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## **Seasonal survival in a non-hibernating Mediterranean garden dormouse population**

Adrià Viñals-Domingo<sup>\*1</sup>, Sandro Bertolino<sup>2</sup>, Germán López-Iborra<sup>3</sup> and José Antonio Gil-Delgado<sup>1</sup>

<sup>1</sup> Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Carrer del Catedràtic José Beltrán Martínez, 2, 46980, Paterna (Valencia), Spain

<sup>2</sup> Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina, 13, 10123, Turin, Italy

<sup>3</sup> Departamento de Ecología/IMEM Ramon Margalef, Universidad de Alicante, Carretera de San Vicente del Raspeig s/n, 03690, San Vicente del Raspeig, (Alicante), Spain

Corresponding author: [avido2@uv.es](mailto:avido2@uv.es)

### **Abstract**

The seasonal survival pattern of a garden dormouse *Eliomys quercinus* population was studied in a Mediterranean agricultural field area from East Spain, a geographical location in which this species does exhibit no hibernation. Individuals were captured from nest - boxes checked monthly during a four year period. Data were analysed using an open population Cormack–Jolly–Seber model including sex, age class and season as factors. Best models included the effect of age and differences in survival between adult males and females. Survival rate was more variable between seasons in males than in females or juveniles. Maximum adult male survival was reached in autumn, decreased in winter and dropped to very low values in spring and summer. Survival of adult females was higher and presented a less marked seasonal pattern. Seasonal survival of juveniles was fairly constant along the year. Recapture probability also varied seasonally and was twice in winter than in the rest of the year. The local annual survival rate obtained in adult females exceeded the survival rate observed in some garden dormouse populations from Italy, but it was considerably lower in comparison to the values obtained in South Spain and France. The possible energetic consequences of the constant sexual activity exhibited by this garden dormouse population and the effect of other factors such as the availability of food and social interactions between individuals seem to influence in the seasonal variations in survival rate for this rodent species in this agricultural habitat.

**Keywords:** Dormouse, *Eliomys*, Survival, Mediterranean, Agricultural land

## Introduction

Understanding the factors involved in animal population dynamics is a basic issue in conservation biology (Beissinger and Westphal 1998; Lebreton et al. 1992). All animal species are characterized by a trade-off between the energetic cost of reproduction and their consequent possibilities to survive (Huber et al. 1999; Koivula et al. 2003). In addition, many species must also cope with other external factors as the variation of environmental conditions and the seasonal limitation of available resources (Lebl et al. 2011; Lindström 1999). Among mammals, different strategies have been observed referring how species can confront these constraints. For instance, big sized and long living species are able to cope with difficult seasons investing a higher effort in survival whereas reproduction events are restricted only to favourable periods (Healy et al. 2014; Lindstedt and Boyce 1985). Nevertheless, seasonal changes in local conditions can represent an important challenge for some groups of short living species as small mammals (Merritt et al. 2001).

A particular example of small mammal group adapted to a wide range of environmental conditions can be found in dormice species (Bertolino et al. 2016; Lebl et al. 2011). This rodent family is characterized by some particular traits such as the possibility to hibernate during unfavourable periods and the ability to skip reproduction when resources are scarce (Bieber 1998; Pilastro et al. 2003; Turbill et al. 2011). All these characteristics have been suggested as main factors explaining the high survival rates and the relative long lifespan observed in some populations of fat dormouse *Glis glis* and hazel dormouse *Muscardinus avellanarius* in north and central Europe (Bieber et al. 2012; Juškaitis 2014; Lebl et al. 2011). On contrary, information related to other dormice species and habitats is still scarce in literature, especially those from Mediterranean areas where inactivity period can be shorter or even absent (Gil-Delgado et al. 2006; Moreno 1984).

The garden dormouse *Eliomys quercinus* is a medium-sized small mammal that occupies many different European habitats (Bertolino et al. 2008; Moreno 2002; Storch 1978). Across its distributional range, the life-history tactics of this rodent vary considerably. Thus, whereas short periods of activity and a single litter per year have been documented in northern habitats; Mediterranean populations showed a complete lack of inactivity and reproduction events occur throughout the year (Bertolino and Currado 2001; Gil-Delgado et al. 2006). In this study, we analyse the seasonal survival rate of the garden dormouse in a Mediterranean agricultural field recently colonized where the species do not enter winter hibernation.

## Material and methods

### *Study area*

The study was conducted in a citrus tree plantation of 16.92 ha, located in Sagunto (Valencia), Spain (39° 42' N, 0° 15' W, 30 m a.s.l.) near the Mediterranean coast. The complete area is

covered by orange (*Citrus sinensis*) and mandarin (*Citrus reticulata*) trees. The climate is Mediterranean with mild winters and temperatures that do not normally drop below 5° C and hot summers of up to 40° C (Ninyerola et al. 2005). Further information about the study is available (Gil-Delgado et al. 2005).

## Methods

Around 40-60 nest-boxes (14 × 14 × 20 cm; 30 mm entrance hole diameter) were distributed randomly through the study area. The number of nest-boxes varied in some months for theft. Nest-boxes were checked at least once per month between January 2009 and January 2013, with the aim to reduce disturbance to dormice and other species that occupied them. All individuals found into the nest - boxes were picked up with the use of a pair of steel scissor tongs protected with rubber covers on the edges that ensured that animals could be immobilized and transferred to cylindric plastic containers with perforated lids for the shortest time possible. During the handling procedure, no animal showed significant levels of visual stress or signs of pain. Later, animals were weighted by an electronic scale to the nearest centigram. All dormice heavier than 10 g were provided with a numbered ear tag (National Band and Tag Co. model 1005 - 1, Newport, Kentucky, USA) and aged according to their weight and fur colour in three different categories: adults (more than 60 g), juveniles (between 45 and 60 g) and pups (less than 45g) (Abad 1987; Moreno 1988; Palacios 1974). Sex and reproductive status of adults and juveniles were determined according to their external sexual characteristics. Both first captured and recaptured animals were immediately released into the same nest-box after handling.

