 1 m grid was subdivided into 20 × 20 cm squares. Image transformation tools (Perspective; Distort; Free Transform) were used to manipulate the electronic grid so that 1 m gridline intersections matched relevant cane placements (Fig. 3B). Still images, captured from video footage at the first frame at which an animal appeared, were pasted onto the image as a new layer (Fig. 3C). To ensure alignment with the reference photograph, additional layers were set to semi-transparency (<50%) and aligned according to notable environmental features, that is, buildings, trees, fences etc.

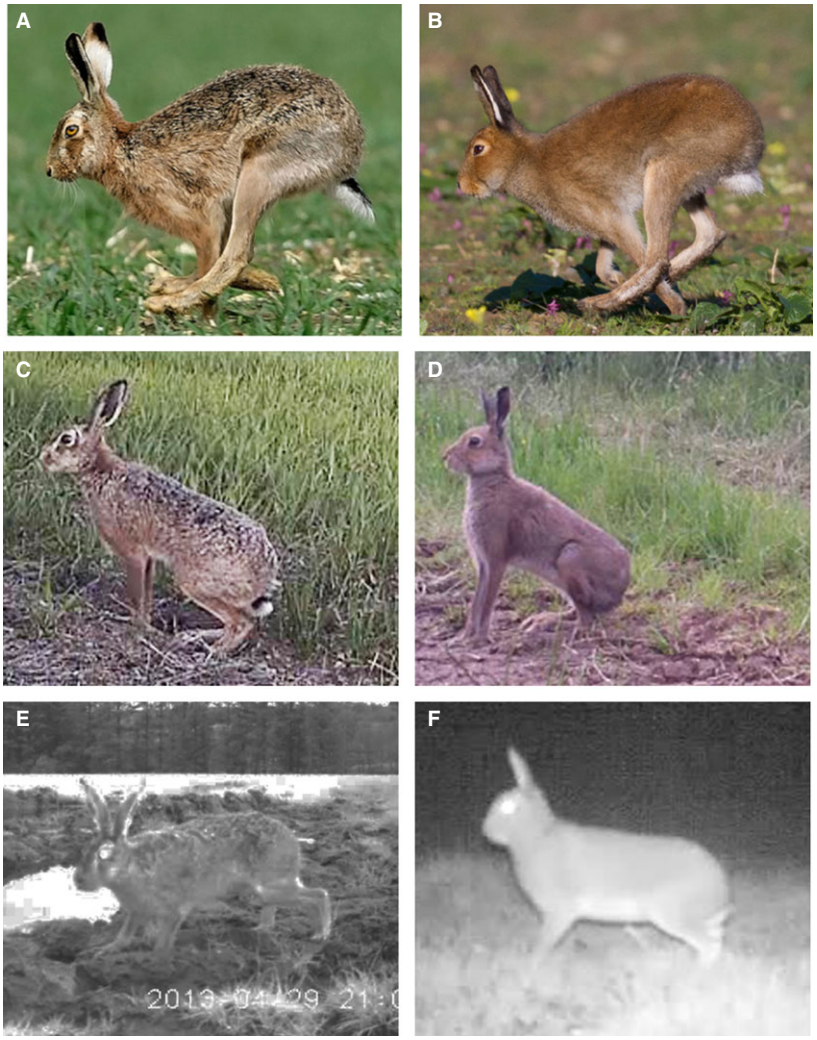

Figure 2. Photographs of (A) European hare *Lepus europaeus* (©Nigel Blake) and (B) Irish hare *Lepus timidus hibernicus* (©Shay Connolly) extracted with permission from Caravaggi et al. (2015), demonstrating clear intraspecific differences enabling species ID from both diurnal (C, European hare; D, Irish hare) and nocturnal (E, European hare; F, Irish hare) camera trap footage.

Data points were highlighted using a white circle placed at the foremost foot of any animal detected. The electronic grid was the topmost layer and set to 50–75% transparency (Fig. 3D). The calibrated grid was used to measure the direct central distance (d_i) to a point adjacent to the ith detection, and the perpendicular distance from the central line to the ith detection (p_i). All distances were estimated to the nearest 20 cm. These data were used to estimate the radial distance (r_i) and the angle (a_i) to each detection trigonometrically, where $a_i = sin^{-1}\left(\frac{p_i}{d_i}\right)$ (Fig. 3E). θ_i (i.e., the zone of detection) was derived by doubling a_i and converting to radians. Means of r and θ across all relevant detections were used in a separate REM for each 1 km square. Field validation of the accuracy and precision of r_i and θ_i estimated from the *ex situ* overlaid grid is provided in Data S1. Mean ± standard error detection zone parameters, r and θ, were comparable between diurnal (3.73 ± 0.21 m, 0.34 ± 0.02°) and nocturnal (4.16 ± 0.24 m, 0.32 ± 0.02°) detections.

There were no data available on the daily activity budgets of hares in Ireland. Thus, speed of movement, v (distance travelled in 24 h) was derived from GPS-telemetry data provided by Schai-Braun et al. (2012) and Zaccaroni et al. (*unpublished data*) who independently recorded mean 24 h movement-distances for European hares in Austria and Italy as 890 ± 163 m (mean ± SE) and 890 ± 75 m, respectively. GPS fix frequencies were 1 every 10 minutes between 6 PM and 8 AM, and 1 every 4 h at other times, in the Italian study, and 1 fix per hour in the Austrian study. Daily distance traveled was calculated as the mean of the summed distances between each fix

