Original Investigation

Forest management affects individual and population parameters of the hazel dormouse *Muscardinus avellanarius*

Giulia Sozio\(^a\), Fabiola Iannarilli\(^a\), Ilaria Melcore\(^a\), Matilde Boschetti\(^b\), Daniele Fipaldini\(^a\), Matteo Luciani\(^a\), Davide Roviani\(^c\), Andrea Schiavano\(^d\), Alessio Mortelliti\(^a,e,∗\)

\(^a\) Department of Biology and Biotechnology “Charles Darwin”, University of Rome “La Sapienza”, Viale dell’Università 32, 00185 Rome, Italy
\(^b\) Department of Biology, University of Pisa, Via A. Volta 4/6, 56126 Pisa, Italy
\(^c\) Department of Life Science, University of Siena, Via Aldo Moro 2, 53100 Siena (San Miniato), Italy
\(^d\) Department for Innovation in Biological, Agro-food and Forest Systems (DIBAF), University of Tuscia, Via San Camillo de Lellis snc, 01100 Viterbo, Italy
\(^e\) Fenner School of Environment and Society, Australian Research Centre for Environmental Decisions, National Environmental Research Program, The Australian National University, Canberra, ACT 0200, Australia

**Article info**

**Abstract**

Several studies have shown that forest management (e.g. for timber production) affects mammal communities. Nevertheless, we still lack a detailed understanding on how different management practices influence individuals and populations. The overarching goal of our work was to investigate the demographic response of the hazel dormouse (*Muscardinus avellanarius*) to forest management. We focused on a set of key individual (survival and litter size) and population (abundance of individuals) parameters to test whether forest management affects dormice and which habitat variables are responsible for such effects. We surveyed a dormice population for 3 years in a continuous forest in central Italy including sites subjected to different management regimes: 5 coppiced stands (2 recently coppiced and 3 old coppice stands), 2 abandoned stands with regrowing forest and 3 high forest stands. We found a strong effect of forest management on hazel dormice, acting mainly through the variation in food resources. Regrowing forests were the most suitable stands for dormice, whereas recent coppices were the most unsuitable, with an ephemeral presence of a few individuals. Old coppices and high forest stands were both able to sustain local populations but at lower densities and with a higher mortality and/or emigration of younger and/or weaker individuals than the regrowing forest. Through our detailed analyses we were able to uncover the demographic mechanism underlying the effects of forest management on hazel dormice populations; our findings strongly suggest that maintaining an heterogeneous successional composition may be the most effective strategy for the conservation of this species.

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**Introduction**

Throughout the centuries most Eurasian forests have been intensively modified by coppicing, grazing and litter raking to the extent that very few areas have remained untouched (Bengtsson et al., 2000; Speckter, 2003). Forest management has provided important resources and economical revenues for centuries and still plays a major role in modern societies (FAO, 2010). Forest management is known to affect the richness and composition of mammal communities (Bogdziewicz and Zwolak, 2014; Fisher and Wilkinson, 2005; Paillet et al., 2010), making this subject-area a research priority for mammalogists. Forest harvesting is known to have species-specific impacts on mammals. Habitat generalists are usually favored by forest harvesting, whereas habitat specialists are usually more impacted (Bogdziewicz and Zwolak, 2014). Previous research focusing on small mammals has mainly targeted community parameters (Bowman et al., 2001; Carey and Harrington, 2001; Etcheverry et al., 2005; Kirkland, 1990; Panzacchi et al., 2010; Sullivan et al., 2009) or the abundance of target species (Capizzi et al., 2003, 2002; Gorini et al., 2011; Savola et al., 2013; Sullivan and Sullivan, 2001), whereas little has been done on the effects of forest management on individuals (e.g. individual survival and female fecundity). Furthermore, previous research efforts have mainly focused on ground-dwelling species (Ecke et al., 2002; Kirkland, 1997), whereas little has been done on arboreal species (predominantly squirrels, Carey and Harrington, 2001; Carey et al.,...
1999; Wauters et al., 1997), which are known to be more threatened by forest management practices (Bogdziewicz and Zwolak, 2014).