## Statistical analysis

Cormack–Jolly–Seber (CJS) model, an open population capture–recapture model that provides separated estimates of the apparent local survival ( $\phi$ ) and the recapture ( $p$ ) probabilities, was used (Cooch and White 2006). Each monthly revision of nest-boxes was considered a capture occasion (45 in total, after excluding 5 occasions with no captures). Variations in revision dates between months were taken into account by considering unequal time intervals between capture occasions. We started with models that considered the effect on survival of the factors age (adults and juveniles), sex (males and females) and season (t), defined as: winter (December, January and February); spring (March, April and May); summer (June, July and August) and autumn (September, October and November). Seasonal variation in monthly survival was modelled forcing the survival in the three consecutive months within a season to be the same and constant between years. The age effect was modelled by including a different juvenile survival parameter for the intervals between capture occasions until 87 days after marking. After that time juvenile survival is considered the same than adults. This specific age interval of 87 days was selected based on the observations of the minimum number of days in which an individual marked as a pup was recaptured again showing all the characteristics of an adult; and contrasted by previous references on the time needed for a dormouse to reach sexual maturity (Santini 1983).

Seasonal apparent survival was calculated by raising the monthly apparent survival to the third power, considering that the monthly apparent survival was constant within a season. Annual apparent survival was calculated by multiplying the four seasonal survivals included in a year. All models were performed in the software Mark (White and Burnham 1999) considering different combinations of three main factors: sex (s), season (t) and age (a). A set of candidate models was designed considering

the different combinations of factors potentially affecting survival while recapture probability was only modelled as variable between seasons or constant (see Table 1). Goodness of fit (GOF) tests was performed with the most general model considered using the program RELEASE (Burnham et al. 1987). The parametric bootstrap implemented in program mark was also used for testing the goodness of fit and variance inflation factor (c) was calculated according to Cooch and White (2006). Akaike's information criterion corrected for small sample sizes (AICc), as implemented in Mark program, was used to order the different models generated according to their plausibility (Burnham and Anderson 2002). We used Akaike weights (w), to obtain estimates of apparent survival and recapture probability through model averaging using the subset of models whose weight was  $>0.1$ . Differences in the number of annual marked and recaptured individuals and between sexes and years were tested using contingency tables. All other statistical analysis were performed using the SPSS statistical package, v.17.0 (SPSS Inc. Chicago, IL, USA).

## Results

### Capture-Recapture data

In total, 279 dormice were captured and marked during the study period: 78 adults, 29 juveniles and 172 pups. From the total number of individuals marked, 80 (28.67 %) were recaptured during 124 different instances: 53 dormice were recaptured once, 17 individuals were recaptured twice, 5 were recaptured three times, 3 were recaptured four times, and 2 individuals were recaptured five times. Based on the age classes, 30 out of 172 pups marked (17.4%) were recaptured in consecutive sessions. 9 out of 29 juveniles (31.03%) marked were recaptured whereas 41 out of 78 adults (52.56%) were trapped again (Table 2). There were no significant differences in the number of animals captured and recaptured per year during the whole period ( $\chi^2_{(3)} = 1.86, p = 0.6011$ ). Regarding the number of adult individuals trapped per year, no variation in the number of males and females was observed per year during the whole study period ( $\chi^2_{(3)} = 4.594, p = 0.204$ ). Maximum observed lifespan was 334 days for a female and 250 days for a male, both of them found as new born pups in the study area.

### Model evaluation

The GOF tests of the most general model ( $\phi(s^*a^*t)$ ,  $p(t)$ ) provided by the program RELEASE were far from significance (TEST 2,  $\chi^2_{(17)} = 1.64$ ; TEST 3,  $\chi^2_{(22)} = 2.58$ , both  $p > 0.9$ ), thus there were no significant departures from assumptions of CJS model. The bootstrap goodness of fit test of the general model was also not significant ( $p = 0.430$ , 100 runs in the bootstrap) and the variance inflation factor was close to 1 ( $\hat{c} = 0.973$ ) showing that there was no overdispersion. In a first step we fitted two versions of the most general model for survival, with capture probability constant or variable along seasons, and the second one presented lower AICc value (Table 3) thus in subsequent models capture probability was considered to vary among seasons. Among these models, the lowest AICc value was obtained for the model with survival of adult males variable seasonally and the survival of adult females and juveniles constant ( $\phi(\sigma^{\text{ad}}(t) \text{ } \text{ } \text{ad}(.), \text{juv}(.)); p(t)$ ). However, a model considering the additive effect of sex and season on adult survival while survival of juveniles was constant ( $\phi(\text{ad}(s+t), \text{juv}(.)); p(t)$ ) was almost as good as the first model ( $\Delta\text{AICc} = 0.87$ ; Table 2). In the third best model survival variation was additive for juveniles and adult males and females.

Best models always included an effect of sex on adult survival. Model averaging estimates from the three best models showed that female survival was higher than that of male survival during most of the year. Seasonal variation of survival was higher marked for males than for females or

juveniles (Fig. 1). Seasonal survival of males, calculated from monthly survival, was relatively low in winter (0.32), decreasing dramatically in spring (0.11) and summer (0.14) and increasing again in autumn (0.99). Females showed a similar trend with values higher than males (winter: 0.66, spring: 0.55; summer: 0.54) but showing a lower apparent survival in autumn (0.77). Regarding juveniles, survival (both sexes pooled) in winter (0.16) and autumn (0.20) was lower compared to the values observed in adults, while values were similar to adult males in spring (0.14) and summer (0.13). Male annual survival, calculated from seasonal values, is much lower (0.005) than the annual survival rate of adult females (0.15).

The probability of recapture of individuals in the nest-boxes showed also a significant seasonal variation (Fig. 2). Recapture probability was higher in winter (0.63, SE = 0.08), and lower in the rest of the year with similar values in spring (0.36, SE = 0.08), summer (0.24, SE = 0.07) and autumn (0.33, SE = 0.07).

