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Bad hare day: very low survival rate in brown hare leverets

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Increased postnatal leveret mortality has been identified as the proximate factor explaining the decline of European brown hare *Lepus europaeus* populations in Europe. However, direct measurements of survival rates are non-existent as the leveret's cryptic behaviour makes them very difficult to study. Previously, leveret survival rates calculated using hunting bag statistics or capture–mark–recapture methods have been estimated to lie between 5% and 56% for the period between the start (January) and the end (October) of the breeding season. Such indirect approaches are known to yield inaccurate results compared to direct survival measurements. Hence, we applied novel detection methods and radio-tagged 63 wild-born leverets (aged between 1 and 22 days at capture) in two different populations in the Swiss lowlands. We located the tagged individuals daily to monitor individual fates and to directly calculate survival probabilities. We found that leveret survival is negatively influenced by precipitation. However, when leverets use edge habitats, survival is positively influenced. Daily survival rate and survival probability for the first month of life were found to be 0.94 and 0.18 respectively. Such low survival is alarming and to prevent further declines in populations of brown hares, it will be essential to mitigate against these excessive losses. Therefore, we suggest measures aimed at increasing the area of suitable habitat for leverets, where they can grow up safely (e.g. shelter from predators and bad weather).

Keywords: conservation, Cox proportional hazards model, daily survival rates, Kaplan–Meier, radio telemetry, thermography, weather effect, wildlife detection dog

Since the 1960s numbers of brown hares in many European countries have drastically declined (Smith et al. 2005). This decline was particularly severe in Switzerland (Pfister et al. 2002, Olesen and Asferg 2006), resulting in today's population density of only 3.4 hares per 100 ha of suitable hare habitat (Hoffmann 2016). As under ideal conditions hare densities can reach up to 340 hares per 100 ha (Abildgård et al. 1972) and typical densities are between 15 and 60 hares per 100 ha (Smith et al. 2005) this is an alarmingly low level. The reasons for the European-wide decline of brown hare numbers are diverse, of an interacting nature and still not fully understood (Tapper and Parsons 1984, Hutchins and Harris 1996, Marboutin et al. 2003, Smith et al. 2005, Olesen and Asferg 2006). The effect of increased predation pressure due to changes in habitat characteristics (shortage of shelter, altered predator–prey interactions) has likely been magnified by unfavourable climate and an increase in predator numbers (Slamečka et al. 1997, Schneider 2001, Smith et al. 2004, Olesen and Asferg 2006). Increased leveret mortality – i.e. low recruitment – has been identified as one of the principal determinants for the decline in European brown hare populations observed all over Europe (Marboutin and Peroux 1995, Haerer et al. 2001, Bensinger 2002, Olesen and Asferg 2006). Neonatal survival can be a key factor affecting population dynamics of certain species (Pepin 1989, Gaillard et al. 1993, Marboutin and Peroux 1995, Hackländer et al. 2001, Marboutin et al. 2003).

The precocial leverets are fully exposed to their environment since they are not provided with shelter by a nest or den. Thus, climatic factors can negatively influence leveret survival when suitable shelter in terms of vegetation cover is missing (Meriggi and Alieri 1989, Hackländer et al. 2002). Even though they are equipped with a cryptic fur coat and are difficult to locate using scent (Conover 2007), once detected, leverets easily fall prey to various predators including foxes, mustelids, birds of prey as well as domestic cats and dogs (McLaren et al. 1997, Marboutin and Hansen 1998, Olesen and Asferg 2006). Only after three to four weeks are they able to escape approaching danger. Before that, leverets freeze and crouch to remain inconspicuous. Furthermore, the mechanical processing of agricultural fields can have up to 100% lethal consequences (Grendelmeier 2011). Consequently, the first weeks in a brown hare's life are most critical regarding their survival (Marboutin and Peroux 1995).

