Survival, movements, home ranges and dispersal of hares after coursing and/or translocation

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Front cover, small photographs from top row:
A deep water fly trap anemone Phelliactis sp., Yvonne Leahy; Common Newt Lissotriton vulgaris, Brian Nelson; Limestone pavement, Bricklieve Mountains, Co. Sligo, Andy Bleasdale; Garden Tiger Arctia caja, Brian Nelson; Violet Crystalwort Riccia huebeneriana, Robert Thompson; Coastal heath, Howth Head, Co. Dublin, Maurice Eakin; Meadow Saffron Colchicum autumnale, Lorcan Scott

Bottom photograph: An Irish hare Lepus timidus hibernicus wearing a GPS-radio collar, Neil Reid.
Survival, movements, home ranges and dispersal of hares after coursing and/or translocation

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Contents

Executive Summary ........................................................................................................... i
Acknowledgements .......................................................................................................... i

1 Introduction .................................................................................................................. 1

2 Methods ....................................................................................................................... 2

2.1 Funding ..................................................................................................................... 2

2.2 Ethics ......................................................................................................................... 2

2.3 Conflicts of Interest ................................................................................................. 2

2.4 Experimental design ............................................................................................... 2

2.5 Animal tagging ........................................................................................................ 3

2.6 Collar testing ............................................................................................................. 4

2.7 Tracking .................................................................................................................... 5

2.8 Outcomes ................................................................................................................ 5

2.9 Movements .............................................................................................................. 6

2.10 Home ranges ......................................................................................................... 8

2.11 Dispersal ................................................................................................................. 8

3. Results ....................................................................................................................... 9

3.1 Outcomes ................................................................................................................. 9

3.2 Activity ..................................................................................................................... 15

3.3 Daily movements during the first week ................................................................. 17

3.4 Daily home ranges during the first week ............................................................... 17

3.5 Movements over six months .................................................................................. 18

3.6 Weekly home ranges over six months ................................................................... 18

3.7 Dispersal ................................................................................................................... 19

4 Discussion .................................................................................................................. 22

4.1 Recommendations ................................................................................................. 25

4.2 Conclusions ............................................................................................................. 26

5 Bibliography & Relevant Literature ........................................................................... 27
Executive Summary

Hare coursing is the pursuit of a hare by long dogs. In Ireland, up to 6,000 hares are caught from the wild each year by long netting and held in captivity for up to eight weeks. Hares are given a head start and coursed in an enclosed arena by two muzzled greyhounds where the object is not to kill the hare, but judge the dogs on their ability to turn the hare from a straight course. The first dog to do so wins the match. The hare escapes under a baffle through which the dogs cannot follow. Over 98% of hares survive and are released back into the wild. In addition to animal welfare objections, the anti-coursing lobby has questioned the survival of coursed hares after their release back into the wild, sometimes in unfamiliar territory.

In this study, 40 hares were fitted with GPS-radio collars and were tracked for up to six months in a factorial experimental design with 10 translocated coursed, 10 untranslocated coursed, 10 translocated uncoursed and 10 untranslocated uncoursed hares.

Two hares released shortly before sunset were killed in road traffic collisions (unrelated to either coursing or translocation) during their first night; no mortalities were recorded for hares released during the morning.

Movements, home ranges and dispersal of hares that remained in the vicinity of release sites were similar between the cohorts once translocated hares, which moved significantly further and had larger home ranges during the first few days after release, had settled.

Fewer coursed than uncoursed hares remained in the vicinity of the release site six months later with more coursed hares disappearing during the study though the causes remain unknown. There was no evidence that coursed and/or translocated hares suffered higher levels of mortality than control hares. There were no differences in coursed and uncoursed hares in their spatial behaviour after release. Movements, home range size and dispersal were similar between cohorts once translocated hares, which moved significantly further and had larger home range sizes during the first few days, had settled.

This is the first assessment of the movements, home ranges and dispersal of coursed hares after their release back into the wild and provides evidence to support current Government coursing licence conditions on where and when to release coursed hares. Translocated hares did not suffer higher mortality and settled quickly suggesting the impacts of translocation after coursing may be limited. Releasing hares during daylight, preferably as early as possible, may provide time for animals to settle before darkness.

Questions remain on the survival and dispersal of coursed hares and it is suggested that any future studies should consider using mobile phone (cellular) or satellite collars (now small enough for hares), mounted on straps impervious to fraying and failure, to minimise collar losses and maximise known outcomes. Complete genetic sampling of coursed hares would help to answer further questions relating to post-release survival and reproduction.

Acknowledgements

Dr Ferdia Marnell was the NPWS Project Client Officer. Thanks to the Irish Coursing Club (ICC), the Chief Executive Mr DJ Histon, Conor Foley, John Curtin and John Troy for cooperating with the research, organising permissions for access to release sites, the provision of coursed hares and supporting the netting of wild control hares. NPWS Conservation Rangers, Killian Brennan and Hugh McLindon, inspected hare handling, collaring and release procedures. Many thanks to the landowners and farmers who granted access to their land for tracking. Thanks to Mr Ian Valentine, Kilrush Airfield Ltd. for piloting the helicopter for aerial searches.
1 Introduction

Hare coursing is the pursuit of a hare by long dogs. Coursing can be ‘open’, where the hare is chased in situ being flush from its form (its daylight lie-up site) or ‘closed’, where it is caught and transported to a coursing field. In Europe, coursing persists in Spain and Portugal and notably Ireland. The Irish hare (Lepus timidus hibernicus) is a game or quarry species and can be hunted during an open season from the 26th September to the 28th February each year (under the Wildlife Act 1976 as amended). Unlike in other European countries, hares are not traditionally shot in Ireland but instead are hunted on foot with a pack of harrier hounds or, more popularly, coursed using greyhounds. The Irish Coursing Club (ICC) consists of 70-80 local coursing clubs distributed all over the country but concentrated in the south. Up to 6,000 hares are captured from the wild each year under Government licence by long netting (Reid et al., 2007). Nets 1.5 m tall and sometimes tens of metres long are hung from forked sticks to create a pouch at ground level. These are placed across likely exit routes from an area to be walked over by a line of beaters such that hares flushed from their daily forms run into the net (Wyman, 1997). Target areas include unimproved rough pasture with substantial cover of rushes, Juncus species, in which hares shelter during daylight hours. Hares may be ear tagged for individual identification commonly using coloured and/or numbered lamb ear tags and boxed and transported to a local holding paddock. Captive hares are given about a 75 m head start before being pursued by two muzzled greyhounds within an enclosed football field-sized arena where the object is not to kill the hare but turn it from a straight course. The dog responsible for turning the hare (identified as the one wearing either a white or red collar) wins the match. The average course lasts less than 40 seconds (Reid et al., 2007). Regional heats and tournaments are held with the best dogs competing at a National meeting. Dogs are selectively bred with their pedigree documented for many generations. Hares escape through a baffle at the end of the coursing field through which the dogs cannot follow and are returned to a holding paddock. Throughout up to eight weeks in captivity (Kelly, 2020), hares are supplementary fed with, for example, oats and grain, willow, apples etc. And receive veterinary treatment including being dosed with a broad spectrum anthelminthic such as Ivermectin, to rid them of parasitic ticks, lice and worms (Reid et al., 2007). The introduction of compulsory dog muzzling, and the sharing of best practice in captive hare husbandry between clubs, has improved survival rates significantly (Reid et al., 2007) which was last reported at more than 98 % annually (Murphy, 2013; Kelly, 2020). Coursing licences state that the same numbers of hares must be released back into the wild as far as possible at the same locations from which such numbers were captured though this may result in hares being inadvertently translocated and released into unknown territory provided a similar number are released, as was caught, at each site. Habitually the same sites are used year-on-year for the capture and release of hares and they are often owned and managed by farmers who are members of the local coursing club. As such, suitable habitat may be left unimproved, predators such as foxes may be controlled and other forms of hare hunting may be prohibited. As a result, so-called hare preserves may be associated with a higher hare population density than comparable areas in the wider countryside (Reid et al., 2010a, 2010b) though the direction of this relationship has been questioned (Kelly, 2020).