## Discussion

Our research represents one of the few garden dormouse population studies conducted by checking nest-boxes, in comparison to other studies in which individuals were captured by using live traps (Amori et al. 2015; Schaub and Vaterlaus-Schlegel 2001). Despite the methodological difference, we captured a high number of animals belonging to all age classes and sexes, evidencing that the use of nest-boxes represents an appropriate method to capture garden dormice, as it has been extensively applied to other dormouse species (Juškaitis 2006; Madikiza et al. 2010; Viñals et al. 2012). Furthermore, this technique allowed us to include the sample of some individuals that do not enter easily in traps as altricial pups, juveniles and lactating females (Drickamer et al. 1999; Lewellen and Vessey 1999; Truszkowski 1974). In effect, due to its advantages, we expected also that nest-boxes could provide a safer environment for dormice increasing in consequence the number of recaptures in a simplified habitat as orange groves (Czeszczewik et al. 2008). But contrary to our expectations, the number of recaptures obtained in our study was low, and only a few individuals were recaptured more than once. Curiously, this particular pattern also agreed with reports from other habitats where it was suggested that garden dormice were not recaptured more frequently because these rodents could avoid entering in live traps based on their previous experience (Amori et al. 2015, Vaterlaus-Schlegel 1997). In our case, we cannot exclude that other causes as our handling protocol, could have a negative impact on the permanence of dormice in the nest-boxes, forcing perhaps some individuals to move to an alternative canopy tree or burrow nest, reducing in consequence the number of recaptures (Bertolino and Cordero di Montezemolo 2007; Shibata et al. 2004). For instance, we observed that after a litter was found and handled, the female occasionally relocated all the pups to a different nest-box nearby. A similar anti-predatory strategy regarding the use of different nesting places has also been reported in the edible dormouse *Glis glis* as consequence of the handling procedure or the presence of natural predators (Kukalová et al. 2013; Pilastro 1992).

The annual survival rate estimated in garden dormice in orange groves was low, in concordance with other authors that describe this rodent as a short-living species (Amori et al. 2015; Schaub and Vaterlaus-Schlegel 2001). We found that male adults in orange groves showed a monthly survival rate comparable to the lowest values estimated in North and Central Italy, for which sex differences, however, were not considered (Amori et al. 2015). Survival of females in our study area, despite being higher than male's during most of the year, was lower in comparison to other populations in South Spain (Amori et al. 2015) and Central Europe (Vaterlaus-Schlegel 2001).

Differences in survival between populations are not linked to the presence of hibernation. Amori et al. (2015) found higher annual survival (0.38) in a population in Southern Spain, where hibernation did not occur than in two populations on mountain areas in Italy where snow cover is present for several months in winter, and whose annual survival was similar to our estimates. In addition, annual survival estimated in a Central European population where dormice hibernate between November and March was very similar (0.38) to the one reported in South Spain (Schaub and Veterlaus-Schlegel 2001). For many hibernators such as dormice species, an increase in the period of activity represents a higher energetic cost, due to the extended reproduction effort, and survival costs due to a higher exposure to predators and other intraspecific interactions (Lebl et al. 2011; Turbill et al. 2011; Schaub and Vaterlaus-Schlegel 2001). However, despite that the avoidance of hibernation might have demographic implications in our population, these comparisons suggest that other factors could be more important to determine variation in annual survival among populations.

Our best models found a clear effect of sex, age and season on survival. In our study female survival was higher than male survival in all seasons except autumn. In previous studies, Amori et al. (2015) seem to have not analysed the effect of sex on survival, while Schaub and Veterlaus-Schlegel (2001) found an additive sex effect in their second best plausible model considering bimonthly survival variation. According to this model female survival rate was up to 15% higher than male survival rate. In our population, out of autumn, female monthly survival was 25-70% higher than male survival, a difference even larger if transformed to bimonthly survivals, which could have facilitated the detection of the effect of sex despite the lower sample size in our study. Schaub and Veterlaus-Schlegel (2001) expected lower survival for garden dormouse males since they do not assist in offspring rearing, but try to mate again and take more risks than females. Our results agree with this prediction but raise the question of why between sex difference is larger in our population than in theirs in Central Europe. Extended reproductive season could be a potential explanation but as we showed before there is not a clear relation with the lack of hibernation. Studies conducted with other dormouse species such as hazel dormouse and fat dormouse found variability in the effect of sex in survival. Some authors found that dormouse males survived more than females during the breeding season as a response to the cost of lactation (Berg and Berg 1990; Juškaitis 2013) while other studies found no significant differences between sexes (Lebl et al. 2011, Mortelliti et al. 2014).

Seasonal variation of survival was also found in Central Europe by Schaub and Veterlaus-Schlegel (2001), that estimated survival close to 1 in their winter (November to February) and bimonthly survival rate out of winter varying between years between 0.72 and 0.96. These last estimates are quite larger than equivalent bimonthly survival for males in our study area out of autumn (0.22-0.47 calculated as the square of monthly estimates) and somewhat larger than same parameters for females (0.66-0.75). Therefore, difference in annual survival between our study population and that of Schaub and Veterlaus-Schlegel (2001) is not explained by the lack of hibernation, since survival during spring and summer is lower in Sagunto, especially for males. A possible explanation for the low survival in spring could be the high cost derived from the long periods of reproduction in autumn and winter (Baudoin 1980, Mann 1976; Fietz et al. 2004). In the case of summer, the high temperatures and the scarcity of food typical of this season could suppose the main reason of mortality in Mediterranean habitats as it has been found in other rodent species (Moreno and Kufner 1988, Sunyer et al. 2016). For instance, Santoro (2017) reported a decrease in the abundances of wood mouse *Apodemus sylvaticus* and Algerian mouse *Mus spretus* in South Spain for this season. Similar results were also evidenced by Saiz-Elise (2012) in a community of small mammals in a mountainous area of East Spain. However, we cannot rule out the possibility that in summer dormice moved to other better insulated nests available such as arboreal natural nests or cavities, reducing their detectability. A similar strategy has been suggested for this and other dormouse species (Moreno 2012; Madikiza et al. 2010; Panchetti et al. 2004, Shibata et al. 2004).