We here focus on the hazel dormouse (Muscardinus avellanarius), a forest-dependent arboreal rodent. Compared to other sympatric rodents such as Apodemus and Myodes spp., this species has a longer life-span (3–5 years; Bright and Morris, 1996), lower reproductive rates (usually up to two litters per year; Juškaitis, 2003) and lower population densities (Bright and Morris, 1996). The hazel dormouse is strictly associated to forested areas with high shrub cover which is used for shelter and as main source of food (mainly fruits, flowers, leaves and invertebrates; Juškaitis, 2008). The species is highly sensitive to habitat loss and fragmentation (Bright and Morris, 1996; Mortelliti et al., 2014, 2011, 2010) and has relatively low ability to move outside forest areas (Mortelliti et al., 2013). According to the IUCN Red List of threatened species, the conservation status of the hazel dormouse is Least Concern (Amori et al., 2008b). However, local populations are declining due to anthropic activities; therefore the species is listed in the Annex IV of the Habitat Directive. A detailed understanding of the effects of forest management on the demography of the hazel dormouse is thus expected to provide important outcomes for conservation practitioners.

Previous studies have found that the presence of this species is associated with early successional stages, which are characterized by a higher diversity of shrubs (Berg, 1996; Bright and Morris, 1990; Capizzi et al., 2002; Juškaitis, 2008; Vilhelmsen, 2003). These studies help us to identify the most suitable management practice and successional stage for dormice populations, but they still do not help us to explain how different management practices and stages influence the populations of this rodent. At which ecological scale are the effects of forest management exerted, and on which biological parameters? How do individual-scale factors influence the response at the population level (Sutherland and Freckleton, 2013)? Answering to these questions will require an “holistic approach” (Lidicker, 1988) that is, the simultaneous examination of several parameters at multiple ecological scales (e.g. individuals- and population-level parameters).

The aims of this study were:

(1) To test whether different forest management regimes and stages affect a set of key biological parameters of dormice populations (individual-level parameters: survival and fecundity; population-level parameter: abundance of individuals);

(2) To identify which are the habitat variables (i.e. the proximate causes) responsible for the effects of forest management on each biological parameter.

We expected that forest practices favoring the development of a complex shrub structure would determine an increase in individual survival and fecundity, which would in turn lead to a higher population abundance (Juškaitis, 2008).

Material and methods

Study area

The study was conducted in central Italy within the regional protected area “Selva del Lamone” (200–428 m a.s.l; Fig. 1).

The climate of the area is Mediterranean, with rainfalls mainly concentrated in late autumn – early winter, with an occasional second peak in spring (mean temperatures: winter 6°C, spring 16°C, summer 21°C, autumn 10°C; mean rainfalls: winter 260 mm, spring 180 mm, summer 150 mm, autumn 500 mm). The study area is a large (approximately 2000 ha) continuous block of deciduous woodland dominated by Quercus cerris; other relevant tree species are: Acer monspessulanum, A. campestre, Fraxinus ornus, Ostrya carpinifolia and Q. pubescens. Several sections of the forest are subject to different management practices (more details below).

Study design

Forest management practices are here considered as “treatments”; our study was designed to sample at least two spatial replicates per treatment. To maximize the independence between treatments we made sure that each area had been managed (e.g. coppiced) independently from the others. To minimize spatial correlation and the movement of individuals between grids we selected sites 300–1300 m apart. The only exception was grids RC1 and OC1 (Fig. 1), which were 30 m apart, in two adjacent stands independently managed (i.e. coppiced in different occasions) and separated by a country road not representing a barrier for dormice. No inter-grid movements were observed during the entire study period even between the two adjacent stands. We sampled a total of ten sites with different management regimes: regrowing stands (hereafter RG; 2 grids: RG1, RG2), recently coppiced stands (hereafter RC; 2 grids: RC1, RC2), old coppice stands (hereafter OC; 3 grids: RC1, RC2, RC3) and high forest (hereafter HF; 3 grids: HF1, HF2, HF3). RG sites are formerly cultivated and/or grazed areas which have been left unmanaged for the last 20 years; they are characterized by a high density of young trees and shrubs. Coppiced areas are managed for timber production; recent coppices were logged 1–5 years ago and are characterized by a very low tree density with regrowing shrubs; old coppices are more mature stages (logged 20–30 years ago) with a higher tree density. High forest stands are the most mature areas, they have no longer been used for timber production for the past 35–40 years and are dominated by high, old trees (most of them older than 50 years) scattered at low density. More quantitative measurements on the characteristics of the different stands are provided as part of results.

