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Source: Wildlife Biology, 2021(3)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00840

**Wildlife Biology 2021: wlb.00840**
doi: 10.2981/wlb.00840

Subject Editor: Stephanie Kramer-Schadt. Editor-in-Chief: Ilse Storch. Accepted 15 June 2021

# Scared as a hare: effects of capture and experimental disturbance on survival and movement behavior of European hares

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Capture and handling of wildlife is an important component of wildlife studies, and hunting can be a central tool for wildlife management. However, human-caused disturbance of animals can cause various negative effects on individuals. Thus, an increased understanding of different disturbances on animals will allow improved mitigation of human stressors for wildlife, and provides the basis for data-censoring when using information obtained from captured individuals. Here, we investigated the effects of capture and handling, as well as experimental disturbance, on the movement behavior of GPS-collared European hares *Lepus europaeus*. Of 28 hares captured in box traps, three died during handling to fit GPS collars, likely due to acute stress. Apart from an 11% decrease in activity in both sexes the first four days after capture compared to later, capture events had no significant effects on subsequent movement behavior. Hares that were disturbed experimentally, i.e. flushed with or without a shotgun shot fired, moved on average (± SD) 422 ± 206 m directly subsequent to the disturbance, leading to a spatial displacement of their short-term home range and an increased daily home range size on the disturbance day. Home range sizes returned to their before disturbance size on the following days, but hares remained further from field edges and spent more time in short vegetation in the days after simulated hunting, though this effect was comparatively small. Overall, our findings indicate that hares only marginally changed their movement behavior in response to short-term disturbances. Therefore, capture and hunting disturbance should not have severe negative effects on the movement behavior of individuals, but future studies should aim to reduce acute capture-related stress to avoid mortalities. We recommend that researchers should censor the first four days after capture from their analyses to avoid using potentially biased data.

Keywords: anti-predator behavior, disturbance, escape behavior, GPS, hunting, *Lepus europaeus*

Human-caused disturbance can induce stress in wildlife, e.g. leading to reduced breeding success, displacement from preferred feeding areas, changes in activity times and in some cases reduced survival (Rodriguez-Prieto and Fernandez-Juricic 2005, Kight and Swaddle 2007, Ciuti et al. 2012, Gaynor et al. 2018). Increasing encroachment of people into nature call for a better understanding of such disturbance effects in order to mitigate them.

Bio-logging devices, such as GPS and accelerometers, can be very useful to study the effects of human-caused disturbance, because they greatly improve our understanding of animal movement, and behavior (Hebblewhite and Haydon 2010, Foley and Sillero-Zubiri 2020). However, the capture, handling and tagging of individuals for research in itself are a source of disturbance that can cause stress and altered energy expenditure, movement and behavior of the studied animals (Tudorache et al. 2014, van der Hoop et al. 2014, Graf et al. 2016). If handling and tagging related stress affects animal behavior and movement over longer-term periods (weeks-years), it can vitiate research findings (Jewell 2013). Thus, it is crucial to assess potential negative effects of capture and tagging. This is often not the case. For example, Godfrey and Bryant (2003) reported that of 836 published papers only 10.3% investigated the impact of radio-tagging on their study species.

In general, any human-caused disturbance can be seen as a form of (non-lethal) predation event, and will often trigger anti-predator behaviors by wildlife (Frid and Dill 2002). Apart from capture and handling for research, another substantial type of human-caused disturbance is hunting, leading to altered behavior and space use (Sunde et al. 2009, Chassagneux et al. 2019). Individuals can respond toward spatio–temporal variation in predation risk (including hunting) via altered time allocation and vigilance (Lima and Dill 1990, Kotler et al. 2002). That is, they can choose when, and where to be active, e.g. by adjusting their daily home range size and location or by selecting for different habitat types, and by altering activity budgets to reduce predation risk (Kotler et al. 2004).

The European hare *Lepus europaeus* (hereafter hare) has well-developed anti-predator behaviors, as it is prey to numerous predators, most often the red fox *Vulpes vulpes* and a common quarry species (Lindström et al. 1994, Panek 2009, Knauer et al. 2010). For example, hares show anti-predator behaviors, such as altered movement speed and local avoidance of high-risk areas, in response to predator scent and disturbance by humans and dogs (Weterings et al. 2016, Mayer et al. 2020). Moreover, anti-predator behaviors by hares depend on habitat composition. Tall structure-rich vegetation provides cover from predators by resting hares (Verdolin 2006, Neumann et al. 2012), and Weterings et al. (2018) showed that hares increasingly use high vegetation with increasing local red fox activity. Additionally, hares moved greater distances in response to disturbance by a leashed dog and two humans in low, but not high, vegetation (Weterings et al. 2016). However, depending on habitat structure, hares might use short vegetation and remain further from field edges to detect and escape predators (Focardi and Rizzotto 1999, Mayer et al. 2020). Moreover, to our knowledge no studies exist on potential capture and tagging effects, despite numerous radio-tracking studies on hares (Zaccaroni et al. 2009, Avril et al. 2012, Petrovan et al. 2013, Schai-Braun et al. 2014, Ullmann et al. 2018).