Like in other populations that present hibernation, in our study area there is also one season with very high monthly survival ( $>0.9$ ), that is Autumn. A possible explanation for this result is that in this season there is a high availability of oranges, a main food in the diet of garden dormouse in this area, could provide enough resources to reduce the mortality in the population (Gil-Delgado et al. 2010). Seasonal variation of survival was more marked in males, and we found that in winter male survival was reduced by a third in comparison to autumn's value. The lower survival of male during winter might have resulted from a higher mobility when searching for the few females in oestrus available (Greenwood 1980; Waterman et al. 2007). But also due to the aggressive territorial behaviour showed by the breeding females raising their litters (Baudoin 1980, Bertolino et al. 2001).

In the case of juveniles, our results showed a constant and low survival rate throughout the year. It is generally assumed that both the smaller body size as well as the lack of experience can represent two decisive factors increasing mortality in small mammals (Koivunen et al. 1996; Promislow and Harvey 1990). However, it is likely that the low juvenile apparent survival could also be reflecting the effect of dispersion (Dobson 1982; Goundie and Vessey 1986). Previous information studying the space use in garden dormouse described the social structure of this rodent as a composition of sedentary groups of adults that occupy relatively small home-ranges of few hectares and juveniles that are forced to disperse to other patches (Badouin 1980; Bertolino et al. 2003; Vaterlaus 1998). In addition, our study site is inserted in a continuous and homogeneous farmland where resources are available throughout the year and where no important barriers limit dispersion. Secondly, the number of juveniles captured was relatively low compared to the number of litters and also considering that reproductive events occurred through the year (Viñals et al. 2012). Finally, we have evidences of two individuals marked previously as pups and found dead in a different orchard about 1500 m away from our study area; evidencing that juvenile dormouse may disperse relatively long distances. Juvenile dispersion is not completely comprehended in garden dormouse but it has been observed how juvenile of other dormice species can cover longer areas depending on the availability of resources and the necessity of finding new territories (Cornils et al. 2017; Juškaitis 1997).

Dormice have expanded recently in the orange groves of Eastern Spain as a result of a recent colonization event (Gil-Delgado et al. 2006). Previous studies from our same area evidenced a significant high reproductive capacity for the species based on the constant occurrence of births throughout the year the high litter size (5.4 pups/litters) and the communal nesting strategy between females (Viñals et al. 2012, 2017). We think that this reproductive success can be a key factor explaining this fast expansion. Although it is still needed more information on the causes that determine variation of survival in this population it is known that abundance, recruitment and survival of some rodent species can be reduced in agricultural habitats such as orchards due to the constant management and transformations (Sullivan et al. 2004). It is fundamental to have a better knowledge of the spatial ecology of this species to understand the dynamics of this population and to predict the risk of local extinction, something that has been already detected in other populations (Bertolino 2017; Moreno et al. 2016). Special attention will need to be paid also to assess the negative effects of climate change expected in areas of South Europe (Bindi and Olesen 2011), which has been highlighted as a potential threat of extinction to garden dormouse and other some small mammals species occurring in the edge of their distributional range (Maiorano et al. 2011; Santoro et al. 2017). Considering that the garden dormouse is a currently showing a significant decline in many parts of Europe (Bertolino 2017), this information is needed in order to develop a conservation strategy.

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## References

- Abad PL. 1987. Biología y ecología del lirón careto (*Eliomys quercinus*) en León. *Ecología* 1, 153-159.
- Amori G, Bertolino S, Masciola S, Moreno S, Palomo J, Rotondo C, Luiselli L. 2015. Aspects of demography in three distinct populations of garden dormouse, *Eliomys quercinus*, across Italy and Spain. *Rend. Lincei* 1-12.
- Baudoin C. 1980. Organisation sociale et communications intraspecifiques d'un hibernant. BSc thesis, University of Franche-Comte, 1.
- Beissinger SR, Westphal MI. 1998. On the use of demographic models of population viability in endangered species management. *J. Wildl. Manage.* 62(3), 821-841.
- Berg L, Berg Å. 1999. Abundance and survival of the hazel dormouse *Muscardinus avellanarius* in a temporary shrub habitat: a trapping study. *An. Zool. Fennici* 39, 159-165.
- Bertolino S, Currado I. 2001. Ecology of the garden dormouse (*Eliomys quercinus*) in the Alpine habitat. *Trakya University Journal of Scientific Research B* 2(2), 75-78.
- Bertolino S, Viano C, Currado I. 2001. Population dynamics, breeding patterns and spatial use of the garden dormouse (*Eliomys quercinus*) in an Alpine habitat. *J. Zool.* 253(4), 513-521.
- Bertolino S, Cordero di Montezemolo N, Currado I. 2003. Home ranges and habitat use of the garden dormouse (*Eliomys quercinus*) in a mountain habitat in summer. *Acta Zool. Acad. Sci. Hung.* 49(1), 11-18.
- Bertolino S, Cordero di Montezemolo N. 2007. Garden dormouse (*Eliomys quercinus*) nest site selection in an alpine habitat. *Ethol. Ecol. Evol.* 19(1), 51-60.
- Bertolino S, Amori G, Henttonen H, Zagorodnyuk I, Zima J, Juškaitis R, Meinig H, Kryštufek B. 2008. *Eliomys quercinus*. The IUCN Red List of Threatened Species 2008: e.T7618A12835766
- Bertolino S. 2017. Distribution and status of the declining garden dormouse *Eliomys quercinus*. *Mamm. Rev.* 47(2), 133-147
- Bieber C. 1998. Population dynamics, sexual activity, and reproduction failure in the fat dormouse (*Myoxus glis*). *J. Zool.* 244 (2), 223-229.
- Bieber C, Juškaitis R, Turbill C, Ruf T. 2012. High survival during hibernation affects onset and timing of reproduction. *Oecologia* 169, 155-166
- Bindi M, Olesen JE. 2011. The responses of agriculture in Europe to climate change. *Reg. Environ. Change* 11(1), 151-158.

- Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH. 1987. Design and analysis methods for fish survival experiments based on release - capture, American Fisheries Society Monograph 5, Bethesda, Maryland, USA, 437 pp.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science Business Media.
- Cooch E, White G. 2006. Program MARK: A Gentle Introduction, 4th edition. Available at: <http://www.phidot.org/software/mark/docs/book/>.
- Cornils JS, Hoelzl F, Rotter B, Bieber C, Ruf T. 2017. Edible dormice (*Glis glis*) avoid areas with a high density of their preferred food plant-the European beech. *Front. Zool.* 14(1), 23.
- Czeszczewik D, Walankiewicz W, Stanska M. 2008. Small mammals in nests of cavity-nesting birds: Why should ornithologists study rodents? *Can. J. Zool.* 86(4), 286-293.
- Dobson FS. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.* 30, 1183-1192.
- Drickamer LC, Feldhamer GA, Mikesic DG, Holmes CM. 1999. Trap-response heterogeneity of house mice (*Mus musculus*) in outdoor enclosures. *J. Mammal.* 80 (2), 410-420.
- Fietz J, Schlund W, Dausmann KH, Regelman M, Heldmaier G. 2004. Energetic constraints on sexual activity in the male edible dormouse (*Glis glis*). *Oecologia* 138(2), 202-209.
- Gil-Delgado JA, Marco E, Paredes M, Vives-Ferrándiz C. 2005. Seasonal clutch size variation of multi-brooded bird species: comparisons between breeding season and latitudes. *Ibis* 147, 206-212.
- Gil-Delgado JA, Cabaret P, Declercq S, Gómez J, Sánchez I. 2006. Winter reproduction of *Eliomys quercinus* (Rodentia) in the orange groves of Sagunto (Valencia, Spain). *Mammalia* 70, 76-79.
- Gil-Delgado JA, Mira O, Viñals A, Gómez J, Banyuls N, Vives-Ferrándiz C. 2010. Diet of the garden dormouse (*Eliomys quercinus* Linnaeus 1766) in orange groves: seasonal variation and use of available resources. *Mammalia* 74(2), 147-151.
- Goundie TR, Vessey SH. 1986. Survival and dispersal of young white-footed mice born in nest boxes. *J. Mammal.* 67(1), 53-60.
- Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28(4), 1140-1162.
- Waterman J. 2007. Male mating strategies in rodents. In: *Rodent Societies: an Ecological and Evolutionary Perspective* (Eds. Wolff JO, Sherman PW), pp. 27-41. Chicago: University of Chicago Press
- Healy K, Guillerme T, Finlay S, Kane A, Kelly SB, McClean D, Kelly DJ, Donohue I, Jackson AL, Cooper N. 2014. Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. Lond. B, Biol. Sci.* 281(1784).
- Huber S, Millesi E, Walzl M, Dittami J, Arnold W. 1999. Reproductive effort and costs of reproduction in female European ground squirrels. *Oecologia* 121(1), 19-24.

- Juškaitis R. 1997. Ranging and movement of the common dormouse *Muscardinus avellanarius* in Lithuania. *Acta Theriol.* 42, 113-122.
- Juškaitis R. 2006. Nestbox grids in population studies of the common dormouse (*Muscardinus avellanarius* L.): methodological aspects. *Pol. J. Ecol.* 54(3), 351-358.
- Juškaitis R. 2014. Summer mortality in the hazel dormouse (*Muscardinus avellanarius*) and its effect on population dynamics. *Acta Theriol.* 59(2), 311-316.
- Koivula M, Koskela E, Mappes T, Oksanen TA. 2003. Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. *Ecology* 84(2), 398-405.
- Koivunen V, Korpimäki E, Hakkarainen H. 1996. Differential avian predation on sex and size classes of small mammals: doomed surplus or dominant individuals? *Ann. Zool. Fenn.* 33: 293-301.
- Kryštufek B, Hudoklin A, Pavlin D. 2003. Population biology of the edible dormouse *Glis glis* in a mixed montane forest in central Slovenia over three years. *Acta Zool. Acad. Sci. Hung.* 49(1), 85-97.
- Kukalová M, Gazárková A, Adamík P. 2013. Should I stay or should I go? The influence of handling by researchers on den use in an arboreal nocturnal rodent. *Ethology* 119(10), 848-859.
- Lebl K, Bieber C, Adamík P, Fietz J, Morris P, Pilastro A, Ruf T. 2011. Survival rates in a small hibernator, the edible dormouse: a comparison across Europe. *Ecography* 34(4), 683-692.
- Lebreton JD, Burnham KP, Clobert, J, Anderson DR. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62(1), 67-118.
- Lewellen RH, Vessey SH. 1999. Estimating densities of *Peromyscus leucopus* using live-trap and nestbox censuses. *J. Mammal.* 80(2), 400-409.
- Lindstedt SL, Boyce MS. 1985. Seasonality, fasting endurance, and body size in mammals. *Am. Nat.* 125(6), 873-878.
- Madikiza ZJK, Bertolino S, Baxter RM, Do Linh San E. 2010. Nest box use by woodland dormice (*Graphiurus murinus*): the influence of life cycle and nest box placement. *Eur. J. Wild. Res.* 56, 735-743.
- Maiorano L, Falcucci A, Zimmermann NE., Psomas A, Pottier J, Baisero D, Rondinini C, Guisan A, Boitani L. 2011. The future of terrestrial mammals in the Mediterranean basin under climate change. *Philos. Trans. R. Soc. B* 366(1578), 2681-2692.
- Mann CS. 1976. Étude du cycle annuel, de la démographie, de l'écologie et du comportement vis à vis de l'espace du lérot *Eliomys quercinus* dans le Briançonnais. BSc thesis, University of Paris VI.
- Merritt JF, Lima M, Bozinovic F. 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. *Oikos* 94, 505-514.
- Moreno S. 1984. Biometría, Biología y Dinámica poblacional del lirón careto, *Eliomys quercinus* (L.) en Doñana. PhD Thesis. University of Granada.