Previously, data on leveret survival has most commonly been obtained using hunting bag statistics, revealing age and sex distribution of the population under investigation (for

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a list of publications investigating juvenile survival rates see Table 1). When a pregnant female is killed during hunting, one can count the embryos of the current litter to extrapolate fertility. Another method involves counting placental scars in the females' reproductive tract. These scars represent the number of leverets the female gave birth to during the current reproductive season. Either way, assuming unbiased shooting of juveniles and adults, comparison of the number of offspring produced and the proportion of juveniles in the hunting bag, reveal indirect survival data. Using this approach, leveret survival rates for the period between the start (January) and the end (October) of the breeding season were estimated to lie between 5% and 50% (Table 1, Frylestam 1980, Hansen 1992, Marboutin et al. 2003). Another approach are capture–mark–recapture methods, where the percentage of recaptured (marked) animals reveal indirect survival rates given that capture effort is constant or statistically corrected for. Such methods reported survival rates between 24% and 56% (Table 1, Abildgård et al. 1972, Marboutin and Peroux 1995). Yet, direct measurements of survival would reveal more accurate data since less assumptions have to be made with respect to non-selective hunting practices, constant capture effort or unbiased detection probabilities. In order to obtain direct survival data, we need to follow the fate of individual leverets. As leverets behave very cryptically, methods for systematic detection have not been available so far. Hence, we are still lacking direct survival data for the youngest age group in brown hares.

This study aims at quantifying leveret survival rate by monitoring the fate of wild radio tagged leverets in two low-density brown hare populations in the Swiss lowlands. We applied novel detection methods: handheld and airborne thermal imaging and a wildlife detection dog. We collected data daily to obtain accurate measurements of survival. We investigated the effect of weather (precipitation and minimum temperature), and the use of a common crop (sugar beet, *Beta vulgaris* subsp. *vulgaris*) on leveret survival. In addition, we were interested if the use of edge habitat had a positive or negative effect on their survival.

Material and methods

The study was carried out between 2013 and 2015 in two different brown hare populations in Switzerland – 'Reinach' (47°28′47.760″N, 7°35′03.879″E) and 'Selzach' (47°11′48.615″N, 7°27′59.658″E), 33 km apart. The climate at the study sites can be characterized as moderate continental with a mean annual temperature of 10°C, a mean annual relative humidity of 77% and a mean annual precipitation of 900 mm (Meteo Schweiz). 'Reinach' was located at an elevation of 310 m a.s.l. and was 1.01 km^2 in size whereas 'Selzach' was located at an elevation of 430 m a.s.l. and was 3.1 km^2 in size. Population densities were medium to high (3–11 hares per 100 ha, Zellweger-Fischer 2015) compared to the rest of Switzerland (3.4 hares per 100 ha) but low compared to populations outside Switzerland (15–60 hares per 100 ha, Smith et al. 2005). The mean field size was 1.1 ha for both study sites and there had been no hare hunting for the previous 30 years. Both study sites included a mixture of agricultural landscape interspersed with some ecological compensation areas (hedges, fallow land, extensively used grassland, etc.). The fields were mainly cultivated with wheat, grassland, sugar beet and corn with little differences between the two study sites.

We did not collect data on the abundance of specific predators, but the following potential leveret predators were present in the study areas: mammals: domestic cat *Felis silvestris catus*, domestic dog *Canis lupus familiaris*, red fox *Vulpes vulpes*, European polecat *Mustela putorius*, stone marten *Martes foina*, pine marten *Martes martes*, European badger *Meles meles*, wild boar *Sus scrofa*; birds: grey heron *Ardea cinerea*, white stork *Ciconia ciconia*, red kite *Milvus milvus*, black kite *Milvus migrans*, common buzzard *Buteo buteo*, common kestrel *Falco tinnunculus*, tawny owl *Strix aluco*, Eurasian eagle owl *Bubo bubo*, long-eared owl *Asio otus*, barn owl *Tyto alba*, rook *Corvus frugilegus*, carrion crow *Corvus corone* and common raven *Corvus corax*.

