



# Survival rates on pre-weaning European hares (*Lepus europaeus*) in an intensively used agricultural area

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## Abstract

The primary cause of the long-term decline in European hares' (*Lepus europaeus*) population throughout Europe is widely assumed to be the intensification of agriculture. A critical component in this population dynamics is seen in the survival of leverets from birth to reproductive age. In European hares, the first stage of life until weaning has been sparsely studied, in particular habitat selection, movements and survival rate, as juveniles' precocial lifestyle is dominated by any kind of anti-predation behaviour. In the present study, free-living and pre-weaning European hares were detected systematically by thermography ( $n = 394$ ), being radio-tagged or marked ( $n = 229$ ) from birth until the fifth week of life to research the early juvenile survival and proximate causes of mortality. Kaplan-Meier survival curves were computed overall and in relation to the strata of season, sex and type of daytime resting place. The survival rate of radio-tagged leverets was 0.35 in the first month of life, and 0.63, 0.52 and 0.44 for the first, second and third week of life, respectively. Approximately 21.6% and 50% of all confirmed deaths occurred during the first 7 and 13 days after birth. By the end of the 4th week of life, the mortality rate caused by predation, suspected predation, agricultural practices and unexplained cases was 41.7%, 36.7%, 11.7% and 10.0%, respectively. There was no significant difference in survival between the sexes and seasons. In contrast, young hares died more frequently as a consequence of choosing a hiding place without shelter during the daytime.

**Keywords** *Lepus europaeus* · Leveret survival · Kaplan-Meier · Predation · Telemetry · Thermography

## Introduction

Since the 1960s, the population of the European hare (*Lepus europaeus*) has declined dramatically across Europe (Edwards et al. 2000; Flux and Angermann 1990). Although the European hare is classified globally as being of 'least concern' by the International Union for Conservation of Nature (IUCN) (Hackländer and Schai-Braun 2019), in consequence of the population trend and decline in hunting bags, the hare has been given the conservation status 'near threatened' or even 'threatened' on various red lists of endangered species, e.g. in

Austria, Germany and Switzerland (Duelli 1994; Meinig et al. 2009; Spitzenberger 2005). Despite the long-term decrease, the European hare is still widespread in its historical range and is considered to be an important game species (Flux and Angermann 1990; Hackländer and Schai-Braun 2018), which leads to a conflict arising between protection and sustainable use. In this context, the number of studies on adult and sub-adult European hares and related species has increased in various biological disciplines in recent decades. The findings thereof significantly improved the understanding of the ecological relationships of this species in today's cultural landscape, e.g. habitat associations (Meichtry-Stier et al. 2014; Reitz and Léonard 1994; Vaughan et al. 2003); reproductive biology (Frylestam 1980; Roellig et al. 2011); energetics and nutrition (Hackländer et al. 2002b; Reichlin et al. 2006; Stalder et al. 2019); activity patterns (Homolka 1986; Schai-Braun et al. 2012; Zaccaroni et al. 2013); agricultural practices (Kaluzinski and Pielowski 1976; Marboutin and Aebischer 1996); survival, predation and hunting (Erlinge et al. 1984; Hummel et al. 2017; Marboutin et al. 2003; Panek et al. 2006; Pépin 1989; Reynolds and Tapper 1995; Stoate and Tapper

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1993); and also diseases (Frölich et al. 2003; Lamarque et al. 1996; Posautz et al. 2015).

The primary cause of this long-term decline in hare populations throughout Europe is widely assumed to be agricultural intensification (Pépin and Angibault 2007; Smith et al. 2004), particularly by farmland management practices (Tapper and Barnes 1986). Some studies have shown that the fecundity in European hares is not affected and concluded that it may not have had any effect on long-term population trends (Bensinger et al. 2000; Blottner 2001; Göritz et al. 2001). In addition, other factors such as precipitation, low environmental temperatures or predation act on a smaller scale or are secondary factors (Hackländer et al. 2002a; Smith et al. 2005).

Consequently, the persistent agricultural development results in the loss of crop and landscape diversity (Jennings et al. 2006; Vaughan et al. 2003), and ultimately in reduced habitat quality (Hackländer et al. 2002b; Schai-Braun et al. 2015), which may affect leveret survival (Hummel et al. 2017). However, the hypothetical effect mechanisms and interactions between the multiple environmental factors on the survival of hares were not precisely known. Indeed, only in recent years have broader research efforts led to a better understanding of these interrelationships (e.g. Hummel et al. 2017; Jensen 2009; Meichtry-Stier et al. 2014; Schai-Braun et al. 2015; Smith et al. 2005; Voigt and Siebert 2019; Zellweger-Fischer et al. 2011).