Here, we investigated movement distances, shifts in home range size and centroids and habitat associations of European hares in response to 1) capture and handling and 2) simulated hunting, human approaches, GPS data download and control treatments (no disturbance). We hypothesized that hares show anti-predator behaviors in response to capture, with responses being more pronounced in the first days after capture compared to the following days (in which we expected hare movement and activity to normalize). Further, we expected more pronounced anti-predator responses after hunting disturbance (hares were flushed and a shotgun shot fired) compared to human approaches (hares were only flushed) and data download (hares were not flushed). In regard to specific anti-predator responses toward disturbance, we predicted that hares reduce their spatial movement (after the initial escape response) to reduce the probability of subsequent detection, leading to decreased daily home ranges in the days subsequent to the disturbance. Moreover, if hares avoid areas where the disturbance occurred, we predicted shifts in daily home range centroids. Finally, we predicted that hares select for areas that enable them to detect approaching threats, i.e. for shorter vegetation and areas further from field edges. Regarding capture effects, we additionally investigated hare survival of tagged hares for the first eight weeks after capture.

## Material and methods

### Study area and hare captures

Our study area was located in Syddjurs municipality of Jutland, Denmark (Fig. 1), and was dominated by arable fields interspersed with pastures, game fields, forest, fallow and buildings (Mayer et al. 2018). We captured 28 hares (10 females and 18 males) in spring and summer 2014, 2018 and 2019 (Table 1), using 30 box traps that were set in pairs along the edges of agricultural fields. All traps were coupled with camera traps (set on a pole ca 5 m from the trap) that sent a picture via the cellphone network every 6 h, allowing us reach the closed traps between 0.5 and 8 h. Due to the fixed time interval of pictures, we could not estimate how long hares had been in the trap. We transferred captured hares into a canvas cone, sexed them and fitted them with a GPS collar (e-obs A1, e-obs GmbH, Gruenwald, Germany) without anesthesia. Handling took ca 10–15 min. The collars weighed 60 g, making up < 2% of the hares' body mass. GPSs recorded one-hourly GPS positions throughout the day in 2014 and 2018, and one position every 15 min in 2019. We obtained vector data of all land parcels from the Danish Ministry for Food, Agriculture and Fisheries (<https://kortdata.fvm.dk>; downloaded May 2014). For these land parcels, we recorded vegetation type and measured ground vegetation height once per month, grouped into four categories: no vegetation (ploughed, raked and freshly sawn fields), 1–25, > 25–50, > 50 cm (Mayer et al. 2018).

### Disturbance experiments

Disturbance experiments were conducted in 2018 and 2019, using 12 GPS-collared hares, six in 2018 and six in 2019 (six males and six females, Table 1). These individuals consisted of all hares that had a functioning GPS collar at the time we conducted the experiments. We conducted all experiments > 3 months after individuals were GPS-collared, and after the agricultural harvest period and before the spring green up, i.e. between September and the beginning of April (62% of experiments were conducted between October and December; the hare hunting season in Denmark). We distinguished between four disturbance types (Table 1): 1) 'control', which we arbitrarily assigned to days without any known disturbance, 2) 'data download', in which one or two observers downloaded GPS data from the hares' GPS collar using a UHF beacon. Depending on vegetation structure and weather conditions, we had to be approximately 50–300 m from the hare for data download, which sometimes resulted in disturbance of the hare (in ca one out of ten data downloads). 3) 'Flushed without shot': two observers approached a hare using the UHF beacon of the GPS collar, homing in on the hare until it fled. 4) 'Flushed and shot fired': two observers approached a hare using the UHF beacon, homing in on the hare and fired a shotgun shot in the air when the hare escaped, simulating a hunting situation. All disturbance experiments were conducted during the late morning, between 09:30 and 13:00 h, when hares were typically inactive (Schai-Braun et al. 2012, Mayer et al. 2018) and people are typically active, and the exact time of the disturbance was recorded (or arbitrarily assigned during the late morning for controls). The duration of each disturbance ranged between 5 and 10 min, depending how quick we detected the hare (independent of the disturbance type). We left at least one week between each disturbance type for hares to resume to their normal behaviors.