Dormice were captured by using wooden nest-boxes (average size 18 × 21 × 10 cm) placed on trees at a height of 1.5–2 m, with the entrance hole (3 cm of diameter) pointed toward the trunk (Morris et al., 1990). Nest-boxes were placed in 4 ha grids, composed by 36 nest-boxes (6 × 6 lines) spaced 40 m. The distance between nest-boxes was comparable to other studies on this species (Juškaitis, 2006). Given the home-range size of the hazel dormouse (up to

Fig. 1. Aerial photo of the study area: the “Selva del Lamone” nature Reserve in central Italy. The labels locate the position of each sampling grid: RC = recent coppice; RG = regrowing forest; HF = high forest; OC = old coppice.
1 ha; Juškaitis, 2008) it is expected that several nest-boxes may be included in an individual home-range (Amori et al., 2008a), increasing the chance of individual recapture. Grids with a higher density of nest-boxes may have an effect on population parameters and are thus not recommended for population ecology studies (Juškaitis, 2006).
visits, we only used count data from the first visit so that sampling effort was homogeneous and the abundance index was consistent across the years. We stress that the abundance index here considered is conceptually analogous to a density index because the size of sampled grids was constant. We used GLMMs so that we could take into account temporal autocorrelation in the data by using sampling grid and sampling session as random effects. As AIC values for model comparison are not reliable with GLMM (Müller et al., 2013), we used Wald's tests to evaluate the significance of each variable (Bolker et al., 2009). As the variable "Management" is a categorical variable, to evaluate all possible comparisons between the four management types we run the analyses with RC (recently coppiced), then RG (regrowing forest) and finally OC (old coppices) as reference category (step 1). Continuous variables (step 2) were standardized so that we could compare the betas of different variables. To keep our models as simple as possible, avoiding over-parameterization and collinearity issues, we individually tested all the variables listed in Table 1 (univariate models) and applied the Benjamini and Hochberg (1995) correction on p-values. The aim of running univariate models was to evaluate the significance of each variable and to provide support for the importance of several aspects of habitat quality. Models were fitted by using package lme4 (Bates et al., 2011) for R.

**Litter size**

Litter size (number of pups per female) was modeled with a GLM (Generalized Linear Model) with a Poisson distribution. We used GLMs rather than GLMMs because of the lack of temporal autocorrelation issues (litter size was never obtained from the same individual) and because multiple captures from the same grid were taken into account by the fixed factors. A categorical variable was included to account for the effect of “age” of the litter (with presumed lower litter size with increasing age due to natural mortality): age 1 = weight < 5 g, closed eyes; age 2 = weight 5–8 g, open eyes, low mobility; age 3 = weight > 8 g, mobile. We included management (step 1) or habitat variables (step 2) as predictors for the models. As for abundance analyses, variables were standardized prior to analyses and their significance was tested with Wald’s test. Models were fitted by using R (R Core Team, 2013).

Sample size for analyses was: 209 for survival analyses, 42 for litter size analyses, 240 for population level analyses (10 grids sampled on 24 occasions).

**Results**

**Characterization of sites**

The different management practices are discriminated by several of the vegetation and trophic features here considered (ANOVA tests; Appendix A). In particular, regrowing forests are characterized by a high level of shrubs cover and diversity and a high cover of Crataegus spp., Rosa canina and Prunus spinosa, while recent coppices have low number of trees, lower height of canopy, lower cover of shrubs selected as important species for dormouse and a low level of shrub richness (Appendix A). Old coppices and high forests show similar values, intermediate between the other two forest types.

**Dormouse population dynamics**

A total of 209 individual dormice were captured during the three-years of the study; 64% were caught in RG stands, 18% in HF, 16% in OC and only 2% in RC stands.

Population abundance varied considerably across seasons and sampling grids (Fig. 2). Maximum observed abundance was 17 individuals (corresponding to a density of 4.25 individuals/hectare), recorded in November 2010 and in May 2011 in the two regrowing forest grids (RG1 and RG2).

**Individual survival**

Only 4 individuals were captured in RC grids and they were never recaptured, therefore we excluded these data from the CMR analyses due to the low sample size.

