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ORIGINAL ARTICLE

Should rehabilitated hedgehogs be released in winter? A comparison of survival, nest use and weight change in wild and rescued animals

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Abstract

The rehabilitation of sick or injured wildlife and their subsequent release back into the wild is considered important, not only for the welfare of the individual animal but also for the conservation and management of endangered and threatened wildlife. The European hedgehog *Erinaceus europaeus* has declined by 25% in Britain over the last decade and is the most common mammal admitted to wildlife rehabilitation centres in Britain, with a large proportion of individuals admitted to gain body weight overwinter prior to release in the spring. Consequently, many thousands of hedgehogs are housed overwinter which incurs significant costs for rehabilitation centres, and has potentially animal welfare issues, such as, stress in captivity, reintroduction stress, increased mortality risk and impaired or altered behaviour. To determine if releasing rehabilitated hedgehogs during autumn and winter had an effect on their survival, body weight or nesting behaviour, we compared these factors between 34 rehabilitated hedgehogs with 23 wild hedgehogs across five sites in England over four different winters. Overwinter survival was high for both wild and rehabilitated hedgehogs, with a significant decrease in survival across both groups when hedgehogs became active post hibernation in spring. We found no differences in the survival rates up to 150 days post release, in weight change, or nest use between wild- and winter-released rehabilitated hedgehogs. Our results suggest that under the correct conditions, rehabilitated hedgehogs can be released successfully during winter, therefore avoiding or reducing time in captivity.

Keywords Rehabilitation release · Overwinter survival · Hibernation · Radio-telemetry · Hedgehog · Reintroduction stress

Introduction

The rehabilitation of sick or injured wildlife and their subsequent release back into the wild is considered an important tool in the conservation and management of endangered and threatened wildlife (Molony et al. 2006; Guy et al. 2013; Mullineaux 2014). However, welfare of the individual should be of primary concern throughout the rehabilitation process and the goal of rehabilitation should be to ensure that individuals are released in a physical and physiological condition that enables them to survive equally as well as wild individuals (Mullineaux 2014). Despite this, the reported success of rehabilitation varies considerably (Guy et al. 2013; Mullineaux 2014) with few studies conducted into the survival of released, rehabilitated animals (Molony et al. 2007). Given that, rehabilitated individuals are often considered to have a lower chance of survival compared to wild individuals as a result of reintroduction stress, impaired foraging ability and increased mortality risk (Molony et al. 2006) and altered ranging behaviour (Tolhurst et al. 2016), the lack of studies in this field needs addressing to provide evidence to inform rehabilitation practice.

In Britain, at least 70,000 casualties are admitted to wildlife rescue centres annually (Grogan and Kelly 2013), with the European hedgehog *Erinaceus europaeus* being the most common mammal species admitted (Molony et al. 2006; Mullineaux 2014). An extended period of monitoring post-

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release is considered an essential part of the rehabilitation processes; however, this is not universally adopted (Guy et al. 2013). Previous studies have monitored the survival and movements of rehabilitated and translocated hedgehogs (Morris 1997, 1998; Molony et al. 2006), but these have not addressed the survival and movement patterns of rehabilitated individuals over the winter hibernation period which is considered a critical phase in the annual cycle of the hedgehog and has previously been identified as a period of high mortality (Kristiansson 1990).

For small heterothermic mammals such as hedgehogs, hibernation overwinter is essential to avoid seasonal stresses of reduced resource availability and elevated endothermic demands (Geiser 1998). Hibernating mammals will reduce their energy requirements, activity levels, and physiological processes in response to low environmental temperatures and reduced food availability (Buck and Barnes 1999; Sendor and Simon 2003; Németh et al. 2009; Cooper and Withers 2014). Critical to overwinter survival is the ability to attain a minimum body mass prior to the onset of hibernation ensuring the individual has enough fat reserves to maintain warmth and metabolic processing, and failure to achieve a critical mass prior to hibernation may increase the risk of mortality (Kristiansson 1990; Csorba 2003; Jensen 2004; Bunnell 2009; Cooper and Withers 2014). Consequently, rapid mass gain in the period leading up to hibernation is common (Buck and Barnes 1999; Haigh et al. 2012). Several authors have attempted to identify a minimum weight by which hedgehogs will have a greater chance of survival over winter (e.g. Morris 1984; Jensen 2004); however, this is likely to be context-dependent and vary with climate and latitude (Haigh et al. 2012) and be higher in Northern Europe where the winters are typically harsher and longer in duration (Kristiansson 1990).