Objections to hare coursing in Ireland focus on animal welfare concerns with some in the anti-coursing lobby, such as the Irish Society for the Prevention of Cruelty to Animals (ISPCA), questioning the survival of coursed hares after their release back into the wild and raising concerns about their release into unfamiliar territory (Kelly, 2020). A previous study radio-tracked nine coursed hares demonstrating survival up to 11 weeks after release (the end of the study) but there were no control animals and no analysis of the effects of translocation (Preston et al., 2006).

This study aimed to assess survival and behaviour of coursed hares after their release back into the wild. The specific objectives were to compare: i) relocation rates and ii) movements (including home range sizes and dispersal) between coursed and uncoursed, and,
translocated and untranslocated hares to examine their impacts both in isolation, and together. These data may help inform Government in decision making when granting licences for hares to be taken from the wild for coursing.

2 Methods

2.1 Funding

This study (Project Identifier Code: 1302_THMS20) was commissioned and funded by the National Parks and Wildlife Service (NPWS), Department of Housing, Local Government and Heritage (see www.npws.ie) and awarded under open competitive tender (at ETENDERS https://irl.eu-supply.com) to Queen’s University Belfast (www.qub.ac.uk/schools/SchoolofBiologicalSciences).

2.2 Ethics

The proposed research protocol was peer-reviewed by two academics working in the field of animal behaviour who reported to the Faculty of Medicine, Health and Life Sciences Research Ethics Committee at Queen’s University Belfast, who approved the proposal on 24th March 2021 (Faculty REC Reference No. MHLS 20_124 amended 4th February 2022). The Irish Coursing Club (ICC) were not involved in experimental design, including sample size determination, data collection, analysis, or interpretation. Queen’s University Belfast was not responsible for, or otherwise involved in, the coursing of hares with already coursing hares being collared just before their release back into the wild. The Irish Coursing Club were licenced by NPWS to capture live hares under Section 34 of the Wildlife Act 1976 to 2018 (as amended) and to attach a tag to a wild animal under Section 32 (for licences see www.npws.ie/licencesandconsents/hare-coursing). To facilitate the current research, an additional condition was added to the ICC licence stating that “the ICC and its affiliated clubs shall co-operate with […] the study”. Uncoursed hares were netted from the wild. The author was licenced to capture protected wild animals for scientific purposes under the Wildlife Act Sections 23 and 34 (Licence No. C55/2021) and to attach a tag to a wild animal under Section 32 (Licence No. 05/2021). NPWS Conservation Rangers, Killian Brennan and Hugh McLindon, inspected hare handling, collaring and release procedures. Fieldwork was covered by Risk Assessment, Lone Working protocols and Professional and Public Liability Insurance.

2.3 Conflicts of Interest

The author was an employee of Queen’s University Belfast and declared no conflict of interest having never been involved with hare coursing, or the Irish Coursing Club, in any capacity, other than being the subject of research.

2.4 Experimental design

A fully factorial 2x2 experimental design was used with two interacting treatments. Treatment one consisted of 20 coursed and 20 uncoursed hares, Treatment two consisted of 20 translocated and 20 untranslocated hares, with both treatments interacting such that half of each overlapped with the other i.e. 10 translocated coursed, 10 untranslocated coursed, 10 translocated uncoursed and 10 untranslocated uncoursed hares, were used (the latter group being the wild control group). This approach was adopted to tease apart the potential impacts of coursing and translocation in isolation and together. The total sample size (40 hares) was restricted by the logistical considerations of how many animals could be tracked simultaneously, and funding. The sample size exceeded the number of individual hares GPS-radio tagged in other recent studies (for example, 25 hares in Mayer et al., 2021; 32 hares in Gigliotti et al., 2018 and 34 hares in Ullmann et al., 2022).
Twenty hares had been coursed by the Irish Coursing Club in the normal operation of the National Coursing meeting at Clonmel, Co. Tipperary in early February 2022. Coursed hares may have spent up to eight weeks in captivity. Hares were collared the day after the National meeting with 10 released at their original site of capture and 10 released into unfamiliar territory, at a site other than where they were captured. Translocated courséd hares were relocated between counties having been brought from other coursing districts. A further 20 hares were captured from the wild using long nets. These hares were temporarily held in boxes until the full cohort had been caught before each was collared, with 10 released at their site of capture and 10 released into unfamiliar territory. Translocated uncoursed hares were relocated locally with a minimum distance between capture and release of 3 km, where animals were taken across a river approximately 5 m wide with few crossing points, though most animals were translocated further. Due to the sensitivity around hares, and hare coursing, in Ireland the locations of capture and release remain confidential. A total of 34/40 hares (85%) were collared and released on the 8th February 2022 (including both courséd cohorts) with the remaining six hares (15% - all uncoursed) caught from the wild and released four days later on 12th February 2022.

2.5 Animal tagging

Hares were tagged with Litetrack RF60 GPS collars (Figure 1) supplied as a single made-to-order batch under open competitive tender from LOTEK Ltd. (www.lotek.com/products/litetrack-60). All animals were weighed to the nearest 100 g. GPS collars were 175 g which was ≤5 % of the average body weight of tagged hares measured at 3.4 kg (n=40). Collars were programmed to collect a SWIFT GPS fix once every hour such that battery life and storage capacity would enable collection of a minimum of six months of spatial data. Each collar had a mortality sensor such that should it remain motionless for 24 hours, it recorded the date and time motionlessness started whilst the rate of the radio signal beeps doubled alerting the researcher, enabling recovery. Collar VHF (very-high frequency) radio beacons were programmed to be active 10am-5pm GMT daily to enable animals to be detected, triangulated and their data downloaded using an UHF (ultra-high frequency) radio channel activated from about 50 m away. Data downloads occurred during daylight hours when animals were lying up in their forms undisturbed. Collars were assembled with cotton stitching ensuring they dropped off after the stitching degraded in the natural environment.
2.6 Collar testing

The operation and programming of each collar was initially tested for 24 hours prior to deployment. Collars were hung from wooden pegs 30 cm (12 inches) above ground level replicating their approximate height and orientation when attached to a sitting hare. Pegs were placed in a 6x7 grid with 3 m spacing between collars in an improved grassland field. The coordinates for their actual positions were measured out on the ground relative to fixed features e.g. a wall and hedge line such that their positions could be accurately mapped using Google Earth Pro aerial imagery georeferenced in ArcMap 10.8 (ESRI, California, USA). All VHF signals were confirmed as detectable using a Sika radio receiver and flexible yagi antennae (www.lotek.com/products/biotracker-vhf-receiver). All mortality beacons were confirmed to activate after 24 hours of no motion. GPS fixes (one per hour) were downloaded from each collar using the UHF radio channel to confirm remote data download was operational.

The distance between each GPS fix and the known coordinates of each collar was calculated using the Near function in the Spatial toolbox for ArcMap. After exclusion of three fixes with errors 13-32 km from the test grid (fixes where only two to three satellites were found), collars had an average error of 7 m per hourly fix with an average maximum error of 39 m per collar and maximum single GPS error of 264 m. Thus, even when collars were motionless (replicating a hare lying up during daylight) there may be apparent movement, usually in the region of tens of metres per hour, attributable solely to GPS locational error. As all collars were equally subject to this source of error its effects are unlikely to have biased the results compared between experimental cohorts.

All collars were cleared of test data and deactivated until just before deployment. During actual deployment on an animal, each collar was activated and its radio beacon confirmed as signalling before attachment.
2.7 Tracking

After release, animals were relocated by triangulation of their daily VHF beacons after one week with spatial data downloaded. Animals were subsequently relocated with data downloaded once per month up to the 18th August 2022 (191 days or 6.3 months after release).