- Moreno S. 1988. Reproduction of garden dormice (*Eliomys quercinus lusitanicus*) in southern Spain. *Mammalia* 52(3), 401–407.
- Moreno S, Kufner, MB. 1988. Seasonal patterns in the wood mouse population in Mediterranean scrubland. *Acta Theriol.* 33(7), 79-85.
- Moreno S. 2002. *Eliomys quercinus* (Linnaeus, 1766). Lirón careto. In: (L.J. Palomo and J. Gisbert, eds.). Atlas de los mamíferos terrestres de España. Dirección general de la conservación de la naturaleza-SECEM-SECEMU, Madrid. pp. 432 – 435.
- Moreno S, Palomo LJ, Fernández MC., Sánchez-Suárez C., Santoro, S. 2016. Pérdida de diversidad en la comunidad de micromamíferos del Parque Nacional de Doñana durante las últimas cuatro décadas. *Galemys* 28, 31-39.
- Moreno S. 2012. Lirón careto – *Eliomys quercinus*. In: Enciclopedia Virtual de los Vertebrados Españoles. Salvador A, Cassinello J. (Eds.). Museo Nacional de Ciencias Naturales, Madrid.
- Mortelliti A, Santarelli L, Sozio G, Fagiani S, Boitani L. 2013. Long distance field crossings by hazel dormice (*Muscardinus avellanarius*) in fragmented landscapes. *Mamm. Biol.* 78(4), 309-312.
- Ninyerola M, Pons X, Roure JM. 2005. Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Bellaterra.
- Palacios F. 1974. Contribución al estudio de la biología y ecología del lirón careto, *Eliomys quercinus* Linnaeus, 1766, en Iberia central. Parte I: Crecimiento, reproducción y nidificación Doñana *Acta Vertebr.* 1, 171–231.
- Panchetti F, Amori G, Carpaneto GM., Sorace A. 2004. Activity patterns of the common dormouse (*Muscardinus avellanarius*) in different Mediterranean ecosystems. *J. Zool.* 262(3), 289-294.
- Pilastro A. 1992 Communal nesting between breeding females in a free-living population of fat dormouse (*Glis glis* L.). *Boll. Zool.* 59, 63–68.
- Pilastro A, Tavecchia G, Marin G. 2003. Long living and reproduction skipping in the fat dormouse. *Ecology* 84(7), 1784-1792.
- Promislow DE, Harvey PH. 1990. Living fast and dying young: A comparative analysis of life - history variation among mammals. *J. Zool.* 220(3), 417-437.
- Santini L. 1983. I roditori italiani di interesse agrario e forestale. CNR, Monograph AQ/1/232, Padova.
- Santoro S, Sanchez-Suarez C, Rouco C, Palomo LJ, Fernández MC, Kufner MB, Moreno S. 2017. Long-term data from a small mammal community reveal loss of diversity and potential effects of local climate change. *Curr. Zool.* 63(5), 515-523.
- Schaub M, Vaterlaus-Schlegel C. 2001. Annual and seasonal variation of survival rates in the garden dormouse (*Eliomys quercinus*). *J. Zool.* 255(1), 89-96.
- Shibata F, Kawamichi T, Nishibayashi K. 2004. Daily rest-site selection and use by the Japanese dormouse. *J. Mammal.* 85(1), 30-37

- Storch G. 1978. *Eliomys quercinus* (Linnaeus, 1766) – Gartenschläfer, in: Niethammer J, Krapp F. (Eds.). Handbuch der Säugetiere Europas Band 1. Rodentia I (Sciuridae, Castoridae, Gliridae, Muridae). Akademische Verlagsgesellschaft, Wiesbaden, pp. 208–225.
- Sullivan TP, Sullivan DS, Hogue, EJ. 2004. Population dynamics of deer mice, *Peromyscus maniculatus*, and yellow-pine chipmunks, *Tamias amoenus*, in old field and orchard habitats. Can. Field Nat. 118(3), 299-308.
- Sunyer P, Muñoz A, Mazerolle MJ, Bonal R, Espelta JM. 2016. Wood mouse population dynamics: Interplay among seed abundance seasonality, shrub cover and wild boar interference. Mamm. Biol. 81(4), 372-379.
- Truszkowski J. 1974. Utilization of nest boxes by rodents. Acta Theriol. 19 (29), 441-452.
- Turbill C, Bieber C, Ruf T. 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proc. R. Soc. Lond. B, Biol. Sci. 278 (1723), 3355-3363.
- Vaterlaus C. 1998. Der Gartenschläfer (*Eliomys quercinus* L.). Ökologie, Populationsstruktur und die Verbreitung in der Schweiz. PhD Thesis, University of Basel.
- Vaterlaus-Schlegel C. 1997. The garden dormouse (*Eliomys quercinus* L.) in the Petite Camargue Alsacienne (nature reserve, Alsace, France). An ecological study by trapping and radio tracking. Natura Croatica 6(2), 233-241.
- Viñals A, Bazán T, Gil-Delgado JA, Gómez J. 2012. No evidence for seasonal litter size variation in a Mediterranean garden dormouse (*Eliomys quercinus* Linnaeus 1766) population. Mammalia 76(1), 77-80.
- Viñals A, Bertolino S, Gil-Delgado JA. 2017. Communal nesting in the garden dormouse (*Eliomys quercinus*). Behav. Process. 135, 25-28.
- White GC, Burnham KP. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (suppl.): 120–138.

**Table 1** Set of models considered for survival of garden dormouse and their biological significance with respect to survival variation. Factors considered are age (*a*), sex (*s*) and season (*t*). No sex or age effect was considered for recapture probability (*p*) that was modelled as variable seasonally (*p*(*t*)) or constant (*p*(.)). Sex effect in juvenile survival was only included in the first model ( $\phi(s*a*t); p(t)$ ), thus in the remaining models no difference in male and female juvenile survival was considered.

