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Abstract. Evidence from the only woodland study in the U.K. of the non-native edible dormouse shows (using nest boxes inspected monthly), that whilst some or much breeding occurs in most years, non-breeding years also occur. This is understood to relate to the number of tree species flowering in spring and the amount of flower production. Morris & Morris (2010) used a small sample to show that some adult animals do not appear in the nest box inspection records during the non-breeding years, but are present during the next breeding year. We have subsequently refined and increased the database, collating information on a sample of 222 glis (136 female, 86 male) known to be alive for between 5 and 13 years during a continuous study period of 18 years. The number of old animals (living to at least five years) recorded in nest boxes is significantly different between years of breeding and non-breeding with up to 90 % absent. There is no evidence that they move elsewhere in the isolated wood. Both males and females displayed this trait. The paper discusses alternative explanatory options interpreted from this. The applied science impact is that if 18 month hibernation is proven the time and cost implications for population control planning are severe. Future research is aimed at demonstrating the reality.

Introduction

The edible dormouse (*Glis glis* L.) is an alien pest species in Britain and was introduced in 1902 (Morris 2008). There is only one known meta-population of this species in the U.K., located across the Chilterns area (Morris 2008). Glis is a long-lived arboreal mammal generally associated with deciduous forest with dense understorey, high trees and a well connected canopy (Milazzo et al. 2003). Their reproduction correlates with years of good tree flowering such as beech (Burgess et al. 2003, Pilastro et al. 2003), which leads to some years with a high level of breeding and some years with no breeding at all. They live above ground during the active season (late spring to autumn) (Gaisler et al. 1977) and go into hibernation around October in the U.K. where they are inactive for about seven months (Morris 1998). In England, it is known that glis use underground chambers as hibernation sites, utilising features such as rotten tree stump roots and old rabbit warrens (Morris & Hoodless 1992, Brooks et al. 2012). Edible dormice are long lived in comparison to other small rodent species and have been known to live more than nine years in the wild in the U.K. (Morris & Morris 2010). Pilastro et al. (2003) showed that free living dormice can reach a longevity of nine years in Italy and that adult animals will make up a higher proportion of the population than overwintered juveniles (less than one year old). This is a strategy of increased longevity and lower rates of reproduction with long periods in hibernation. Typically, hibernation in mammal species is restricted to periods of cold or dry weather (Buck & Barnes 1999). Bieber & Ruf (2009) have shown that in outdoor enclosures with ad lib food, dormice in non-reproductive condition may return to hibernation during the summer after active periods of as little as two weeks. They suggest this is a method of predator avoidance when tree based food is low.

In Britain, edible dormice can cause unacceptable nuisance and damage in houses and to forest trees (Thompson 1953, Jackson 1994, Morris 2008). Control strategies in houses by trapping aim to clear the infestations but are both expensive and appear to be required annually as re-infestation is apparently very common. Glis control in forests has been considered (especially for newly emerging isolated populations) but, as yet, not implemented in the U.K.

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At the main study site in England Morris & Morris (2010) noted during a period of six years or more a difference in twelve wild individual glis seen in nest boxes between breeding and non-breeding years – where many were completely absent from nest boxes in non-breeding years. However, it is unknown where these missing animals go during non-breeding years but they subsequently re-appeared in the trapping history. Using a much larger and longer sequence of data from the same study site, this paper examines a large number of individuals recorded to explore similar questions and any potential implication for pest control.

Material and Methods

A study site in the Chilterns where European beech (*Fagus sylvatica*) is the dominant species was originally set up by Pat Morris in 1996 and since then the nest boxes have been checked at least once per month during each active season. The wood is ca. 100 ha and isolated on all sides by farmland and a dual carriageway road, with the exception of several hedges. Permanent marking using PIT tags has been used to identify individuals since 1996. During each box check, information such as individual identification, weight, reproductive condition, and sex were recorded. A calendar of captures was then created to enable us to determine the number of dormice "known to be alive" at any given time (because they were captured again later) even if they are only occasionally seen in the nest boxes. In 2008 75 more nestboxes were added at the edges of the wood and monitored as above. Marked individuals known to have lived (known to be alive) for at least five years were identified. Five years was considered a reasonable minimum period needed to create a database of captures of individual animals seen across multiple breeding and non-breeding years suitable for analysis. The number recorded in nest boxes of those known to be alive was compared between breeding and non-breeding years using ANOVA. ANOVA was also used to explore whether the average emergence weight of all animals is different after non-breeding years in comparison to breeding years.

