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Population dynamics and nest site selection of the Hazel dormouse *Muscardinus avellanarius* in Austrian Alps shrubby deciduous woodland habitats.

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Abstract

Studies of *Muscardinus avellanarius* (Linnaeus, 1785) predominantly originate from the edges of its European range and therefore are not easily extrapolated to alpine habitats. Thus, we surveyed a population in the Triebener Moos (Styria/Austria) from 2012 to 2018 using 100 dormouse nest-tubes at 4 study plots. In total, 113 dormice were captured and measured. Overall sex-ratio among adults was even and body mass increased from May to September. Our results show highest population densities in August and in September varying annually between 1.73 and 3.98 individuals per hectare. Annual percentage of nest tubes used by *M. avellanarius* averaged 31%, with a high inter-annual variation in nest-tube occupancy. Principal Component Analysis (PCA) showed that the number of occupied nest tubes decreased with declining diversity of food plants and increasing tree cover.

Introduction

The range of *Muscardinus avellanarius* (Linnaeus, 1785) extends from the Mediterranean to southern Sweden, and from western France to eastern Russia (Mitchell-Jones et al. 1999, Hutterer et al. 2016). With the exception of some Mediterranean ecosystems (Soarce et al. 1998, Sara et al. 2001), *M. avellanarius* spends winter in hibernation (Juškaitis 2008) from October to May (Bright & Morris 1996). Studies of its population biology and habitat use predominantly originate from the edges of its European range, e.g. England (Bright & Morris 1990), Sweden (Berg & Berg 1998, 1999), Lithuania (Juškaitis 2008) and Denmark (Vilhelmsen 2003). Whereas knowledge on *M. avellanarius* in the northern part of its range has increased (review in Juškaitis et al. 2015), we still lack detailed studies of the species in the Alps (c.f. Kahmann & Frisch 1950, Wachtendorf 1951, Catzeflis 1983). Different habitat conditions (climate, vegetation, land use etc.) prompted Büchner & Lang (2014) to question whether the results of these investigations are conferrable to populations in Germany and the same doubts apply to *M. avellanarius* in Austria. The conservation status of *M. avellanarius* in the European Union (FFH directive 92 / 43 / EEC, appendix IV) deteriorated from favourable (report period 2007–2012) to unfavourable-inadequate (report period 2013–2018). In addition, population declines are reported from England (Goodwin et al. 2018), Denmark (Vilhelmsen 2003),

Sweden (Berglund & Persson 2012), and Belgium (Verbeylen 2009, Verbeylen et al. 2017). Together with possible negative effects of global climate change (Goodwin et al. 2018), these circumstances require better knowledge of the species' biology and habitat use. Our recent long-time survey (data from 2011–2018) in the alpine valleys contributes to this. Alongside other long-term monitoring studies in various parts of Europe, it provides the basis for a more efficient protection of this endangered species.

Optimal habitats of *M. avellanarius* are known to be rich in shrubs, with scattered trees (Bright & Morris 1990, Juškaitis 2008, Juškaitis & Büchner 2010). Hence, we chose shrubby, sparse deciduous forest areas for our research. Thus, our study might serve as an exemplary for *M. avellanarius* population biology in the centre of its European range. It focuses on the following issues:

- When does *M. avellanarius* mainly use artificial nest sites, and which population densities can be inferred from this?

- When are the first young of the year observed?

- What are summer and autumn body weights of adult dormice, and are there sex-specific differences?

- Which locations does *M. avellanarius* use as nest sites in shrubby, sparse deciduous forests?

Material and Methods

Study sites: The study area (Triebener Moor, WGS84: 14°30' E, 47°30' N, 700 m a.s.l.) is situated in the Paltental in Austria, a longitudinal alpine valley between the foothills of the Eisenerz Alps in the north and the Lower Tauern in the south. Typically for a valley basin, inversions and fog are frequent, with moderately cold winters (average temperature in January: –4 °C) and moderately warm summers (average temperature in July: 16 °C). Mean annual precipitation amounts to 1,306 mm, with the summer maximum in July (158 mm) being almost threefold of the winter maximum in January (54 mm). Annually, 135–150 days are frost-free, and snow cover duration usually extends from November to March, reaching a maximum depth in February (meteorological data: Prettenthaler et al. 2010). Flooding by the Palten river has become rare following extended regulation and during our study period, only one inundation occurred, caused by a long period of torrential rain in July 2012.