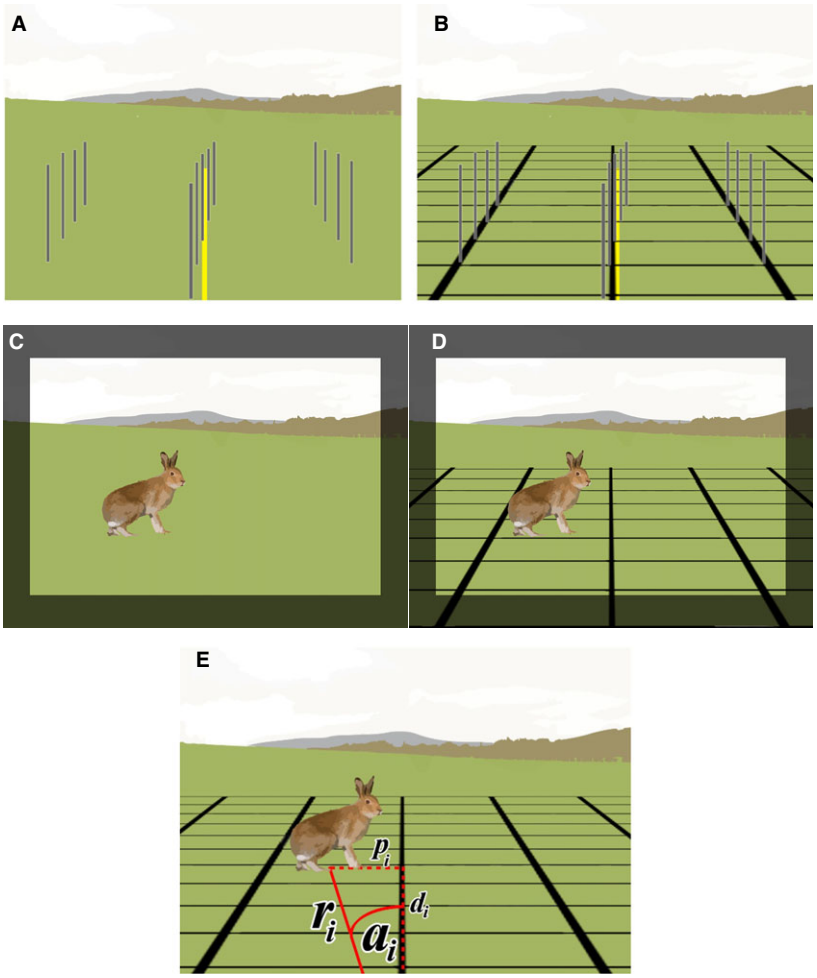

Figure 3. Step-wise demonstration of *ex situ* data extraction from still camera-trap images. A base reference photograph with bamboo canes placed at 1 m intervals along the center of the field of view, up to a maximum of 5 m, and 1 m parallel to the central line at 1 m intervals (A). A 1 × 1 m grid, subdivided into 20 × 20 cm squares (20 cm sub-grid omitted here for clarity), was created and transformed so that each 1 × 1 m square junction coincided with cane placements (B). Still camera-trap images extracted from videos were overlaid using 50% transparency and aligned according to consistently identifiable landscape features (C). The calibrated grid was moved above both images (D); the simulated detection (in this case represented by a hare *Lepus* sp.) has been kept uppermost for clarity (the grid would usually be uppermost). (E) r_i and a_i values were calculated trigonometrically from direct central (d_i), and perpendicular (p_i) distances. The random encounter models (REM) parameter $\theta = 2a_i$.

per animal, per day. The home ranges of European hares in Austria (0.12 ± 0.03 km^2; Schai-Braun et al. 2014) and Italy (0.13 ± 0.09 km^2, Zaccaroni *unpublished data*) were comparable to Irish hares in Northern Ireland (0.14 ± 0.02 km^2; Reid (*unpublished data*) from minimum convex polygon analysis of radio-telemetry data published originally as Reid et al. 2010). Activity patterns, and, hence, detection probability, of both species were likely to be similar (i.e., nocturnal) throughout the study period.

It was suggested that a minimum total of 10 detections are required for the calculation of reasonably precise density estimates (Rowcliffe et al. 2008). However, while all sites surveyed returned in excess of 10 detections, the number of images of the less populous species in areas of sympatry frequently fell below this threshold (see Data S2). Thus, species-specific densities were then calculated by multiplying the overall hare density, D, in each 1 km square by the proportional detection of each species within each square. Approximations of 95% confidence intervals around calculated densities, D, were obtained using nonparametric, resample-with-replacement bootstrapping estimates of detections for each survey square (i.e., within each group of 20 camera traps). Thus, variance estimates were obtained from each 1 km survey square. As with D, we calculated mean variance in each

zone of invasion, and species-specific estimates via *post hoc* splitting of data according to proportional detection. This method facilitates the description of variation *between* sites (wherein each cluster of 20 cameras was non-independent), *within* each zone of invasion, as opposed to treating all survey sites within zones of invasion as spatially contiguous (nonindependence of n^i cameras), and, hence, obscuring spatial variation. Each resample-with-replacement bootstrapping analysis was based on 1000 iterations (see http://rpubs.com/kkeenan02/density-bootstrap), using the program R (R Core Team, 2015).

Optimizing camera trapping effort

To minimize future (re-)survey effort, we derived optimal camera trapping protocols defined as: the trade-off between time per camera placement and the number of placements. Estimates of mean density, and estimates of 95% confidence intervals, for each 1 km survey square (s_i) were calculated as a function of survey effort using randomly selected data representing variable numbers of camera traps (n_i) across days (t_i), where t_i was sequential, with a total of 1820 possible combinations ($s_{max} \times n_{max} \times t_{max}$). To generate these estimates, and for each combination, camera trap detection data were subjected to nonparametric random-resample-with-replacement bootstrapping, with 5000 iterations (http://rpubs.com/arcaravaggi/REMmultiboot). In order to identify optimal parameters, linear models were constructed with the width of confidence intervals derived from bootstrapping as the dependent variable and n_i and t_i as independent variables. The point at which confidence intervals were substantially affected by a change in survey effort was identified via regression coefficients from stepwise reductions in n_i and/or t_i.

Distance sampling

Nocturnal road-based line transects (Fig. 3) were surveyed using a 3×10^6 candlepower spotlight from a platform on a high clearance vehicle elevating the observer's head height >2 m above ground level, that is, above most hedgerows during winter 2012–13. Two surveyors were present to ensure consistency of identification. Surveying from linear features, such as roads, may lead to biased abundance estimates as target animals may not be distributed randomly with respect to human activity. It is possible to partially mitigate against this by accounting for density gradients with respect to transects (Marques et al. 2013). However, fully accounting for survey bias and error requires *a priori* knowledge of the true population density, and an estimate of the density gradient obtained by, for example, surveying transect perpendicular to the road (Reid and Montgomery 2010). However, hare density in Ireland is subject to considerable localized spatial variation, and it was not economically, nor practically viable to conduct night walked transects away from the road network. To maximize detection of the invasive species, which occurs at low densities and is widely distributed, transects were continuously driven at 10–15 kph, pausing only when a hare was sighted to record relevant data. Surveys were conducted over a total of 42 nights during winter 2012–13, beginning 1 h after sunset, and continuing for 8 h or until prevailing conditions (e.g., rain, hail) made further surveying impractical. Hare activity is greatest during winter, which includes the start of breeding, whilst the absence of domestic livestock from fields and low vegetation height increases the probability of detection. A network of transects, half of which ran approximately south-east to north-west with the remainder running south-west to north-east, were selected along minor roads, totalling 698 km, to cover the known invasive range of European hares in Northern Ireland (see Caravaggi et al. 2015). The region is densely covered by minor roads such that few areas are >300 m from the nearest road. The primary measurements of each hare or cluster were: location of each hare detection measured to the nearest 10 m using a Garmin eTrex 30 GPS; angle, taken as degrees from North; cluster size (i.e., number of hares); species identity; radial distance of the cluster from the observer, measured using a laser range finder, Leica LRF 900 Scan. The perpendicular distance from the road to each cluster was calculated using ArcGIS.