Generally, a critical component of population dynamics in birds and mammals is seen in the survival of juveniles to reproductive age. The estimated generation time of about 2 years in European hares (Marboutin et al. 2003) is relatively short, and consequently, variations in survival of juveniles could have significant effects on population growth and viability (Ronget et al. 2018). Therefore, the survival strategy of the species in connection with the influence of environmental factors in the respective habitat is of existential significance. A number of studies investigated the survival of European hares as they are a key factor for population dynamics. Normally, these were indirectly calculated at a population scale from estimates of spring and autumn population densities, annual female reproduction and analysis of hunting bags as well as directly from capture-mark-recapture (CMR) experiments (Haerer et al. 2001; Marboutin and Hansen 1998; Marboutin and Peroux 1995; Pépin 1989). Telemetry was also performed on adult hares and older juveniles to measure direct survival rates (Devillard and Bray 2009; Marboutin et al. 1990; Misiorowska and Wasilewski 2012; Reitz and Léonard 1993). All studies concerned with the indirect recalculation of juvenile losses reveal a high mortality rate of juveniles between 50 and 90% within the first year of life. In contrast, telemetric studies of adult and especially older juveniles showed much lower mortality rates, even during the dispersal phase (Devillard and Bray 2009; Gillis 1997), with slight area-

dependent variations. From this, it becomes obvious that the main losses occur during the phases of pre-weaning and pre-dispersal. In particular, food quality and a positive energy balance may play a major role in this process (Hackländer et al. 2002b; Hummel et al. 2017; Schai-Braun et al. 2015) as well as various anti-predation strategies in the precocial European hare (Focardi and Rizzotto 1999; Holley 1993). For related species such as the snowshoe hare (*Lepus americanus*) and the mountain hare (*Lepus timidus*), a high mortality rate was proven in the first weeks of life (Dahl 2005; O'Donoghue 1994). Besides two investigations, one unpublished (Bray 1998) and one recently published (Karp and Gehr 2020), there are no studies on the European hare that have directly calculated the survival rate of pre-weaning leverets, neither from systematically captured juvenile animals from the wild nor in an experimental approach under field conditions.

The reasons for this are likely to be found in the challenges involved in studying a species in the wild whose lifestyle is shaped by inconspicuousness, motionlessness and perfect use of shelter, reducing the detection probability and ultimately decreasing the risk of predation in the first weeks of life.

The present study aims to fill the gaps of knowledge by characterising the survival of leverets within the first weeks of life. This may contribute to a better understanding of hares' early ecology and population dynamics, and possibly also be a stimulus for applied research on habitat improvements in the modern agricultural landscape.

## Materials and methods

### Study area

The study was performed from 2004 to 2010 in the Hildesheimer Boerde landscape, which belongs to the Central European loess zone, part of the North German Plain (study site: N 52.244°/E 10.116°). Hildesheimer Boerde is a slightly undulating, less structured, large-scale agricultural landscape and is mainly characterised by cultivation of winter cereals (44%), sugar beet (25%), maize (16%) and potatoes (up to 5%). On a seven-step scale, soil fertility and yield capacity achieve the 'extremely high' category, the best value (NIBIS@-Map Server 2018). Due to this intensively managed agriculture, forests are completely absent and grassland and copses are found rarely and are isolated. Other wooded landscape elements, such as hedges and lines of trees, are slightly more frequent but limited to roadsides and field paths. An Atlantic climate prevails, with an average annual precipitation of 646 mm and temperature of 10.4 °C. The overall size of the study area was approximately 1800 ha. The population density estimated by spotlight counting (Langbein et al. 1999) averaged from 20 to 52 hares per km<sup>2</sup> in spring and 30 to 68

hares per km<sup>2</sup> in autumn. Compared with the federal average density of hares (Sliwinski et al. 2019), the study area featured a medium to high density of hares. Hares are hunted once a year, mostly in the first 2 weeks of December.

### Detection of leverets and seasons

In the lapse of time between leaving the daytime hideout and returning to it (Broekhuizen et al. 1986; Broekhuizen and Maaskamp 1980), leverets can be detected by an observer. A thermal imager infra-red camera (Palm IR 250-D; Raytheon Company Inc., Waltham, MA, USA) equipped with a 100-mm telephoto lens was used to detect leverets. The 320 × 240 pixel microbolometer detector array was able to differentiate thermal radiation between objects and their direct surroundings of 0.2 °C, so warm objects like mammals could be detected easily. Although the thermal imaging camera ensures a reliable detection of small and distant warm objects, instant identification of different species, e.g. leveret, hedgehog or rat, was difficult due to the low resolution. Behaviour, size and shape of the detected object, as well as the experience of the observer, determined a worthwhile approach in most cases. Once a warm target had been located, the object was approached on foot until identification by torch was possible.