Model	Survival variation
$\phi(s*a*t); p(t)$	Different seasonal variation in each combination of age and sex
$\phi(ad(s*t), juv(t)); p(t)$	Different seasonal variation in adult males and females and juveniles
$\phi(s+a+t); p(t)$	Additive seasonal variation in adult males and females and juveniles
$\phi(ad(s*t), juv(.)); p(t)$	Different seasonal variation in adult males and females, constant juvenile survival
$\phi(ad(s+t), juv(.)); p(t)$	Additive seasonal variation in adult males and females, constant in juveniles
$\phi(\text{♂}ad(t) \text{♀}ad(.), juv(.)); p(t)$	Seasonal variation of survival of adult males, constant for adult females and juveniles
$\phi(\text{♂}ad(.), \text{♀}ad(t), juv(.)); p(t)$	Seasonal variation of survival of adult females, constant for adult males and juveniles
$\phi(ad(s), juv(t)); p(t)$	Constant survival in adult males and females, seasonal variation in juveniles
$\phi(t); p(t)$	Seasonal variation with no effect of sex or age
$\phi(ad(t), juv(.)); p(t)$	Seasonal variation in adults and constant survival in juveniles
$\phi(ad(s), juv(.)); p(t)$	Constant survival in adult males and females and juveniles

**Table 2** Compact version of the matrix of capture–recapture data for garden dormouse in orange groves used in the survival analysis. Individuals are classified by age and sex and data are summarized by pooling seasons for all study years. Seasons of the following year are marked with +1. No individual was captured one year or later after release, thus additional columns of seasons would contain zeros as the last spring. a) Adult males; b) Adult females; c) Juveniles of both sexes. For every season all the data from the months included in this season have been summed. Seasons definition is as follows: winter (December, January and February); spring (March, April and May); summer (June, July and August); and autumn (September, October and November). Notation is as follows:  $R_i$  is the number of marked individuals released in occasions  $i$  included in a release season;  $r_i$  is the total number of individuals recaptured to those released at each season; the cell  $ij$  contains the number of individuals released at each season and recaptured for the first time at  $j$ . Given that each season includes several capture and release occasions there are recaptures within the same release season.

a) Adult males

Seasonal event j								
Release season	$R_i$	Winter	Spring	Summer	Autumn	Winter+1	Spring+1	$r_i$
Winter	30	7	6	0	0	0	0	6
Spring	30		4	0	0	1	0	5
Summer	9			0	6	0	0	6
Autumn	24				6	10	0	16

b) Adult females

Seasonal event j								
Release season	$R_i$	Winter	Spring	Summer	Autumn	Winter+1	Spring+1	$r_i$
Winter	19	7	5	0	0	0	0	5
Spring	22		6	8	1	0	0	15
Summer	13			2	3	1	0	6
Autumn	8				0	7	0	7

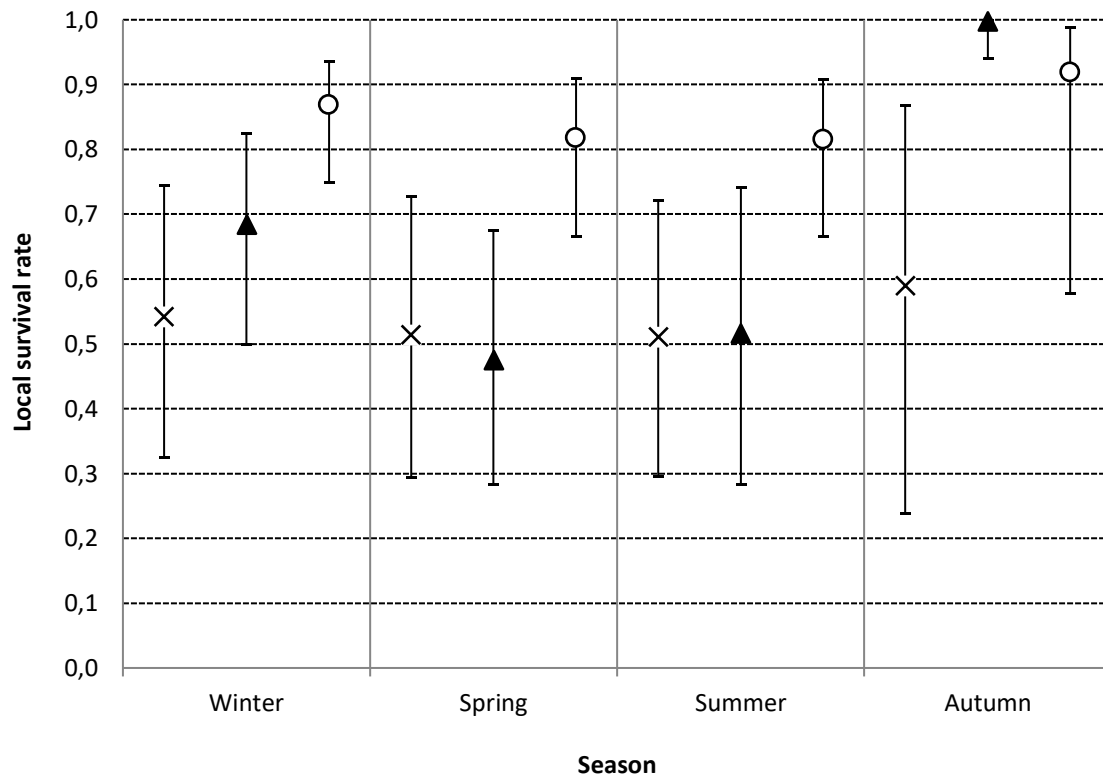
c) Juveniles (both sexes)

Seasonal event j								
Release season	$R_i$	Winter	Spring	Summer	Autumn	Winter+1	Spring +1	$r_i$
Winter	9	2	0	0	0	0	0	0
Spring	12		2	1	0	0	0	3
Summer	8			0	0	0	0	0
Autumn	7				1	3	0	4