Until 2009, animals below 100 g were not PIT tagged due to limited resources. From 2009 onwards, nestling young were PIT tagged – making it possible to accurately determine birth year. Moreover, the only recorded non-breeding year since 2009, was 2012. Known individuals recorded in this non-breeding year were analysed using a chi-squared test to see if the ratio of adults: overwintered juveniles (age ratio) was significantly differed from a null hypothesis of 50:50,

indicating whether juveniles of the previous breeding year (who have lower pre-hibernation weights than adults) had to become active. We have noted animals living up to 14 years at this study site and Pilastro et al. (2003) showed dormice living an average of nine years, indicating that there is a greater proportion of adults to overwintered juveniles at any given time. Therefore, a ratio of 50:50 adults to juveniles was chosen as the null hypothesis as a conservative estimate. Some animals were also radio collared prior to hibernation in 2009, 2010 and 2012 to see where they over-wintered and spent the subsequent summer months.
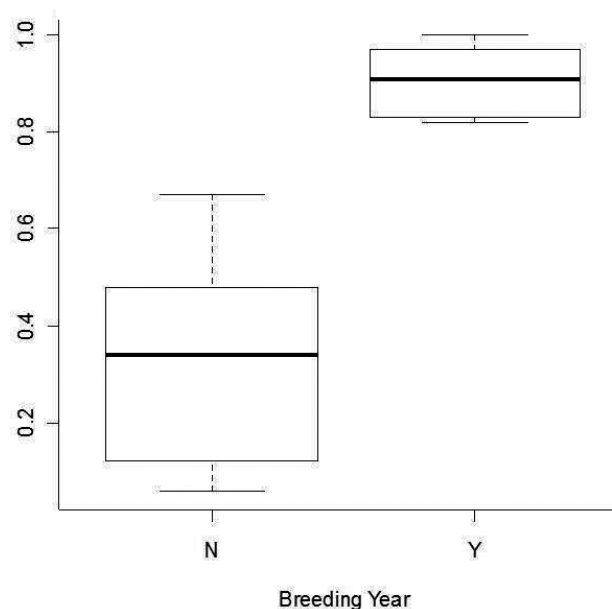

Fig. 1. Box and whisker plot showing the proportion of 222 long-lived animals captured in nest boxes out of those known to be alive in breeding (Y) and non-breeding (N) years from 1997-2012. The upper and lower quartile, the maximum and minimum values are displayed.
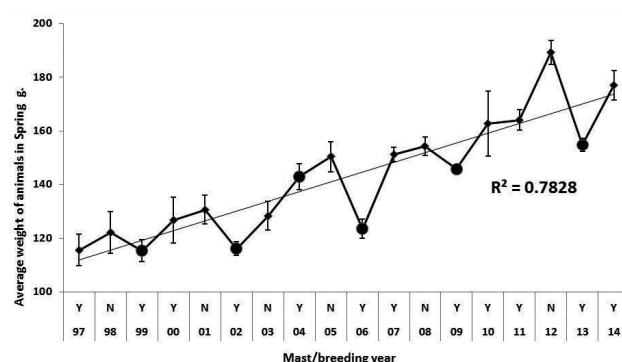

Fig. 2. The average spring emergence weight of all animals in breeding and non-breeding years (Y = breeding/mast year, N = non-breeding/non-mast year) from 1997 to 2014. Filled circles = emergence weight the spring after a non-breeding year.
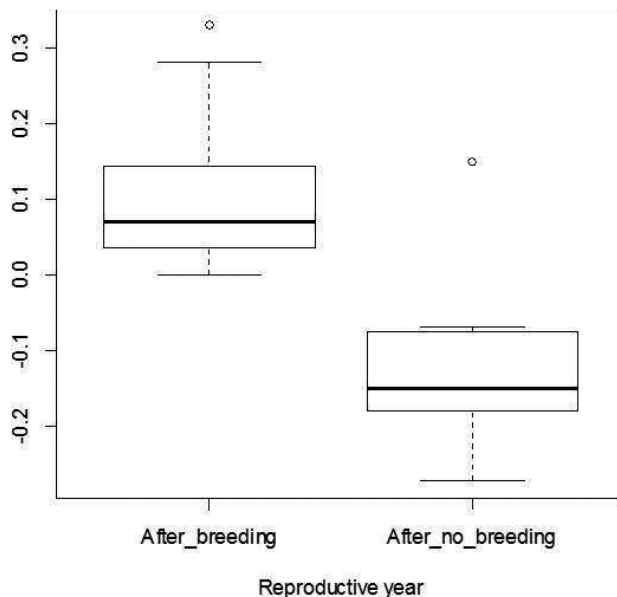
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Fig. 3. Box and whisker plot showing the proportional change in average spring emergence weight from the previous year's emergence weight, after breeding years and non-breeding years from 1997 to 2014. The median, upper and lower quartile, the maximum and minimum values are displayed.