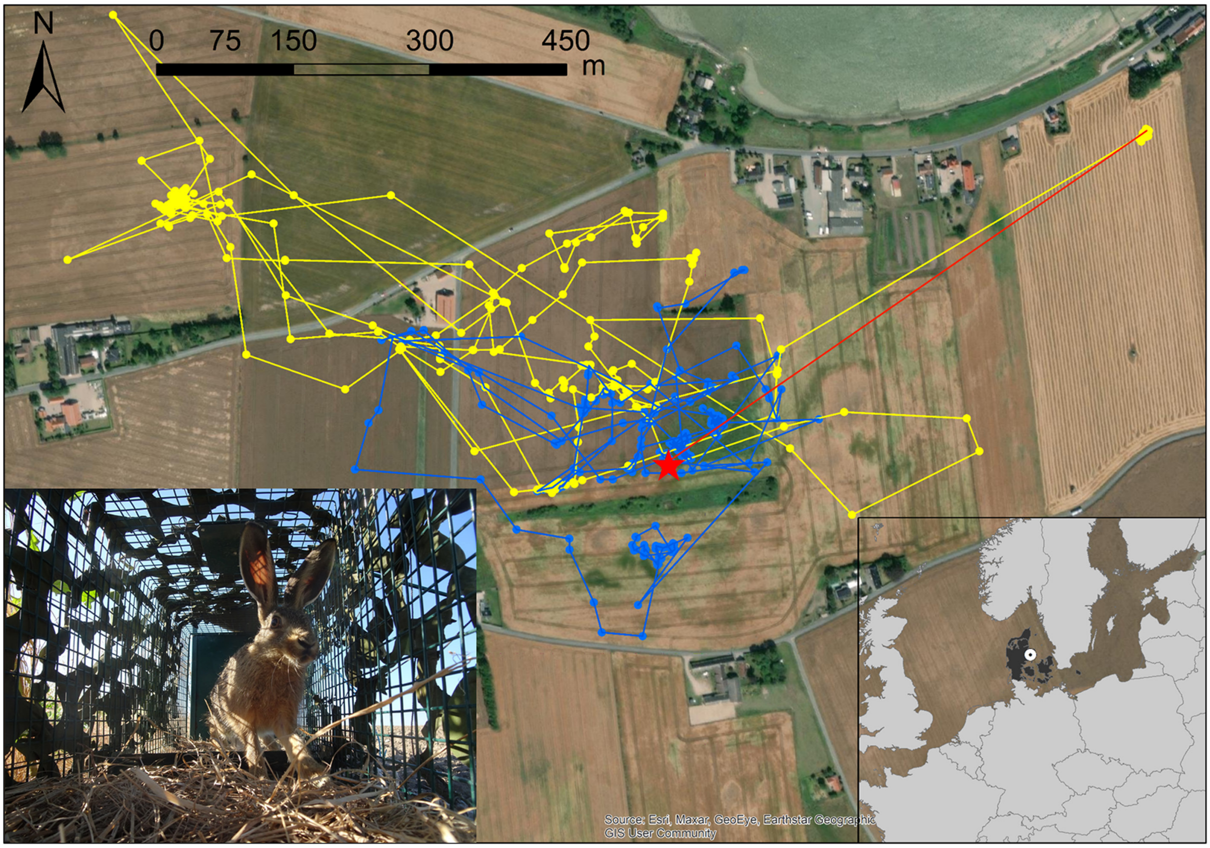


Figure 1. Main map: example of the movement path of a GPS-collared hare that was exposed to a simulated hunting disturbance (flushed and shotgun shot fired). GPS positions (dots) were recoded every 15 min. Lines represent the hare's schematic movement path. Blue lines and dots represent the period three days (and the hours of the disturbance day) before the disturbance, and yellow lines and dots represent the period three days (and the hours of the disturbance day) after the disturbance. The red star indicates the location of the hare when disturbed and the red line its escape movement path. The inset map shows the location (white dot) of our study area in Denmark. The picture shows a hare inside a box trap.

## Data preparation and statistical analyses

### *Capture effects*

To evaluate potential effects of capture on hare survival, we calculated the proportion of tagged hares that were alive each week during the first eight weeks after capture, and used a two-tailed Fisher's exact test to assess weekly differences in the proportion of hares that survived after capture (Casas et al. 2015). As we only obtained data from collared hares, we did not have a 'true' control, i.e. from hares not captured and collared. Thus, to examine potential effects of capture and GPS-collaring on movement behavior, we investigated changes in spatial movement patterns for the first 14 days after capture (Table 2, Supporting information). We chose this period, because a longer period would not have allowed us to disentangle between capture effects and behavioral changes related to vegetation height and other factors (e.g. changes in population density, predator abundance, etc.). It was previously shown that hare home range size and habitat selection changes seasonally due to changing vegetation height (Mayer et al. 2019). This was especially important during the capture period (82% of captures occurred in May and June), with the proportion of fields covered by > 25 cm high vegetation increasing from 39% in May to 61% in June. Thus, by restricting our analysis to short-term changes, we considered other potentially confounding factors constant.

As measure of daily area use and activity, we calculated the daily home range size based on 95% kernel density estimates (KDE) using the R package 'adehabitatHR' (Calenge 2006), using the reference method to estimate the smoothing parameter h, since it is generally less variable than least-squared cross validation (Hemson et al. 2005). As KDE estimates were highly correlated to daily 95% minimum convex polygons (Pearson rank correlation: $R = 0.92$, $t = 64$, $p < 0.001$), we deemed them reliable, especially, because we were mostly interested in relative changes between days. To investigate spatial shifts in hare core area use, we calculated the centroid of daily 50% KDEs using the R package 'sp' (Pebesma et al. 2012) and then calculated the straight-line distance between these centroids from day to day (e.g. the centroid shift from day 1 to day 2, from day 2 to day 3 etc.). To investigate the effect of capture on distance moved, we calculated the straight-line distance between consecutive hourly GPS positions (data with 15 min fix rate were subsampled to hourly GPS positions to be comparable). We initially did this separately for periods when hares were generally active (from 18:00 h to 10:00 h) and inactive (11:00–17:00 h) (Mayer et al. 2018), but then merged these analyses, as there were no differences in the effect of days after capture. More-