Leverets were located using thermal imaging technology and a specifically trained wildlife detection dog. We used a handheld device (FLIR Scout TS-32r Pro, FLIR systems, Inc., USA) operated from the back of a slow driving pick-up truck and searched for leverets until vegetation density did not allow target detection anymore. For areas with progressed vegetation height and density we used an aerial system equipped with a small thermal imaging sensor (FLIR Photon 320 or FLIR Quark 640, FLIR systems). Where vegetation was closed, and thermal imaging was not suitable we used a wildlife detection dog trained on the scent of leverets. The dog indicated their presence by lying flat on the ground at a distance of about 30 cm. We searched for leverets during 26 months of the years 2013 (mid-February–start October), 2014 (start February–end October) and 2015

Table 1. Juvenile survival rates over the whole breeding season (January–October) as reported in the literature. Note that the survival estimation for this study represents survival for the first month of life instead of the whole breeding season, and is thus not directly comparable to the estimates listed in this table.

Reference	Estimated leveret survival	Method for survival estimation	Country
Abildgård et al. 1972	56% (♂)/44% (♀)	Capture–mark–recapture models No mammalian predators at the study site	Denmark
Marboutin and Peroux 1995	47% (♂)/24% (♀)	Capture–mark–recapture models	France
Pépin 1989	25–50%	Embryo counts combined with hunting bag statistics	France
Hansen 1992	19–31%	Placental scar counts combined with hunting bag statistics	Denmark
Pielowski 1981	23%	Captures	Poland
Marboutin et al. 2003	14–29%	Placental scar counts combined with hunting bag statistics	France
Frylestam 1980	16–27%	Placental scar counts combined with hunting bag statistics	Sweden
Wasilewski 1991	6.2–14.4%	Age distribution in hunting bag	Poland
Möller 1977	5–33%	Embryo counts combined with hunting bag statistics	Germany

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(mid-January–end October). For more details on detection methods see Karp (2020). Leverets younger than two weeks (roughly assessed from a distance) were hand-captured whereas older leverets were caught using a landing net. We only used landing nets with a soft front to prevent injuries to the leveret. In total, 63 individual leverets from 40 different litters were caught and radio tagged (PIP2, Biotrack). Litters were defined as individuals joining the same doe for suckling. Body measurements (length and width of the skull, ear and foot length and body weight) were taken as in Bray et al. (2002) and combined with a general visual estimation to determine the age of the leverets. Using the results from the body measurements, the general visual estimation and pictures, all 65 leverets were reassessed at the end of the study to increase accuracy of the final age determination. Leverets were between 1 and 22 days old (mean ± SD = 8 ± 6.2 days) upon first capture. After cutting some hairs, a skin adhesive commonly used in human surgery (EPIGLUE, Meyer–Haake) was used to attach radio tags (<3 g), which were glued onto the skin between the shoulder blades also using the surrounding hairs for better tag attachment. We were unable to determine the leveret's sex because at the age of captures morphological features did not yet allow explicit discrimination. Six individuals were caught a second time after they had lost their first radio tag. Individuals were recognized either because of having the old (but unfunctional) tag still on or because we could see signs from the fallen-off tag (haircut and/or glue residuals). All methods were approved and the study permit for both study sites was issued by the Economic and Health Affairs Dept of the Canton of Basel-Landschaft, Switzerland (permit nr BL443).

Individuals were located using a Lintec flexible 3-element Yagi antenna and a SIKA radio tracking receiver (Biotrack). Time span between consecutive relocations never exceeded 55 h. Ninety-five per cent of the relocations took place within 36 h, and the average time between relocations was 24.1 ± 6.7 h (mean ± SD). Leverets were located at different day- and night times and were monitored until they lost their tag, the signal of the tag was lost, or until they were found dead. Differentiation between lost signal and lost tag was only possible in those cases where we found the tag (n = 58). Whole carcasses were recovered and frozen to be dissected at a later stage. Cause of death of the recovered carcasses was assessed by staff members of the Centre for Fish and Wildlife Health, University of Bern (FIWI) according to standard procedures.

Radio transmitters were equipped with a mortality sensor continuously adjusting pulse rate according to ambient temperature. Hence, whenever we did not see the animal, we always knew whether it was alive or dead due to the transmitter's pulse rate. In 27% of the relocations we did not see the animal but we always went close enough in order to determine the land-use type the leveret was in and whether it was located at the edge of a field (less than five meters distance to the field-edge). Data on precipitation and temperature were obtained from two different weather stations from the Federal Office of Meteorology and Climatology: 'Grenchen' (428 m a.s.l.) and 'Binningen' (315 m a.s.l.). Distance to the according study site was 4.4 km and 6.9 km respectively. In addition to the weather data used in the survival analyses we opportunistically also took our own local measurements of temperature and rain.