Experience in the field suggested that collar VHF beacons were undetectable much beyond approximately 350 m. During each visit, the extent over which hares ranged, as observed from data downloaded on any previous visit, was walked whilst scanning through all collar radio frequencies to find animals if they were not immediately detectable from their last known position. All minor roads, and many farmers lanes and tracks, were driven at 10-15 kph out to approximately 5 km from each release site with a roof-mounted omnidirectional antennae with continuous scanning of all missing collar radio frequencies. Sites were further searched from the air on 3rd June 2022 by privately chartered helicopter, piloted by Mr Ian Valentine (Kilrush Airfield www.kilrushairfield.com). A yagi antenna was fixed to one of the helicopter skids pointing directly behind the aircraft (Figure 2). A spare collar was placed on the airfield at a known location and the aircraft flown at the lowest allowable altitude of 500 ft (152 m) directly away from the collar until the signal was lost at approximately 800-1,000 m suggesting detection distances may have been up to three times further from the air than ground-based surveys. Sites were flown circling outward. Any potential signals detected from the air were investigated further from the ground (both by vehicle and on foot) immediately after landing.

![Figure 2 a) The helicopter used to search for missing hares from the air showing b) the fixing of the yagi antennae to the skid.](image)

2.8 Outcomes

The fate of each tagged hare was classified at the end of the study as: i) never located after release, ii) relocated but subsequently lost, iii) collar removed, iv) collar retrieved with suspected evidence of death (e.g. animal-vehicle collision, predation) and v) relocated alive. Variation in the proportion of hares classified by outcome was tested across experimental cohorts using 2x2 or 2x4 χ2 Contingency tests with the former comparing two cohorts (each
with 20 hares) and the latter four cohorts (each with 10 hares). The probability of relocating a hare throughout the six months was compared between cohorts using Kaplan-Meier survival analysis and Log Rank Mantel-Cox tests.

2.9 Movements

GPS fixes were cleaned to remove single points falling well beyond each study site (more than tens of kilometres) indicative of GPS error associated with too few satellites being used for triangulation.

Hare movement was measured as step lengths i.e. the distance between successive hourly GPS locations. As 12% of GPS fixes were missing, due to too few satellites being detected, movements were standardised per hour. That is, the distance between points two hours apart was divided by two, and so on, to express movements in metres per hour (m/hr).

Hare activity patterns (average hourly movements across the 24-hour period) was described by a boxplot of step lengths with variation analysed using a Generalised Linear Mixed Model (GLMM) fitting Hour of the day as a Fixed Factor and HareID as a Random Factor to account for repeated measures of each animal throughout the study. Sunrise and sunset times varied from 4-8am and 5-9pm respectively between February during mid-winter (initial release) and June during mid-summer (four months after). Thus, not only was it necessary to adjust for daylight savings (BST to GMT) but also to standardise any activity profile relative to date-specific local sunrise and sunset creating a daylight and darkness offset. Hourly movements were described as a boxplot of step lengths offset relative to sunrise and sunset (both adjusted to a value of zero). Activity in daylight was given as the number of hours into daylight (up to local midday) and activity in darkness given as the number of hours into darkness as a negative integer (up to local midnight). Based on their observed activity pattern, the 24-hour period was subsequently split into an Active period and Inactive period.

It was not simply a matter of adding all consecutive step lengths together to get a measure of the total distance travelled by each individual due to the problem of missing GPS fixes. To account for missing data, the average mean value for each hare’s rate of movement, in metres per hour, for each day’s Active and Inactive periods was calculated and multiplied by the number of hours in that day’s Active and Inactive periods. The sum of the Active and Inactive estimates provided a total daily estimate. This multiplicative method essentially filled in the average movements for missing values specific to each day, for each hare, and allowed the total distance covered by each hare, every 24 hours, to be estimated. To avoid the creation of any artefacts by imputing missing data, the estimated total distance travelled each day was linearly regressed with the summed total distance travelled each day for hares where all 24-hourly fixes were obtained i.e. those days when there were no missing data as sufficient satellites were found for each fix. These two were near perfectly correlated ($r^2=0.994$; Figure 3) with only a 0.5 m average difference between the estimated value and true value out of 1.7 km/24hrs (i.e. estimated values were within 0.03 % of the true value). Thus, this method was used to estimate total distances covered by hares when not all hourly movement values were present.
Figure 3 Linear regression between the actual total summed distance moved by hares every 24 hours when 24 GPS fixes were successfully collected, and the distance estimated as the sum of the active and inactive periods’ hourly averages multiplied by their duration each day.

Total estimated daily movements were analysed every day over the first week after release to examine immediate effects of experimental treatments. Total estimated distance travelled every 24 hours was fitted as the dependent variable in a GLMM with Day fitted as a continuous covariate and sex, coursing, translocation and their interaction as fixed factors and HareID fitted as a Random Factor. This analysis was repeated and restricted to the first four days and last three days of the first week. Two further models were fitted, one restricted to the Active period and another to the Inactive period with identical model structure.

Total estimated daily movements were also analysed every week over the 27 weeks (6.3 months) during which spatial data were collected to examine longer-term effects. GLMMs of total estimated distance travelled every 24 hours were fitted again but this time with Week as a continuous covariate and sex, coursing, translocation and their interaction as fixed factors and HareID fitted as a Random Factor. Again, this analysis was repeated and restricted, this time to Weeks 2-15 i.e. excluding Week 1 and Weeks 16-27. Two further models were fitted, one for the Active and another for the Inactive period with identical model structure.
2.10 Home ranges

Spatial analyses were conducted using the program Ranges 9 v4.01 (Anatrack Ltd, England [www.anatrack.com]). A hare’s home range i.e. the extent of the area used by the animal expressed in hectares, was defined as the 95% kernel polygon enclosing GPS fixes while their core range was defined as the 50% kernel (Figure 4). These were drawn using subsets of the data to produce daily home ranges for the first week and weekly home ranges over the duration of the study. Home range size was fitted as the dependent variable in GLMMs with either Day or Week fitted as a continuous covariate as appropriate and sex, coursing, translocation and their interaction fitted as fixed factors and HareID as a Random Factor.

2.11 Dispersal

Ranges 9 estimated the distance between the release site of each animal and each of its subsequent GPS locations. This distance was fitted as the dependent variable in a GLMM with Week fitted as a continuous covariate and sex, coursing, translocation and their interaction as fixed factors and HareID as a Random Factor.

Figure 4 An example of a translocated coursed hare’s GPS locations (red dots), home range (9.8 ha 95% kernel polygon: outer boundary), core range (2.8 ha 50% kernel: inner boundary), and step length movements (dashed lines) during Week 2 when the animal had settled after the disturbance of the first few days, immediately after release. During Week 2, this animal’s average step length was 68 m/hr, the furthest single movement was 530 m with the animal travelling on average 1.7 km/24hrs and 11.6 km/week.
3. Results

3.1 Outcomes

There was no difference between experimental cohorts in the proportions of hares never located after release, or, those that were relocated after release but subsequently disappeared (Table 1). Taken together, these disappearances accounted for 19/40 hares (47.5 %) throughout the study. Only two animals that went missing were relocated again, and in both cases, this was when they spontaneously reappeared within their usual home ranges having not been located during a previous tracking bout. No missing hares were found as a result of driven and aerial surveys, though known hares were detected from the air when passing nearby their home ranges.

A total of 5/40 hares (12.5 %) removed their collars by slipping them over their heads (Table 1). They were discovered still bolted closed indicating too loose a fit. Animals removed collars on average 38 days (range 0-128 days) after release. The collar of one untranslocated uncoursed hare was reported to be found by a farmer among straw used as cattle bedding after opening a round bail. The collar was closed and intact with no apparent evidence of predation or death (no blood/flesh/hair). The mortality sensor indicated that movement stopped 4.2 months after release within an improved grassland field within the animal’s core home range. The collar lay motionless for four days before a single sudden 730 m movement to the farmyard where its signal was eventually traced some weeks later. How it found its way into a straw bale could not be determined but there was no evidence that the animal had died by either predation or agriculture (it was thus recorded as a collar removed rather than a death).