Current guidance from various animal welfare and conservation organisations on the release weight of rehabilitated hedgehogs states that individuals should be at least 600 g before release in late autumn/early winter (Hedgehog hibernation weight – a collaborative view n.d.). Despite this, many rehabilitators habitually keep hedgehogs in care over winter (even if this weight is achieved), under the assumption that they will have low survival if released (e.g. Sainsbury et al. 1996). This is not only costly to the wildlife rehabilitator and limits the housing space available for new individuals arriving at centres but also prolongs the duration that individuals spend in care. Longer captivity times can result in animal habituation and loss of behavioural skills that are relied upon for successful survival in the wild (Miller 2000).

The aim of the study was to compare overwinter survival, body weight changes and nesting behaviour between wild and rehabilitated hedgehogs. We hypothesise that under the correct circumstances there would be no difference in overwinter behaviour and survival rates of hedgehogs released during winter compared to their counterparts. Results of this study will inform hedgehog rehabilitation practice and further highlight the need for scientific studies to provide evidence in support of rehabilitation practice and release protocols.

Methods

Ethics statement

All work was conducted under a Natural England Licence (20121788) and following approval by the ethical review committees of the School of Animal, Rural and Environmental Sciences, Nottingham Trent University (ARE10), and the School of Pharmacy and Biomolecular Sciences, University of Brighton.

Study sites and animals

Rehabilitated hedgehogs were from the Royal Society for the Prevention of Cruelty to Animals (RSPCA) wildlife rehabilitation centres. Rehabilitated hedgehogs' admission weights ranged from 0 g (born in captivity) to 530 g. Hedgehogs that weighed under 150 g were bottle fed and weaned at between 150 and 175 g ($n = 4$), and all others ate independently. No distinction was made between hand-reared and weaned hedgehogs in the analysis. All individuals had passed a veterinary health check prior to release. Where possible, hedgehogs were released back to sites where they were found. All other hedgehogs were released at sites deemed suitable for hedgehogs; selection criteria included available suitable habitat located away from main roads (to reduce the chances of road mortality) and for the site to have minimal or no local badger (*Meles meles*) activity or reported badger setts nearby, as previous hedgehog releases in such areas resulted in high rates of predation (Doncaster 1992; Morris and Warwick 1994).

The study took place at five study areas across Southern and Central England over four winters. The rehabilitation release sites, UK grid references and winters were as follows: Pett (TQ8741 1402) (2010-11); Seddlescombe (TQ7832 1817) (2011-12); a local nature reserve in Brighton (TQ 3262 0723) (2011–2013) and a suburban area of Brighton (TQ3130 0415) (2013–2014). Wild hedgehogs were also studied in Brighton (TQ2627 0694) (2013–2014) and at Nottingham Trent University's Brackenhurst Campus near Southwell, (SK 6946 5243) (2012–13 and 2013–14). In Brighton, wild hedgehogs were located in residential gardens following reports from a local hedgehog community group. At Brackenhurst, wild hedgehogs were located during nocturnal searches using one million candle power spotlights. The majority of wild hedgehogs were caught in October prior to winter hibernation, while the rehabilitated individuals were

released throughout autumn and winter. Release of rehabilitated hedgehogs was timed so that mean night temperature was above 0 °C for at least 2 days before release and forecast for minimum temperature to be above 0 °C for 5 days post release. Rehabilitated hedgehogs were 'soft'-released at dusk, by placing a nest-box which contained bedding and food, at the release site, from which the hedgehog could leave and re-access. The boxes were checked daily after release to check the hedgehog had moved, and if no hedgehog was present, the box was removed. Hedgehog ages were classed as either 'adults' (known to have survived at least one winter season) or 'young of year' (yet to experience a winter season), and gender was recorded.

Radio tracking

All hedgehogs were tagged with VHF radio transmitters weighing approximately 7 g (Biotrack, Wareham, Dorset) following the methods described by Young et al. (2006). All radio transmitters weighed less than 5% body weight (range 0.54–1.79%), meeting the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011). Radio-tracking took place using a Sika radio tracking receiver fitted with a flexible Yagi three-pronged antenna (Biotrack). Hedgehogs were also individually marked with coloured heat shrink tubing to aid identification and weighed prior to release using an electronic balance (Glasby and Yarnell 2013). Rehabilitated hedgehogs were located via radio-tracking once per day for 3 days after release. All hedgehogs were located in their nests at least once per week between their release date and the following spring, and the location of each nest was recorded using a Garmin GPSmap 62 handheld GPS. The radio-tracking survey period was split into three-time periods in an attempt to identify periods of differing survival over autumn, winter and spring. These were 'autumn' (before 31st of October), 'winter' (between 1st of November and 31st of March) and 'spring' (after 1st of April). From the 1st of March, location data was taken at least three times a week to identify hedgehog activity after hibernation. Once a hedgehog has been identified as moving nests after the 1st of March, nocturnal radio tracking commenced in order to relocate and weigh hedgehogs and to remove their radio-transmitters. Weight change over winter was calculated as the difference between the weight when first radio-tagged and released, to the date the animal was first caught after the 1st of March. The last weight of the animal would depend on when hedgehogs became active after hibernation in relation to when they were recaptured, so that individuals that had been active for some time are likely to have recovered weight lost over winter, whereas those that were captured soon after becoming active are likely to weigh less than before winter, increasing variation in this variable.