Hare density and abundance (±95% confidence limits) were calculated using Distance 6.0 (Thomas et al. 2010). The assumption that survey effort equalled 1 (i.e., an unobstructed, 360° field of view throughout the survey period) on all transects was violated due to variations in topography, habitat and rural development(s); hills, hallows, hedgerows, trees, tall vegetation and housing/buildings in close proximity to the road occasionally entirely obscured the surveyor's view, rendering survey effort <1. Previous Northern Ireland Irish Hare Surveys (e.g., Reid et al. 2010) utilized point transects placed at 200 m intervals along road-based line transects. This allowed 869 km of minor road to be surveyed continuously, but provided a means by which to estimate survey effort whilst stationary. At each point, surveyors, using a handheld 360° protractor, estimated the total, unobstructed field of view of a circle 250 m in radius. Measurements were taken in degrees. Data were transformed into the proportion of a complete circle that was visible without obstruction (ranging from 0–1). The mean survey effort calculated from 3660 point transects surveyed throughout Northern Ireland during 2010 (the last major survey conducted) was 0.65 (Reid, *unpublished data*). Thus, we adopted this

value as a better estimate of likely survey effort along continuous driven line transects to account for likely obfuscation. Three commonly used detection functions were tested: uniform cosine, half-normal cosine and hazard-rate simple polynomial (Buckland et al. 2004). The parsimony of each model was evaluated using Akaike's Information Criterion (AIC), with the best model being selected on the basis of the lowest AIC value (Akaike 1973). The single, best fitting detection function was used to estimate mean hare density (both species combined) ±95% confidence limits. Species-specific densities were then calculated, assuming similar detection functions, by multiplying the overall mean hare density by the appropriate proportion of invasive-native sightings, obtained using the Distance Sampling method, above, within each zone of invasion: native species allopatry and shallow and deep sympatry.

Results

A total of 456 hare detections were recorded during 43 680 h of camera trapping (Table S1). REM estimates suggested that, at the local scale, within the squares sampled, the density of native species was largely unaffected by the initial invasion of the European hare, with 3.0 (95% CI 2.4–3.9) Irish hares per km^2 being observed in the zone of native allopatry, compared to 3.1 (95% CI 2.6–3.7) Irish hares per km^2 in shallow sympatry of the peripheral range of the European hare. However, native species density was significantly reduced within deep sympatry of the core range of the invasive species, with 1.0 (95% CI 0.8–1.1) Irish hare per km^2. Overall REM hare densities (both species combined) were 18.8% higher in the invader's core range at 5.7 (95% CI 5.0–6.7) hares km^2 than its peripheral range, of which 93% that is 4.7 (95% CI 4.2–5.7) hares per km^2 had a European-like phenotype (Fig. 4A). The total population derived from REMs was estimated at 1068 (95% CI 888–1258) European hares within its invasive range and 4943 (95% CI 4019–6240) Irish hares within the entire 1652 km^2 study area.

A total of 267 hares were detected during spotlight transects (Table S2). A hazard-rate, simple polynomial detection function fitted the frequency distribution of detection distances best (Fig. 5). Distance sampling density estimates described a similar pattern of invasion and impact on native species to that described by camera trap REM estimates (Fig. 4). However, the Distance Sampling estimate described a lower mean density of the native species in shallow sympatry with 1.2 (95% CI 0.9–1.3) compared to 1.7 (95% CI 1.5–1.8) Irish hare per km^2 in native species allopatry. In contrast to REM results, Distance Sampling suggested no further decline in native species abundance in deep sympatry; however, hare densities

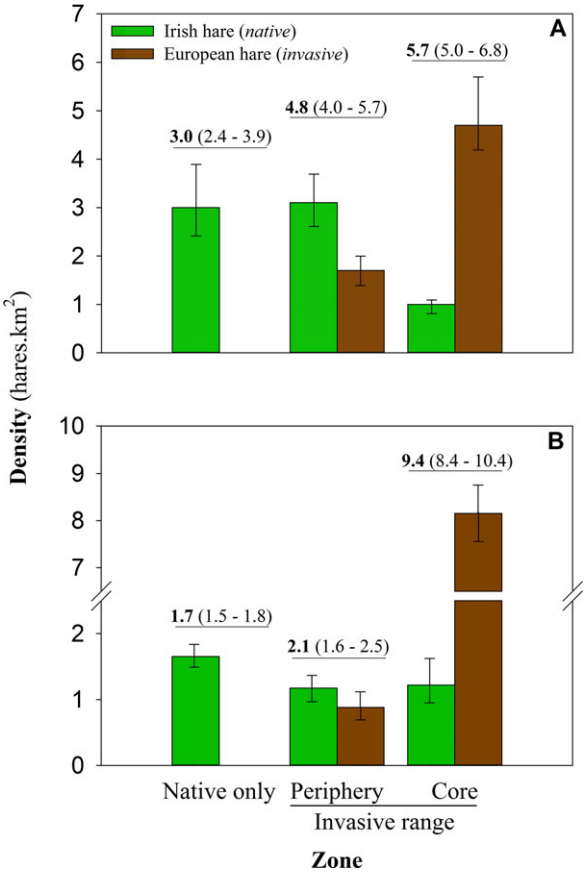

Figure 4. Species replacement as demonstrated by native and invading hare densities (hares per km^2 ± 95% CIs) derived from (A) the random encounter model (REM), using camera trapping data and (B) Distance sampling using nocturnal spotlight surveys in three zones: (i) native species only, (ii) invasive species peripheral range and (iii) invasive species core range. Numbers above the bars show the absolute hare density (both species combined) with 95% CIs in parentheses. Note: the split *y*-axis in part (B) which facilitates comparisons between both methods with respect to the species replacement process. For site-specific (i.e., individual 1 km survey square) REM densities and other additional data see Data S3.

were 7.9 times higher in the invader's core range with 9.4 (95% CI 8.4–10.4) hares per km^2 compared to native allopatry, of which 87% that is, 8.2 (95% CI 7.5–8.8) hares per km^2 had a European-like phenotype (Fig. 4B). Distance Sampling estimates where survey effort was assumed to be 0.65 were on average 1.5× higher than those assuming survey effort = 1. The total populations derived from Distance Sampling was substantially lower than those obtained from the REM estimated at 382 (95% CI 341–444) European hares compared to 416 Irish hares (95% CI 369–481).