Statistical analyses

We used a Cox proportional hazards model to quantify the effect of weather and habitat characteristics at bedding sites on survival of leverets in their first months of life at the two study sites. As time origin we chose age (in days) to allow for a sufficient number of animals at risk at any one time to estimate daily survival. However, this precluded the estimation of an implicit age effect in the model. As weather variables we tested how precipitation and minimum temperature affected leveret early survival whereas for habitat characteristics we included an edge effect (binary variable defining whether the bedding site was close, i.e. less than 5 m, or further away from field edges) and sugar beet (binary variable defining if bedding site was situated in a sugar beet field or not). We did not have enough data to quantify the effect of other crop or habitat types. Since most of leverets were found in sugar beet fields, we chose to specifically investigate this crop type. As the location of death could not be reliably determined in many cases and in the case of precipitation and minimum temperature we assumed that the effect of adverse weather conditions on survival would not be immediate, we calculated for all model covariates a mean value over the past three days preceding relocation. In the case of the binary variables edge and sugar beet we calculated the percentage of times bedding sites were situated close to the edge or within sugar beet fields over the past three days respectively. Finally, we included a random term for year and litter in the survival model to account for within year and within litter correlation structure in the data. The Cox proportional hazard model was estimated using the coxme function from the coxme package in R (Therneau 2015). We tested the proportional hazard assumption using scaled Schoenfield residuals for a model without random terms (cox.zph function, Therneau 2015). In the end we estimated daily survival from the model survival curve and compared this estimate to daily survival estimated from a Kaplan–Meier survival curve (i.e. without accounting for model predictors) in order to compare survival estimates to other lagomorphs such as the snowshoe hare *Lepus americanus* or the Tehuantepec jackrabbit *Lepus flavigularis* (providing KM survival data).

Results

The radio tagged leverets (63) were monitored between 2 and 34 days (mean ± SD = 8 ± 6) post tagging. This resulted in 505 days of observation. Daily survival for the first month (28 days) for the Cox proportional hazard model was $S_{daily\ cox} = 0.94$ and $S_{daily\ KM} = 0.93$ for the Kaplan–Meier estimate (Fig. 1). Furthermore, we found a relevant litter and year effect (Table 2). The Cox proportional hazard model showed a positive effect of field edges on early leveret survival (hazard ratio = 0.57, $HR_{95low} = 0.32$, $HR_{95high} = 1.00$; Table 2, Fig. 2) as well as a negative effect of precipitation ($HR = 1.48$, $HR_{95low} = 1.01$, $HR_{95high} = 2.15$; Table 2, Fig. 3).

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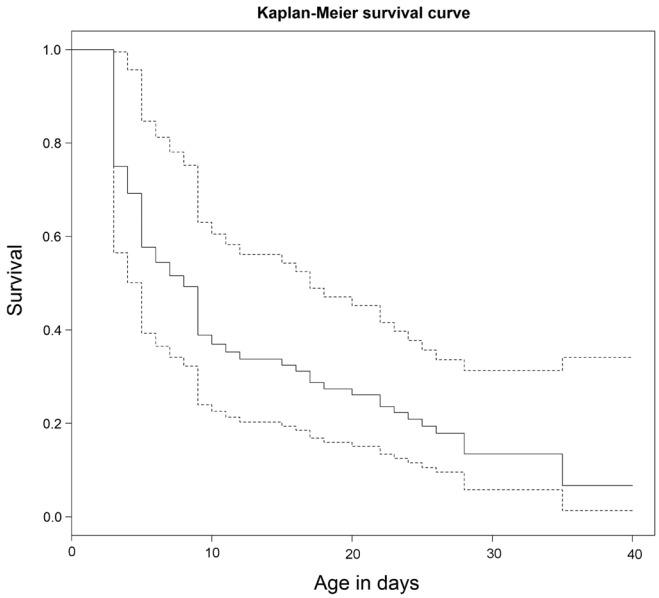


Figure 1. Kaplan–Meier survival curve (–) with 95% confidence bounds (– –). The oldest leveret in the study lost its tag and was right censored at the age of 39 days.