Analysis

Hedgehog fate was determined as either 'surviving', 'died' or 'unknown'. Survival during a survey period (autumn, winter or spring) was confirmed if an individual was relocated alive or had moved nests in the following season. An animal was recorded as having died if it was found dead during the study period. If an individual was not re-caught due to tag loss/failure, or animal disappearance, then the fate was recorded as being unknown. The total number of days alive was calculated for each hedgehog between the first date of radio-tag attachment and release, to the last date known to be alive (i.e. the date that the hedgehog was recaptured, and the tag removed or the last date of recorded nest movement). The total number of days alive was also calculated for each individual during the study and also for each survey period. The first day alive was either the day the individual was first radio-tagged and released, or if already tagged, as the first day of the study period (autumn, winter or spring). The last day alive was either the day the animal was found alive and had its tag removed, or in the situation where the animal could not be relocated due to disappearance or tag failure and loss, the day which the individual was known to have moved nest or was last seen alive. The number of days alive was used in right-censored Kaplan-Meier survival analysis to compare survival rates of wild and rehabilitated individuals (Kaplan and Meier 1958). That is, only hedgehogs that were known to have died were recorded as such, and for hedgehogs where fates were unknown, they were assumed to have survived up to the last movement between nests and assumed to have dropped out of the survey at that point in time. Kaplan-Meier survival analysis was conducted for all hedgehogs pooled, and by all hedgehogs pooled across season, by treatment (wild or rehabilitated) and by treatment up to 150 days into the study. The survival curves of wild and rehabilitated were compared up to 150 days as the sample sizes (number of individuals still being tracked) beyond this time period was greatly reduced (mostly to due tag removal, loss or disappearance of individuals), making statistical comparisons dependent on a few individuals. Individual hedgehogs were treated independently in each survey period for this analysis, so that a hedgehog tracked over the entire survey period was included in the survival estimates across all three survey periods. Survival rates between the two groups were tested with a log-rank test. Survival rates of all hedgehogs were compared between seasons to ascertain whether season influenced survival as this is likely to inform release protocols. All survival analysis was conducted in R (R Core Team 2014) using the 'survival' (Therneau 2015) and 'survminer' (Kassambara and Kosinski 2018) packages.

Changes in hedgehog weight (g) were assessed using variables: 'start weight' (weight of individual at the start of the radio-tracking period); 'last weight' (last known recorded

weight of individual during the study); 'weight change' (the difference in 'start weight' and 'last weight'); 'daily weight change' ('weight change' divided by the number of days between the start and last weights were recorded); and 'percentage weight change' (proportional weight loss over winter per individual). Nesting rate (number of nests used by individuals per 100 days) was recorded as the number of nests reported as being used by each individual over the duration of the radio-tracking period ∗ 100. The total number of days individuals were radio-tracked was also recorded and compared between wild and rehabilitated individuals.

To test whether overwinter behaviour of hedgehogs varied by age or gender, a preliminary analysis of only the wild hedgehogs was conducted to determine whether these variables required factoring into analyses. All data was tested for homogeneity with a Bartlett test, and for normality using a Shapiro-Wilk test. To compare differences in over winter behaviour between gender (male versus female), age (adults versus young of year) and wild versus rehabilitated hedgehogs, independent *t* tests were used where assumptions of normality and homogeneity were met, and Mann-Whitney *U* tests used otherwise. Unless specified all values represent means ± 1 standard error. All analysis was conducted in R (R Core Team 2014).

Results

A total of 57 hedgehogs were tracked over four winters between 2010 and 2014, comprising 34 rehabilitated (21 males, 6 females and 7 unknown) and 23 wild hedgehogs (13 females and 10 males) (Table 1). Two tags fell off soon after attachment giving 55 individuals tracked. The age profiles of hedgehogs differed between wild and rehabilitated hedgehogs, with the majority (74%) of wild hedgehogs comprising adults, whereas the majority (91%) of the rehabilitated hedgehogs were young of the year.

Hedgehogs were radio-tracked on average 133.76 ± 5.7 days ($n = 55$), with wild hedgehogs being tracked for significantly longer ($n = 23$; mean = 158.7 ± 6.89) than rehabilitated hedgehogs ($n = 31$; mean = 115.84 ± 7.04) (t test: $t = 4.392$, df = 51.50, p value < 0.001), due to the rehabilitated individuals being released throughout the winter period, compared to the wild individuals that entered the study in late autumn or early winter.