Results

Glis identified as living at least five years numbered 222. The oldest male animal was born in 2000 and is currently (in 2014) 14 and two females bred in 2013 at 13 years old. A one-way ANOVA shows that the percentage of animals recorded in nest boxes out of those known to be alive was significantly higher in breeding years (ca. 90 %) in comparison to non-breeding years (ca. 35 %) (f = 44.55, p = 1.053e-05, p < 0.001) see Fig. 1. Both males and females displayed this behaviour. Those that were found in non-breeding years were mainly seen in the early summer, e.g. none of 19 individual old glis captured in 2012 (of a total 151 known to be alive) were found after the first week in August.

ANOVA also shows that the average spring emergence weight of all animals handled was significantly lower after a non-breeding year than after a breeding year (ca. –15 % *vs.* +7 % of the previous year) (f = 15.06, p = 0.0013, p < 0.01), see Figs. 2 and 3. Despite this, linear regression shows that the average spring emergence weight has significantly increased over time from 115-174 g (t = 7.67, p = 0.67e-07) with an R^2 value of 0.78.

Forty seven individual adults and 104 "juveniles" (animals born the previous year 2011) were recorded in total in 2012. This is a ratio of 31:69 (31 % adults: 69 % juveniles). The chi-squared test showed a significant difference between the ratio of adults to juveniles from the null hypothesis of 50:50 (χ^2 = 21.57, df = 1, p = 3.508e-06) and the opposite of the result from Pilastro et al. (2003).

Discussion

The results demonstrate that the majority (ca. 65 %) of long-lived animals known to be alive are not seen in the nest boxes at all during non-breeding years, whilst only 10 % of the same animals are not seen in breeding years. Although many individuals in a population may not be occupying nest boxes in any given inspection, PIT tagging to individually mark animals helps to establish which ones we know are alive even without recording them entering nestboxes in any particular year because they are handled in succeeding year(s). Bieber & Ruf (2009) have shown in outdoor enclosures that well fed glis have the capability to go into summer "hibernation" when reproduction is inactive. This may explain where wild glis in England go during non-breeding summers.

The results of our study also show that the average spring emergence weight of all animals is significantly lower after non-breeding years in comparison to after breeding years. This supports our theory that these animals have been in summer hibernation and for a second winter and have therefore used up more body fat reserves than if they were active and feeding throughout the previous summer. An alternative would be that they were active within our study site but not captured and were significantly lighter entering hibernation. We have no evidence of this since we so rarely caught old adults during non-breeding years (e.g. 0 of 151 known to be alive were handled in autumn 2012).

Other reasons for animals missing from nest boxes in non-breeding years could include migration to another part of the wood or to some other food rich location then return next year. If so, they might be expected to be the normal weight which does not explain the spring emergence weights being lower after non-breeding years. Moreover, many additional boxes were installed in the peripheral area of this isolated wood in 2008 supplementing the core boxes used in this study. Very few adults from the core area have been noted in these peripheral boxes, suggesting no wholesale movement of individuals within or whilst moving off the site. Also, similar trends in glis numbers seen in nest boxes were observed in both core and periphery areas, although that data has not yet been fully analysed. The same individuals were logged over many years and applying the concept of trap-happy and trap-shy individuals is not appropriate nor supported by the results, it would require that

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most of the individuals in the population changed from one state to another each year – even if many were captured only once per year.

Average post hibernation emergence weight has significantly increased over the past 18 years whilst the frequency of breeding years has also increased. Could this be a result of climate change? Beech is a characteristic species of woodlands in the Chilterns. Schmidt (2006) showed that beech flowering and seed production was higher in years preceded by a warm summer opposed to those preceded by a cool summer. Moreover, Overgaard et al. (2007) has shown that the frequency of beech mast years has increased in Sweden, although the exact reason for this remains unknown. Our data also suggests very few poor beech flowering years recently – only twice in the past nine years, 2008 and 2012. Natural succession of the trees at the study site could result in a greater food supply as the species age and mature, but little seed is produced before the beech is 60 years old in a canopy forest. Production of seed reaches a maximum at age 80-140 (Coed Cymru 2011) and most beech stands in our study wood fall into this age range.