The woodland consists of a vast Alder swamp (*Alnion glutinosae*) interspersed with patches dominated by Grey alder (*Alnetum incanae*) and White willow (*Salicion albae*) along the banks of the river Palten, where sparse forests edges with Fen (Phragmitetae) and Forb stands (Filipendulion) connect to the dense deciduous stands. The sparse tree canopy enables growth of a dense shrub layer (predominantly Grey alder *Alnus incana*, Black alder *A. glutinosa*, Black elder *Sambucus nigra*, Willows *Salix* sp., Silver birch *Betula pendula*, and Common snowball *Viburnum opulus*).

Nest tubes: To study *M. avellanarius* population density and nest site selection, we used plastic nest tubes (25 x 6 x 6 cm) with a wooden tray inside protruding from the nest tube opening by approx. 5 cm, meant to facilitate access for the animals (Chanin & Woods 2003, Bright & MacPherson 2002). In each of 4 study plots (A: north, B: east, C: middle, D: west) we placed 25 nest tubes at a height of 1–3 m above the ground on branches of trees and shrubs.
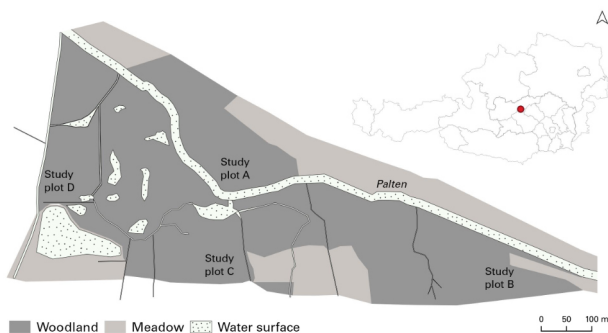

Fig. 1: Location of the study area and the study plots A–D.

Population density: To estimate minimum population density, nest tubes were examined monthly in the years 2011, 2012, 2015 and 2016 from May to October. Dormice found dwelling in the tubes were examined and their body mass (60 g 0,5 g; Kern & Sohn GmbH), age and sex (adult animals) were recorded. We distinguished 2 age classes: adult animals (mass >14 g) and juveniles (mass <7 g); ambiguous individuals (mass of 7 to 14 g) were excluded from

further analyses. To include an edge effect into population density estimates (Kenneth, & Anderson 1985, Tioli et al 2009) we added a 25 m wide boundary surrounding each study plot, resulting in the following sizes: Plot A: 10.7 ha; B: 12.5 ha; C: 9.3 ha and D: 9.9 ha.

Annual percentage of nest tubes utilised: In addition, every year (from 2011 to 2018) in October (except for 2018: in June), after the onset of hibernation, we collected the nesting material from the nest tubes. According to Meyer et al. (2002), Teerink (1991) and Tester & Müller (2000) *M. avellanarius* can unequivocally be identified by species-specific features of medulla and hair texture. Hence, we verified species-specific utilisation of nest tubes by microscopic analyses of hair found in the nesting material. We used these presence data to calculate local abundance as percentage of nest tubes used by *M. avellanarius.*

Habitat attributes: We mapped the vegetation in 2011 and 2017 to determine the influence of different vegetation parameters on the occurrence of *M. avellanarius*. The following variables were recorded within a 3 m radius around each nest tube: height of the herb layer, cover of herb, shrub and tree layer, and number of shrubs providing food suitable for *M. avellanarius*. According to Juškaitis & Büchner (2010), Juškaitis (2007), Juškaitis (2008) and Kahmann and Frisch (1950), we considered the following plants as relevant: Alder buckthorn *Rhamnus frangula* (= *Frangula alnus*), Black elder *Sambucus nigra*, Mountain ash *Sorbus aucuparia*, Common snowball, berries from *Rubus* sp. and *Ribes* sp., Bird cherry *Prunus padus*, European spindle *Euonymus europaeus*, Fly honeysuckle *Lonicera xylosteum*, Norway spruce *Picea abies*, Alder *Alnus* sp., Willow *Salix* sp., and Silver birch *B. pendula*.