Survival

A total of 36 (63%) hedgehogs were alive at the time of tag removal and were deemed to have survived the winter. Seven (12%) individuals were known to have died during the study, comprising four wild individuals and three rehabilitated. Cause of death was attributed to road traffic accidents ($n = 3$, 43%), predation by badgers ($n = 3$, 43%) and one hedgehog (14%) was likely to have died from starvation due to a lack of fat reserves as identified at necropsy. All rehabilitated hedgehogs that died were predated by badgers. The fate of 14 (3 wild and 11 rehabilitated) hedgehogs (25%) could not be determined due to combination of tag loss/failure or the hedgehog not being recaptured. Therefore, the survival rate of hedgehogs whose fate was known was 83% ($n = 42$).

Kaplan-Meier survival analysis showed that hedgehog survival over winter was 0.961 ± SE 0.028 after 100 days, falling to 0.257 ± SE 0.791 after 200 days (Fig. 1). However, only 10 individuals were tracked over 181 days, reducing sample size, which resulted in lower survival probabilities towards the end of the study. There was a significant difference in overwinter survival between wild and rehabilitated hedgehogs (log rank test: chi-squared = 5.6, d.f. = 1, $p = 0.017$) (Fig. 2). However, the two survival curves only diverged after 150 days, in response to very

Table 1 Number of wild and rehabilitated hedgehogs monitored over four winters between 2010 and 2014, across five study sites in England. The total number of hedgehogs per site are shown as well as number of adults, young of the year (YoY), sex (if known) and whether the hedgehogs originated from the wild (wild) or from rehabilitation centres (rehab). Sites were as follows: Pett; Sedd = Seddlescombe; BrLNR = Local Nature Reserve Brighton; Brsub = Suburban Brighton; and Brack = Brackenhurst Campus

			Wild				Rehab			
Year	Site	Total No.	YoY	Adult	Male	Female	YoY	Adult	Male	Female
2010–11	Pett	8					6	2		
2011–12	Sedd	7					6	1	6	1
2012–13	BrLNR	12					12	0	8	4
2012–13	Brack	10	1	9	4	6				
2013–14	BrLNR	2					2	0	1	1
2013–14	Brsub	8	1	2	1	2	5	0	5	0
2013–14	Brack	10	4	6	5	5				
	Totals	57	6	17	10	13	31	3	20	6

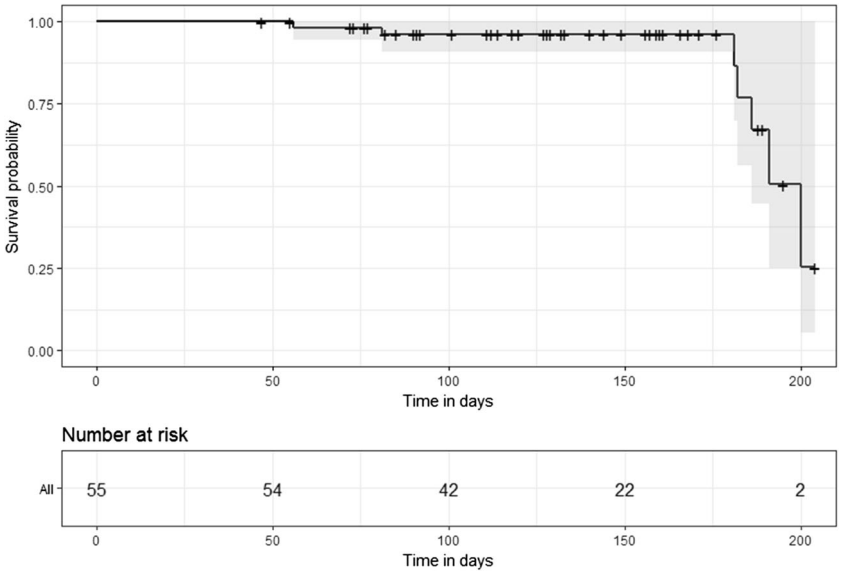

Fig. 1 Kaplan-Meier survival curve and risk table from 55 wild and rehabilitated hedgehogs radio-tracked through time (days) over four winters (October to May 2010–2014) in England. The risk table shows the number of hedgehogs still known to be alive and participating in the study. Shaded area represents 95% confidence interval

few rehabilitated hedgehogs being tracked for more than 150 days. Therefore, a survival analysis on the first 150 days that each hedgehog was involved in the study was conducted that found there was no significant difference between wild and rehabilitated hedgehog survival (log rank test: chi-squared = 0.4, d.f. = 1, $p = 0.542$) (Fig. 3). Due to a lack of significance in survival between the first 150 days after release between wild and rehabilitated hedgehogs, the survival data across both treatments was pooled to enable a comparison between seasons. There was a significant difference in hedgehog overwinter survival rate by season, with survival rates being lowest in spring, compared to autumn and winter (log-rank test: chi-squared = 18.5, d.f. = 2, $p < 0.0001$) (Fig. 4).