There was no difference between cohorts in the number of confirmed deaths (Table 1). Two hares (one translocated coursed and one untranslocated uncoursed) were killed in animal-vehicle collisions occurring on a National and Regional road within 460 m and 425 m from their respective release sites. Mortality sensors indicated that one was killed 2.5 hrs and the other 8.7 hrs after release. At one location, a roadkill fox (Vulpes vulpes), otter (Lutra lutra) and stoat (Mustela erminea) were also found within 300 m of the recovered collar along a straight stretch of National road with notably fast traffic. One roadkill hare was scavenged by a fox four days after death and carried 620 m away to be buried in the bank of a stream. The collar of a translocated coursed hare was recovered recording mortality 5.5 months after release with the collar still bolted closed with evidence of either predation or scavenging with fox tooth marks evidencing chewing on the external rubber housing and associated blood and flesh. This single death, either by natural causes followed by scavenging or predation, cannot be attributed to that animal having been coursed and translocated 6 months before.

Coursed hares were significantly more likely to be lost from the study (17/20 = 85 %) than uncoursed hares (11/20 = 55 %) and thus significantly fewer were relocated alive at six months after release (5 % compared to 40 %). The translocated coursed cohort was the only group to have no animals remaining on site by Week 23 (5.5 months). The rate of loss of coursed hares from the study was significantly faster than uncoursed hares (Kaplan-Meier $\chi^2_{df=1}= 4.032$, $p=0.045$, Log Rank Mantel-Cox $\chi^2_{df=1} = 5.811$, $p=0.016$) with the 95% Confidence Intervals of relocation six months after release between 0-15 % for coursed hares and 19-61 % for uncoursed hares (Figure 5a).

There was no difference in the rate of loss of translocated and untranslocated hares (Kaplan-Meier $\chi^2_{df=1}= 0.004$, $p=0.949$, Log Rank Mantel-Cox $\chi^2_{df=1} = 0.058$, $p=0.810$) with the 95 % Confidence Intervals of relocation six months after release between 2-38 % for translocated hares and 6-44 % for untranslocated hares (Figure 5b).

Loss of coursed hares was attributable to 5/10 (50 %) of translocated coursed hares removing their collar by scratching the strap until it wore through (Figure 6) within on average 16 days (range 0-32 days); a behaviour not observed in any other cohort. Destroying collars was not
associated with coursing as none of the untranslocated coursed hares wore through their strap and it was not associated with translocation as none of the translocated uncoursed hares wore through their collars. Nevertheless, untranslocated coursed hares were lost from the study faster than either uncoursed cohort (whether translocated or not) because more disappeared from the study (8/10) than any other group (Table 1).

One collar whose strap was worn through was recovered from a hare’s form after flushing the animal 16 days after the collar stopped moving with the animal observed alive 44 days after release. On several occasions during tracking, groups of hares (up to six individuals) were observed where some were wearing collars and some were not. It was suspected that some of the uncollared animals may have been experimental animals that had removed their collars. After the last spatial data were collected 6.3 months after release, the Irish Coursing Club recaptured three of the studied hares in the course of their normal netting operations during October and November 2022 (all three were uncoursed with two translocated and one untranslocated). These animals were alive 8.0 - 9.5 months after release. Two of these animals had been tracked for the full six-month study, but one had been last located in April. Thus, records were updated to recode the outcome for this individual as alive at six months. However, its spatial data arrived too late to be included in analyses presented here.

Due to the loss of collars, coursed hares were tracked for half the time of uncoursed hares with on average 40 and 97 days respectively (Table 2).

The outcome for hares at six months was unrelated to their original body weight (Kruskal-Wallis $df=4 = 3.665$, $p=0.453$; Figure 7).
Table 1  Outcome for 40 collared hares after six months. Numbers are individual counts of hares. Indentation indicates the outcome was a subset of the hierarchical category above. Statistical differences between cohorts were tested using a 2x2 or 2x4 $\chi^2$ Contingency tests as appropriate for two or four cohorts respectively. Bold font and asterisks highlight outcomes that differed significantly between cohorts. $\infty$ indicates a complete difference in outcome i.e. that outcome occurred in one cohort only.

<table>
<thead>
<tr>
<th>Outcome at 6 months after release</th>
<th>Coursing Coursed</th>
<th>Coursing Uncoursed</th>
<th>Translocated Translocated</th>
<th>Translocated Untranslocated</th>
<th>Coursing translocated</th>
<th>Coursing untranslocated</th>
<th>Uncoursed translocated</th>
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<th>TOTAL</th>
<th>$\chi^2$</th>
<th>df</th>
<th>p</th>
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<td>6</td>
<td>5</td>
<td>28</td>
<td>4.29</td>
</tr>
<tr>
<td>Disappeared</td>
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<td>8</td>
<td>7</td>
<td>11</td>
<td>7</td>
<td>11</td>
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<td>8</td>
<td>5</td>
<td>3</td>
<td>18</td>
<td>4.76</td>
</tr>
<tr>
<td>Never located after release</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>5</td>
<td>2</td>
<td>5</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>7</td>
<td>1.46</td>
</tr>
<tr>
<td>Relocated but subsequently disappeared</td>
<td>7</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>5</td>
<td>6</td>
<td>2</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>11</td>
<td>4.39</td>
</tr>
<tr>
<td>Collar retrieved (removed by animal)</td>
<td>7</td>
<td>3</td>
<td>7</td>
<td>3</td>
<td>7</td>
<td>3</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>10</td>
<td>9.07</td>
</tr>
<tr>
<td>Stripped overhead (still bolted closed)</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>0.69</td>
</tr>
<tr>
<td>Strap failed (worn through)</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>0.83</td>
</tr>
<tr>
<td>Dead (carcass or evidence of death)</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0.83</td>
</tr>
<tr>
<td>Relocated alive at 6 months</td>
<td>1</td>
<td>8</td>
<td>4</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>9</td>
<td>5.16</td>
</tr>
<tr>
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<td>20</td>
<td>20</td>
<td>20</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>40</td>
<td></td>
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</tr>
</tbody>
</table>

$IWM$ 145 (2023) Survival and behaviour of coursed hares
Figure 5 Kaplan-Meier plot showing declining probability of relocating a hare (solid lines) ± 95 % Confidence Intervals (shading) comparing a) coursed and uncoursed and b) translocated and untranslocated hares over six months after release. These two groupings (n=20 in each) were further broken down into c) four cohorts (n=10 in each): uncoursed untranslocated, uncoursed translocated, coursed untranslocated and coursed translocated. For simplicity, 95 % Confidence Intervals have not been shown in c) but are reported as text next to each line.
Figure 6 Examples of three Litetrack RF60 collars (LOTEK Ltd.) where coursed translocated hares slashed through the strap with their hind nails with evidence of gnawing the payload barrel. There was no evidence of predation or other extrinsic sources of mortality.
### Table 2