Optimization of camera trapping protocols, .that is, spatiotemporal bootstrapping (Fig. 6A), with *post hoc* analyses suggested that 12 cameras placed *in situ* for 5 days in 13

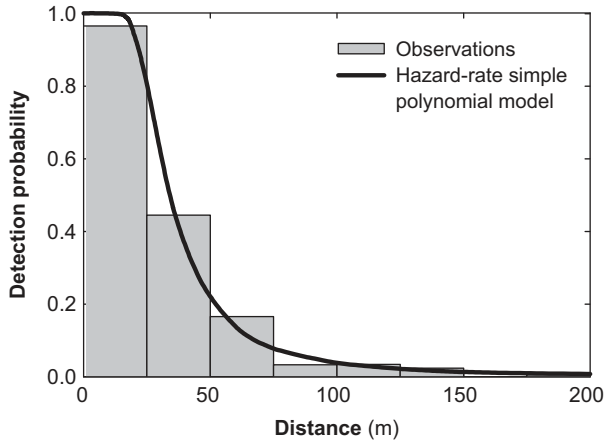

Figure 5. The relationship between the number of hares detected (within 25 m interval bins) and perpendicular distance (m) from transects (i.e., roads) fitted with a hazard-rate simple polynomial detection function.

squares (18 720 camera hours) would provide largely comparable mean density estimates with substantially overlapping 95% confidence intervals with those obtained from 20 cameras for 7 days in 13 squares (43 680 camera hours), that is, the full dataset (Fig. 6B). Thus, total survey effort could be substantially reduced (by 57%) without detrimentally impacting density estimates or their precision (Fig. 6C).

Discussion

Spatial patterns of change in invasive and native hare species densities between zones of native allopatry and the shallow and deep sympatry of the invader's peripheral and core ranges, were captured using remote sensing camera trap REMs and direct observation line transect Distance Sampling. Both methodologies capture the species replacement process, with significantly lower native hare abundance in deep sympatry compared to allopatry. However, each method produced a substantially different estimate of absolute density and abundance. REM-estimated densities were on average 1.4× higher for both species in all zones, with the exception of the European hare in its core range, where REM estimates were 1.6 times lower than Distance Sampling. Studies comparing density estimation methods have reported mixed success, with some reporting comparable results (e.g., Zero et al. 2013; Anile et al. 2014), while others reported considerable discrepancies (e.g., Rovero and Marshall 2009; Cusack et al. 2015). However, these studies surveyed single sites, within which methods were compared across the same spatial scale.

Differences in density estimates in the present study, therefore, may be due to differences in scale and duration over which the data were collected. The Distance

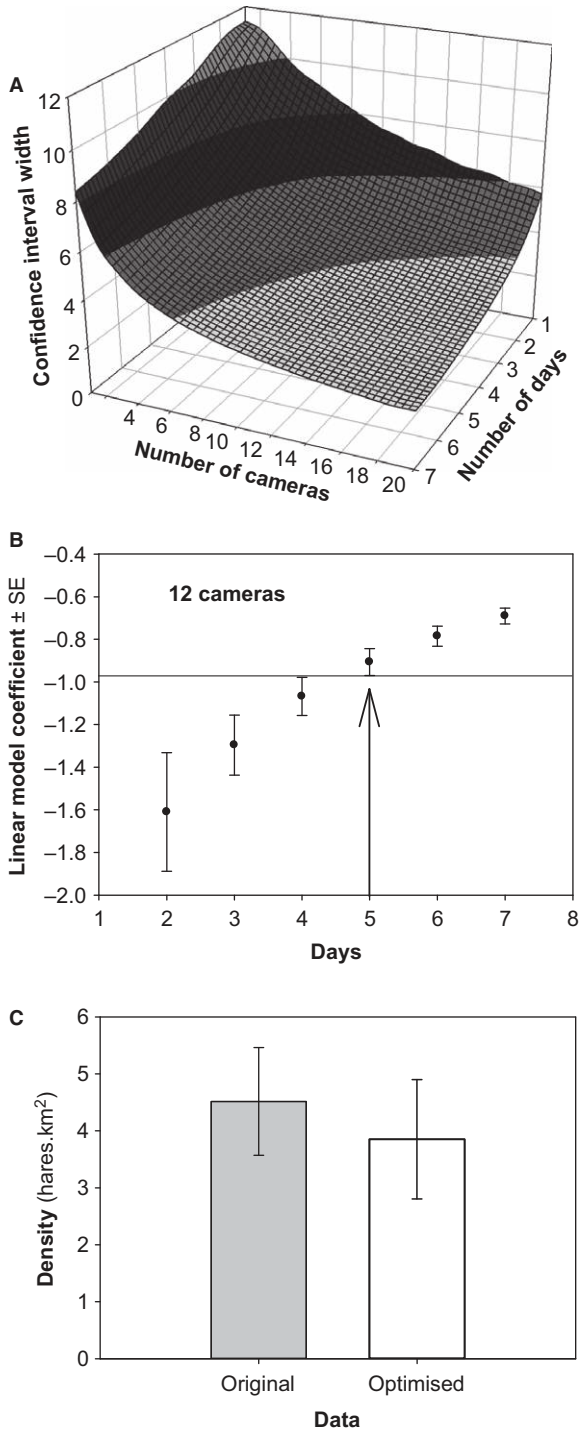

Figure 6. Reduction in future survey effort via (A) spatiotemporal variation in the width of 95% confidence intervals of random encounter model (REM) density estimates derived from nonparametric resample-with-replacement bootstrapping of camera trap data, and (B) the identification of a significantly different regression coefficients with stepwise reductions in t_i, here for n_{12}, (C) Hare densities (hares per km^2 ± 95% CIs) derived from original camera trap data (20 cameras for 7 days) and the optimization protocol (12 cameras for 5 days).

Sampling survey covered a study area of 1652 km^2 where the scanning of each field took seconds, whereas the camera traps were deployed in an area totalling 13 km^2 distributed as 1 km squares throughout the entire study area, and where constant surveys of each trap location spanned 7 days (168 h). Consequently, the spatiotemporal quality of the data collected per unit area varied from coarse to fine resolution. Spatial variation in encounter rates for example rare, or widely distributed species, has been shown to negatively affect Distance Sampling density estimates (Zero et al. 2013). Certainly within our study area, the Irish hare population exhibited significant spatial autocorrelation (Caravaggi et al. 2015), having a 'clumped' distribution e.g., in the south-east of the study site (Fig. 3). Thus, calculating an average density across the entire study area likely obscures spatial variation. Hare detectability during spotlight surveys of line transects is affected by local topography, being negatively associated with 'hilliness' (Caravaggi et al. 2015). Hills and hollows within surveyed fields can hide animals from view and are difficult to account for when estimating survey effort. Thus, our assumed estimate of survey effort (0.65) may be a source of error. Furthermore, it is probable that individuals which do not move, or which are positioned with their backs to the observer, are not detected, especially at greater distances, as the reflectivity of their *tapetum lucidum* remains hidden. Hares may lie low, or hide, prior to detection when disturbed by movement, noise, or incidental illumination, reducing the probability of detection and subsequently suppressing density estimates. However, the Distance Sampling detection function estimates the proportion of objects missed during surveys, thus accounting for these potential sources of bias. In contrast, camera trap surveys have near constant survey effort within their field of view, and detectability, given a focal species of sufficient physical size and a relatively homogenous landscape, is constant within the infrared cone of detection across cameras and sites. Thus, the quality of data is affected by the duration of survey and the placement of the camera traps. We used a random placement of cameras within 1 km^2 squares to avoid bias of survey effort *within*-squares, thus conforming to the REM ideal (Rowcliffe et al. 2008). Probability of detection was most likely affected, therefore, by the density of cameras and the composition of focal 1 km squares (the unit area for the camera-trap study and from which estimates of variance were obtained), the latter being almost certainly the most important factor. Having such a small sample size (n = 13) split into native allopatry, and invasive peripheral and core ranges, resulted in a large degree of variation between density estimates of individual squares (1.9–11.6 hares per km^2; Table S1). Thus, the zonal population estimates derived from our REM are inherently vulnerable to localized stochastic variation. One solution may be to distribute cameras, not within squares within each zone of invasion but rather randomly throughout each zone of invasion to cover a spatial scale more comparable to that covered by Distance Sampling. However, this method would substantially increase transport and staff costs in terms of driving greater distances between widely distributed camera trap sites.