Gender and age differences in over winter behaviour of wild hedgehogs

There were no significant differences ($p > 0.05$) in any of the variables ('start weight'; 'last weight'; 'weight change'; 'daily weight change'; 'percentage weight change' 'nesting rate'; and 'number of days tracked') between wild male ($n = 10$) and female ($n = 13$) hedgehogs (Table 2). Adult wild hedgehogs ($n = 17$) were significantly heavier than young of the year ($n = 6$) at the start and end of the study, respectively (Table 2). However, there was no significant difference between adults and young of the year regarding weight change over winter, daily weight change or in the number of nests used per 100 days (Table 2). Therefore, hedgehogs of all ages

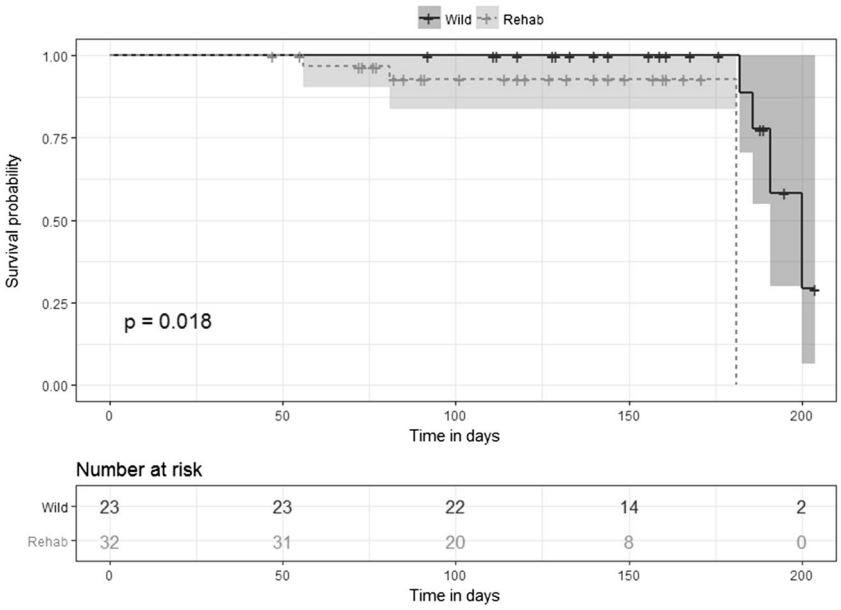

Fig. 2 A comparison of Kaplan-Meier survival curves and risk table between wild ($n = 23$) and rehabilitated ($n = 34$) hedgehogs radio-tracked through time (days), over four winters (October to April 2010–2014) in England. The risk table shows the number of hedgehogs still known to be alive and participating in the study after number of days. The p value is the significance level of the log-rank test between the survival curves of wild and rehabilitated hedgehogs. Shaded areas represent 95% confidence intervals

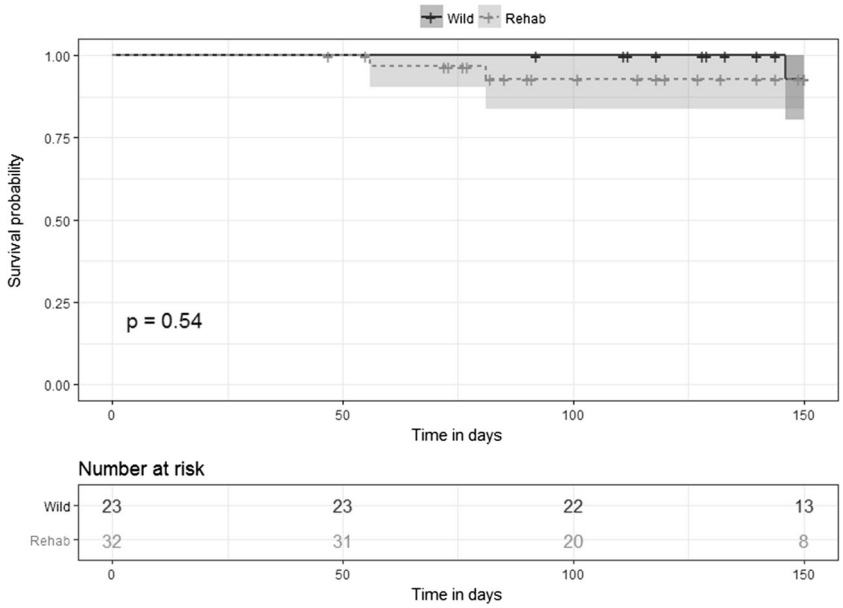

Fig. 3 A comparison of Kaplan-Meier survival curves and risk table between wild ($n = 23$) and rehabilitated ($n = 34$) hedgehogs radio-tracked through time (days), over the first 150 days that individuals participated in the study, across fours winters (October to April 2010–2014) in England. The risk table shows the number of hedgehogs still known to be alive and participating in the study after number of days. The p value is the significance level of the log-rank test between the survival curves of wild and rehabilitated hedgehogs. Shaded areas represent 95% confidence intervals

and genders were pooled for comparisons in over winter behaviour between wild and rehabilitated conspecifics.