Forty individual hares showing the experimental cohort to which each belonged, their sex, weight and duration of tracking with the final outcome 6 months after release. Averages are given as means ± 1 standard deviation.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Hare_ID</th>
<th>Sex</th>
<th>Weight (kg)</th>
<th>Release date (first data)</th>
<th>End date (last data)</th>
<th>Days tracked</th>
<th>Outcome at 6 months</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coursed translocated</td>
<td>33</td>
<td>M</td>
<td>3.7</td>
<td>08/02/2022</td>
<td>08/02/2022</td>
<td>0</td>
<td>Collar retrieved within &lt;24hrs</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>M</td>
<td>3.4</td>
<td>08/02/2022</td>
<td>08/02/2022</td>
<td>1</td>
<td>Dead. Road traffic collision.</td>
</tr>
<tr>
<td></td>
<td>32</td>
<td>M</td>
<td>3.6</td>
<td>08/02/2022</td>
<td>11/02/2022</td>
<td>3</td>
<td>Collar retrieved</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>M</td>
<td>3.3</td>
<td>08/02/2022</td>
<td>19/02/2022</td>
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<td>Collar retrieved</td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>F</td>
<td>3.8</td>
<td>08/02/2022</td>
<td>24/02/2022</td>
<td>16</td>
<td>Not relocated</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>M</td>
<td>3.4</td>
<td>08/02/2022</td>
<td>24/02/2022</td>
<td>16</td>
<td>Not relocated</td>
</tr>
<tr>
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<td>30</td>
<td>M</td>
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<td>08/02/2022</td>
<td>04/03/2022</td>
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<td>Collar retrieved</td>
</tr>
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<td></td>
<td>26</td>
<td>F</td>
<td>3.8</td>
<td>08/02/2022</td>
<td>12/03/2022</td>
<td>32</td>
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</tr>
<tr>
<td></td>
<td>31</td>
<td>M</td>
<td>3.0</td>
<td>08/02/2022</td>
<td>24/03/2022</td>
<td>44</td>
<td>Collar retrieved</td>
</tr>
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<td>F</td>
<td>3.7</td>
<td>08/02/2022</td>
<td>24/07/2022</td>
<td>166</td>
<td>Dead. Likely fox predation.</td>
</tr>
<tr>
<td></td>
<td>7M:3F</td>
<td></td>
<td>3.5 ± 0.3</td>
<td></td>
<td></td>
<td>31 ± 49</td>
<td></td>
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<td>F</td>
<td>3.5</td>
<td>08/02/2022</td>
<td>08/02/2022</td>
<td>0</td>
<td>Never relocated after release</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>M</td>
<td>3.1</td>
<td>08/02/2022</td>
<td>08/02/2022</td>
<td>0</td>
<td>Never relocated after release</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>F</td>
<td>3.3</td>
<td>08/02/2022</td>
<td>08/02/2022</td>
<td>0</td>
<td>Never relocated after release</td>
</tr>
<tr>
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<td>9</td>
<td>M</td>
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<td>15/02/2022</td>
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<td>Collar retrieved</td>
</tr>
<tr>
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<td>08/02/2022</td>
<td>26/02/2022</td>
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</tr>
<tr>
<td></td>
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<td>M</td>
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<td>08/02/2022</td>
<td>26/03/2022</td>
<td>46</td>
<td>Not relocated</td>
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<tr>
<td></td>
<td>11</td>
<td>M</td>
<td>3.5</td>
<td>08/02/2022</td>
<td>26/03/2022</td>
<td>46</td>
<td>Not relocated</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>M</td>
<td>3.3</td>
<td>08/02/2022</td>
<td>22/04/2022</td>
<td>73</td>
<td>Not relocated</td>
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<tr>
<td></td>
<td>3</td>
<td>F</td>
<td>3.4</td>
<td>08/02/2022</td>
<td>03/06/2022</td>
<td>115</td>
<td>Not relocated</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>M</td>
<td>3.4</td>
<td>08/02/2022</td>
<td>18/08/2022</td>
<td>191</td>
<td>Relocated alive at 6.3 months (study end)</td>
</tr>
<tr>
<td></td>
<td>6M:4F</td>
<td></td>
<td>3.4 ± 0.2</td>
<td></td>
<td></td>
<td>50 ± 62</td>
<td></td>
</tr>
<tr>
<td>Uncoursed translocated</td>
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<td>08/02/2022</td>
<td>0</td>
<td>Never relocated after release</td>
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<td>38</td>
<td>F</td>
<td>3.7</td>
<td>08/02/2022</td>
<td>08/02/2022</td>
<td>0</td>
<td>Never relocated after release</td>
</tr>
<tr>
<td></td>
<td>39</td>
<td>F</td>
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<td>08/02/2022</td>
<td>09/02/2022</td>
<td>1</td>
<td>Dead. Road traffic collision.</td>
</tr>
<tr>
<td></td>
<td>36</td>
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<td>08/02/2022</td>
<td>19/02/2022</td>
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<td>Not relocated</td>
</tr>
<tr>
<td></td>
<td>29</td>
<td>M</td>
<td>3.5</td>
<td>12/02/2022</td>
<td>01/03/2022</td>
<td>17</td>
<td>Collar retrieved</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>M</td>
<td>3.6</td>
<td>12/02/2022</td>
<td>20/06/2022</td>
<td>128</td>
<td>Collar retrieved (inside round bale)</td>
</tr>
<tr>
<td></td>
<td>41</td>
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<td>3.2</td>
<td>12/02/2022</td>
<td>16/08/2022</td>
<td>185</td>
<td>Relocated alive at 6.1 months (study end)</td>
</tr>
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<td>22</td>
<td>M</td>
<td>3.2</td>
<td>12/02/2022</td>
<td>16/08/2022</td>
<td>185</td>
<td>Relocated alive at 6.1 months (study end)</td>
</tr>
<tr>
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<td>M</td>
<td>3.5</td>
<td>08/02/2022</td>
<td>16/08/2022</td>
<td>189</td>
<td>Relocated alive at 6.2 months (study end)</td>
</tr>
<tr>
<td></td>
<td>37</td>
<td>F</td>
<td>3.3</td>
<td>08/02/2022</td>
<td>08/10/2022</td>
<td>242</td>
<td>Recaught alive 8.0 months later (study end)</td>
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<tr>
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<td>6M:4F</td>
<td></td>
<td>3.3 ± 0.5</td>
<td></td>
<td></td>
<td>96 ± 99</td>
<td></td>
</tr>
<tr>
<td>Uncoursed untranslocated</td>
<td>17</td>
<td>M</td>
<td>3.2</td>
<td>08/02/2022</td>
<td>08/02/2022</td>
<td>0</td>
<td>Never relocated after release</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>F</td>
<td>3.2</td>
<td>08/02/2022</td>
<td>25/02/2022</td>
<td>17</td>
<td>Not relocated</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>F</td>
<td>2.6</td>
<td>08/02/2022</td>
<td>07/03/2022</td>
<td>27</td>
<td>Collar retrieved</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>F</td>
<td>4.5</td>
<td>12/02/2022</td>
<td>03/06/2022</td>
<td>111</td>
<td>Not relocated</td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>M</td>
<td>3.4</td>
<td>08/02/2022</td>
<td>03/06/2022</td>
<td>115</td>
<td>Not relocated</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>M</td>
<td>3.1</td>
<td>08/02/2022</td>
<td>18/08/2022</td>
<td>191</td>
<td>Relocated alive at 6.3 months (study end)</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>M</td>
<td>3.9</td>
<td>08/02/2022</td>
<td>18/08/2022</td>
<td>191</td>
<td>Relocated alive at 6.3 months (study end)</td>
</tr>
<tr>
<td></td>
<td>19</td>
<td>F</td>
<td>3.3</td>
<td>08/02/2022</td>
<td>10/10/2022</td>
<td>244</td>
<td>Recaught alive 8.0 months later (study end)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>M</td>
<td>3.0</td>
<td>08/02/2022</td>
<td>24/11/2022</td>
<td>289</td>
<td>Recaught alive 9.5 months later (study end)</td>
</tr>
<tr>
<td></td>
<td>6M:4F</td>
<td></td>
<td>3.3 ± 0.5</td>
<td></td>
<td></td>
<td>119 ± 107</td>
<td></td>
</tr>
</tbody>
</table>
Figurę 7 Boxplot of hare body weights at release and outcomes six months later.