**Step 1**: the top model set (Table 2) included two models within 2ΔAICc. Recapture probability was influenced by season, being lower in warm months (July and August) than in the rest of the year (Appendix B).
Forest management influenced individual survival. Individuals in RG forest had the highest survival, whereas the survival of individuals in OC and HF stands was significantly lower (Fig. 3, Appendix B). Other models including different parameterizations of forest management had considerable less support according the adopted model selection criteria (Burnham and Anderson, 2002).

The effect of body weight was positive, with heavier individuals surviving more than lighter ones (Fig. 4A and B, Appendix B).

In the top ranked model (Table 2) forest management interacted with body weight: the effect of body weight in determining survival probability was weaker in RG stands than in other grids (i.e. there was a smaller difference in survival probability between thin and heavy individuals in RG forest compared to other stands; Fig. 4A and B). It should also be noted that for heavier individuals (>21 g), survival probability was approximately the same, irrespective of forest management (Fig. 4A and B). In the second ranked model (Table 2) the effect of body weight and forest management on survival was additive, i.e. the effect of body weight did not vary amongst grids under different forest management.

Table 2
Step 1 – Final set of Cormack–Jolly–Seber models ranked according to AICc, with survival as a function of forest management. Covariates are specified in brackets; hypothesis with alternative groupings of management types are in square brackets (see Material and methods for details). phi = survival probability, p = recapture probability, AICc = Akaike’s Information Criterion, AICc wgt = Akaike’s weight, Num. Par = number of estimated parameters, HF = high forest, OC = old coppice, RG = regrowing forest.

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Model</th>
<th>ΔAICc</th>
<th>AICc wgt</th>
<th>Num. Par</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>phi</td>
<td>0.00</td>
<td>0.43</td>
<td>6</td>
</tr>
<tr>
<td>1</td>
<td>phi(weight × [RG vs OC and HF]) p(season)</td>
<td>-0.75</td>
<td>0.30</td>
<td>5</td>
</tr>
<tr>
<td>2</td>
<td>phi(weight × [RG vs OC and HF]) p(season)</td>
<td>-2.37</td>
<td>0.13</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>phi(weight × [RG vs OC and HF]) p(season)</td>
<td>-2.48</td>
<td>0.13</td>
<td>8</td>
</tr>
<tr>
<td>4</td>
<td>phi(weight × [RG vs OC and HF]) p(season)</td>
<td>-7.67</td>
<td>0.01</td>
<td>4</td>
</tr>
</tbody>
</table>
Table 3
Step 2 – Final set of Cormack–Jolly–Seber models ranked according to AICc, with survival as a function of trophic resources and vegetation variables, and recapture probability as a function of season (summer versus rest of the year). Covariates are represented in brackets (see Table 1 for details on the covariates). phi = survival probability, p = recapture probability, AICc = Akaike’s Information Criterion, AICc wgt = Akaike’s weight, Num. Par = number of estimated parameters.

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Model</th>
<th>ΔAICc</th>
<th>AICc wgt</th>
<th>Num. Par</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>phi(weight + Simpson) p(season)</td>
<td>0.00</td>
<td>0.41</td>
<td>5</td>
</tr>
<tr>
<td>2</td>
<td>phi(weight + * Simpson) p(season)</td>
<td>0.55</td>
<td>0.31</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>phi(weight + * Cra.spp) p(season)</td>
<td>3.11</td>
<td>0.09</td>
<td>5</td>
</tr>
<tr>
<td>4</td>
<td>phi(weight + Richness) p(season)</td>
<td>4.46</td>
<td>0.04</td>
<td>5</td>
</tr>
<tr>
<td>5</td>
<td>phi(weight + Rot.can) p(season)</td>
<td>4.51</td>
<td>0.04</td>
<td>5</td>
</tr>
<tr>
<td>6</td>
<td>phi(weight + Pru.sp) p(season)</td>
<td>6.45</td>
<td>0.02</td>
<td>5</td>
</tr>
<tr>
<td>7</td>
<td>phi(weight + Lon.sp) p(season)</td>
<td>8.07</td>
<td>0.01</td>
<td>5</td>
</tr>
<tr>
<td>8</td>
<td>phi(weight + Cor.mas) p(season)</td>
<td>9.11</td>
<td>0.00</td>
<td>5</td>
</tr>
</tbody>
</table>

Step 2: the top model set included two models within 2ΔAICc (Table 3). In the top-ranked model survival was expressed as function of the Simpson’s Index of shrubs diversity and body weight, with an additive effect. Increasing shrub diversity and higher body weight led to an increase of individual survival; the effect of body weight did not vary among grids under different forest management (Fig. 4C, Appendix C).