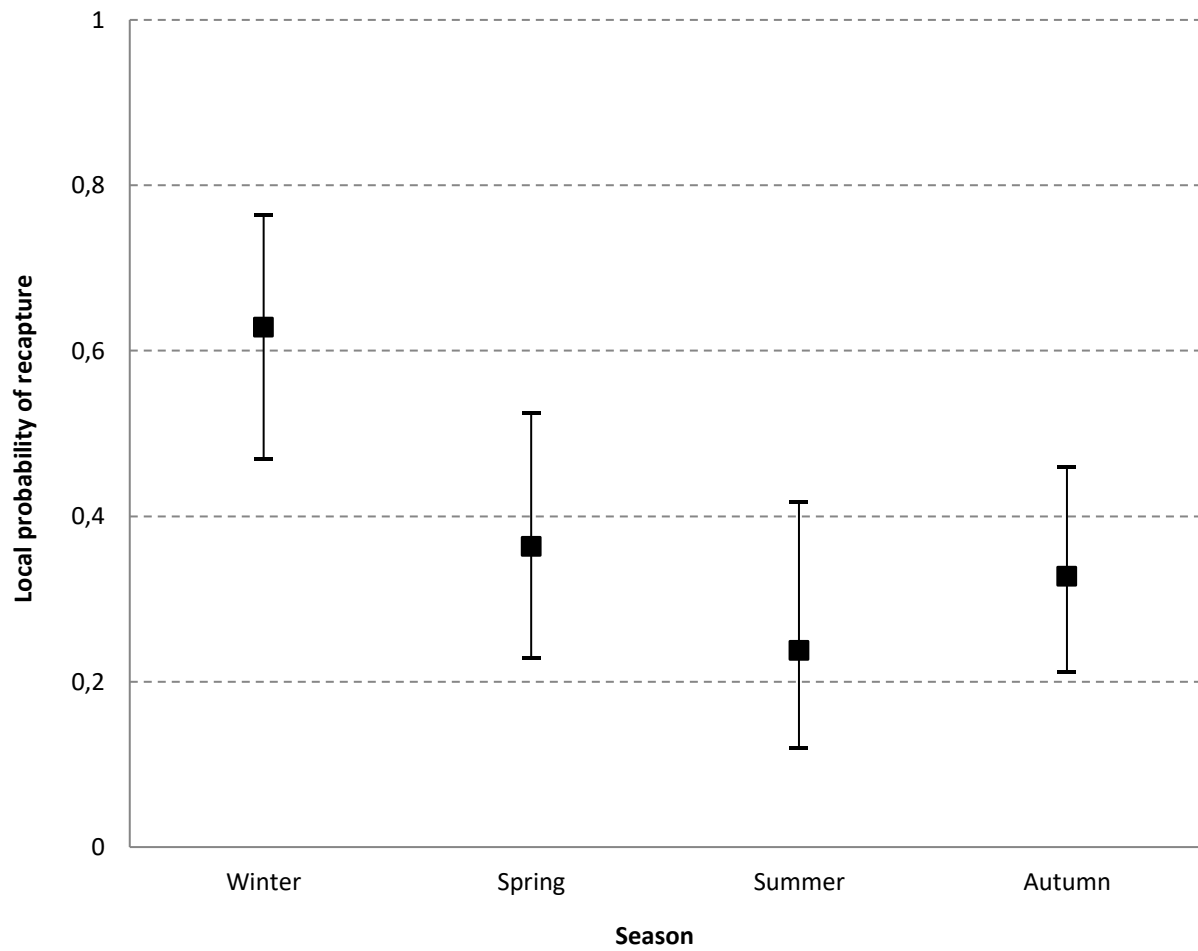
**Table 3** Model selection for garden dormice in orange groves. (AICc: value of the Akaike's information criterion corrected for small sample size;  $\Delta$ AICc: difference between AICc of each model and the best model AICc, K: number of estimated parameters; AICc w: Akaike weight). First two alternative models for probability of recapture (p) were checked and several models for survival were tested using the best model for p.

Model	AICc	Delta AICc	K	Deviance	AICc w
Probability of recapture (p)					
$\phi (s*a*t); p (t)$	441.21	9.40	19	342.70	0.005
$\phi (s*a*t); p (.)$	444.98	13.17	16	353.86	0.001
Apparent survival ( $\phi$ )					
$\phi (\text{♂ ad } (t) \text{ ♀ ad } (.), \text{ juv } ()); p(t)$	431.81	0.00	10	354.71	0.497
$\phi (ad(s+t), \text{ juv } ()); p (t)$	432.68	0.87	10	355.58	0.322
$\phi (s+a+t); p(t)$	434.48	2.67	10	357.38	0.131
$\phi (ad(s*t), \text{ juv } ()); p(t)$	436.85	5.03	13	352.86	0.040
$\phi (ad(s*t), \text{ juv } (t); p(t)$	441.84	10.03	16	350.72	0.003
$\phi (ad(t), \text{ juv } ()); p(t)$	444.82	13.01	9	369.96	0.001
$\phi (ad(s), \text{ juv } ()); p(t)$	447.01	15.20	7	376.55	0.000
$\phi (t); p(t)$	447.72	15.90	8	375.06	0.000
$\phi (\text{♂ ad } (.), \text{ ♀ ad } (t), \text{ juv } ()); p(t)$	451.80	19.99	10	374.70	0.000
$\phi (ad(s), \text{ juv } (t)); p(t)$	452.19	20.38	10	375.08	0.000





**Fig. 1** Monthly apparent survival for the *Eliomys quercinus* population occurring in Spanish orange groves ( $\pm$  95% Confidence Interval), calculated through model averaging using the three best models of Table 2. Empty circles (○) correspond to adult females, black triangles (▲) correspond to adult males and black crosses (X) correspond to juveniles. The models assume that this value is equal for all the months within a season. Seasons definition is as follows: winter (December, January and February); spring (March, April and May); summer (June, July and August); and autumn (September, October and November).



**Fig. 2** Recapture probability rate ( $\pm$  95% Confidence Interval) of *Eliomys quercinus* in orange groves per season, calculated through model averaging using the three best models of Table 2. Seasons definition is as follows: winter (December, January and February); spring (March, April and May); summer (June, July and August); and autumn (September, October and November).