The trigger for possible summer hibernation remains unknown. Whilst breeding in the wild is thought to relate to the amount of available beech mast (Burgess et al. 2003), the captive study by Bieber & Ruf (2009) used ad lib food on their study animals. They demonstrated that some animals still went into hibernation during the summer and some did not breed despite having an unlimited food supply. Ten percent of our old animals were not found in breeding years when food is relatively plentiful, this may reflect the background level of summer hibernation or the background random chance of not finding any particular individual in a nestbox on any of the days we inspected. Bieber's study was important in demonstrating the (captive) capability of the species to survive in hibernation during winter, the following summer and subsequent winter. We would concur with Kager & Fietz (2009) that breeding is related to the plentiful spring flowering of trees that pre-empts a good mast year (unless severe frost or drought kills the developing fruits, Piovesan & Adams 2005), not the mast itself. This was corroborated by Lebl et al. (2010) who showed a positive effect of a spring supplementary feeding experiment. Moreover, if normal weight loss over winter is about 20 %, consistent with other hibernators, then some of our largest animals of ca. 300 g were theoretically fat enough to hibernate for 18 months and still emerge within the normal range of body weights seen in spring.

Animals may go into summer hibernation to avoid predators and/or avoid expending unnecessary energy when there is little nutritious food in the area, resulting in no opportunity to successfully breed. If they bred, the resultant young will not have sufficient food resources to both grow and fatten up in time for the onset of winter hibernation, given that they will have barely 6-8 weeks in which to do so after being weaned and the adults will have depleted the available food already. In which case, why do some older glis appear above ground and active during non-breeding years? The results of this study show that the majority (69 %) of all animals (i.e. all ages) seen in nest boxes in 2012 (a non-breeding year) were born in 2011. A likely explanation is that these young animals did not gain enough weight in their first year to survive more than one winter in hibernation, and therefore had no choice but to emerge and stay active. A limitation to this explanation is that only one year was analysed. This is because animals under 100 g were not PIT tagged until 2009 as it was previously thought these individuals were unlikely to survive the winter. Weight is not a precise method of determining age as this study has recorded a few examples of nestlings gaining over 150 g within two months prior to hibernation (in a good food year) so without microchipping young animals still in the nest, it is difficult to determine the following spring from weight alone exactly in which year animals were born. The only non-breeding year to occur since 2009 was 2012 and therefore the only year used in the analysis. Future data could be analysed to test this theory.

This species can be a chronic pest problem causing damage and nuisance (Trout & Mogg, in press). Summer hibernation by a significant proportion of the local population would make planning and executing short term population control operations problematic. Locating animals would be difficult when they are underground in concealed chambers only to emerge the next year when (apparently successful) control has ceased. Longer term solutions would need to be investigated and implemented to permanently reduce pest problems. The hibernation habits and social nature of this species should be considered. Controlling animals at the hibernation site could be a humane, effective and safe solution that could be investigated in future work, i.e. if they can be drawn to artificial hibernacula. Summer hibernation means that permanent marking of animals is necessary to really understand the population dynamics of this species. Without this, it would be difficult to determine true population level and trends and survival results would be misinterpreted.

Radio tracking has so far been unable to determine where animals go during non-breeding years, this is because radio tracking studies have not been operational during a non-breeding summer due to budget limitations. Whilst there have been reports of long term hibernation in some other mammals species (e.g. 250-350 days for a captive marsupial, Geiser 2007), there is no proof reported for wild living glis Hoelzl et al. (2015). Although the findings of this study support the theory of winter + summer + winter hibernation (> 500 days), other explanations cannot yet been ruled out. Further research to confirm if wild glis in England go into summer hibernation is ongoing using radio location of hibernacula. Whether they behave the same way when living in buildings and the implications of this on planning appropriate population control is under investigation. The mast production years may be related to the climatic variables the year before as the flower anlagen may be developed the previous year, thus potentially giving a warning of a good or poor glis breeding season. Summer hibernation in non-breeding years would have significant implications on pest control in buildings by requiring a two year control programme. That many properties have repeated infestations tacitly supports the non-capture of some individuals – either from trap-shy individuals or from those hibernating in the summer, or re-infestation via poor glis proofing of houses.

Acknowledgements

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