Rowcliffe et al. (2008) state that a key underlying assumption of the REM is that targets move randomly relative to camera placement. Selective placement, example along a trail, violates this assumption, and may lead to overestimation of focal species densities. This was a key consideration in the current study as hares are known to habitually use paths between foraging sites. However, hares will make use of multiple entrance/exit points. Moreover, hares do not follow field boundaries, instead preferring to cross the open field directly. There is no evidence that the species differed in this regard. Thus, the methodology described herein was appropriate with regards to the species ecology. Recaptures also present an additional potential source of bias. Failure to properly account for recaptures may lead to inflated density estimates. However, the REM was developed as an alternative to capture-recapture studies which utilize individual markings and repeated detections to estimate population density and abundances. As such, accounting for resampling is an inherent feature of the REM. Obvious recaptures should of course be removed prior to analysis.

Distance Sampling assumes the random placement of transects, thereby approximating a uniform distribution of targets. However, road-based transects present particular challenges, and results may be inherently biased. For example, the assumption of uniformity is violated as targets are unlikely to be detected on roads (Marques et al. 2010). Moreover, nonuniformity may be expected given certain species traits (e.g., avoidance of field margins). However, temporal trends may nevertheless be explored if the assumption of constant bias is met. The use of roads in the present study was justified as: (1) we surveyed a rare species at very low density, thus continuously driven line transects afforded the greatest likelihood of detection; (2) the survey area in Mid-Ulster has a high density of minor roads (hares are rarely >300 m from a road though we acknowledge that undulating topography is nevertheless an issue); (3) we followed, and extended upon, many of the same transects used in the original European hare survey in 2005–06, so as to ensure comparability of results.

Differences in the spatial allocation of effort between Distance Sampling and camera trapping surveys may have led to differing absolute estimates, but the relative spatial

pattern of invasive-native species replacement was comparable. One of the major drawbacks of the REM is its requirement for *a priori* knowledge of daily movement patterns of the focal species. Given the lack of high temporal resolution GPS-telemetry for Irish and European hares in Ireland, it is impossible to say whether their daily movement patterns were similar to those of European hares in Austria and Italy, from which we obtained input data (Schai-Braun et al. 2012; Zaccaroni et al., *unpublished data*). The landscape of our study area consisted of small, agricultural fields, 76% of which were improved or rough grassland (EEA 2010). The country has a temperate climate, with regular rainfall. In contrast, the Austrian study took place in a landscape of small arable fields (Schai-Braun et al. 2012), whilst the Italian study took place in a landscape dominated by woodlands and vineyards in a Mediterranean climate (Zaccaroni et al. 2013). Furthermore, it is conceivable that movement was affected by interspecific interactions, i.e., local density of congenerics. However, despite these considerations, both the Austrian and Italian data converged on the same mean distance travelled per day of 890 m. In addition, the home ranges of European hares in Austria and Italy were comparable to those of Irish hares in Northern Ireland, suggesting that the use of these daily movement data for hares in the present study is not unreasonable.

Previous studies have reported hybridization between European and Irish hares (Hughes et al. 2009), with the invader's range expanding (Caravaggi et al. 2015). Recent data suggest a hybrid prevalence of ≥30%, with bidirectional mating and at least 2nd generation hybrids (Prodöhl et al. 2013). It is possible, therefore, that we detected hybrids during both surveys, particularly in the invader's peripheral range. However, given the phenotypic plasticity demonstrated by *L. europaeus* x *L. timidus* hybrids (Lönnberg 1905; Gureev 1964; cited in Thulin et al. 2006), this potential source of bias is unquantifiable without the utilization of genetic techniques to accurately identify hybrid individuals. In addition to hybridization, Irish hare populations in the invader's core and peripheral ranges are likely subject to displacement via interspecific competition for resources (i.e., food, mates). While more physically robust than continental mountain hares, Irish hares have evolved in the absence of direct ecological competition, and, hence, may exhibit a degree of naivety when faced with a more aggressive invader. We recommend the investigation of aspects of leporid ecology for which we are currently data deficient, e.g., relative fecundity and the prevalence of parasites or pathogens, so that we may have a more comprehensive and detailed understanding of the factors driving the species replacement process.

It is important that the invasive-native species replacement process undergoes surveillance and monitoring in the future. To this end, maximizing survey effort, in terms of the number of independent sites surveyed, would be beneficial to provide robust data. Non-parametric, resample-with-replacement bootstrapping optimization algorithms suggested that survey effort could be reduced by 57%. If we assume investment of the same *total* survey effort, the optimized camera trapping protocol would have allowed us to survey an additional 17 × 1 km^2 squares, thereby increasing the number of independent sites by 30%. If future surveillance adopts similar guidelines, it is likely that more robust zonal estimates of density will be acquired (i.e., larger sample sizes within zones), and, hence, provide improved resolution in monitoring the observed invasive-native species replacement process. Given the rapidity with which invasive species can spread and become established, we recommend recurrent surveys extending beyond the zone of invasion to monitor the status of both the native and the invader. It has been suggested that the European hare population in mid-Ulster was introduced in the 1970s, expanding at 0.73 km $year^{-1}$ between 2005 and 2013–14 (Caravaggi et al. 2015). The Swedish example, wherein European hares displaced the native mountain hare *L. timidus*, from over 210 000 km^2 of its former range (Jansson and Pehrson 2007), represents a stark reminder of the potential outcome of inaction in Ireland.