Table 1. Overview of all GPS-collared hares and of the sample size separately for the different disturbance types.

| Hare ID | Date captured | Fate | Number of GPS days | Sex | Disturbance 'control' | Data download | Flushed without shot | Flushed and shot fired | Total disturbances |
|---|---|---|---|---|---|---|---|---|---|
| D1 | 11 May 2014 | died while collaring | | male | | | | | |
| H1 | 16 June 2014 | battery stopped | 57 | female | | | | | |
| H2 | 13 May 2014 | battery stopped | 152 | female | | | | | |
| H3 | 30 May 2014 | unknown | 21 | female | | | | | |
| H4 | 31 May 2014 | unknown | 26 | female | | | | | |
| H5 | 1 June 2014 | battery stopped | 141 | male | | | | | |
| H6 | 9 June 2014 | battery stopped | 177 | male | | | | | |
| H7 | 25 April 2018 | battery stopped | 264 | male | 4 | 1 | 1 | 1 | 7 |
| H8 | 28 April 2018 | likely predated | 93 | male | | | | | |
| H9 | 4 May 2018 | likely predated | 17 | male | | | | | |
| H10 | 7 May 2018 | battery stopped | 315 | female | 4 | 3 | 2 | 3 | 12 |
| H11 | 10 May 2018 | battery stopped | 313 | female | 4 | 5 | 1 | 1 | 11 |
| H12 | 8 June 2018 | likely predated | 3 | male | | | | | |
| H13 | 25 June 2018 | run over by a car | 384 | male | 4 | 3 | 5 | 1 | 13 |
| H14 | 25 June 2018 | unknown | 282 | female | 5 | 3 | 4 | 2 | 14 |
| H15 | 9 July 2018 | battery stopped | 303 | female | 4 | 2 | 2 | 3 | 11 |
| D2 | 16 July 2018 | died while collaring | | male | | | | | |
| H16 | 15 August 2018 | unknown | 19 | male | | | | | |
| H17 | 3 May 2019 | battery stopped | 235 | female | 3 | 1 | 2 | 2 | 8 |
| H18 | 4 May 2019 | battery stopped | 237 | male | 3 | 2 | 1 | 1 | 7 |
| H19 | 5 May 2019 | unknown | 165 | male | 3 | | | 1 | 4 |
| H20 | 7 May 2019 | battery stopped | 234 | male | 3 | 3 | 2 | | 8 |
| H21 | 11 May 2019 | battery stopped | 141 | male | | | | | |
| H22 | 12 May 2019 | unknown | 74 | male | | | | | |
| H23 | 19 May 2019 | battery stopped | 216 | male | 3 | 2 | 1 | 1 | 7 |
| H24 | 23 May 2019 | battery stopped | 212 | female | 3 | 1 | 2 | | 6 |
| D3 | 23 May 2019 | died while collaring | | male | | | | | |
| H25 | 25 May 2019 | run over by a car | 49 | male | | | | | |
| Total | | | 4130 | | 43 | 26 | 23 | 16 | 108 |

over, to investigate hare activity, we calculated the number of hourly GPS positions of inactive hares, i.e. consecutive positions < 15 m apart (which is ca 3 × the GPS location error), defined as 'time spent inactive'. Finally, to investigate if hares use areas with increased visibility in the days after capture, we calculated the straight-line distance of each GPS position to the closest field edge (of any field), and assigned the ground vegetation height to each GPS position, categorizing positions as being in > 25 cm high vegetation (lower visibility, more cover) versus lower vegetation (higher visibility). We then used generalized linear mixed models (GLMM) of the R package 'lme4' (Bates et al. 2015) to investigate changes after capture by including the days after capture (as category), sex and their interaction as fixed effects, and the hare ID as random intercept (Table 2). Distance moved and distance to field edges were log-transformed to account for non-normal residual distribution.

### *Disturbance experiment*

For the disturbance experiment, we used two temporal windows of data to distinguish between immediate (hours) and longer-term (1–3 d) responses towards the disturbance: 1) the hour before, during and after the disturbance (for the analyses of distance moved and distance from field edges) and 2) three days before, the day of the experiment and three days after the experiment (all analyses; Table 2, Supporting information). We could not investigate long-term effects (> 3 d) as they coincided with new experimental disturbances.