Two search variants were performed depending on the field size, the height of vegetation and the associated reduced detectability of warm objects at ground level at a greater distance. Usually, the landscape was scanned from the back of a pick-up truck, driven along field roads and across uncropped fields, e.g. bare soil, stubble fields or cover crops. Searching from both sides of the truck and using the elevated position of the camera at about 3.5 m above the ground resulted in a more favourable detection performance and probability, as the latter strongly depends on the angle of elevation for distant objects. In addition, fields were also crossed on foot and searched using a GPS-guided meander-like pattern at a maximum distance to each transect part of 200 m. The detectability of leverets was assumed to be at least 130 m for this camera type, resulting in a detection overlap area between two adjacent transects. Transects were always defined crosswise to any existing seed rows in order to ensure the highest possible detectability of leverets. The combination of the two variants resulted in an almost complete scan of the fields.

The investigation was performed during two seasons per year because detection of warm objects in dense crops and other vegetation is virtually impossible. Season I incorporated data from early February to late May, and season II incorporated data collected after cereal harvest, from mid-July to the end of September, which coincided with the end of hares' main reproductive phase. The searches were conducted exclusively at night, beginning 60 min after sunset at the earliest, and lasting between 4 and 7 h per night depending on the season.

### Capturing, handling, tagging and age determination

A permit allowing the capturing, handling, tagging and radio-tracking of leverets was issued by the Lower Saxony Institute for Consumer Protection and Food Safety (LAVES, Germany, Department 3 Animal Health, permit number: 33.12-42502-04-16/2083). Leverets were caught directly by hand, since they showed no signs of resistance or made no attempts to escape. Larger animals were captured with a landing net (diameter 1 m) fitted with a 5-m handle. To avoid further disturbance from the immediate surroundings, the subsequent procedure was carried out away from the capture site by transporting the leveret in a small box. Data for the capture location was saved in the handheld GPS by averaging positions over a 10-min period (horizontal accuracy 1.7 m ± 0.3 m). Capturing took place one and a half hour after sunset at the earliest, but in most cases after suckling to reduce potential handling effects.

During handling, care was taken to provide a quiet environment, and the animal's head was always covered. For subsequent recognition after the transmitter had dropped off, a numbered metal ear tag (Model 1005-3; National Band & Tag Co., Newport, KY, USA) was attached to each animal. Leverets weighing less than 400 g were fitted with lighter 1.4 g vhf-transmitters (Model PIP, 150 MHz, 12 cm antenna; Biotrack Ltd., Wareham, UK). Otherwise, heavier and more powerful 4.0 g vhf-transmitters were used (433 MHz, 6.5 cm antenna, AWEK fl-electronic GmbH, Braunschweig, Germany), so that in both options, the ratio of body mass to transmitter weight did not exceed 1.4% (3–5% as rule of thumb: Kenward 2001). A surgical adhesive (EPIGLU®, Meyer-Haake GmbH Medical Innovations, Ober-Mörlen, Germany) was used for attaching the transmitters. The fur of the interscapular region was parted, and some glue was applied to the underside of a transmitter. The transmitter was then carefully glued onto the undercoat but not to the skin, aligned along the body axis. Afterwards, the leveret's hair was folded over each side and over the top of the transmitter, which was glued once more to these sides, while the antenna resting along the back was directed slightly upwards. After the glue had dried for approx. 1 min, the leveret was again placed in the capture box and released immediately at the initial capture site. To reduce the effect of repeated disturbance, transmitters were never re-glued to the same animal. Leverets were held captive for a maximum of 9 min.

The age at first capture was estimated from the nearly linear allometric relationship between skull length and weight (Bray et al. 2002). To maintain accuracy of this appraisalment, some animals were captured and measured two to three times. Otherwise, the age of relocated animals was determined based on the time gap since the initial detection.

## Monitoring leverets

Since leverets remain at their habitat and show no pronounced dispersal behaviour in the first weeks of life, homing (Mech and Barber 2002; White and Garrott 1990) was applied as the ultimate method for tracking their life status. Telemetry was performed by a three-element yagi antenna and a receiver suitable for the used frequency type (SIKA, 150 MHz, Biotrack Ltd., UK; FME 434, 433 MHz, AWEK fl-electronic GmbH). Each leveret was located up to five times a week, at different times during the day and night, until death of the animal, transmitters falling off or transmitter failure was confirmed. The signal was always localised within a range of 0.5 m<sup>2</sup>, and the averaged position was stored in a handheld GPS. Visual confirmation was often omitted, especially in dense vegetation, to avoid disturbing the leverets or attracting predators. In such cases, life status was determined retrospectively by the well-documented exact positions, their changes over time or entry of a final stage. Lost transmitters were searched for by a truck-mounted telemetric system at an antenna height of 8 m to increase detection probability. Additionally, the last location of an animal, known to be alive, was checked by thermography several times at night to reduce the likelihood of a transmitter failure.

## Data processing and analysis

All data preparation and analyses were modelled in R 3.5.3 (RCoreTeam 2018) by using the following R packages: ‘survival’ for computing survival analyses (Therneau 2018), ‘survminer’ (Kassambara and Kosinski 2018) and ‘ggplot2’ (Wickham 2016) for summarising and visualising the results of survival analysis.