In the second ranked model (Table 3) body weight interacted negatively with the Simpson’s Index of shrubs diversity: the effect of an increase of shrubs diversity was stronger for thinner individuals than heavier ones. Other models including single species and habitat variables had considerable less support according the adopted model selection criteria (Table 3).

Table 4
Step 1 – Dormouse abundance as a function of forest management. Model parameters (β) and standard errors (SE) are shown for each variable in the model. Fitted model: GLMM with a Poisson distribution with logarithmic link; random factors: sampling session, sampling grid. Variable significance was tested with a Wald test (N = 240; 24 sampling occasions on 10 grids). The variable Manag is a categorical variable; in order to evaluate all possible comparisons between management types we run the analyses with RC (recently coppiced), then RG (regrowing forest) and finally OC (old coppices) as reference category.

<table>
<thead>
<tr>
<th>Term</th>
<th>Variance</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Session</td>
<td>0.73</td>
<td>0.85</td>
</tr>
<tr>
<td>Grid</td>
<td>0.22</td>
<td>0.47</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Term</th>
<th>β</th>
<th>SE</th>
<th>Wald’s test</th>
<th>Significance p</th>
</tr>
</thead>
<tbody>
<tr>
<td>RC as reference category</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>−2.70</td>
<td>0.71</td>
<td>−3.80</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Manag (RG)</td>
<td>3.82</td>
<td>0.77</td>
<td>4.98</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Manag (OC)</td>
<td>1.60</td>
<td>0.76</td>
<td>2.11</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Manag (HF)</td>
<td>1.77</td>
<td>0.76</td>
<td>2.33</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>RG as reference category</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>1.12</td>
<td>0.38</td>
<td>2.93</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Manag (RC)</td>
<td>−3.82</td>
<td>0.77</td>
<td>−4.98</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Manag (OC)</td>
<td>−2.22</td>
<td>0.46</td>
<td>−4.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Manag (HF)</td>
<td>−2.05</td>
<td>0.46</td>
<td>−4.45</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>OC as reference category</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>−1.10</td>
<td>0.37</td>
<td>−3.00</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Manag (RG)</td>
<td>2.22</td>
<td>0.46</td>
<td>4.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Manag (RC)</td>
<td>−1.60</td>
<td>0.76</td>
<td>−2.11</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Manag (HF)</td>
<td>0.17</td>
<td>0.45</td>
<td>0.38</td>
<td>0.71</td>
</tr>
</tbody>
</table>

Step 1 and Step 2. We found 7 litters in HF, 12 litters in OC and 23 litters in RG. Mean litter size (±standard deviation) was 4.3 (±2.0), 4.8 (±1.3), 4.5 (±1.8) respectively in HF, OC and RG. Litter size was not influenced by forest management (GLM analyses with management categories, all p > 0.5) or by the habitat variables (GLM analyses with variables listed in Table 1, all p > 0.05).

Litter size

Discussion

Our study showed a strong effect of forest management on a hazel dormouse population in central Italy. We found that the effect of management was acting at different ecological scales: the individual-level (direct effect on individual survival) and the population level (abundance of individuals). Forest management affects key variables (e.g. abundance and diversity of resources) which in turn affect individual and population variables of the hazel dormouse. We found that the regrowing forest was the most suitable stand for hazel dormice. Regrowing stands are characterized by a high density of young trees and abundant and diverse shrubs (Appendix A) which provide a high amount and diversity of food resources, as well as protection from predators and nesting sites (Berg, 1996; Juškaitis, 2008).