3.2 Activity

Hourly movements of hares varied throughout the 24-hour period ($F_{df=23, 5443} = 227.95, p<0.001$; Figure 8a). Hares spent most of the day motionless in their forms with any apparent movement likely attributable to GPS error. Accounting for the drift in daily sunrise and sunset times, hares were most active in the hour before and after sunrise and sunset (Figure 8b) being 2.5 times as active at sunrise as sunset (Figure 8a). There was a low level of activity throughout the night. Thus, the active period of the day was defined as one hour before sunset until one hour after sunrise and the inactive period as one hour after sunrise until one hour before sunset.
Figure 8 Boxplot (median, interquartile range and 95 % Confidence Interval) of hare movements in metres per hour *i.e.* step lengths between successive GPS fixes throughout **a)** the 24-hour period showing nocturnal (dark grey), crepuscular (light grey) and diurnal activity (no shading). The earliest and latest sunrise and sunset times varied from 4-8am and 5-9pm between mid-winter (initial release in February) and mid-summer (four months after release during June) respectively. **b)** shows the same but with daily activity folded over date-specific local sunrise and sunset (both represented by 0) with hourly offsets during night shown as negative integers and day as positive integers adjusted for daylight savings (BST to GMT). This removes the drifting of sunrise and sunset times and standardised activity relative to the date-specific light-dark cycle.
### 3.3 Daily movements during the first week

The distance travelled by hares decreased significantly over the first week (Days 0-7: \( F_{df=7,209} = 10.128, p<0.001 \)) from an average of 3.6 (95% CI: 3.1 - 4.2) km during the day of release (Day 0) dropping over the next four days before stabilising thereafter (the average of Days 4-7 was 1.9 (1.6 – 2.3) km/24hrs). There was no difference between the sexes (\( F_{df=1,209} = 0.043, p=0.835 \)) or coursed and uncoursed hares (\( F_{df=1,209} = 0.046, p=0.830 \); Figure 9a). Translocated hares moved significantly further than untranslocated hares during the first four days only (Days 0-3 average for translocated hares was 3.4 (2.7 – 4.1) km/24hrs which was 1.5 times further than untranslocated hares at 2.3 (1.5 – 3.1) km/24hrs (Days 0-3: \( F_{df=1,106} = 4.121, p=0.045 \); Figure 9b). However, translocated hares settled by Day 4 with no difference between the movements of either group thereafter (Days 4-7: \( F_{df=1,103} = 0.015, p=0.904 \); Figure 9b). There was no interaction effect between coursing and translocation i.e. no difference between any of the four cohorts (\( F_{df=1,209} = 0.040, p=0.842 \)). Translocated coursed and translocated uncoursed cohorts had greater movements during the first four days i.e. translocation had the same effect on coursed and uncoursed hares (Figure 9c). Samples sizes of the number of hares contributing spatial data each day were comparable between cohorts throughout the first week (Figs. 9d & e).

Daily active period movements (dusk, night and dawn) significantly declined through the first week (Day: \( F_{df=1,215} = 54.426, p<0.001 \)) from 3.4 (2.9 – 3.9) km on the day of release (Day 0) to an average of 1.7 (1.3 – 2.0) km/active period on Days 4-7 reflecting the majority of the variation in the 24-hourly pattern described above. There were no effects of sex, coursing, translocation or their interaction on apparent movements during what would otherwise be the inactive period.

### 3.4 Daily home ranges during the first week

In common with daily movements, daily home ranges (95% kernels/24hrs) decreased in area significantly throughout the first week (Day: \( F_{df=1,215} = 16.877, p<0.001 \)) from an average of 60 (38 – 84) hectares during Day 0 to an average of 14 (10 - 17) ha/24hrs during Days 4-7. There were no effects of sex (\( F_{df=1,215} = 0.364, p=0.547 \)) or coursing (\( F_{df=1,215} = 0.090, p=0.764 \)) on daily home ranges during the first week. Translocated hares had an average home range of 68 (33 – 103) ha during the first three days (Days 0-2), which was substantially greater than untranslocated hares with an average of 18 (1 – 59) ha (Days 0-2: \( F_{df=1,78} = 3.543, p=0.064 \)). Thereafter, home ranges were similar between translocated and untranslocated hares (Days 3-7: \( F_{df=1,131} = 0.007, p=0.934 \)). Home ranges did not vary between the four cohorts during the first week (\( F_{df=1,215} = 0.280, p=0.597 \)). Its notable that untranslocated uncoursed hares (the wild control group) had the lowest variation in daily home ranges during the first week (the blue line in Figure 9h). Patterns in daily core ranges (50% kernels/24hrs) were the same as 95% kernels and are not reported for simplicity.

A single individual translocated uncoursed hare (a male) made a notably unusual and large exploratory movement over the course of the night during Day 2. During this excursion, it crossed a river twice (outbound and inbound journeys) in locations where there were no bridges and navigated throughout unfamiliar territory circumnavigating the entire study site before returning to near its release site. This accounted for the peak in home range during Day 2 in the translocated and uncoursed cohorts (Figs. 9f-h). Similarly, a single untranslocated uncoursed hare (also a male) moved away from the release site during the night of Day 4 before returning accounting for the smaller peak in this cohort (Figure 9h). Removal of both individuals from the sample resulted in relatively smooth declines in movements and home ranges throughout the first week but their movements were real and not GPS artefacts, and as such, there was no a priori basis for their removal and they were thus retained in analysis.
3.5 Movements over six months

The average daily distance covered by hares each week decreased significantly throughout the six-month study (Week 1-27: $F_{df=1,2492} = 154.986, p<0.001$) with a notable drop between Week 1 (the week of release) and Week 2 with a marginal decline in activity thereafter (Figure 10). There was no difference between the sexes ($F_{df=1,2492} = 0.235, p=0.628$), coursed and uncoursed hares ($F_{df=1,2492} = 0.222, p=0.637$; Figure 10a), translocated and untranslocated hares ($F_{df=1,2492} = 1.117, p=0.291$; Figure 10b) or their interaction ($F_{df=1,2492} = 0.654, p=0.419$; Figure 10c) throughout the six months. The average daily distance covered by a hare was 1.7 (1.4 – 2.0) km/24hrs/week. Movements of coursed hares appeared to decline markedly after Week 16 (Figure 10a) but this reflected a decline in the number of individual hares contributing spatial data which had dropped to two individuals in the coursed group compared to eight individuals remaining in the uncoursed group by Week 16 (Figure 10d). To be conservative, the data were re-analysed excluding Week 1 and Weeks 16-27 i.e. excluding initial movements including the disturbance of handling, tagging and release and the period of poorest sample size towards the end of the study. During Weeks 2-15, coursed hares moved 1.5 (1.1 – 1.9) km/24hrs/week which was about 200 m less than uncoursed hares at 1.7 (1.4 – 2.0) km/24hrs/week but this difference remained not statistically significant ($F_{df=1,1576} = 0.919, p=0.338$) and within the variation observed between individuals.

The ratio of the duration of active-to-inactive periods each 24-hours shifted from the release of hares in early-to-mid February during winter with 17 hours of activity (dusk, night and dawn) and seven hours of inactivity (daylight) per day up to the summer solstice during late June with seven hours of activity and 17 hours of inactivity per day. After the solstice the ratio shifts back toward more hours of darkness. Average daily movements during active and inactive periods showed a significant effect of Week (Week 1-27: $F_{df=1,2493} = 546.942, p<0.001$ and $F_{df=1,2447} = 162.137, p<0.001$ respectively) with active movements shortening (from 2.2 km/active period in Week 1 to approximately 522-680 m/active period throughout most of the summer months) and inactive movements lengthening (from 281 m/inactive period in Week 1 to 820 m/inactive period in Week 20 when the solstice occurred) before drifting back in the other direction again. There were no effects of sex, coursing, translocation or their interaction on either active or inactive period movements as reflected by the 24-hourly analysis above.

3.6 Weekly home ranges over six months

Weekly home ranges (95 % kernels/wk) decreased in area significantly throughout the six months study (Week: $F_{df=1,351} = 8.930, p=0.003$), initially from an average of 55 (41 – 69) ha during Week 1 to 15 (1 – 30) ha by Week 2. Home ranges were unaffected by sex ($F_{df=1,351} = 0.986, p=0.321$) or coursing ($F_{df=1,351} = 0.845, p=0.359$). Translocated hares had an average weekly home range of 32 (19 – 45) ha which was substantially larger than untranslocated hares with home ranges of 15 (1 – 30) ha ($F_{df=1,351} = 2.801, p=0.095$): a weak but persistent effect throughout the six months (Figure 10g). There was no interaction between coursing and translocation ($F_{df=1,351} = 0.137, p=0.711$).