Survival curves were computed for the radio-tagged leverets using the non-parametric Kaplan-Meier estimator (Kaplan and Meier 1958). This procedure allows the use of censored data as well as staggered entry of animals during the course of a study (Pollock et al. 1989).

The survival object within the survival function was created by the arguments time, time2 and event. Time and time2 are defined as the corresponding leverets’ age in days, starting from tagging until the occurrence of the event group censor or death. Animals were considered as censored from the time of detachment or loss of the radio transmitter, even if the animal was found dead or alive later on, e.g. shot in the following hunting seasons or directly by visual confirmation. In cases of signal loss and unsuccessful search by thermography in the following nights in the surroundings of the last locations where animals were known to be alive, the animal was assigned to the event group ‘dead’. The same classification applied to the finding of carcasses or tissue parts such as bones, organs, fur with skin remnants or blood.

In this study, the causes of death were determined by checking for signs on the dead animal and in the vicinity of the killing site or the site where the carcass had been found (Brand et al. 1975; Dolbeer et al. 1996). Furthermore, the assessment of event groups or causes of death also considered the place where the radio transmitter had been relocated, e.g. close to a fox’s den or a built-up area, and the agricultural activity in the vicinity of the daytime resting place. The cause of the event group ‘dead’ was categorised into ‘unknown’, ‘agricultural practices’, ‘predation’ and ‘assumed predation’. The latter two categories were assigned very restrictively. The impact of pesticides or diseases as a possible cause of death or sublethal effects was not investigated.

A recent study has shown that leverets performed a pronounced change in habitat between daytime and nighttime (Voigt and Siebert 2019), which is related to nursing behaviour. This fact was taken into account in the analysis. The daytime locations of radio-tagged leverets were categorised into ‘concealed’ and ‘open’. Concealed habitats included all animals that were either found well hidden by vegetation, or animals that had changed their daily resting place from ‘open’ to ‘concealed’ with increasing age. On the other hand, all animals localised during the day with vertical openness or on bare soil were counted as ‘open’ daytime users.

A web-based calculator (Conrad 1998-2019) was used to assign the time of the hares’ detection between the beginning of civil twilight in the morning and the end of civil dawn in the evening to day locations and vice versa to night locations.

The observed number of death events of the survival curves was compared with the non-parametric log-rank test (Pollock et al. 1989), each for the variables season (season I or II), sex (male or female) and daytime user type (open or concealed).

## Results

### General results

In total, 394 individual hares were detected by thermography during the study period, of which 70% were found in season I and 30% in season II. Of these, 229 animals were radio-tagged and marked between 2004 and 2010 (Table 1).

Depending on the weather conditions, size of the leverets and the surface structure of the field, leverets could be detected by thermography between 4 and 247 m (average of 26 m) regardless of the season. The estimated age at first detection for all animals ranged from birth to approx. 100 days at a median of 6 days (SE = 0.506, SD = 9.05), but there was a difference between season I and season II with a median of 5 and 11 days, respectively (Mann-Whitney  $U = 5816.0$ ,  $n_1 = 226$ ,  $n_2 = 95$ ,  $p < 0.001$  two-tailed; see also additional file 1). The retention time, which is defined as the interval from tagging to dropping off or loss of the vhf signal, had a mean of

**Table 1** Number of detected and radio-tracked hares per year and season

	2004	2005	2006	2007	2008	2009	2010	Total
Season I	34 (9)	32 (22)	57 (26)	37 (24)	50 (35)	36 (26)	30 (25)	276 (167)
Season II	10 (-)	13 (3)	17 (6)	24 (11)	26 (17)	13 (13)	15 (12)	118 (62)
Total	44 (9)	45 (25)	74 (32)	61 (35)	76 (52)	49 (39)	45 (37)	394 (229)

The number of leverets detected by thermography is given for each year and season; the number of radio-tracked and marked animals for the survival analysis is given in brackets

11 days (SD = 7.7, 95th percentile = 24, maximum 50). This resulted in a period monitored by telemetry until the end of the first month of life and covered almost the entire period until weaning. The sex ratio of all captures was balanced (48.3% males and 51.7% females).

### Survival rates

The entire survival rate of radio-tagged leverets amounted to 0.33 at the end of the first 40 days of life, and 0.63, 0.52, 0.44 and 0.37 for the first, second, third and fourth weeks of life, respectively (Fig. 1a).

The curves A (survival ~ all radio-tagged leverets), B (survival ~ season) and C (survival ~ sex) had no abrupt steps, and a uniformly decreasing survival rate for all age groups, with the exception of the first 2 to 3 days of life. This also applied to user type 'open' (survival ~ daytime user type), but only from the tenth day of life. A consistent decreasing course indicated that there were no time points within the complete suckling period in which leverets were subject to a comparatively increased mortality rate (see also additional file 2).