We applied a Mann-Whitney U-test to compare annual means of vegetation parameters from 2011 and 2017. For dimension reduction of data and to achieve an overview of linear relationships between *M. avellanarius* presence and vegetation parameters a Principal Component Analysis (PCA) was performed. Correlated vegetation parameters were excluded using the Spearman-correlation matrix, remaining variables were standardised. We used the package FactoMineR of the statistics programme R (Lê et al. 2008) to calculate the principal components. Those with eigenvalues ≥ 1 were considered relevant for the interpretation of our data, and were tested for Spearman rank correlations with *M. avellanarius* presence data of the years 2011–2018.

Results

Population dynamics and abundance (Tab. 1 and Fig. 2): In the years 2011, 2012, 2015, and 2016, in total 113 *M. avellanarius* were captured in the nest tubes. Numbers were highest in August (2011 & 2015) and in September (2012 & 2016), resulting in estimated population densities varying annually between 1.73 and 3.98 individuals per hectare (ind./ha). Plot C showed the highest numbers, with an overall mean population density of 2.74 during the whole study period, and a maximum density of 6.47 ind./ha (August 2011 & July 2015). Densities were lower in Plot B (mean 1.52 ind./ha; maximum 5.62 ind./ha in August 2015), and lowest in plots A and D (<1 ind./ha; maximum in July 2015, A: 4.69 ind./ha, D: 3.65 ind./ha).

Tab. 1: Monthly population densities (adult individuals occupying nest tubes per hectare) of *Muscardinus avellanarius*; averages of the four study plots A-D). - = no data; values in parentheses are absolute changes since the previous month.

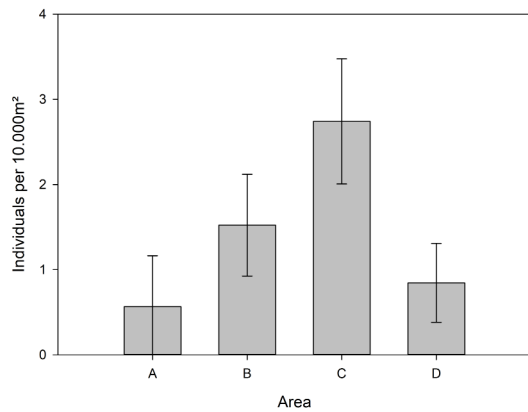| Month \ Year	2011	2012	2015	2016
May	-	-	1.41	0.2
June	-	-	3.05	0.67
July	1.13	0	3.65	1.28
August	2.98 (+1.85)	0.94 (+ 0.94)	3.98 (+ 0.33)	1.26 (−0.02)
September	1.54 (−1.44)	1.73 (+0.79)	1.48	1.97
October	0.5	0.77	0	0.51

Fig. 2: Mean population densities of *M. avellanarius* (pooled means from 2011, 2012, 2015 and 2016 for each study plot A–D).

Nest box occupancy (Figure 3): Annual percentage of nest tubes used by *M. avellanarius* from 2011 to 2017 averaged 30.71% (minimum: 15% in 2012: 61% in 2015). Omission of 2015 as an outlier reduced mean annual nest box occupancy to 25.67%.
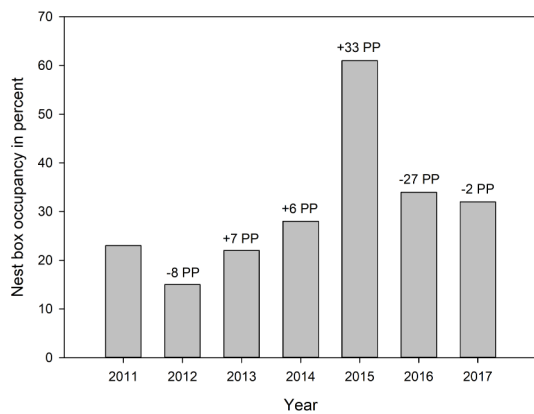

Fig. 3: Annual percentage of tubes utilised by *M. avellanarius* from 2011 to 2017 throughout the study area.