The purpose of this study was to evaluate the efficacy of the REM as a conservation tool in monitoring native and invasive leporids in Northern Ireland, using Distance Sampling as a corroborative methodology. We conclude that both camera trap random encounter models, and Distance Sampling, provide estimates of density and abundance that reflect relative changes in local leporid densities between different zones of invasion, thus capturing and describing an invasive-native species replacement process. With regard to camera trap surveys, increasing the number of independent sites surveyed by minimizing the number of cameras deployed and the duration of their deployment per site is likely to maximize future sample sizes providing more robust and precise estimates of local density and abundance. These data provide further support for the hypothesis that the invasive European hare poses a threat to the native Irish hare.

Data accessibility

Camera trap and Distance sampling raw data are available from Figshare (http://figshare.com/s/89016efaffc611e48b0806ec4bbcf141).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. *Ex situ* estimation of REM paramaters and validation
Figure S1. Simulated detection validation
Figure S2. Simulated density estimation
Data S2. Random encounter model and distance sampling density estimates
Table S1. Density estimates from REM
Table S2. Density estimates from Distance Sampling

Data S3. Explanation of *post hoc* stratification of Distance Sampling estimates
Figure S3. Density estimates based on in-program stratification
Table S3. Density estimates stratified by zone and species
Table S4. Density estimates stratified by zone
Table S5. Population density estimates of European and Irish hares derived *post hoc* from Table S4.

Supporting Information 1

Ex-situ estimation of REM parameter validation

Studies utilising the REM have largely estimated the maximum zone of detection parameters by means of operator camera activation (Rowcliffe *et al*, 2008; Manzo *et al.,* 2011; Anile *et al.,* 2014; Carbajal-Borges *et al.,* 2014). However, refinement of the method led to the zone of detection being derived from individual detections, i.e. the mean position of each animal at the point of first detection (Rowcliffe *et al.,* 2011). To record these data, researchers must either examine all recorded images *in-situ*, estimate the location of each animal in the landscape, and measure each parameter empirically, or return to the field to take relevant measurements after sorting the images *ex-situ*.

Processing camera trap data can be extremely time consuming, particularly if video footage is being recorded rather than still images. In this study, we found that the focal species (European and Irish hares) accounted for only 3.6 hours (3%) of 120 hours of video footage recorded. The study area was set in agricultural land and consisted of small fields, so it was not surprising that approximately 75% of all records featured domestic livestock. Identification of animals and measurement of REM parameters from detections *in-situ* was thus impractical given both the individual and cumulative duration of detections, and the low resolution of camera playback screens which made recognition of distant animals difficult (i.e. confusing hares with rabbits). Re-visiting sites to measure r_i and a_i, while possible, was not considered to be practical given constraints of time and cost. To address these considerations, we developed a protocol for the *ex-situ* estimation of r_i and a_i from camera trap images using a modified field protocol and a simple grid system using readily available image manipulation software (see main Methods of primary report).

Ex-situ parameter estimation

To simulate the location of an animal, a small metal disc was tossed into the field of view of a camera trap, and then replaced with a medium-sized backpack (40 x 27 cm) representing a hare. The camera trap was set as described in the main Methods of the primary report. Data were collected from 10 data points in each of 10 fields (n=100). Fields were chosen *a priori* based on subjectively-discerned differences in aspect and vegetative composition so as to mimic the variety of habitats encountered while undertaking farmland surveys. Thus, field composition included pasture, reed (*Juncus* sp.)-dominated rough grassland, and unimproved land, across a variety of aspects. The distance (r_i) to the backpack from the camera (given false origin coordinates 0,0) was measured from the foot of the camera mount using a tape measure. The angle (a_i) to the backpack from the camera was measured using a handheld compass, following Rowcliffe *et al.* (2008, 2011). A cane grid was erected and a reference photograph taken for *ex-situ* data extraction (see the main Methods of the primary report, and Fig. 1).

Comparisons between r_i and θ_i measured *in-situ* and derived *ex-situ* were examined using linear regression. To establish the performance of both input datasets, densities were calculated from both *in-* and *ex-situ* data, using a range of sample sizes from groups of 10, 20, and 30 detections, selected at random. Rowcliffe *et al.* (2008) suggest a minimum of 10 detections are required for adequate performance of the REM. Thus, we used two multiples of this minimum requirement. Confidence intervals of 95% were estimated using non-parametric, resample-with-replacement bootstrapping, with 1000 iterations where the unit of variance was the number of detections, i.e. resampled according to sample group size. Data analyses were carried out using the program R (R Core Team, 2014). Temporal (t) and distance-travelled (v) parameters followed their descriptions in the Methods section of the main manuscript.

Results

Simulated detections were distributed throughout the zone of detection (Fig. S1a). Radial distances (r_i) estimated using the *ex-situ* method were significantly positively correlated with *in-situ* measurements ($F_{1,98}$= 2430.70, $p < 0.001$, $R^2 = 0.98$; Fig. S1b). There was a mean difference of 27cm (95% CI 23-31cm) between the methods. Precision declined at distances beyond 6m though the correlation remained statistically significant ($F_{1,14}$= 15.47, $p < 0.001$, $R^2 = 0.75$; Fig. S1b insert), with a comparable mean difference of 22cm between the methods but substantially greater variation (95% CI 6-38cm). *In-situ* measured and *ex-situ* estimated angles (a_i) were also significantly positively correlated ($F_{1,98}$= 410.57, $p < 0.001$, $R^2 = 0.90$; Fig. S1c), with a mean difference of 0.07 radians (95% CI 0.06-0.08) equivalent to 3.97° (95% CI 3.29-4.65°). Simulated REM density estimates did not differ significantly between models using *in-situ* measured and *ex-situ* estimated input parameters over sample sizes of 10, 20 and 30 detections (Fig. S2).