For visual representation of the effect of relevant model predictors we show marginalized adjusted survival curves (i.e. averaged over all random effects, Fig. 2, 3). There was no statistical evidence for an effect of sugar beet (HR = 0.66, HR_{95low} = 0.38, HR_{95high} = 1.13; Table 2), minimum temperature (HR = 1.13, HR_{95low} = 0.71, HR_{95high} = 1.79; Table 2) or study site (HR = 1.78, HR_{95low} = 0.67, HR_{95high} = 4.72; Table 2). Inspection of the Schoenfeld residuals of the marginal Cox model indicated no violation of the proportional hazard assumption. Details on fate determination and possible cause of death can be found in the Supplementary material Appendix 1.

Our own opportunistic local weather measurements showed that leverets can survive extreme weather conditions from the day of birth on. We measured temperatures as low as −2.3°C and even simultaneous exposure to rain and temperatures below 1.5°C on a ploughed acre (no shelter from the rain) did not result in immediate death of the leveret. As we never observed the event of death, we do not know whether the leverets were eventually predated being alive or already dead (hypothermia or disease).

Discussion

Even though increased leveret mortality is recognized as an important factor explaining negative population trends in brown hares (Marboutin and Peroux 1995, Haerer et al. 2001, Bensinger 2002, Olesen and Asferg 2006), direct measurements of leveret survival rates were non-existent due to methodological limitations in the past. Here we report for the first time directly measured survival estimates of leverets in the wild by monitoring the fate of radio tagged individuals. We found very low survival of leverets from birth to four weeks of age (28 days): nearly all mortality (82%) occurred during this first and most vulnerable period. We also found that the fate of siblings was not independent. In the beginning, leverets are least mobile and thus most vulnerable to predators or agricultural machines. Furthermore, the risk of death from exposure to wet and or cold weather is higher at birth due to the increased surface to volume ratio of small bodies leading to increased heat loss and energy expenditure (Jones et al. 2005, Nowak and Poindron 2006). Consequently, as leverets grow larger, they become less vulnerable

Table 2. Results of the Cox proportional hazard model.

Fixed effects	β	Hazard ratio	model SE	Lower 95% CI	Upper 95% CI	p-value
Study site	0.58	1.78	0.50	0.67	4.72	0.25
Edge	–0.57	0.57	0.29	0.32	1.00	0.05
Sugar beet	–0.42	0.66	0.28	0.38	1.13	0.13
Minimum temperature	0.12	1.13	0.23	0.71	1.79	0.61
Precipitation	0.39	1.48	0.19	1.01	2.15	0.04
Random effects	SD					
Year	0.51					
Litter	0.38					
	LPL	df				
Mixed model	19.17	7				
Model w/o random effects	17.63	5				

SE = standard error; CI = confidence interval; SD = standard deviation; LPL = log partial likelihood; df = degrees of freedom.

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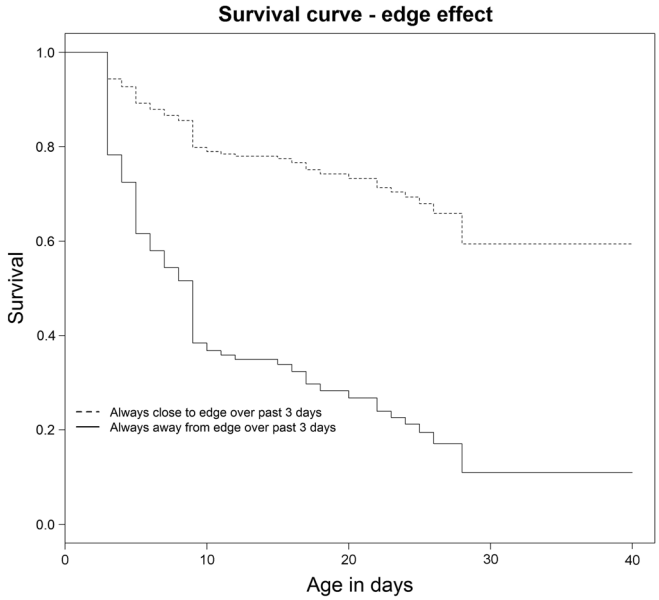