In common with movements, average home ranges declined markedly in the coursed group after Week 16 reflecting the drop in sample size of individual hares contributing spatial data (Figure 10d). Re-analysis excluding Week 1 and Weeks 16-27 suggested no change in home ranges between Week 2 to Week 15 (Weeks 2-15: $F_{df=1,220} = 0.074, p=0.785$). Weekly home ranges in Weeks 2-15 were unaffected by sex ($F_{df=1,220} = 1.644, p=0.201$), coursing ($F_{df=1,220} = 0.577, p=0.448$), translocation ($F_{df=1,220} = 1.713, p=0.192$) or their interaction ($F_{df=1,220} = 0.464, p=0.497$). Males tended to have larger weekly home ranges than females at 28 (18 – 38) ha and 17 (3 – 31) ha respectively, coursed hares tended to have slightly smaller home ranges than uncoursed hares at 19 (7 – 32) ha and 25 (15 – 36) ha respectively and translocated hares tended to have larger home ranges than untranslocated hares at 28 (16 – 39) ha and 17 (4 – 29) ha respectively (though none of these were different statistically). There were no effects of sex, coursing, translocation or their interaction on weekly core ranges (50 % kernels/wk).
3.7 Dispersal

Hares dispersed away from their respective release sites by around 800 (600 – 900) m during the first week before drifting another 200 m or so further over the next four months out to on average 1 (0.8 – 1.2) km (Week 1-16: \(F_{df=1,379}=59.179, p<0.001\)). Dispersal did not differ between the sexes \(F_{df=1,220}=0.813, p=0.368\), coursed and uncoursed hares \(F_{df=1,220}=0.784, p=0.376\), translocated and untranslocated hares \(F_{df=1,220}=0.173, p=0.678\) or their interaction \(F_{df=1,220}=0.004, p=0.947\); Figure 11).
Survival and behaviour of coursed hares

Figure 9 Average daily movement (in kilometres per 24 hours) ± 1 standard error comparing a) coursed and uncoursed, b) translocated and untranslocated and c) all four cohorts of hares. Samples sizes in individual hares for d) coursed and uncoursed and e) translocated and untranslocated hares. Home ranges (the extent of 95% kernel polygons) in hectares comparing f) coursed and uncoursed, g) translocated and untranslocated and h) all four cohorts of hares.
Figure 10  Average daily movements per week (in kilometres per 24 hours per week) ± 1 standard error comparing a) coursed and uncoursed, b) translocated and untranslocated and c) all four cohorts of hares. Sample sizes for d) coursed and uncoursed and e) translocated and untranslocated hares. Home ranges (the extent of 95 % kernel polygons in hectares) comparing f) coursed and uncoursed, g) translocated and untranslocated and h) all four cohorts of hares. The shaded area from Weeks 16-27 indicates that caution should be taken in interpreting results due to a small sample size of coursed hares contributing spatial data.
Figure 11 Dispersal as measured by the average distance from the release site each week (in kilometres) ± 1 standard error comparing all four cohorts of hares. The shaded area from Weeks 16-27 indicates caution should be used in interpreting results due to the small sample size of individual hares contributing spatial data.

4 Discussion

This was the first study to attempt to assess the survival, movements and behaviour of coursed hares after their release back into the wild.

Five out of forty hares (12.5 %) managed to slip their collar over their head, with it remaining bolted closed, indicating too loose a fit. There was no difference in the numbers that managed this between the experimental cohorts. There is always a trade-off between over tightening a collar to ensure fit and under tightening a collar to avoid causing the animal distress. In all cases, collars were fitted to leave space for two fingers to be comfortably slipped between the collar strap and the hare’s throat. In virtually all cases, collars were tightened to the same notch.

Five out of ten (50 %) of the translocated coursed hares removed their collars by fraying the straps until they failed (wore through) usually within a month of release. This indicated an engineering failure where strap material was vulnerable to being compromised by hares scratching and gnawing. The supplier of the collars (LOTEK Ltd.) were informed and responded that no such problems had been reported by other researchers who had tagged similar hare species (for example, the European hare *L. europaeus*) with comparable collar models. All collars were from the same made-to-order batch and there is no reason to believe their quality should have varied between those deployed on different cohorts of hares. Why strap failures were not distributed randomly across the cohorts and clustered in the translocated coursed cohort is unknown. It was not an effect of having been coursed as none of the untranslocated coursed hares destroyed their collars; and it was not an effect of translocation as none of the translocated uncoursed hares did so either. Whilst it could be speculated this behaviour may be the result of the combined effects of coursing and translocation (greater stress leading to lower tolerance for collar wearing) there was no evidence whatsoever to support such a supposition and the role of random chance and statistical stochasticity cannot be ruled out when quantifying outcomes for cohorts of just ten individuals. For future studies, any manufacturer of collars for studying Irish hares should be
alerted to the potential for strap failure and should ensure straps are made from material impervious to being frayed and slashed.

Nineteen out of forty hares (47.5%) were either never located after release (7/40 or 17.5%), or, relocated but subsequent disappeared (12/40 or 30%) indicating collar failure or dispersal far enough offsite to be beyond detection during walked, driven and aerial surveys. All radio receiving equipment (Sika receivers and yagi antennae) were fully serviced by LOTEK Ltd. before the study commenced and all collar VHF radio beacons were confirmed as signalling and detectable before animals were released. All collars had exactly the same programming schedule files uploaded i.e. the VHF radio beacon signalled for the same period each day for each collar. Nevertheless, it was noted that several collars had signal strengths appreciably weaker than others making detection and triangulation more challenging and loss seemingly more likely. For example, one animal was not located after release until the very last day of tracking (6.3 months later) during which it went undetected during regular VHF scans but was accidentally connected to when downloading data from another animal using the UHF channel (it was lying up beside the tracked target animal). This chance discovery allowed the signal strength of that collar to be checked by walking away from the animal’s known position with it being undetectable at little over 100 m (a very short distance). Examination of this animal’s GPS data suggested it was constantly within the study site; its home range was coincident with another hare which was reliably detected on each visit. Another example was a hare recaptured by the Irish Coursing Club eight months after release. This animal had been successfully tracked from February to April remaining in the vicinity of the release site. It disappeared and went undetected from May through to August despite walked, driven and aerial searches. Yet it was recaptured nearby the release site with its track showing it within the vicinity throughout the study. These incidences, and the generally short average detection distances of approximately 350 m at ground level (the approximate length of a field within the study areas), raised questions about the reliability of the collars and may suggest that at least some missing animals may not have dispersed beyond the study sites, but their collars may have experienced technical issues. That said, there was no evidence by which to differentiate potential collar failures from potential dispersal events and no reason to suppose collar failures, if they did occur, were not randomly distributed across the cohorts of hares. The outcome for animals that disappeared remains unknown but it is reasonable to assume that most must have dispersed beyond the search area of approximately 5 km around each study site. For those animals successfully tracked, the average dispersal distance from the release site was only about 1 km even after several months. Irish hares are known to be relatively sedentary from previous tracking studies (Wolfe & Hayden, 1996; Jeffrey, 1996; Reid et al., 2010b) with the current study providing no direct evidence for long distance dispersal i.e. no animals were located more than a few kilometres from the release sites despite wider searches. That said, if some missing animals had dispersed offsite, failure to acquire their spatial data would lead to any sample of GPS locations being biased; by definition successfully detected animals may have moved less.