Age classes (Figure 4): Out of 113 live captures, 70 times a dormice was classified as adult (mass > 14 g) and 14 times as juvenile (< 7 g); the remaining ambiguous 29 animals (mass of 7 to 14 g) were excluded. Juveniles were trapped from June to August.
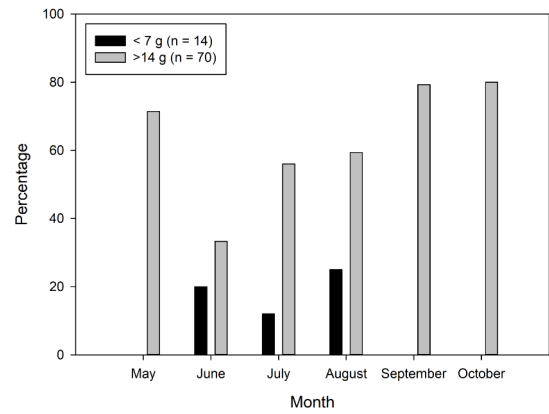

Fig. 4: Monthly percentages of live-captured *M. avellanarius* assigned to age classes. Pooled data from 2011, 2012, 2015 and 2016; rest to 100%: unassigned captures

Sex ratio: With 34 males to 36 females, overall sex ratio among adults approached 1:1. When monthly captures were analysed separately, we found a slight skew towards males in July (m : f = 1.3), a pronounced female bias in August (m : f = 0.6), and a male bias in September (m : f = 1.6).

Body Mass (Table 2 and Figure 5): In summer (June to August) adult *M. avellanarius* body mass averaged 18 g (9 males) and 18 g (15 females) and in autumn (October and November) 24 g (15 males) and 23 g (12 females). In September, adult males were significantly heavier than the females. The small sample size in October allowed no statistical analysis for this month.

Tab. 2.: Statistical comparison of sex-specific monthly body mass of *M. avellanarius* captured throughout the study. df...degrees of freedom; ∅...mean body mass.

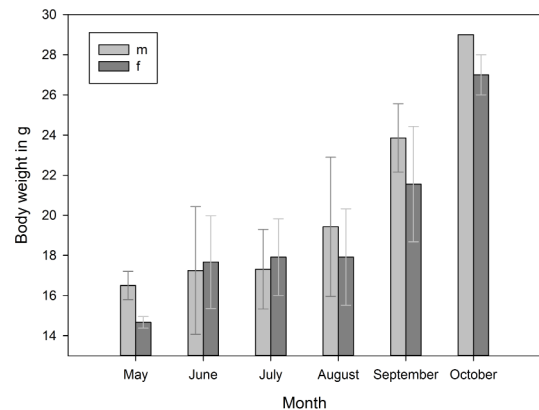|	g(∅), ♂	g(∅), ♀	Mann-Whitney U / t-Test
May	17 (n = 2)	15 (n = 3)	N/A
June	17 (n = 2)	18 (n = 3)	N/A
July	17 (n = 8)	18 (n = 6)	p = 0.577, t = 0.573 (df = 12)
August	19 (n = 7)	18 (n = 12)	p = 0.276, t = −1.125 (df = 17)
September	24 (n = 14)	22 (n = 9)	p(U) = 0.044; U = 31.00
October	29 (n = 1)	27 (n = 3)	N/A

Fig. 5: Monthly body weights of male (m) and female (f) *M. avellanarius* captured throughout the study.

Nest site selection: Vegetation parameters did not change significantly between 2011 and 2017 (height of herb layer: $U = 4732$, $p = 0.5$; cover of herb layer: $U = 4917$, $p = 0.839$; cover of shrub layer: $U = 4330$, $p = 0.093$; cover of tree layer: $U = 4437$, $p = 0.161$; and number of plant species: $U = 4674$, $p = 0.407$). Hence, we used pooled means of both years for further analyses. Cover and height of the herb layer were correlated ($p < 0.05$; Spearman, $r^s = 0.695$) and hence cover of the herb layer was excluded from the PCA. The PCA (Table 3) revealed three principal components that explained 68.96 % of the variance. Number of occupied nest tubes decreased with decreasing diversity of food plants and increasing tree cover (Principal Component 2; $p < 0.001$; Spearman, $r^s = -0.424$). Other correlations with nest tube occupancy were not significant, for either density of shrub layer (PC1; $p < 0.155$; Spearman, $r^s = -0.143$), or herb layer height and nest tube height (PC3; $p < 0.292$; Spearman, $r^s = -0.106$).

Tab. 3.: Factor loadings of the components of the PCA (loadings > 0.6 are bold).