We calculated the escape distance, defined as the distance moved by the hare directly subsequent to the disturbance (i.e. the straight-line distance between the GPS position of the hare before the disturbance and the following position), as well as the distance moved in the hour directly before and the hour directly subsequent to the disturbance. GPS data with 15-min fix rate (from 2019) were again subsampled to an hourly fix rate to be comparable. Moreover, we used the same response variables as for the capture effects analyses (described above; Table 2). Additionally, we calculated the time spent outside the hares' home range after disturbance to investigate changes in space use. To do so, we estimated the 95% KDE home range size of the three-day period prior to the disturbance and then counted the number of GPS positions outside this home range separately for the day after the disturbance and three days after. We used GLMMs to investigate effects of disturbance and included sex, the disturbance type, period (before disturbance versus after disturbance) and the interaction of disturbance type and period as fixed effects and hare ID as random intercept (Table 2). Moreover, we initially included a categorical variable describing whether an individual was previously flushed or not in the analysis, but found no effect on spatial movements, and consequently removed this variable from the main analysis. In line with this, Weterings et al. (2016) previously showed that hares do not habituate to disturbance.

## Model selection

For all analyses, we created a set of candidate models (Supporting information), and performed model selection using Akaike's information criterion corrected for small sample size

Table 2. Overview of the analyses separately for 1) capture effects and 2) disturbance experiments of 25 GPS-tagged European hares *Lepus europaeus*.

| Response variable | Fixed effects | Random intercept | Model link |
|---|---|---|---|
| 1) Capture effects | | | |
| log (Distance moved (m $h^{-1}$)) – active hares | Days after capture + Sex + Days after capture: Sex | hare ID | Gaussian |
| log (Distance moved (m $h^{-1}$)) – inactive hares | Days after capture + Sex + Days after capture: Sex | hare ID | Gaussian |
| Number of inactive GPS positions | Days after capture + Sex + Days after capture: Sex | hare ID | Poisson (log) |
| Daily 95% KDE home range size | Days after capture + Sex + Days after capture: Sex | hare ID | Gaussian |
| 50% KDE centroid shift (m) | Days after capture + Sex + Days after capture: Sex | hare ID | Gaussian |
| log (Distance from field edge (m)) | Days after capture + Sex + Days after capture: Sex | hare ID | Gaussian |
| In > 25 cm high vegetation | Days after capture + Sex + Days after capture: Sex | hare ID | Bernoulli (logit) |
| 2) Disturbance experiment | | | |
| log (Distance moved (m $h^{-1}$)) | Sex + Period + Disturbance type + Period: Disturbance type | hare ID | Gaussian |
| Daily 95% KDE home range size | Sex + Period + Disturbance type + Period: Disturbance type | hare ID | Gaussian |
| Number of GPS positions outside the three day before-disturbance home range | Sex + Period + Disturbance type + Period: Disturbance type | hare ID | Poisson (log) |
| log (Distance from field edge (m)) | Sex + Period + Disturbance type + Period: Disturbance type | hare ID | Gaussian |
| Proportion of positions in > 25 cm high vegetation | Sex + Period + Disturbance type + Period: Disturbance type | hare ID | Bernoulli (logit) |

($AIC_c$) (Anderson and Burnham 2004), selecting the model with the lowest $AIC_c$ (Murtaugh 2009), using the R package 'MuMIn'(Barton 2016). If ΔAICc was < 10 in two or more of the most parsimonious models, we performed conditional model averaging of these candidate models (Bolker et al. 2009). There was no correlation between the fixed effects in any analyses (all $r < 0.6$). Parameters that included zero within their 95% confidence interval were considered uninformative (Arnold 2010). We validated models by plotting the model residuals versus the fitted values (Zuur et al. 2010). All statistical analyses were carried out in R ver. 4.0.3 (<www.r-project.org>).

## Results

### Capture effects

We captured 28 hares, of which three males died while fitting the GPS collar, likely because of intensive stress during handling. For the remaining 25 hares, we obtained 3–384 d of GPS data (mean ± SD: 165 ± 113 d, Table 1). There were no significant differences in the weekly percentage of survival during the first eight weeks after capture, with 96% surviving the first week after capture (24 of 25 hares), and an average of 97% surviving per week during weeks 2–8 after capture (Fisher's exact test: $p = 0.07$).

The movement and activity of hares changed little in the days after-capture (Supporting information). Hares spent more time inactive in the first four days after capture (mean ± SD: 11.2 ± 4.1 h) compared to the next six days (9.6 ± 4.6 h), equivalent to a 11% decrease in activity during the first four days after capture, and females generally spent more hours inactive than males (Fig. 2, Supporting information). Moreover, females spent more time in > 25 cm high vegetation than males, but there were no clear patterns regarding changes in the days after capture although this variable was retained in the best model (Fig. 2, Supporting information). We did not detect changes in hourly distance moved in the days after capture (not included in the best model; Supporting information). Distance moved by active hares was best explained by sex, with males generally moving greater distances than females (mean ± SD: 121 ± 142 versus 49 ± 69 m), whereas distance moved by inactive hares did not differ between sexes (Supporting information). Males had larger daily home ranges (95% KDE) than females, but home range size did not change in the days after capture (Supporting information). Hares shifted their core home range (50% KDE) centroid on average (± SD) 139 ± 147 m per day, with shifts being larger in males than females, but centroid shifts did not change in the days after capture (days after capture was included in the best model, but uninformative; Fig. 2, Supporting information). Finally, the distance from field edges was not explained by any variable (sex was included in the best model, but did not improve model fit compared to the intercept only model; Supporting information).