Albeit not statistically significant (log-rank test:  $N = 229$ ,  $\chi^2 = 3.4$ ,  $df = 1$ ,  $p = 0.06$ ), survival rates tended to be lower in season I (median survival = 15 days) than in season II (23 days).

Males seemed to have a slightly lower survival rate between the fourth and 20th day of life than females (Fig. 1c). This was also expressed by the median survival, which was 9 days for males and 17 days for females. However, there was no significant difference between the sexes in the overall survival rate due to the wide confidence intervals (log-rank test:  $N = 215$ ,  $\chi^2 = 0.5$ ,  $df = 1$ ,  $p = 0.5$ ).

Survival was significantly higher in concealed than in open habitats (median survival time 29 and 2 days, respectively, Fig. 1d, log-rank test:  $N = 164$ ,  $\chi^2 = 24.1$ ,  $df = 1$ ,  $p < 0.001$ ) in terms of daytime habitat use. In concealed habitats, 87% of the leverets survived until 7 days old (SE = 0.104, 95% confidence intervals 0.69–1.00) compared with 19% (SE = 0.112, 95% confidence intervals 0.06–0.60) in open habitats. The difference in mortality between the two habitat type users was particularly high in the first days after birth. At 28 days of age, 50% of the juveniles were still alive in concealed habitats, compared with 5% in open habitats (Fig. 1d). It was also found that 12 out of 50 animals inhabiting initially

open habitats moved to the concealed habitat, where they presumably reduced the risk of being detected and predated during the day.

The survival rate of the leverets depends on the time (days) after marking shows no abrupt change after capture (see additional file 3). Therefore, the possible influence of handling on the survival rate seems to be present but only marginal.

### Causes of mortality

Of the 229 radio-tagged leverets, there was proof of 60 animals (26.2%) dying during the monitoring period. This contrasts with the large number of 105 animals, whose fate could not be determined more precisely. It remains speculative as to what percentage of them can still be counted among the deaths. The number of cases of a transmitter detachment and confirmed survival of individuals amounted to 37.9% of all censored animals (Table 2).

The losses clearly attributable to predation amounted to 42% of the known leveret mortalities, and besides 'predation assumed' 37%, 'agricultural practices' (cultivating, ploughing, mowing) 12%, and 'unknown' mortality causes 10% (e.g. disease, hypothermia, pesticides or unexplained cause).

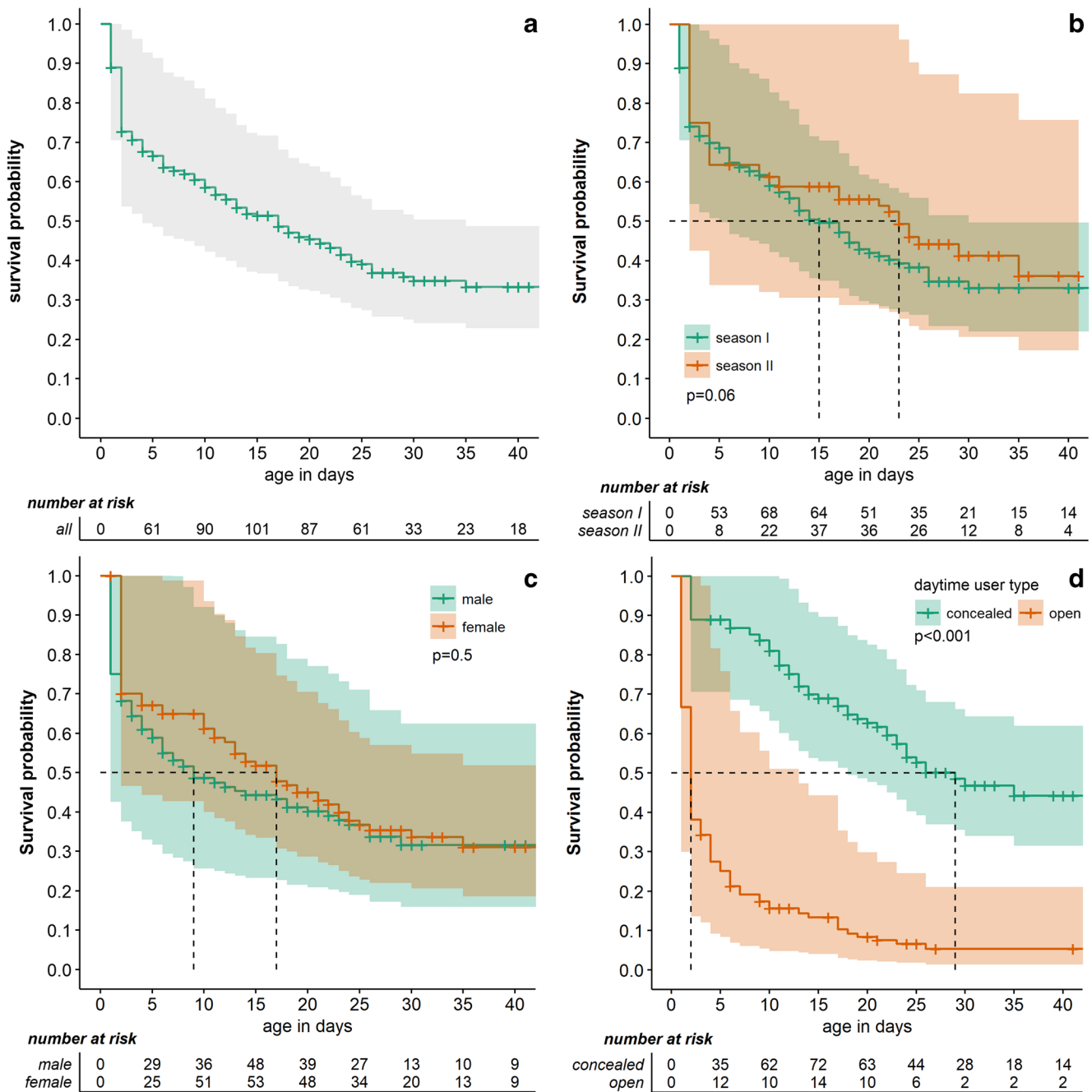
The extent to which pesticides influence the survival rate of leverets could not be clarified in this study.

