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Minimising orphaning in the brown hare *Lepus europaeus* in England and Wales: should a close season be introduced?

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The European brown hare *Lepus europaeus* is an *r*-selected species showing relatively high fecundity, and changes in the hare population can be influenced by the timing of hunting and reproductive activity. Between February and August in Europe, the majority of female hares are either pregnant or suckling young, or both, and if a female is killed during the suckling period, the young hares (leverets) are orphaned and are likely to die of starvation. In England and Wales, in contrast with other European countries, there is no close season when hunting hares is prohibited, and the peak time of hunting in February coincides with the start of reproductive activity. We explore the impact of hunting practices on the risk of death by starvation of dependent young. By modelling scenarios of hunting at the highest documented rate at times of the year based on practices adopted in England and Wales, and by comparing this with the close season practice in Scotland, we quantify seasonally variable risks of orphaning and death by starvation of leverets. Hunting in February leads to a profoundly damaging combination of population shrinkage ($\lambda = 0.534$) and levels of orphaning of leverets corresponding to 7.6% of the year start population and thus providing poor welfare and poor population recovery outcomes for the hare. These illustrative figures compare very unfavourably with the modelled Scottish population which has a growth rate of $\lambda = 1.404$ and levels of orphaning of leverets corresponding to 0.3% of the year start population. We anticipate that these findings will stimulate consideration of the impact of hunting practices, and that increased understanding of the effects of the timing of hunting may aid policy development aimed at protecting dependent young hares.

The brown hare *Lepus europaeus* is found from Britain in the west to Lake Baikal in Russia to the east, and has been introduced elsewhere (e.g. Argentina, Australia, USA). In Europe, populations of hares are perceived to be in decline (Smith et al. 2005); following historic decline, the population in the UK is now believed to be broadly stable (Wright et al. 2014). The main causes of mortality in the hare are: 1) predation, with fox *Vulpes vulpes* predation accounting for up to 76–100% of annual production (Reynolds and Tapper 1995); 2) disease, including European Brown Hare Syndrome, coccidiosis, leporine dysautonomia, toxoplasmosis and pseudotuberculosis (Péroux 1995, Whitwell 1997, Jokelainen et al. 2011); and 3) hunting – organised shoots typically take place in England in February, at the end of the pheasant shooting season; in almost all other European countries, hunting takes place in the autumn.

There is increasing public, scientific and legislative interest in the role of hunting in wild animal population dynamics, and in the welfare of hunted animals (Butterworth 2014, Law Commission 2015). In England and Wales, the Hares Preservation Act 1892 prevents the sale of hares from 1 March to 31 July, but this does not compare to a close season, as hares can be shot during this period, and may then be frozen and sold at other times. Elsewhere in Europe, hares are protected by a close season, for example in Austria, Belgium, Denmark, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Luxembourg, the Netherlands, Poland, Slovenia, Spain, Sweden and Switzerland (Fig. 1). In 2011, Scotland introduced a close season from 1 February to 30 September, through the Wildlife and Natural Environment (Scotland) Act. However, the hare has no close season in England and Wales, and the recently published Law Commission report (Law Commission 2015) identifies that one reason to establish a close season may be "that during certain periods of the year the young of a huntable animal may starve if the mother is killed." Recommendation 17 of the report states "…the Secretary of State or Welsh Ministers should have the power to introduce, alter or remove close seasons or prohibited periods by regulation in connection with any animal species…"

We aimed to examine the effects of different hunting practices on population growth and on the orphaning of