Comparison of wild and rehabilitated hedgehogs over winter behaviour and weight change

The average weight of rehabilitated hedgehogs upon release was 631.74 g ± 13.57 with a range between 391 g and 851 g. The average weight loss for hedgehogs over winter was 110.32 g ± 22.08 which equated to an average loss rate of 0.72 g/day ±0.19 ($n = 39$). There was no significant difference in weight loss or daily weight loss between wild and rehabilitated hedgehogs over winter (wild weight loss = −124.74 g ± 26.82 ($n = 19$), rehabilitated weight loss = −96.61 g ± 35.12 ($n = 20$), Mann-Whitney U test: $W = 180$ $p = 0.792$; wild daily weight loss = −0.79 g/day ± 0.17, rehabilitated daily weight loss = −0.65 g/day ± 0.35, Mann-Whitney U test: $W = 211$, $p = 0.569$). Average percentage of body weight loss across all hedgehogs over winter was 14.11% ± 3.08, with maximum percentage weight loss being 44.01%. There was no

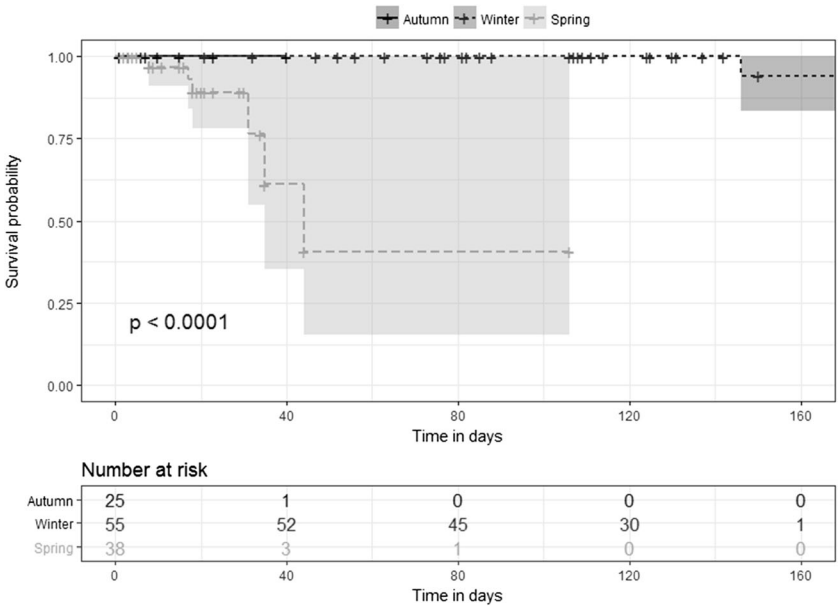

Fig. 4 A comparison of Kaplan-Meier survival curves and risk table for radio-tracked hedgehogs ($n = 57$) through time (days), across three seasons (autumn, before the 31st of October; winter, the 1st of November to 31st of March; spring, after the 31st of March) over winters 2010–2014 in England. The risk table shows the number of hedgehogs still known to be alive and participating in the study after number of days. The p value is the significance level of the log-rank test between the survival curves of hedgehogs' radio-tracked in different seasons. Shaded areas represent 95% confidence intervals

Table 2 Comparisons of over winter weights, number of days tracked and number of nest locations in wild hedgehogs across different age (adult and young of the year) and gender (male and female) classifications from individuals radio-tracked over two consecutive winters between 2013 and 2014 in England. Where, start weight is the weight of individual at the start of the radio-tracking period); last weight is the last known recorded weight of individual during the study; weight change is the difference in start weight and last weight; daily weight change is weight change divided by the number of days between the start and last weights were recorded); nesting rate is the number of nests used per 100 days; and the number of days tracked is the duration that each individual was radio-tracked. All weights are in grams. All values are mean (± standard error). Values in bold indicate a significant difference ($p < 0.05$) in independent *t* tests or non-parametric equivalent