### Disturbance experiment

#### *Distance moved*

Directly subsequent to the disturbance event, hares moved on average (± SD) 454 ± 184 m when a shot was fired (range: 206–759 m), and 399 ± 221 m when disturbed without shot (range: 69–802 m; Fig. 3). During data download, 15 of 26 hares (58%) moved away from their resting spot, whereas individuals did not move on the other occasions (Fig. 3). Hares did not move during the arbitrary control, i.e. the distance moved (7 ± 10 m) was comparable to the GPS location error (5 ± 5 m; as obtained from field tests in the same study area). In the hour after the disturbance events, movement distances returned to the baseline level, i.e. hares generally did not move (Fig. 3, Supporting information). There were no sex differences (Supporting information). When comparing average hourly distances moved (m $h^{-1}$) in the three days before and after the disturbance day, the interaction of period and disturbance type was not included in the highest ranking models (Supporting information).

***Home range size and shift***

Daily home range sizes were larger on the treatment day for hares that were flushed (with and without shot), but they returned to their previous size in the days after the disturbance (Fig. 3, Supporting information). Compared to the home range calculated from the three days before the disturbance, hares spent on average (± SD) 4 ± 5 h outside their home range on the day of the disturbance and the days after the disturbance (Fig. 3, Supporting information). After the control treatment and data download, hares spent on average (± SD) 2 ± 4 h outside their home range on the treatment day and the days after, whereas hares that were flushed (with and without shot) spent 7 ± 6 h outside their home range (Fig. 3, Supporting information).

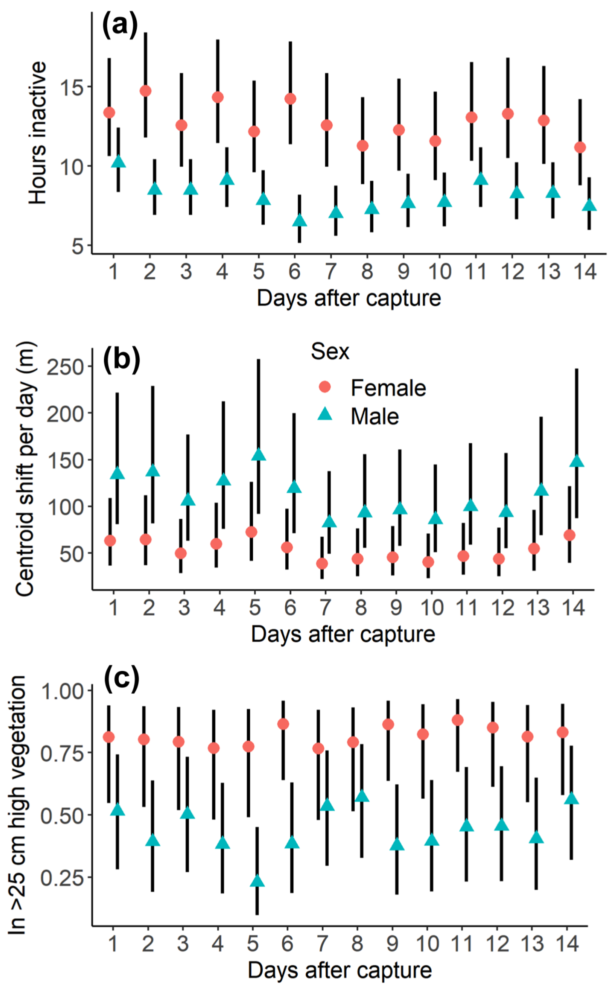


Figure 2. Showing the time spent inactive (a), core home range centroid shift (centroid calculated from 50% KDE; b), and proportion of GPS positions in > 25 cm high vegetation (c) for the first 14 d after capture in 25 GPS-collared European hares.

***Distance from field edges and time in high vegetation***

Hares did not stay further from field edges in the hour directly subsequent to any disturbance (Supporting information), but remained further from field edges during three days after a simulated hunt (shot fired) (Fig. 4, Supporting information). The other disturbance types did not affect how far from field edges hares remained in the days after disturbance (Fig. 4, Supporting information). During the three days after disturbance, hares spent less time in > 25 cm high vegetation after they were flushed (this effect was strongest after a shot was fired), but not after data download and control (Fig. 4, Supporting information).

## Discussion

### Capture effects

To our knowledge, this is the first study to evaluate capture effects in European hares. Hares reduced their activity in the first four days after capture, but we did not detect other effects on movement or space use. This is in line with studies on other mammals that also found limited short-term (< 10 d) effects of capture on animal behavior and space use (Neumann et al. 2011, Northrup et al. 2014, Graf et al. 2016, Jung et al. 2019).