Figure 2. Survival curve displaying the effect for leverets being situated at the edge or in the center of an agricultural field while accounting for other variables in the model.

to bad weather conditions (Jones et al. 2005). In line with this, we found a negative effect of rainfall on leveret survival. However, there was no evidence for a negative effect of temperature (Table 2) which is congruent with other studies that found wetness to be more fatal than low temperatures (Hackländer et al. 2002, Van Wieren et al. 2006, Rödel and Dekker 2012). Soaked fur does not insulate properly and in contrast to dry fur which can isolate leverets enough to survive temperatures down to −8°C, wet leverets will eventually freeze even at temperatures well above frost due to the increased energy demands for thermoregulation (Hackländer et al 2002). Furthermore, the spread of endoparasites such as coccidia or nematodes is favoured by wet weather conditions (Zörner 1996, Stromberg 1997). Nevertheless, our local weather measurements showed that leverets can survive very harsh conditions of rain and low temperatures (subzero). To our knowledge this is the first time wild leverets were directly observed to be exposed to such extreme climatic conditions. This is particularly remarkable as very young leverets (<7 days) spend more energy than they can take up via milk when temperatures fall below 8°C (Hackländer et al. 2002).

Among the habitat related factors, we found a positive effect of edge habitat and sugar beet crop but only the former being significant. Studies on habitat edge effects provide contrasting results. Some studies find elevated predation rates along habitat edges others do not (Møller 1989, Andrén 1995, Phillips et al. 2003, Fernex et al. 2011). Edge effects

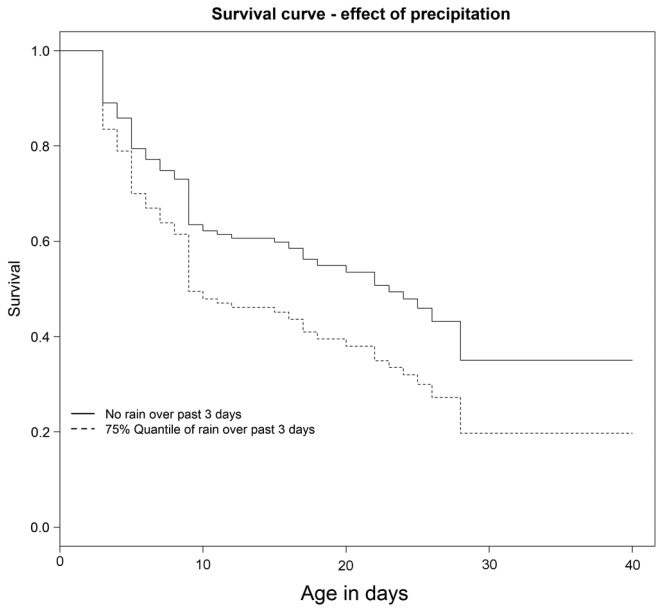


Figure 3. Survival curve displaying the effect of precipitation on the survival of leverets while accounting for other variables in the model.

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Table 3. Information on juvenile survival for some lagomorph species other than the brown hare.

Reference	Species survival	Estimated leveret	Period
O'Donoghue 1994	Snowshoe hare *Lepus americanus*	35%	birth to 30 days
O'Donoghue and Boutin 1995	Snowshoe hare *Lepus americanus*	35%	birth to 14 days
Krebs et al. 2002	Snowshoe hare *Lepus americanus*	38%	birth to 28 days
Rioja et al. 2011	Tehuantepec jackrabbit *Lepus flavigularis*	51%	birth to 19 days
Price et al. 2010	Pygmy rabbit *Brachylagus idahoensis*	43%	Starting at 14 days (emergence) to 126 days
This study	European brown hare *Lepus europaeus*	32%	birth to 14 days
		18%	birth to 28 days