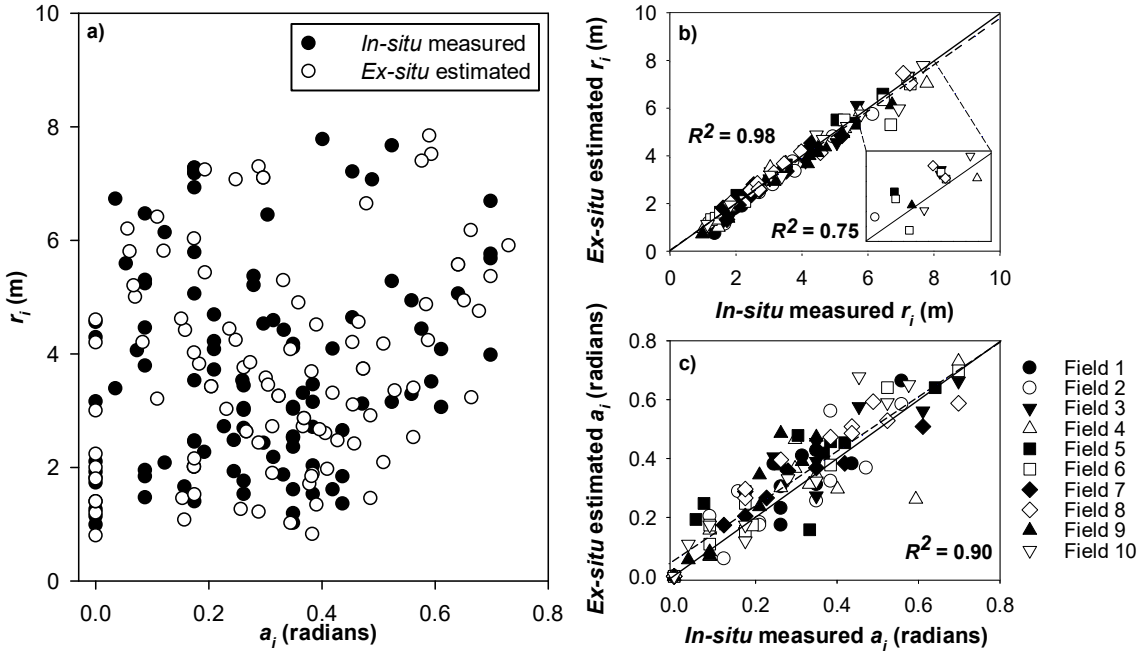

Fig. S1 (**a**) Position of simulated detections (n = 100) relative to the camera (at false origin coordinates 0,0). The zone of detection is assumed to be symmetrical; hence, this plot describes half of the sector. **(b)** Correlations between *in-situ* measured and *ex-situ* estimated. Distances r_i and **(c),** angles (a_i) to random object placements, i.e. hypothetical animal locations. Precision in estimating radial distance begins to decline at a distance of approximately 6m (insert in b). The dashed line represents the observed regression coefficient. The solid line represents a gradient of 1, deviation from which describes inaccuracy.

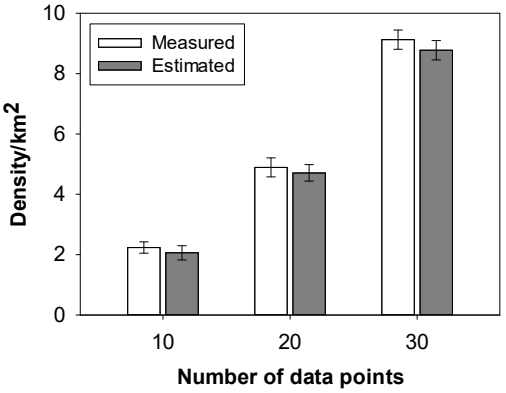

Fig. S2 Density estimates (± 95% confidence intervals) derived from the Random Encounter Model (REM), using measured and estimated radial distances (r) and detection zones (θ) for a range of sample sizes i.e. simulated detections.

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Supporting Information 2

Random Encounter Model and Distance Sampling density estimates

Table S1 Population density estimates derived from the *Random Encounter Model* using camera trapping data for native and invading hares in Mid-Ulster, Northern Ireland during 2013. * highlights three squares of European hare allopatry in the invader's core range within which the native species was entirely absent.

Zone	Square ID	Number of detections	Absolute density Hares.km^2		% European hares	Hares.km^2 European		Hares.km^2 Irish	
Native species allopatry	1	10	2.0	(1.4 - 3.0)	0	0.0	(0.0 - 0.0)	2.0	(1.4 - 3.0)
	2	21	2.6	(2.1 - 3.5)	0	0.0	(0.0 - 0.0)	2.6	(2.1 - 3.5)
	3	23	2.5	(2.0 - 3.2)	0	0.0	(0.0 - 0.0)	2.5	(2.0 - 3.2)
	4	46	4.8	(4.1 - 5.7)	0	0.0	(0.0 - 0.0)	4.8	(4.1 - 5.7)
	$\bar{x}$	**25**	**3.0**	**(2.4 - 3.9)**	**0**	**0.0**	**(0.0 - 0.0)**	**3.0**	**(2.4 - 3.9)**
Invader's peripheral range	5	42	6.8	(5.9 - 8.0)	0	0.0	(0.0 - 0.0)	6.8	(5.9 - 8.0)
	6	17	2.3	(1.7 - 3.1)	18	0.4	(0.3 - 0.5)	1.9	(1.4 - 2.6)
	7	12	1.9	(1.3 - 2.6)	58	1.1	(0.8 - 1.5)	0.8	(0.6 - 1.1)
	8	46	7.0	(6.0 - 8.2)	28	2.0	(1.7 - 2.3)	5.0	(4.3 - 5.9)
	9	62	5.7	(5.0 - 6.7)	85	4.9	(4.3 - 5.7)	0.8	(0.7 - 1.0)
	$\bar{x}$	**36**	**4.8**	**(4.0 - 5.7)**	**38**	**1.7**	**(1.4 - 2.0)**	**3.1**	**(2.6 - 3.7)**
Invader's core range	10	69	11.6	(10.2 - 13.3)	68	7.7	(6.9 - 9.1)	3.9	(3.3 - 4.2)
	*11	51	4.9	(4.5 - 5.5)	100	4.9	(4.5 - 5.5)	0.0	(0.0 - 0.0)
	*12	34	3.7	(3.1 - 4.8)	100	3.7	(3.1 - 4.8)	0.0	(0.0 - 0.0)
	*13	23	2.6	(2.1 - 3.2)	100	2.6	(2.1 - 3.2)	0.0	(0.0 - 0.0)
	$\bar{x}$	**44**	**5.7**	**(5.0 - 6.7)**	**92**	**4.7**	(4.2 - 5.7)	**1.0**	(0.8 - 1.1)

Table S2 Population density estimates derived from *Distance sampling* using night-driven spotlight surveys for native and invading hares in Mid-Ulster, Northern Ireland during 2013.

Zone	Number of detections	Absolute density Hares/km^2		% European hares	Hares/km^2 European		Hares/km^2 Irish	
Native species allopatry	121	1.7	(1.5 - 1.8)	0	0.0	(0.0 - 0.0)	1.7	(1.5 - 1.8)
Invader's peripheral range	83	2.1	(1.6 - 2.5)	43	0.9	(0.7 – 1.1)	1.2	(0.9 – 1.3)
Invader's core range	63	9.4	(8.4 – 10.4)	87	8.2	(7.5 – 8.8)	0.8	(0.7 - 0.9)

Supporting Information 3

Justification for post-hoc stratification of Distance estimates

The program Distance is capable of post-stratification of data according to a given criteria, e.g. species. However, stratification with low numbers of detections can return unrealistic estimates. We calculated density and abundance estimates by: i) counting each transect (i.e. each separate road) individually, post-stratifying by zone and species (Fig. S1c, Table S3); and ii) counting each transect (i.e. each separate road) individually, post-stratifying by zone (Table S4), and calculating species-specific densities post-hoc (Fig. S3d, Table S5).