The fact that three hares died during GPS-collaring is evidence that the immediate capture and handling process is highly stressful for hares. Fatalities during capture were not reported in other hare studies, including our own, despite numerous studies that collared hares for telemetry (Avril et al. 2012, Zaccaroni et al. 2012, Schai-Braun and Hackländer 2013, Schai-Braun et al. 2014, Weterings et al. 2016, Ullmann et al. 2018, Mayer et al. 2019). This raises the question whether fatalities were not reported or did not occur. Consequently, we advocate for the reporting of fatalities (or their absence) in studies using data obtained from captured individuals in order to improve capture and handling methods (Schemnitz et al. 2009). Different methods are used for the capture of hares. The most common ones are box traps (our study, Schai-Braun et al. 2014), driving hares into long nets with beaters (Rühe and Hohmann 2004, Weterings et al. 2016) or dogs (Zaccaroni et al. 2012) or the use of spotlights and hoop nets (Stott 2003). The choice of capture method will predominantly depend on capture efficiency in relation to landscape structure and population density, but the reporting of fatalities or complications would allow the evaluation of the different methods. Moreover, the use of sedatives can help reduce capture stress (Montané et al. 2003), but might not be useful for hares due to the very short handling time, and because it potentially increases predation risk after capture.

We cannot say whether the short-term changes in activity resulted from the capture and time spent in the box trap, the handling itself or the subsequent presence of the GPS collar that the hares had to adjust to. It is likely that all these factors partly played a role. Moreover, the reduced activity after capture might have been caused by other factors, such as altered

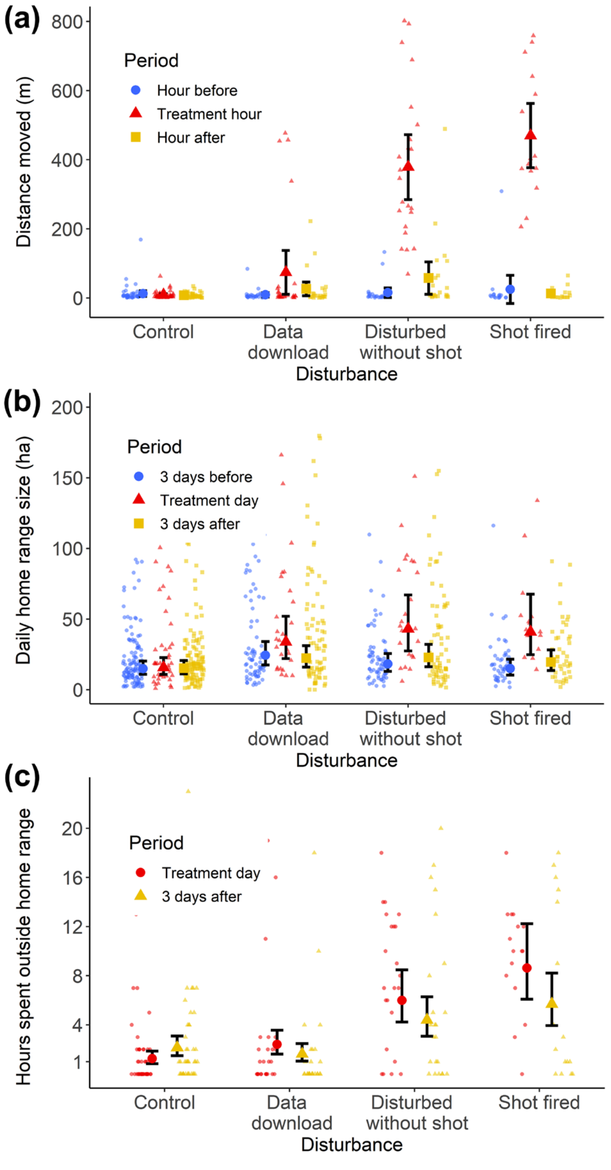


Figure 3. The distance moved by hares (a) in the hour before the disturbance, the hour the disturbance took place and the hour after. Plot (b) shows the daily home range size (estimated as 95% KDE) three days before, on the treatment day and three days after the disturbance. Further, plot (c) shows the hours spent outside the three-day before-disturbance home range on the treatment day and three days after the disturbance. Large symbols represent the mean and bars the 95% confidence interval. Small symbols represent the raw data.

resource availability due to vegetation growth, though this is unlikely considering the short time period. Finally, there might have been other responses to capture and disturbance as measured here, such as increased stress levels (Abreu et al. 2009, Cattet et al. 2014) or reduced reproductive success (Côté et al. 1998).

## Disturbance experiment

The experimental disturbance of hares (both with and without shot fired) caused short-term changes in movement behavior, initiated by a strong escape response, resulting in a spatial displacement on the disturbance day and the days