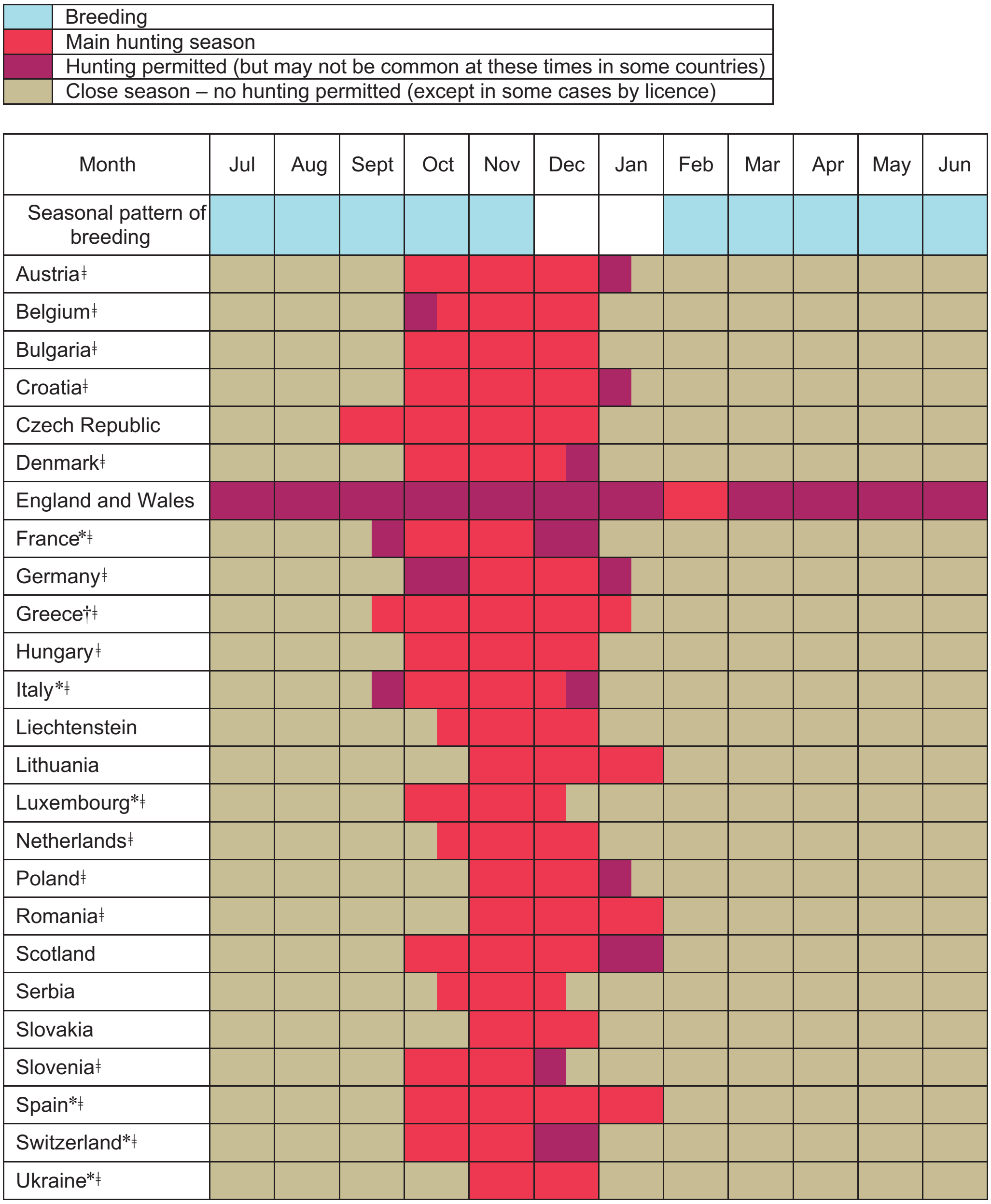


Figure 1. Yearly breeding cycle of the hare (top row), and approximate permitted hunting seasons, main hunting seasons, and close seasons in 24 European countries arranged alphabetically (Great Britain divided into England and Wales, and Scotland; data derived from the literature and from the survey). Close seasons also exist in countries not shown here. *Hunting season may be changed each year (France, Luxembourg, Switzerland, Ukraine) and/or depends on location (France, Italy, Spain, Switzerland). In France, the main hunting season is October and November, but hunting may start in mid-September and continue until the end of December. Hunting with dogs may continue until 1 March. In Italy, hunting may start on the third Sunday in September. In the Lombardy region, it may continue until 8 December. In Luxembourg, the hunting season in 2012/13 was 1 October – 16 December; in 2013/14 it was 1 October – 22 December. In Switzerland, hares are hunted almost exclusively in the canton Graubünden, in October and November. In most of Switzerland there is a licence-based hunting system and hares may be shot in October and November (exact dates depend on the year). In the parts of the country with a territory-based hunting system the close season is 1 January to 30 September. In cantons where numbers of hares are low, hunting is prohibited by cantonal law. †Greece: hunting is allowed on only three days each week from 15 September to 10 January. ‡ Data from the survey as well as from the literature.