Due to the paucity of native species sightings in the core range, post-stratification by zone and species returned wholly unrealistic density and abundance estimates (Fig. S3c, Table S3), for example, 19.7 European hares/km^2 (95%CI 8.96 - 43.46) and 3.4 (95% CI 0.0 - 204,620) Irish hares/km^2.

While post-stratifying by zone and calculating species-specific densities post-hoc returned more reasonable Irish hare estimates for the core range, the European hare density estimate and associated confidence interval for the core remained excessive (19.74 hares/km^2 (95% CI 8.73 - 44.6); Fig. S3d, Table S5). We therefore suggest that the methodology described in the manuscript is appropriate as it provides results that are approximate to those obtained in previous Northern Ireland Irish hare Surveys (Reid *et al*., 2010).

References

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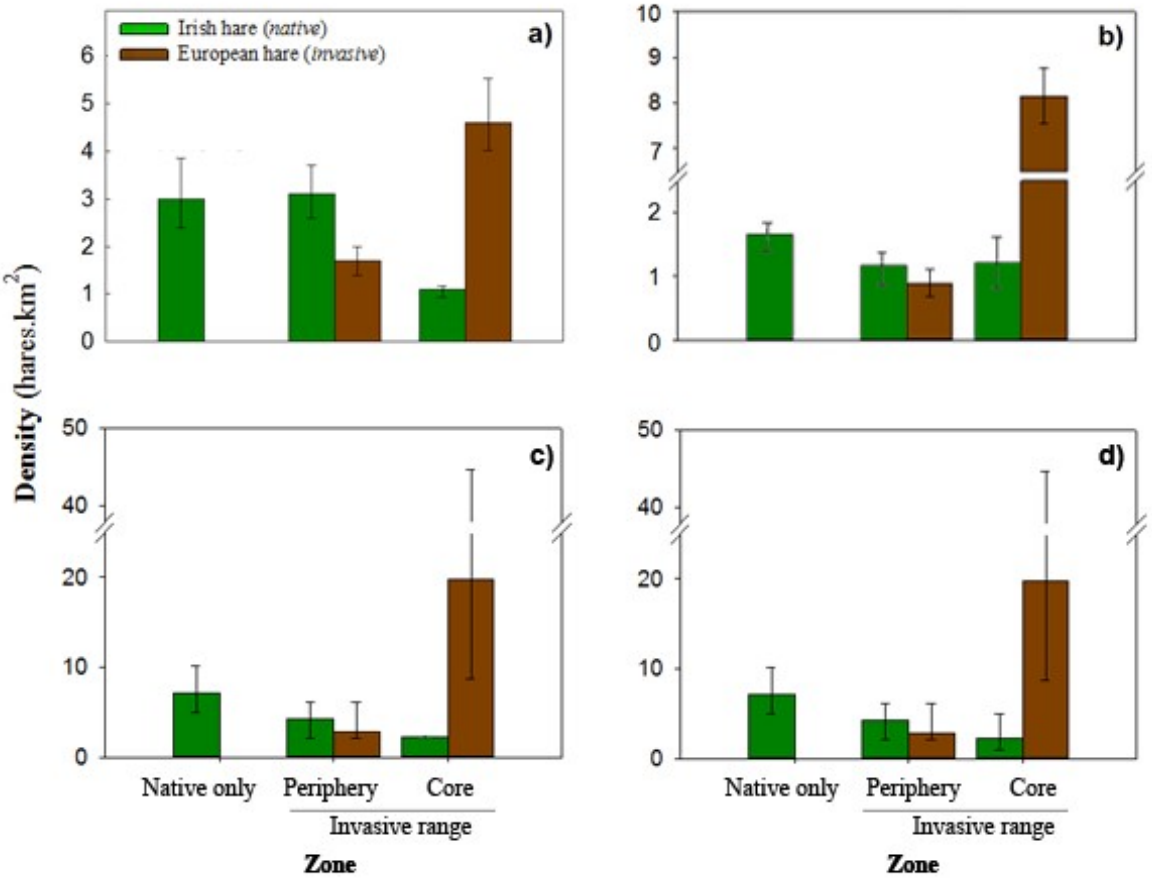

Fig. S3 Species replacement as demonstrated by native and invading hare densities (hares/km^2 ± 95% CIs) derived from **(a)** the Random Encounter Model (REM) using camera trapping data and **(b, c, d)** Distance sampling using nocturnal spotlight surveys in three zones: i) native species only, ii) invasive species peripheral range and iii) invasive species core range. Distance estimates and 95%CI were calculated: **(b)** according to the main Methods described in the primary manuscript; **(c)** post-stratifying by species and zone; **(d)** post-stratifying by zone, and calculating relative species densities *post-hoc*. Error bars are omitted from core Irish hare estimates in **(c)** due to their extreme nature (Table S3).

Table S3. Population density and abundance estimates of hares in Northern Ireland, calculated using the software Distance, stratified by zone and species.

Species	Range	Density (hares/km^2)		Abundance	
European hare	Invasive core	19.7	(9.0 - 43.4)	653	(297 - 1,438)
	Invasive periphery	3.8	(2.2 - 6.4)	2,022	(1,194 - 3,424)
	Native allopatry	0	(0.0 - 0.0)	0	(0 - 0)
Irish hare	Invasive core	3.4	(0.0 - 204,620.0)	113	(0 - 6,772,400)
	Invasive periphery	3.7	(2.2 - 6.1)	1,981	(1,194 - 3,2487)
	Native allopatry	7.2	(4.2 - 12.4)	7,667	(4,437 - 13,250)

Table S4. Population density and abundance estimates of hares in Northern Ireland, calculated using the software Distance, stratified by zone. Species-specific estimates **(Table S5)** were calculated post-hoc based on relative proportions observed during Distance Sampling.

Range	Density (hares/km^2)		Abundance	
Invasive core	22	(3.7 - 50.0)	726	(321 - 1,640)
Invasive periphery	7.1	(5.0 - 10.2)	3,816	(2,665 - 5,465)
Native allopatry	7.2	(4.2 - 12.4)	7,667	(4,437 - 13,250)

Table S5. Population density estimates of European and Irish hares in Northern Ireland, derived from data in **Table S4**, and based on relative proportions observed during Distance Sampling.

Range	European hare		Irish hare	
Invasive core	19.7	(8.7 - 44.6)	2.2	(1.0 - 5.0)
Invasive periphery	2.9	(2.1 - 6.2)	4.3	(2.1 - 6.2)
Native allopatry	0	(0.0 - 0.0)	7.2	(4.2 - 12.4)