Other studies have previously shown that intermediate successional stages of vegetation are the most suitable for this species (Berg, 1996; Bright and Morris, 1990; Capizzi et al., 2002; Juškaitis, 2008; Vilhelmsen, 2003). We add to existing knowledge by showing that two different aspects of shrub resources were important and...
each acted at a different ecological scale (individual survival and population abundance) in determining the observed effect of habitat management. (1) A higher abundance of shrubs, which meant an overall higher amount of food resources (especially fruits), led to a higher abundance of individuals, most likely because it increased the habitat carrying capacity. (2) The diversity of resources, instead, played a role in increasing individual survival: survival in the most diverse stands was twice as high as survival in the least diverse stands (Fig. 4C). A higher diversity of shrub species with different phenology may in fact provide a longer availability of different sources of food throughout the year (Bright and Morris, 1996).

We acknowledge the fact that a high abundance of individuals may imply that the site is a sink, low-quality habitat with a concentration of subordinate or younger individuals (Van Horne, 1983). However, this hypothesis is poorly supported by our data. Individual survival was higher in RG or comparable to other management types and, as clearly shown in Appendix A, the amount of food resources was very high in RG sites. We thus conclude that RG sites clearly represent high quality habitat.

Coppice stands in their initial phase of regrowth (<5 years) proved to be unsuitable habitat for the hazel dormouse, as recent logging resulted in a very open forest with low density of residual trees and with an almost missing shrub component of the vegetation. In this habitat type, in fact, we found only 4 individuals throughout two years of surveys, and these individuals were never recaptured. We are not able to conclude if those individuals were transient individuals in dispersal (passing through and leaving the stand after capture) or if they were resident and died on site. In both cases, however, the presence of dormice is clearly ephemeral and cannot be considered as part of a stable population.

The grids with more mature habitat (old coppice and high forest), instead, proved to be suitable to sustain stable dormice populations, at least during our study period, but at a lower density if compared to regrowing forests.

**Demographic mechanisms**

We found that the effect of body weight on individual survival differed according to forest management. This result may be interpreted in two non-exclusive ways: (1) body weight had a stronger effect in less suitable stands (old coppice and high forest) and was less important in highly suitable grids (regrowing forest); (2) there was a substantial effect of forest management only for thinner individuals. A low body weight may indicate either that the individual is in poor body condition (low body fat) or that it is younger. We therefore propose two possible explanations of this result: (1) the effect of low habitat quality manifested by increasing mortality of weaker individuals, causing low population densities in less suitable habitat (only a few individuals in better body condition survived); (2) in less suitable habitats there was a high rate of emigration (usually related to younger individuals; Juškaitis, 2008). It is possible that both mechanisms acted together; both, however, would determine the pattern we observed: low abundance of individuals in low quality stands and high abundance of individuals in highly suitable stands.

Our preliminary results suggest that management practices do not significantly affect the reproductive success of hazel dormice. We acknowledge, however, that litter size is just one of the components of reproductive success (including, as an example, the percentage of reproducing individuals, the number of litters/year and the survival of newborns Büchner et al., 2003; Juškaitis, 2008; Naim et al., 2011). Further empirical evidence is required to confirm our findings on reproductive success.

In conclusion our results suggest forest management affects the shrub layer of the vegetation which determined the quality of habitats (Appendix A). The higher quality habitats (regrowing stands) were characterized by a higher survival and persistence of weaker and younger individuals which in turn translated to a higher overall abundance of the population. Furthermore our results confirm the key role played by intermediate phases of vegetation growth for this species when compared to earlier and older stages (Juškaitis, 2008).

**Conclusions**

Our study provides an in-depth example on the mechanisms by which human activities exert their effect on a species of conservation concern. Considered that most European native forest habitat is now destroyed, fragmented or degraded, and considered the sensitivity of the hazel dormouse to all these anthropic processes (Bright and Morris, 1996; Mortelliti et al., 2014, 2011, 2008), the appropriate management of the residual, often highly disturbed forests, is mandatory. Our results strongly suggest that maintaining a heterogeneous successional composition may be the most effective strategy for the conservation of this species (Berg, 1996; Bright and Morris, 1990), which is still compatible with timber production. The goal should be to maintain an appropriate shrub layer composition, and it may be achieved by maintaining a dynamic heterogeneous structure of the forest, with the juxtaposition of stands at different successional stages, e.g. by appropriate coppicing cycle and rotation or by periodically allowing the regrowth of vegetation in clearcuts, fields and pastures.

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**Appendix A. Supplementary data**

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2014.12.006.

**References**


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