leverets in England and Wales. First we collated information on hare management practices, close season dates, hunting methods, and quotas via an online survey of biologists, ecologists, game managers and hunters in 24 European countries, for comparison with the situation in England and Wales. In England, it is estimated that between 28 and 69% of hares are removed locally by shooting (Stoate and Tapper 1993). We then modelled and compared the effect of maximal hunting (69%) at different times of year based on practices adopted in England and Wales (no close season) in comparison to practices in Scotland (with close season). This allowed us to quantify seasonally variable risks of orphaning and death by starvation of leverets.

Material and methods

Through published papers, we identified biologists, ecologists, game managers and hunters in 24 European countries for an online survey on hare management practices, close season dates, hunting methods and quotas. We asked how long the close season had been in place; whether any licenced hunting was allowed during the close season; why a close season existed; how hares were hunted; and how quotas were organised. A literature review allowed us to collate biological parameters on hare reproduction in Europe (Table 1).

Review of the literature and consultation with veterinary and animal care staff responsible for rearing orphaned leverets provided the model parameter values for the period of dependency on maternal milk and survival characteristics for orphaned young hares. Milk provides all of the nutrition between day 1 and approximately day 17, and a significant but diminishing component from day 17 to 21 (Hackländer et al. 2002); milk may subsequently supplement the increasingly forage-based diet for more than 67 days (Broekhuizen and Maaskamp 1980). Between days 1 and 17, the chance of survival of an orphaned leveret is virtually zero. After day 17, the survival probability of an individual orphaned leveret increases.

To construct a biologically reasoned deterministic model for population growth and for orphaning rates, we combined data from our consultations and from the literature (Table 1; mean values) to inform model parameters (Table 2). The year was divided into calendar months, and using the model parameters for fecundity and survival, the population growth rate (λ) was calculated. The model was initially run with only adults in the population to establish an equilibrium distribution of ages within the population, in the absence of hunting. This process was repeated until there

Table 1. Literature sources for the compiled biological parameters on hare reproduction used in the model: age structure (percentage of juveniles at end of breeding season), the sex ratio (percentage of females at the time of sampling, usually during the hunting season), annual survival of adults, and survival of young (percentage of juveniles surviving to next breeding season).

Age structure (% young)	Source	Sex ratio (% females)	Source	Survival of adults (%)	Source	Survival of young (%)	Source	No. of leverets born /female/ yr	Source
45	Ceulemans 2009	48	Pintur et al. 2006	49	Wincentz Jensen 2009	14	Wincentz Jensen 2009	10	Ceulemans 2009
50	Pintur et al. 2006	51	Popović et al. 2008	40	Pépin 1987	26	Hansen 1992	7.7	Hansen 1992
47	Popović et al. 2008	48	Wincentz Jensen 2009	51	Marboutin and Péroux 1995	33	Lincoln 1974	13.6	Marboutin and Péroux 1995
51	Wincentz Jensen 2009	53	Hansen 1992	67	Kovács and Ocsényi 1981	27	Devillard and Bray 2009	11.3	Pépin 1989
38	Hansen 1992	52	Lincoln 1974	38	Kovács 1983	22	Marboutin et al. 2003	9.4	Bensinger et al. 2000
41	Lincoln 1974	48	Jennings et al. 2006	36	Broekhuizen 1979	36	Marboutin and Peroux 1995	11	Broekhuizen and Maaskamp 1981
61	Pépin 1987	50	Pépin 1987	75	Wasilewski 1991	38	Pépin 1989	8.5	Almåşan and Cazacu 1976
59	Marboutin et al. 2003	51	Petrovan 2011	56	Andrzejewski and Jezierski 1966	19	Kovács and Ocsényi 1981	12.4	Petrovan 2011
42	Marboutin and Péroux 1995	58	Kovács and Heltay 1981	41	Petrovan 2011	25	Petrovan 2011		
65	Pépin 1989	52	Wasilewski 1991						
46	Bensinger et al. 2000	50	Bresiński 1983						
41	Eskens et al. 1999	50	Almåşan and Cazacu 1976						
52	Kovács and Heltay 1981	77	Dubinský et al. 2010						
62	Broekhuizen 1979								
32	Wasilewski 1991								
54	Bresiński 1983								
57	Beuković et al. 2013								
57	Dubinský et al. 2010								
62	Slamečka 1991								
39	Petrovan 2011								