Specific predators were identified in 16 out of 25 predator kills: red fox (*Vulpes vulpes*,  $n = 5$ ), beech marten (*Martes foina*,  $n = 3$ ), carrion crow (*Corvus corone*,  $n = 1$ ), common buzzard (*Buteo buteo*,  $n = 3$ ), cats (*Felis silvestris catus*,  $n = 2$ ) and one case each for the owl species short-eared owl (*Asio flammeus*) and barn owl (*Tyto alba*). In five cases, predation by buzzards, owls and crows was directly observed. However, some of the animals accounting for predation could have been scavenged by predators after they had died of other causes.

## Discussion

### Survival rates

The abundance and fluctuations in European hare populations are primarily caused by changes in survival rates among juveniles (Jennings et al. 2006; Marboutin and Hansen 1998;



**Fig. 1** Kaplan-Meier survival curves of leverets. Survival is computed generally for all observed hares (a), and for the strata season (b), sex (c) and the daytime user type (d). Along with each curve, the 95% point-wise

confidence band, the median survival (dashed line) and ticks for the censored observations are shown. The given  $p$  values in the subframes b, c and d were calculated in a log-rank test

Pielowski and Raczyński 1976). For the first time, the present study directly calculated low survival rates in leverets of European hares with an average of 33% of all animals surviving the nursing period, regardless of the wide confidence limits. A recently published study from Switzerland (Karp and Gehr 2020), which examined the survival of leverets using the same methodology as in the present study, found a comparatively lower survival rate of 18% at the end of the first month of life. Usually, hares are reproductive from January

until October (Broekhuizen and Maaskamp 1981; Frylestam 1980). Some European studies reveal survival rates in juveniles between 14 and 50% for different habitats (Frylestam 1980; Jensen 2009; Pielowski and Raczyński 1976), and 37% on average in farmland (Pépin 1989). Although the survival rates of the present study were within the range of other studies, they are not directly comparable due to the lack of data between season I and season II (late May until mid-July).

**Table 2** Attribution of leverets' fate. Number and causes of classified events among pre-weaning European hares from birth until end of weaning (percentages were rounded up)

Event group	Cause of event	Number of animals	Percentage within event group
Censored	Unknown	105	62
	Transmitter detachment with survived animal	64	38
Dead	Unknown	6	10
	Predation assumed	22	37
	Predation	25	42
	Agricultural practices	7	12

Several studies reveal both a lack of animals born in the first third of the reproductive period from February to April and a peak of births and surviving leverets between May and August (Hansen 1992; Marboutin and Peroux 1995; Pépin 1989).

In contrast, telemetric studies of older juveniles showed much lower mortality rates (Marboutin et al. 1990; Reitz and Léonard 1993) than the back-calculation of hunting bags for the annual juvenile survival rate, even during dispersal (Devillard and Bray 2009; Gillis 1997), with slightly area-dependent variations. From this, it becomes obvious that the main losses in juveniles occur during the periods of pre-weaning and pre-dispersal.

The estimated survival curves do not reveal any abrupt changes with the exception of up to 3 days after birth. Although the overall loss rate of pre-weaning hares is quite high, there does not seem to be any specific endangered points in time for this period, and mortality affects all age groups equally. During the day, leverets hide at a variable distance from the suckling site (Broekhuizen and Maaskamp 1976), preferably at the margins of field paths and ditches or hedges (Voigt and Siebert 2019), and leave this place only for a short period of time to be suckled. During the nursing period, which usually lasts 4 to 5 weeks (Broekhuizen and Maaskamp 1980), leverets start to feed on green fodder during the second week of life (Martinet and Demarne 1984). The transition in consumption less milk from the female to more vegetable food is depicted as a smooth process, which increases from the 17th day of life (Broekhuizen and Maaskamp 1980). From this time onwards, it could be assumed that the change in diet will also lead to a change in the behaviour of the leverets, which become more conspicuous for predators or die more frequently due to digestive problems. However, this could not be proven in the present study.