	PC1	PC2	PC3
Eigenvalue	1.255	1.178	1.015
Cumulative variance (%)	25.094	48.650	68.958
Nest tube height	0.451	0.171	**−0.712**
Height of herb layer	0.369	0.378	0.008
Cover of shrub layer	**0.751**	−0.239	−0.042
Cover of tree layer	0.385	**0.698**	0.008
Number of plant species	0.450	**−0.679**	0.221

Discussion

Population density estimates and nest tube occupancy: In different parts of its distribution, estimated minimum population densities of *M. avellanarius* ranges from 1–10 individuals per hectare, with a maximum of 15 in optimal habitats (review in Juškaitis & Büchner 2010, Juškaitis 2008, Juškaitis et al. 2015). Our estimates varied from 1.73 to 3.98 ind/ha in August and September. Preceding studies in the Austrian Alps show similar results: in six wetlands in valleys of the Hohe Tauern, the Niedere Tauern and the Kalkalpen, population densities ranged from 1.2 to 2.5 ind/ha (Blatt & Resch 2015, Resch & Resch 2018, Resch et al. 2019). Our results correspond with those reported by the "National Dormouse Monitoring Programme" in England, where average population densities in 83 monitored sites ranged from 1.75 to 2.5 ind/ha (Bright et al. 2006). In common with similar studies, we observed that use of nest tubes or boxes increased with their number and population density usually decreased after removal of artificial nesting opportunities (Juškaitis & Büchner 2010). Chanin & Gubert (2011) and Verbeylen et al. (2017) reported differences in use of nest boxes compared to tubes, impeding comparison of data acquired with different methods.

M. avellanarius abandons nest boxes earlier in the year in the northern compared to the southern part of their range (Juškaitis et al. 2015). Thus, the cool and rainy climate in the Alps might cause the animals to start hibernating earlier and to abandon the nest tubes during September. Low nest tube occupancy in the Alps in October might be skewed and hence not effectively reflecting population density.

Maximal nest tube occupancy rates of 15–61 % appear high compared to data from studies with wooden nest boxes. In Italy, average nest box occupancy rates in spring varied between 0 and 23.3 % (1991–1997), with a maximum of 47.3 % in evergreen-oak forests (*Quercus ilex*; Sorace et al. 1998). Long-term monitoring (1980–1996) of nest boxes in autumn in different forest sites in Germany (Baden-Württemberg) revealed occupancy rates of 0–7 %, increasing to 15 % in some patches (Gatter & Schütt 1999). In Belgium, in 2014–2016 *M. avellanarius* used annually 39 to 48 % of the available nest tubes (32 to 34 % when also nest boxes were included) in a railway verge with dense edge vegetation, with annually 54 to 82 % of the adults and 35 to 53 % of the known subadults being encountered in the nest boxes or nest tubes during fortnightly checks (Verbeylen et al. 2017). In the present study, inter-annual variation in nest-tube occupancy (−27 and +33 percentage points) also was higher than in these studies. Again, the different methods should be considered when comparing population densities from several studies, especially when many nest boxes or tubes were placed in the study areas.

Demographics

We captured the first young of the year in June, i.e. one month earlier than reported for the Alps by Kahmann & Frisch (1950). In *M. avellanarius'* northern distribution range first litters are born in May, occasionally already in April (Juškaitis 1997, review in Juškaitis 2008 Juškaitis & Büchner 2010, Verbeylen 2012).

In accordance with other studies, overall sex-ratio among adults was even and body mass increased from May to September (Juškaitis 2008, Juškaitis & Büchner 2010, Juškaitis et al. 2015). Mean body mass of males in August was 19 g and of females was 18 g which were similar to those reported by Juškaitis & Büchner (2010). In accordance with data from Lithuania (Juškaitis 2001) and Belgium (Verbeylen et al. 2017), we found sex-specific differences in body mass in September. The lower mass of adult females may negatively influence their winter survival (Juškaitis 2008).

Nest site selection

M. avellanarius is a selective feeder and, lacking a caecum (Flower & Lydekker 1891, Storch 1978) to digest cellulose, it relies mainly on foraging blossoms, fruits, and insects (Bright & Morris 1996). Juškaitis (2008) described an optimal hazel dormouse habitat with a high diversity of potential food resources through the changing seasons with an appropriate structure (well developed, unshaded understorey for flowering and ripening of fruits). This is also shown by our results (PCA) for the Austrian Alps, where decreasing diversity of food plants and increasing tree cover probably yielded lower nest tube occupation rates. In accordance with Bright & Morris (1990, 1996) we conclude that Hazel dormice preferred sites with a high species diversity and sparse canopy, where shrub growth intersects with overlapping branches, facilitating movement, exploration, and foraging.

Acknowledgements

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