Table 2. (a) Demographic parameter values used in the models for population change in hares. Birth rate is month-specific, and death rate is month-specific for adults. For juveniles, death rate is higher and is assumed constant throughout in the absence of hunting (affects juveniles from four months old) and orphaning (affects juveniles up to four months old). (b) Percentage of the population in each age cohort at the start of the year, to maintain a stable year start population demographic from year to year with a growing population size, in the absence of hunting (the initial conditions for the model). Am = adult males, Af = adult females, J = Juvenile, m = month.

(a)	Births/adult female	Adult death rate	Juvenile death rate
Jan	0.016	0.09	0.104
Feb	0.309	0.07	0.104
Mar	1.604	0.04	0.104
April	2.286	0.03	0.104
May	2.429	0.03	0.104
June	1.582	0.03	0.104
July	1.348	0.03	0.104
Aug	0.567	0.04	0.104
Sept	0.258	0.05	0.104
Oct	0.096	0.07	0.104
Nov	0.013	0.09	0.104
Dec	0.013	0.09	0.104

(b) Stable population composition	Am	Af	Total J (m1..7)	J(m1)	J(m2)	J(m3)	J(m4)	J(m5)	J(m6)	J(m7)
Percentage in each age cohort	33%	33%	34%	0.3%	0.2%	1%	3%	5%	12%	13%

was no change in the demographic profile from one year to the next, and the profile was then used to generate a 'year start population' to investigate the effect of three close season scenarios on population growth. The model included aging in monthly stages (m1, m2…, m7 and adult) and incorporated the death of adults through natural processes, death of adults due to hunting, death of juveniles through natural processes, death of dependent young due to orphaning through hunting of their mothers, and death of sub-adults (above four months of age) due to hunting. After month 7, the juvenile was considered an adult, and capable of reproducing (though hares reach puberty at different ages depending on when they were born; Lincoln 1974), so individuals of over seven months of age enter the adult population. It was assumed that young hares (of up to four months) are not hunted, because although these young hares can legally be shot (Lincoln 1974), in most cases they remain in hiding, avoiding being flushed by beaters, and so are more likely to avoid being shot (Abildgård et al. 1972, Marboutin et al. 2003). Hares older than four months were assumed to be hunted in proportion to their abundance.

Our model structure did not include variation in birth and death rates caused by changes in factors such as climate, predation or food availability and related to geographic location. The monthly birth and death rates we used can be considered an average of these factors, but in reality, variations will result in large effects on the population dynamics of a fast growing species such as the hare. Our aim was to isolate the qualitative effects of different hunting scenarios. The model is intended to be illustrative rather than quantitative, and is available on request for others to input alternative initial conditions.