The already described abrupt drop in the survival rate during the first days of life is also plausible. This can be explained by the fact that leverets of the genus *Lepus* leave their birth area between the second and fourth day of life to find their own daily hiding place (Broekhuizen and Maaskamp 1976; O'Donoghue and Bergman 1992; Rongstad and Tester 1971). In this study, almost all animals of the age class up to 4 days

were found on bare soil or in fields with a low vegetation height (Voigt and Siebert 2019). Taken together, the change of place from the area of birth and the low coverage can lead to a rise in mortality rate due to an increased conspicuousness and visibility for predators. This is supported by the results of the present study, in which the daytime user 'open' animals die more frequently and faster than the 'concealed' ones or those animals which were born without cover but moved to the next adjacent shelter, therefore having a better chance to survive. The latter also means that the distances to be covered between the daytime hiding place and the suckling place must remain low, which would make leverets less conspicuous for nocturnal predators. A study from Switzerland (Karp and Gehr 2020) confirmed the present results that leverets using edges survived better than animals using the mid of fields. In addition, the survival rate of littermates in the snowshoe hare is not to be assumed independent before the litter breaks up, so litters tend to all live or die as a group (O'Donoghue 1994). Of course, another factor could also be unfavourable weather conditions (Hackländer and Schai-Braun 2018), such as persistent cold and wet periods, which leverets have more problems contend with during the pre-weaning period than with advanced age.

Furthermore, it could be demonstrated that baits were eaten less frequently inside crop fields and wildflower strips than at the edge of these areas (Fernex et al. 2011). Conversely, this means that the edges of agricultural areas are subject to higher predation pressure. However, leverets remain in these areas a short time before and after nursing at night and run the risk of being predated. It could be shown that set-asides contribute to the survival of leverets and, correspondingly, population growth and spring density (Schai-Braun et al. 2020). Apart from a potential improvement in food quality for the females and leverets, the described effect could also be caused by an increased availability of daytime hiding places in areas with a higher proportion of set-asides. These findings are in line with the results of the present study and of Voigt and Siebert (2019), who showed that leverets prefer to hide in cover-rich structures, especially in field track edges, ditches and fallow-like strips.

No significant difference in survival between sexes could be revealed. In contrast, studies show that young males die

more frequently than young females (Marboutin and Hansen 1998; Marboutin and Peroux 1995) in areas without predation and that males disperse more frequently than females (Avril et al. 2011; Bray et al. 2007). Usually, a lower survival rate of males than females is expected because the dispersal behaviour of males rather leads to visibility and conspicuity, which consequently could increase the predation risk (Broekhuizen 1979; Jensen 2009).

### Causes of mortality—predation

Along with the intensification of agriculture, predation is cited as the most frequent cause of loss in European hares (Panek et al. 2006; Schmidt et al. 2004); especially the red fox plays an important role (Erlinge et al. 1984; Jensen 2009; Reynolds and Tapper 1995). Nonetheless, also the potential importance of habitat quality on the impact of predation is highlighted (Vaughan et al. 2003).

In telemetric studies without permanent monitoring and additional technical sensors like mortality or activity, estimating fate or cause of death is often not clearly attributable, in particular, the distinction between true predation and scavenging as well as identifying specific predators. A further complicating factor is that often only a small sample of events is indicated when determining the actual cause of death (Cresswell and Whitfield 1994). Also, in this study, after a careful and restrictive examination, there were relatively few cases where the actual cause of death could be clearly classified (26%). Thus, the results represent only the minimum percentage of the respective loss category. It can be assumed that some animals in the unknown groups of ‘dead’ and ‘censored’ can be added to the groups ‘predation’ or ‘other causes of loss’. To close these gaps of knowledge, there is a need for well-structured surveillance experiments in arable and grassland areas with different predator communities that can assess the impact of scavenging in telemetric studies.

Predation among the daytime user type ‘concealed’ probably only occurs at night by predatory mammals and owls, as leverets tend to hide themselves during the day. On the other hand, the influence of weasels (*Mustela* spp.) during the daytime cannot be excluded and is just as likely.

### Causes of mortality—agriculture

The found low impact of agricultural processing on the mortality rate can be explained by the fact that a relatively high percentage of winter cereals was cultivated in the study area. As a rule, soil tillage for summer crops is limited in time and space, and usually takes place during the day, i.e. at a time when at least 65% of all leverets are in the non-cultivated edge habitats (Voigt and Siebert 2019). This leads to the assumption that the probability that tillage will occur when a non-mobile young animal is staying in the field to be cultivated is

comparatively low. This assumption is supported by the fact that firstly, a maximum of 8% of the causes of death can be attributed to agricultural cultivation in spring (season I) and, secondly, most of the leverets staying in these fields are predated within a short time after birth before they fall victim to agriculture practices. Furthermore, leverets tend to leave these fields to seek shelter in the borders of field tracks, ditches or other natural vegetation (Voigt and Siebert 2019).