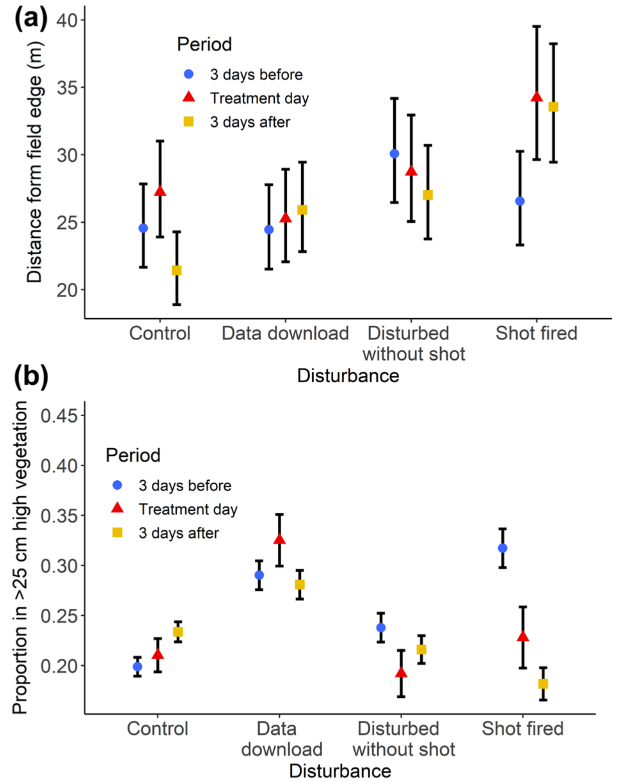


Figure 4. The distance hares remained from field edges (a) three days before disturbance, on the treatment day and three days after disturbance. Further, (b) shows the proportion hare GPS positions that were located in > 25 cm high vegetation three days before disturbance, on the treatment day and three days after disturbance. Symbols represent the mean and bars the 95% confidence interval.

after disturbance as indicated by an increased time spent outside the before disturbance home range (compared to control treatment). Other mammals also showed a spatial displacement in response to hunts (Sunde et al. 2009, Yamaguchi et al. 2020) and other human-caused disturbances (Seip et al. 2007), but this is not always the case (Andersen et al. 1996, Neumann et al. 2009). The effect size of the response partly depended on the disturbance type, with simulated hunts leading to stronger anti-predator behaviors, as indicated by hares remaining further from field edges and spending less time in high vegetation, but apart from this hares reacted similarly to being flushed with or without shot. Interestingly, though this effect was small, hares also moved greater distances on the day of the data download, cautioning that regular fieldwork might affect the behavior of the study animals, which might affect research findings.

The question arises how different types of hunting would affect anti-predator behaviors (Yamaguchi et al. 2020). We speculate that driven hunts with more people and hunting dogs (and more frequent hunts) might result in stronger anti-predator responses (in both space and time) than measured here due to an extended spatio–temporal disturbance. Hares also adjusted space use on a finer scale, i.e. they remained further from field edges and spent more time in short vegetation, likely to have better visibility, thereby increasing the chance of detecting a potential approacher/predator (Focardi and Rizzotto 1999, Mayer et al. 2020), also shown in other species (Lima 1992). In general, the spatial displacement and altered space use probably did not impede the hares' foraging efficiency as they spend more time in low vegetation which is of higher foraging quality (Wilmshurst et al. 1995), though this effect was comparatively small. In contrast to our study, Zaccaroni et al. (2012) found no measurable effects of driven hunts conducted with 10 people and a pack of hunting dogs on home range displacement of hares. However, hunting in this study targeted foxes, and hares were not purposefully flushed as in our study. Hares might generally show pronounced anti-predator behaviors (at least in areas where foxes are present) to avoid detection in the first place or to be able to outrun a predator/approacher.

Our disturbance experiment had several limitations. We only investigated a single disturbance within a given week, and our study design did not allow us to test for longer-term effects of the disturbance or the effect of multiple disturbance events within a short period. Moreover, due to the comparatively small sample size of the disturbance experiment, we could not reliably investigate sex differences. However, sex differences are less pronounced in fall and early winter (Mayer et al. 2019) when we conducted the experiments, probably because this period is outside the hares' mating season (Holley and Greenwood 1984).

## Conclusions

Capture and handling can affect animal movement behavior and can be a large stressor (as evidenced by three mortalities in this study) and therefore, has to be assessed to ensure the best techniques available are being used to reduce negative effects on animal welfare and to avoid biased data. Hares have well developed anti-predator behaviors, which might be the reason why we found overall little effects of capture and disturbance on movement behavior, because hare behavior and activity is generally driven by predator avoidance. Nevertheless, we recommend that researchers should remove data from the first four days after capture to warrant unbiased results, as our data indicated reduced activity during this period after capture. In general, data screening (as shown here) could be used to guide data censoring for individuals. The comparatively limited response towards disturbance indicates that hunting likely is not a major source of disturbance for hares given that hunts are not conducted too frequently.

*Acknowledgements* – We thank Erik Lykke for allowing us to work on his land, Jacob Coleman Nielsen and Lia Schlippe Justicia for assistance with fieldwork. Further, we are thankful for economical funding from the Danish Environmental Agency and the Danish Hunters Association.

*Conflict of interests* – The authors declare no competing financial, personal or other conflict of interest.

*Permits* – All trapping and handling procedures were approved by the Federal Nature Conservation Act (§ 45 Abs. 7 No. 3) and the local nature conservation authority (reference number LUGV V3-2347-22-2013 and 55.2-1-54-2532-229-13) and met the guidelines approved by the American Society of Mammalogists.

### Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.j0zpc86fb> (Mayer et al. 2021).

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