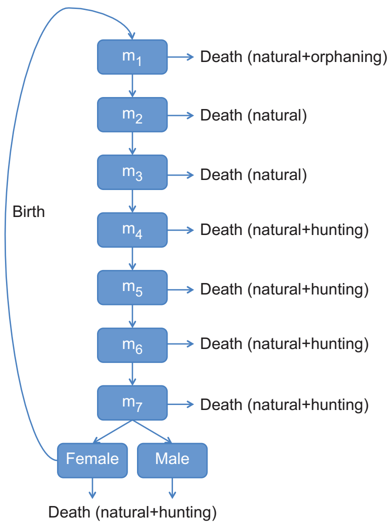
We used the model to examine the effects of different hunting practices on population growth and the orphaning of leverets in England and Wales (Fig. 2). Orphaning is calculated from the percentage of females killed by hunting in the previous month and the average birth rate in that month. Hunting, adult death rate and birth rate are specified for each month of the year (subscript $_t$) and death rate is specific to each age stage (subscript $_a$). We considered three scenarios:

1) no hunting; a calculation of population growth rate with no hunting at all to allow comparison with other scenarios;
2) hunting in February, based on the traditional hunting pattern in England and Wales, with a modelled hunting rate of 69% (Stoate and Tapper 1993) to explore the effects of the highest documented hunting rate;
3) hunting with a close season from the start of February to the start of October as in Scotland – again modelled on the highest documented hunting rate of 69% (Stoate and Tapper 1993).

For each scenario we modelled the effects of removal of a fixed percentage of animals during the hunting period relative to the original year start population (January). We did this by calculating the rate of loss in each month to obtain an equal distribution of animals hunted in each 'open season' month, so that the scenarios could be compared. We then explored the effect of varying the overall rate of hunting by ± 5% (upper/lower bands, λu / λl) to assess the sensitivity of the final population growth rate in each scenario to changes in hunting rate.

Results

Our online survey of hare management practices, close season dates, hunting methods and quotas in 24 European countries revealed (Fig. 1) that close seasons for hares have existed in Belgium, Croatia and Italy for more than 100 years, in Germany for more than 50 years, and in Greece for more than 30 years. In France, the Netherlands, Romania and Spain there has been a close season for more than 20 years, in SU and Poland for more than 10 years, and Slovenia, Hungary and Scotland introduced a close season in the last decade. The survey showed that close seasons have been adopted for reasons of conservation alone (in 12% of countries), welfare alone (6%), and both welfare and conservation combined



$$m1_{t+1} = Female_t \times birth\_rate$$

$$m2_{t+1} = m1_t(1\text{-}death\_rate_{at})\ (1\text{- } orphaning)$$

$$m3_{t+1} = m2_t(1\text{-}death\_rate_{at})$$

$$m4_{t+1} = m3_t(1\text{-}death\_rate_{at})$$

$$m5_{t+1} = m4_t(1\text{-}death\_rate_{at})\ (1\text{- } hunting_a)$$

$$m6_{t+1} = m5_t(1\text{-}death\_rate_{at})\ (1\text{- } hunting_a)$$

$$m7_{t+1} = m6_t(1\text{-}death\_rate_{at})\ (1\text{- } hunting_a)$$

$$Female_{t+1} = 0.5 \times (m7_t - m7_t \times (death\_rate_{at} + hunting_t)) + (Female_t(1\text{-}death_t)(1\text{-}hunting_t)$$

$$Male_{t+1} = 0.5 \times (m7_t - m7_t\ V\ (death\_rate_{at}+hunting_t)) + Male_t(1\text{-}death_t)(1\text{-}hunting_t)$$

Figure 2. Flow diagram of the life of a hare from birth to adulthood, and the modelled elements of risk for a young hare from month 1 (m_1) to month 7 (m_7). After month 7, the juvenile is considered an adult and capable of reproducing, and so it enters the adult population. In the first weeks of life (up to day 17 minimum) it is assumed that the young hare will die through starvation if orphaned. At each month, the young hare experiences risks (predation, disease, etc.); from four months of age the hare experiences the additional risk of hunting.

(71%), and that in many countries (89%), within the 'open season', some form of quota exists to regulate the numbers of hares which may be killed. In 13 countries (72%) no hunting at all is permitted within the close season, and in the remaining five countries (28%; Belgium, Denmark, France, the Netherlands, Poland) hunting within the close season is allowed under special licence, for example, to control local hare populations considered to be damaging crops.