Variable	Gender		Age	
	Male	Female	Adult	Young of year
Start weight	993.71 (30.51)	895.78 (35.07)	**997.3 (27.18)**	**771.35 (38.16)**
Last weight	814.12 (61.39)	802.82 (52.63)	**879.43 (33.83)**	**606.4 (40.86)**
Weight change	−160.75 (40.49)	−98.55 (35.21)	−111.36 (32.99)	−162.22 (43.25)
Daily weight change	−0.94 (0.23)	−0.68 (0.25)	−0.66 (0.20)	−1.16 (0.30)
Percent weight change	−16.40 (3.82)	−11.14 (4.15)	−10.76 (3.23)	−20.62 (5.41)
Nesting rate	1.69 (0.40)	2.22 (0.47)	1.78 (0.35)	2.6 (0.69)
Number of days tracked	163.4 (7.58)	153.38 (10.62)	**166.71 (7.81)**	**132.33 (7.04)**

significant difference in percentage weight loss between wild (13.35% ± 2.88 ($n = 19$)) and rehabilitated (14.84 ± 5.44 ($n = 20$)) hedgehogs during the study (Mann-Whitney *U* test: $W = 227$, $p = 0.309$).

In total, 92 winter nests were utilised by 40 hedgehogs, with between 1 and 7 nests used per hedgehog. An average of 1.74 ± 0.20 nests was used every 100 days by hedgehogs over the study period. There was no significant difference in the rate of nest use between wild ($n = 23$; mean = 1.98 ± 0.32) or rehabilitated hedgehogs ($n = 17$; mean = 1.42 ± 0.2) (Mann-Whitney *U* test: $W = 229.5$, $p = 0.359$). The distance between successive nest sites ranged from 2 to 323 m for wild hedgehogs, and 6–245 m for rehabilitated hedgehogs. There was no difference in the mean distance between successive nests per hedgehog between wild ($n = 17$, 106 ± 16 m) and rehabilitated hedgehogs ($n = 7$, 82 ± 41 m) (*t* test: $t = -0.55$, df = 8, $p = 0.598$).

Discussion

This study is the first to compare overwinter survival, body weight changes and nesting behaviour between wild and rehabilitated hedgehogs to inform hedgehog rehabilitation practice. Our findings show that rehabilitated animals released in winter have similar survival rates, changes in weight and use a similar number of nests to wild conspecifics over similar time periods, suggesting that healthy hedgehogs can be released throughout winter under favourable conditions without affecting survival rates. This would reduce costs to rehabilitators and free up space for incoming unhealthy hedgehogs in need of rehabilitation, as well as reduce the time hedgehogs are in captivity, thereby reducing the potential negative consequence of captivity on natural behaviour required for survival in the wild and so providing an overall positive effect on hedgehog welfare (Miller 2000).

In this study, survival rates were high, with no difference in survival overwinter between wild and rehabilitated hedgehogs within 150 days post release, suggesting that release of rehabilitated hedgehogs will not impact their chances of survival in comparison with wild conspecifics. Overwinter survival of wild adult and juvenile hedgehogs has been recorded as being on average 66% in Southern Sweden (Kristiansson 1990), which is lower than reported here, which may reflect the colder winters and consequent longer hibernation periods experienced at higher latitudes.

Despite low numbers of deaths recorded in this study, some interesting patterns of mortality did emerge which can be used to highlight some advantages of winter release of rehabilitated hedgehogs. The majority of mortality occurred during the spring season, once hedgehogs became active after winter hibernation. This may be expected as hedgehogs will be less active overwinter, and relatively safe in nest sites from major sources of mortality (for review see Turbill et al. 2011), such as road traffic accidents (Huijser and Bergers 2000) or predation (Doncaster 1992). All seven hedgehog mortality events occurred after the 5th of March, and the six animals killed on roads and by badgers were killed after April when they are more likely to encounter such risks due to higher levels of activity. One wild individual died of suspected starvation near the end of winter, and, although this is only one individual, it may suggest that the post emergence time period is associated with increased risks of mortality due to low body condition and a lack of natural prey availability, and that survival post hibernation may be lower than survival over winter per se. However, this is speculation based on the evidence in this study but may

merit further research, so that any negative consequences of releasing rehabilitated hedgehogs at the end of winter are better understood.

Survival rates of released rehabilitated hedgehogs in this study (0.96 ± SE 0.02 after 100 days) are higher than other studies on post release survival in the UK (Morris et al. 1993; Morris and Warwick 1994; Morris 1997; Reeve 1998; Molony et al. 2006). These studies found post release survival rates (corrected by time period) between 0.00 (Morris and Warwick 1994) and 0.55 per 100 days (Molony et al. 2006). The differences in survival rate of post release hedgehogs is likely due to timing of release (greater survival over winter associated with lower chance of encountering sources of mortality) combined with the suitability of release site for hedgehogs. In this study, hedgehogs were released in a range of sites that were regarded as suitable for hedgehogs, namely suitable habitat away from main roads and in areas with a low density of badgers. Despite this all three rehabilitated hedgehogs known to have died were due to badger predation, suggesting that the release sites were not completely badger-free. In other studies that have released hedgehogs, those where releases took place in suburban areas (presumably without badgers, Molony et al. 2006)) and areas without badgers such as on the Island of Jersey (Morris 1997), had higher post release survival rates than those where release sites were predominantly rural (e.g. Morris et al. 1993; Morris and Warwick 1994; Reeve 1998). This highlights the importance of suitable release sites for rehabilitated hedgehogs, with optimal release sites being those that are suburban and free of badgers. This is borne out by current research in the UK showing that hedgehog occupancy and abundance is low in rural landscapes (Hubert et al. 2011; Yarnell et al. 2014; Pettett et al. 2017; Williams et al. 2018; Williams et al. 2018a), which suggests that these habitats are sub-optimal for hedgehogs and should not be used for rehabilitation release and that release into suburban areas without main roads and badgers should increase individual survival rates.