Notwithstanding losses, neither coursed and/or translocated hares had elevated mortality compared to controls. Three hares died during the study. Two (one translocated coursed and one untranslocated uncoursed) were killed in collisions with vehicles on their first evening after release. Both of these cohorts were released at around 3 pm and 5 pm respectively (sunset was at 5:33 pm) compared to 10 am and 11 am (sunrise was at 8:03 am) for translocated uncoursed and untranslocated coursed cohorts. Most hares were released on the same day (8th February) to standardise release dates and the difference in the timing of releases was due to the logistical constraints of travelling between sites and the time spent netting control animals. Licence conditions required all hares to be released during daylight hours, which was the case, but the two cohorts with road kills on the first night had less daylight in which hares could settle before the onset of darkness having been released 30 minutes and 1.5 hours before sunset. This supports coursing licence conditions that all hares should be released back into the wild during daylight hours (the recommendation here is as early as possible), to provide adequate time for them to settle in cover. All hares moved about twice as far on their first day than after they settled, increasing the risk of encountering dangers (so called, extrinsic sources of mortality), in this case road traffic. It was notable in both cases that the roads were busy,
straight stretches of National or Regional road with fast moving traffic, such that at one site several other roadkill mammals were found, suggesting it was a particularly dangerous crossing point for wildlife. Only one animal, a translocated coursed hare, was confirmed as having been predated or scavenged by a fox due to evidence of diagnostic tooth marks and the remains of blood and flesh. Predation is to be expected and the death of a single hare cannot be attributed to this animal having been coursed and translocated six months earlier. Three of the eight hares relocated alive at the end of the study, all uncoursed, were recaptured by the Irish Coursing Club in the course of their normal netting operations for the next coursing season eight to nine months after their initial release, demonstrating survival. It is known from earlier genetic fingerprinting studies of coursed hares that the same animal was caught and tissue sampled across consecutive coursing seasons, indicating interannual survival and release site philopatry (Hughes et al., 2006). Lifespan of wild mountain hares may be as much as 18 years (Angerbjörn & Flux. 1995) but more likely three to seven years (Reid, 2010).

In common with previous tracking studies (e.g. Wolfe & Hayden, 1996; Jeffrey, 1996; Reid et al., 2010b), this study suggested that Irish hares have notably smaller home ranges than other mountain hares in more typical mountain hare habitat, for example, up to 200 hectares in Finnish boreal forest (Kauhala et al., 2005). Irish hares are more comparable in their spatial ecology to European brown hares (L. europaeus) which have similar home ranges in agricultural grasslands (Ullmann et al., 2020). As the seasons progress from winter to summer the ratio of darkness-to-light shifts in northern latitudes such that tracked Irish hares became more active during the day; a trend that reversed after the solstice. There was no effect of coursing, translocation or their interaction on the apparent movements of hares during what would otherwise be their inactive period, suggesting all hares lay up during the day in their forms with little or no appreciable variation in daylight behaviour across the cohorts.

All hares moved significantly more during the first four days after release before settling, with translocated hares moving 1.5 times further, covering 3.8 times the area, of untranslocated controls. Most of this movement happened immediately after release whereupon animals settled into moving about 2 km, and covering about 14 ha per day by Day 4 onwards. Most of this movement occurred during their active period defined empirically by hare activity as one hour before sunset until one hour after sunrise. Irish hares are typically crepuscular, with camera trapping data also showing them more active at sunrise than sunset (Caravaggi et al., 2018). Movements, home ranges and dispersal of hares that remained in the vicinity of the release sites did not differ, after they had settled within the first few days, suggesting the impacts of accidental translocation of hares in returning the same number of coursed animals, as were captured, to a release site, may be limited. Other studies that GPS-radio tracked herbivores (for example, big horn sheep Ovis canadensis or caribou Rangifer tarandus caribou) have also demonstrated little lasting effects of translocation, with comparable survival to controls and little dispersal from release sites (Grant et al., 2019; Werdel et al., 2021).

Fewer coursed than uncoursed hares remained within the vicinity (within a few kilometres) of their release site six months later, not because more died (mortality did not differ between coursed and uncoursed cohorts), but a combination of a larger number of translocated coursed hares removing their collars and untranslocated coursed hares disappearing. The coursed translocated cohort was the only group with no hares remaining on site five and a half months after release. These results could suggest that a higher proportion of coursed than uncoursed hares dispersed beyond the vicinity of the release sites in the first few months after release, but with the outcome for such individuals unknown, the impacts of coursing on individual survival remains poorly quantified.
4.1 Recommendations

GPS radio-collars provided high resolution spatial data (hourly locations to an accuracy of a few metres usually) allowing movements, home ranges and dispersal of coursed hares to be quantified for the first time. Mortality sensors allowed death rates to be compared between coursed and uncoursed and translocated and untranslocated animals. Radio beacon signals were detected from more than a kilometre away with a direct line of sight, but signals were weakened by uneven terrain, low-lying animals, vegetation and landscape clutter (such as buildings). These factors could reduce the effective detection distance to a few hundred metres meaning animals could go missing if they disperse into the farmland matrix much beyond the road network. Lai et al., (2021) were the first to deploy Argos satellite tags on hares (KiwiSat303 collars from LOTEK Ltd.). These were traditionally bulkier than GPS tags due to the requirement to relay locations via a satellite network and the associated transmitter needed. Recent miniaturisation now means these can be fitted to animals the size of a hare while other collars can utilise mobile phone networks in areas of dependable cellular coverage. This has the advantage that animals do not need to be tracked manually using radio beacons. The disadvantage is that such devices have less battery capacity and lifespan due to the energy costs of transmitting data. After cleansing and filtering the data, the collars used by Lai et al., (2021) resulted in a single location per day demonstrating that one Arctic hare (L. arcticus) in Greenland migrated 388 km over 49 days. Such data provides much sparser information about movements, space use and behaviour than that provided by GPS-radio collars. On the other hand it may provide a better means by which to assess survival as data will be returned even for animals that disperse long distances that might otherwise by lost by radiotracking.

Given that the key question about the potential impact of coursing on hares after their release back into the wild focuses principally on survival, and not spatial behaviour, it is recommended that any future follow-up study focuses solely on coursed hares (no control group, no translocated group). This would avoid any subdivision of the sample size that might otherwise limit statistical inference. This would reduce the logistical challenges of any future study by removing the need to net control groups or move animals. Savings from simplification of the methods would allow, for example, greater investment in a larger sample size of cellular or satellite collars to be deployed solely on coursed hares before their release at whatever locations the coursing club(s) would ordinarily use (thus inherently accounting for any translocation if it occurs). Any future study should point out to collar manufacturers the need for collar strap materials to be more durable to reduce losses. Dependability of the remote relay of daily fixes would increase the likelihood of determining known outcomes, i.e., survival.

An alternate method to consider may be the complete genetic sampling of all hares caught for coursing each year with subsequent relatedness analysis, providing a means by which to quantify survival, reproduction and population recruitment. Survival would be demonstrated by the genetic fingerprinting of the same individual across different coursing seasons, reproduction would be demonstrated by hares being related to animals from previous seasons while recruitment would be demonstrated by familial relationships across time. Practically, this could be achieved by sampling of hair follicles from each animal netted each year. Samples could be archived, amassing tens of thousands of samples throughout Ireland over a few years. This would enable high powered genetic analyses, allowing the impact of coursing on hare populations to be further investigated. Local population sizes and their variation over time could be assessed using genetic capture-mark-recapture models. This genetic bank of samples could also support a wide range of research questions on the status, population structure and significance of the Irish hare.
4.2 Conclusions

Coursed hares did not differ from uncoursed hares in their post-release movements, home ranging behaviour and apparent dispersal for those individuals that remained within the vicinity of the release sites.

Translocated hares moved further, and ranged over a larger area, for four days after release before settling into a pattern similar to other hares.

Fewer coursed than uncoursed hares remained in the vicinity of their release sites six months after release. This was not due to differing mortality but instead, collar removals and disappearances, the latter of which may indicate higher dispersal rates not captured by the GPS tracking data of animals that remained within the vicinity of their release sites. Outcomes for animals not relocated remain unknown.

In summary, this study provides evidence that coursed and/or translocated hares did not suffer higher mortality than uncoursed and/or untranslocated control hares while their movements, home ranges and dispersal were all similar after translocated hares settled during their first few days after release. This work provides evidence to support Government coursing licence conditions about where and when to release hares and provides the first assessment of coursed hare movements, home ranges and dispersal after release back into the wild. Due to collar losses, notably among the coursed cohort, questions remain about dispersal and survival of coursed hares after their release. Any future studies should consider cellular or satellite collars and stronger strap material to minimise losses and maximise known outcomes. Other approaches such as comprehensive genetic sampling of coursed hares could resolve questions about subsequent reproduction and population recruitment.
5 Bibliography & Relevant Literature