Our modelled scenario 1, without hunting (Fig. 3a), resulted in a population growth rate $\lambda = 2.381$ (where a value of $\lambda = 1$ denotes no population change, $\lambda > 1$ denotes population growth with time, and $\lambda < 1$ denotes population shrinkage). No leverets are lost due to orphaning as a result of hunting of the mother in the 'no hunt' scenario.

Scenario 2, hunting of 69% of the population in February (Fig. 3b), as representative of the highest documented hunting rate in England and Wales (Stoate and Tapper 1993), led to shrinkage of the population with $\lambda = 0.534$ (upper/lower bounds with $\pm$ 5% λ_u 0.399/λ_l 0.667) across one year, and a significantly shrinking population if maintained over subsequent years. This rate of hunting leads to the orphaning during suckling (and presumed death) of leverets corresponding to approximately 7.6% of the year start population.

Scenario 3, a close season from the start of February to the start of October, as in operation in Scotland (Fig. 3c), with a hunting rate of 69% of the year start population, and with the same number of animals hunted and distributed across each open season month, led to an increase in the population $\lambda = 1.404$ (upper/lower bounds with $\pm$ 5% λ_u 1.233/ λ_l 1.575). This close season scenario leads to the orphaning (and presumed death) of leverets corresponding to approximately 0.3% of the year start population.

Discussion

In this study we provide objective data and an illustrative model of the results of different possible hunting scenarios on hares. In line with the high degree of variation in the model parameters (Table 1, 2), our model cannot be considered to provide absolute or exact outcomes. We hope that this paper will inform discussions on the topic, and aid the possible introduction of a close season in England and Wales. Hopefully, the results will draw the attention of English shooting organisations to the experience of Scotland, which adopted a close season in 2011, from 1 February to 30 September, via the Wildlife and Natural Environment (Scotland) Act.

Although numbers of hares are declining even in countries in which they are not hunted in February, our results show that hunting hares in large numbers (at the upper limit of known levels of hunting, representing perhaps the worst case scenario) at this time of year is likely to be highly damaging both for population persistence and for welfare.

Of the scenarios considered, a close season from the start of February to the start of October, as in Scotland, is most similar to the close season in many other European countries (Fig. 1). Whilst permitting hunting, this scenario provides capacity for population growth, and results in markedly reduced numbers of dependent juveniles being orphaned when compared to the same number of animals hunted in a short 'season' in February, as is typically the case in England and Wales.

If a reduction in the negative welfare impact on young animals of starvation following orphaning is an aim, then creation of a close season protecting the animals from the start of February to the start of October offers the potential to reduce dramatically the numbers of orphaned leverets