In season II, hares were searched and radio-tagged only after harvesting cereals. Therefore, no statements can be made concerning the losses caused by harvesting. The first tillage of the harvested cereal fields takes place at the latest 10 days after harvest. Thus, it can be assumed that in this short interim period, comparatively few leverets are born in the stubble fields and die as a result of cultivation. These fields are not cultivated again until the sowing of winter cereals or the sowing of catch crops in October and mid-September. Between October and January, the reproduction phase of the European hare is largely interrupted and the influence of agricultural cultivation on the risk of death for leverets is consequently also reduced.

Less than 3% of the investigated area was used for the production of hay or energy from biogas, and therefore, no higher losses from mowing were recorded. In contrast, substantial losses can be expected in areas dominated by grass (Barnes et al. 1983; McLaren et al. 1997) which are grown for silage or hay with repeated cutting from May onwards. Naturally, the mortality rate due to agricultural processing is strongly dependent on the crops cultivated, crop rotation and the associated practices (Pépin 1989). For example, the average loss from the use of machinery can amount to up to 15.5% of annual growth (Kaluzinski and Pielowski 1976), but can also reach over 45% in the cultivation of alfalfa (Milanova and Dimov 1990).

### Detection, capture and handling

Although the applied thermographic method is quite time-consuming and expensive, it is nevertheless a suitable approach for systematic detection of leverets in wild populations a few days after birth, this being confirmed by the age range at first detection. It is obvious that the denser the vegetation, the fewer animals can be detected. Thus, the usability and significance of this method or results are limited to periods of low vegetation, and it remains unclear whether the ascertained survival pattern changes with the closing of vegetation and complete covering of the fields. This gap of knowledge could be closed by field experiments, such as those carried out on pregnant snowshoe hares in temporary pens (O’Donoghue 1994; Rongstad and Tester 1971). Furthermore, future research should combine thermal imaging technology with drone technology to extend the entire coverage period by the search in denser vegetation. In addition, this combination



would offer the opportunity of verifying the study area more randomly, which would ultimately improve the prerequisites for statistical methods.

A human-related predation that may affect species behaviour and distribution in various ways is described for hunting (Frid and Dill 2002), and one can assume the same for any kind of handled animals. Ultimately, this study fails to elucidate the extent to which capturing, tagging and relocation had an influence on the choice of the daytime resting places, the overall moved distance and the survival of leverets. In fact, a higher mortality rate could be calculated in the first 5 days of life than in older animals (Fig. 1a). These losses were mainly caused by animals that used the open field during the day (Fig. 1d), whereas animals of the ‘concealed type’ showed a comparatively higher survival rate in the corresponding life stage. In principle, handling effects cannot be excluded in the present study, but they are considered to be moderate due to the minimal human contact and the associated duration of stress, as well as capture after lactation in most cases. However, in a study on the snowshoe hare, the impact from handling was not considered significant (O’Donoghue 1994).

## Conclusions

For the first time, the present study has provided direct evidence that high losses of leverets occur from birth to weaning, which is also related to the availability and use of daytime hiding places (Voigt and Siebert 2019). The findings lead to the conclusion that leveret mortality in the first weeks of life is of outstanding importance for recruitment and possibly also for population dynamics. The improvement in the survival rate of leverets could be achieved by an increase in habitat quality (Hummel et al. 2017; Zellweger-Fischer et al. 2011) as well as food resources (Schai-Braun et al. 2015) or set-asides (Schai-Braun et al. 2020).

The instruments of habitat improvements (ecological focus areas, EFA: European Commission 2013, 2014) are already available in the current Common Agricultural Policy (CAP) or other national agricultural funding schemes. Nonetheless, for various administrative and impractical reasons, these opportunities do not seem to be sufficiently exploited in relation to actual benefits for hares. The habitat improvement measures should be designed to be unattractive to predators (Hummel et al. 2017; Meichtry-Stier et al. 2014), in line with the preference of leverets’ habitat usage (Voigt and Siebert 2019) and the nursing behaviour of the European hare (Broekhuizen and Maaskamp 1980). There is a clear need for studies to evaluate existing ecological knowledge of the early life of European hares in more practical approaches, which are adapted to regional differences in agricultural production methods.

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**Data availability** All data supporting the conclusions of this article are included within the article and its additional files.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All procedures performed in this study were conducted under a permit held by the Institute for Consumer Protection and Food Safety of Lower Saxony (LAVES), Germany (Ethics Committee Dept. 3 Animal Health, permit number: 33.12-42502-04-16/2083). All experiments were performed in accordance with institutional and national laws and ethical principles.

**Consent for publication** Not applicable.

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