likely depend on habitat composition and arrangement as well as predator species and their search pattern (Andrén 1995, Phillips et al. 2003, Cervinka et al. 2013). The negative edge effect reported in some studies has been explained by increased detection probability by opportunistic predators patrolling along field edges (Salek et al. 2009, Fernex et al. 2011, Beerli 2013, Hummel et al. 2017). However, for olfactory predators, the wind characteristics dominating at habitat edges may affect their detection efficiency (Conover 2007). This might be due to turbulences and updrafts – air flow directed upwards lifting the scent particles out of the area where they can be perceived by the predator – occurring at the interface between a change in vegetation height at field edges when the air is moving from the shorter to the taller vegetation (Conover 2007). This phenomenon may explain why we found higher survival for leverets located at the edge of a field. Alternatively, the positive edge effect we found in our study might be explained by the proximity of edges to other fields providing complementary needs to the leverets (shelter, feeding, suckling, etc.). Generally, edge habitat is associated with higher biodiversity and thus considered to be of high quality to both predators and prey (Hansson 1983, Andrén 1995). In this respect, non-crop vegetation such as wild herbs along field edges may provide leverets with suitable food. Finally, we observed some leverets to change between fields at sunset in order to be suckled and then return after suckling. Such 'commuting' leverets were mostly found close to the edge of fields with medium to high vegetation density during the day (hiding) and were being nursed in low vegetation fields (Karp 2019).

Our estimation of brown hare leveret survival for the first days and weeks after birth cannot be compared to data on brown hares from the literature as those represent survival over the whole breeding season from January to October using indirect data. Comparing to other lagomorph species, survival of brown hare leverets seems to be low (Table 3). For snowshoe hares – which have a similar lifestyle compared to brown hares – a similar survival rate has been found by O'Donoghue and Boutin (1995) in contrast to a much higher survival rate found by Krebs et al. (2002) and O'Donoghue (1994, Table 3). According to these three studies on snowshoe hares, it seems that survival does not change very much after two weeks (day 14–28) whereas in brown hares there was a more or less constant increase of mortality from day 14 to day 28 (Table 3). For the endangered Tehuantepec jackrabbit a relatively high survival rate of 51% was calculated for the first three weeks of life (Rioja et al. 2011). Survival rate of young pigmy rabbits *Brachylagus idahoensis* – with a different lifestyle (altricial) – was found to lie between the two other species at 43% for the period between emergence (14 days) and 18 weeks (Price et al. 2010). Being a farmland-specialist, the brown hare might be confronted with a multitude of different factors having a negative effect on its survival compared to species living in more pristine habitat.

Some methodological drawbacks could have led to left-truncation of our data which may have affected our survival estimation (Cain et al. 2011, Gilbert et al. 2014). This includes that we may have missed some leverets in very risky habitats (i.e. unsheltered habitat such as e.g. acres where detection probability by predators is increased and thermal protection is decreased) because they died before we were able to detect them. Additionally, detection probability increased with increasing age and size of the leveret respectively (Karp 2020). This means that very young leverets (in the first week of life) were potentially underrepresented in our sample. Similarly, right-censoring of our data due to unknown mortality as well as not knowing the exact location of death might have further affected our survival estimation and statistical model respectively. Thus, further studies are needed to gain a more comprehensive understanding of early survival in leverets and how it might vary in different populations and habitats types respectively.

This is the first study to report direct measurement of leveret survival in the wild and it reveals a strikingly high mortality rate during the first month of life (82%). Consequently, where populations of brown hares are declining, the first step for conservation actions should be to reduce leveret mortality. In order to achieve this goal, we need to better understand the importance of different causes of mortality. Only then are we able to formulate specific and tailored agri-environmental measures aimed at promoting habitats where leveret survival is increased during the most sensitive first weeks. In this respect, structures with minimal agricultural processing that provide shelter from weather and predation seem to be very important to improve leveret survival. Nonetheless, what exactly constitutes an ideal habitat for leverets still remains largely unknown. Understanding the relative importance of different land-use types in terms of leveret survival and the spatial organization of habitat structures regarding prey accessibility hence are critical aspects for future studies concerning the conservation of brown hares.

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Conflicts of interest – None.
Permits – All methods were approved and the study-permit for both study sites was issued by the Economic and Health Affairs Department of the Canton of Basel-Landschaft, Switzerland (permit nr. BL443).

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Supplementary material (available online as Appendix wlb-00645 at <www.wildlifebiology/appendix/wlb.00645>). Appendix 1.

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