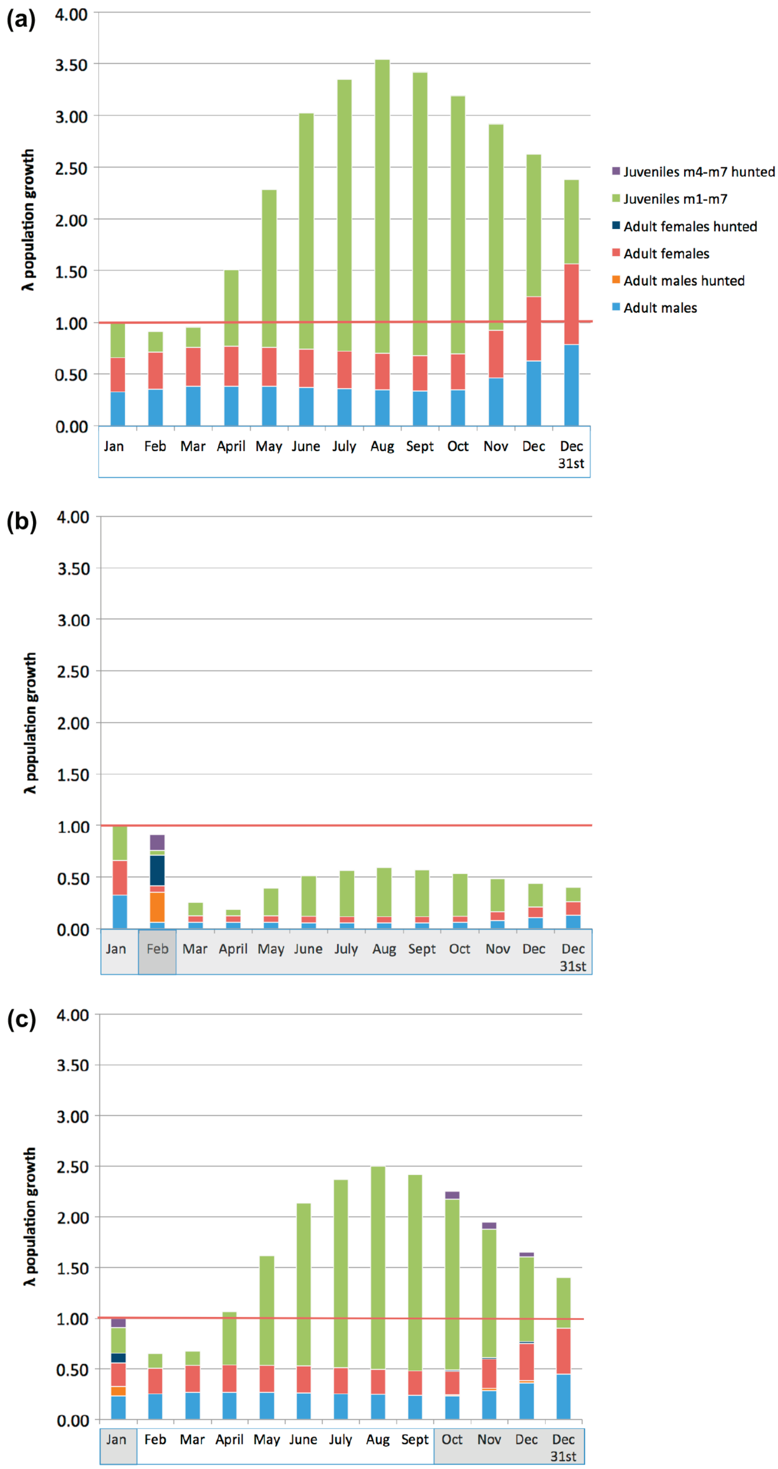


Figure 3. (a) Year 1 model population change characteristics for a modelled hare population with no hunting ('scenario 1') provides a year end population growth rate of $\lambda = 2.381$ (where a value of $\lambda = 1$, indicated by the horizontal red line, denotes no population change, $\lambda > 1$ denotes population growth with time, and $\lambda < 1$ denotes population shrinkage). No leverets are lost due to orphaning as a result of shooting the mother in the 'no hunt' scenario. The bar for each month represents the population at the start of that month, except the bar on the far right (31 Dec) which shows the population on the last day of the year. (b) Year 1 model population change with a maximal reported hunting rate of 69% of the population in February alone ('scenario 2'), as representative of the highest documented hunting rate in England and Wales, leads to shrinkage of the population with $\lambda = 0.534$ (upper/lower bounds with ± 5% λ_u 0.399/λ_l 0.667) across one year. This rate of hunting leads to the orphaning during suckling (and presumed death) of leverets corresponding to approximately 7.6% of the year start population (unshaded box denotes permitted hunting period, grey box denotes main hunting period, when the majority of hunting takes place in England). (c) Year 1 model population change with a close season from the start of February to the start of October as in operation in Scotland ('scenario 3'), with a hunting rate of 69% of the year start population, and with the same number of animals hunted and distributed across each open season month ($\lambda = 1.404$, upper/lower bounds with ± 5% λ_u 1.233/λ_l 1.575); unshaded box denotes the close season (no hunting), grey box denotes the permitted hunting period.

from ca 7.6% to ca 0.3% of the year start population. Our findings therefore very strongly support the use of a close season in England and Wales, in line with the legislative potential offered by the Law Commission report (Law Commission 2015), as a mechanism to help protect dependent young animals from death by starvation following the death of their mother by hunting.

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