The overwinter behaviour of released rehabilitated hedgehogs was similar to their wild counterparts and is similar to other studies that have shown released individuals have innate behaviours that allow them to forage, find and build nests and function in the natural environment following a period in rehabilitation (Morris 1998). The effect of spending a first winter in captivity on hedgehogs' future ability to subsequently successfully breed, forage and survive overwinter is unknown and this would warrant further investigation into the longer-term consequences of overwintering in captivity, although there is no evidence to support this in this study. We found that wild hedgehogs sampled in this study were heavier than their rehabilitated conspecifics at the start and end of the study period, which is to be expected since the majority of the rehabilitated individuals were young of the year compared to the majority of wild animals being fully grown adults. Despite this, released individuals were able to find shelter and build their own nests and at similar rates to their wild counterparts, further supporting our contention that winter release of hedgehogs can be used as a release strategy by wildlife rehabilitators. Furthermore, no differences in weight loss overwinter were observed between wild and rehabilitated hedgehogs. This suggests there are no differences in thermoregulatory capabilities or ability to find environmentally stable hibernation locations or respond to environmental cues across seasons for foraging.

Hibernation weight loss could not be estimated in this study since the majority of hedgehogs became active and are likely to have had opportunity to forage and start to gain weight before individuals were re-caught and weighed. However, our winter weight loss estimates are similar to those recorded in other studies that suggest winter weight loss of between 20 and 40% body weight in over wintering hedgehogs across Northern Europe (Morris 1984; Jensen 2004; Haigh et al. 2012). Current rehabilitation guidance from the RSPCA states that hedgehogs should be over 600 g prior to release between December and March (RSPCA 2013). In this study, the rehabilitated hedgehogs weighed on average 631 g at release, ensuring adequate body condition to survive to the following spring, with the high survival rates confirming that current RSPCA and British Hedgehog Preservation Society guidance on release weights in winter is appropriate (http://www.britishhedgehogs.org.uk/pdf/Hibernation-Weight.pdf). However, not all animals in this study weighed over 600 g upon release, since the study took place before the RSPCA and British Hedgehog Preservation Society guidance was published. Despite this, all animals in this study survived considerable overwinter periods, irrespective of release weight. Those individuals that where known to have died did so due to factors unrelated to body size, i.e. road traffic or badger predation. This suggests that identifying a minimum weight by which individual hedgehogs can be released is problematic. Current guidance is based on studies of weight loss already discussed (Morris 1984; Jensen 2004; Haigh et al. 2012), and further research is required to refine predictions of minimum weight of hedgehogs to survive overwinter. Indeed, the minimum weight will likely be context-dependant, and influenced by local weather conditions, time of year, and age of the individual as well as individual differences in behaviour and physiological condition, and it may be that as long as the hedgehog is healthy (as determined by a veterinarian) that the hedgehogs should be released irrespective of weight, but further research would be useful to help inform this decision.

There were a number of limitations in the study, such as the unbalanced design in ages and gender, different years used across treatments and difficulties associated with tag loss/failure which limited sample sizes. Despite these, the survival and behaviour data clearly show that hedgehogs released in winter will exhibit similar behaviours and survival rates to wild individuals.

Conclusion

In conclusion, this study is the first to compare overwinter survival and behaviour of wild and rehabilitated hedgehogs and demonstrate that rehabilitated hedgehogs survive well if released in winter and exhibit natural behaviours of nest building, while changes in weight are similar to wild counterparts. Based on these findings, we recommend that wildlife rehabilitators can release rehabilitated hedgehogs during winter if the criteria used for release are similar to those used in this study. That is, hedgehogs should weigh over 600 g, have passed a veterinary health check, are soft-released in areas where the individuals were originally found or suburban areas without main roads and badgers, and during periods of mild weather (> 0 °C) over winter. Following these guidelines will reduce the periods of captivity for rehabilitated hedgehogs and allow them to reintegrate into their natural habitats as soon as possible, improving their welfare, whilst reducing the costs of care for the wildlife rehabilitators.

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