

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

2 *Muscardinus avellanarius*

3

4 Giulia Sozio^a, Fabiola Iannarilli^a, Ilaria Melcore^a, Matilde Boschetti^b, Daniele Fipaldini^a, Matteo
5 Luciani^a, Davide Roviani^c, Andrea Schiavano^d, Alessio Mortelliti^{a, e}

6

7 ^a Department of Biology and Biotechnology "Charles Darwin", University of Rome "La Sapienza",
8 Viale dell'Università 32, 00185, Rome, Italy

9 ^b Department of Biology, University of Pisa, Via A. Volta 4/6, 56126 Pisa, Italy

10 ^c Department of Life Science, University of Siena, via Aldo Moro 2, 53100, Siena (San Miniato),
11 Italy

12 ^d Department for Innovation in Biological, Agro-food and Forest systems (DIBAF), University of
13 Tuscia. Via San Camillo de Lellis snc, 01100, Viterbo, Italy

14 ^e Fenner School of Environment and Society, Australian Research Council Centre for
15 Environmental Decisions, National Environmental Research Program, The Australian National
16 University, Canberra, ACT 0200

17

18 Corresponding Author: Alessio Mortelliti; Fenner School of Environment and Society. ANU
19 College of Medicine, Biology & Environment. The Australian National University Canberra ACT
20 0200 Australia T: + 61 2 52737. alessio.mortelliti@anu.edu.au

21

22

23

24 Abstract

25

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

44

45 Keywords: common dormouse, coppice, demography, rodents, survival, timber production.

46

47 Introduction

48

49 Throughout the centuries most Eurasian forests have been intensively modified by coppicing,
50 grazing and litter raking to the extent that very few areas have remained untouched (Bengtsson et
51 al., 2000; Spiecker, 2003). Forest management has provided important resources and economical
52 revenues for centuries and still plays a major role in modern societies (FAO, 2010). Forest
53 management is known to affect the richness and composition of mammal communities
54 (Bogdziewicz and Zwolak, 2014; Fisher and Wilkinson, 2005; Paillet et al., 2010), making this
55 subject-area a research priority for mammalogists. Forest harvesting is known to have species-
56 specific impacts on mammals. Habitat generalists are usually favored by forest harvesting, whereas
57 habitat specialists are usually more impacted (Bogdziewicz and Zwolak, 2014). Previous research
58 focusing on small mammals has mainly targeted community parameters (Bowman et al., 2001;
59 Carey and Harrington, 2001; Etcheverry et al., 2005; Kirkland, 1990; Panzacchi et al., 2010;
60 Sullivan et al., 2009) or the abundance of target species (Capizzi et al., 2003, 2002; Gorini et al.,
61 2011; Savola et al., 2013; Sullivan and Sullivan, 2001), whereas little has been done on the effects
62 of forest management on individuals (e.g. individual survival and female fecundity). Furthermore,
63 previous research efforts have mainly focused on ground-dwelling species (Ecke et al., 2002;
64 Kirkland, 1997), whereas little has been done on arboreal species (predominantly squirrels, Carey
65 and Harrington, 2001; Carey et al., 1999; Wauters et al., 1997), which are known to be more
66 threatened by forest management practices (Bogdziewicz and Zwolak, 2014).

67 We here focus on the hazel dormouse (*Muscardinus avellanarius*), a forest-dependent arboreal
68 rodent. Compared to other sympatric rodents such as *Apodemus* and *Myodes* spp., this species has a
69 longer life-span (3-5 years; Bright and Morris, 1996), lower reproductive rates (usually up to two
70 litters per year; Juškaitis, 2003) and lower population densities (Bright and Morris, 1996). The hazel
71 dormouse is strictly associated to forested areas with high shrub cover which is used for shelter and
72 as main source of food (mainly fruits, flowers, leaves and invertebrates; Juškaitis, 2008). The

73 species is highly sensitive to habitat loss and fragmentation (Bright and Morris, 1996; Mortelliti et
74 al., 2014, 2011, 2010) and has relatively low ability to move outside forest areas (Mortelliti et al.,
75 2013). According to the IUCN Red List of threatened species, the conservation status of the hazel
76 dormouse is Least Concern (Amori et al., 2008b). However, local populations are declining due to
77 anthropic activities; therefore the species is listed in the Annex IV of the Habitat Directive. A
78 detailed understanding of the effects of forest management on the demography of the hazel
79 dormouse is thus expected to provide important outcomes for conservation practitioners.

80 Previous studies have found that the presence of this species is associated with early successional
81 stages, which are characterized by a higher diversity of shrubs (Berg, 1996; Bright and Morris,
82 1990; Capizzi et al., 2002; Juškaitis, 2008; Vilhelmsen, 2003). These studies help us to identify the
83 most suitable management practice and successional stage for dormice populations, but they still do
84 not help us to explain *how* different management practices and stages influence the populations of
85 this rodent. At which ecological scale are the effects of forest management exerted, and on which
86 biological parameters? How do individual-scale effects influence the response at the population
87 level (Sutherland and Freckleton, 2013)? Answering to these questions will require an “holistic
88 approach” (Lidicker, 1988) that is, the simultaneous examination of several parameters at multiple
89 ecological scales (e.g. individuals- and population-level parameters).

90 The aims of this study were:

- 91 1) To test whether different forest management regimes and stages affect a set of key biological
92 parameters of dormice populations (individual-level parameters: survival and fecundity; population-
93 level parameter: abundance of individuals);
- 94 2) To identify which are the habitat variables (i.e. the proximate causes) responsible for the effects
95 of forest management on each biological parameter.

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

100 Material and methods

101 *Study area*

102 The study was conducted in central Italy within the regional protected area “Selva del Lamone”
103 (200-428 m a.s.l; Fig. 1).

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

111

112 *Study design*

113 Forest management practices are here considered as “treatments”; our study was designed to sample
114 at least two spatial replicates per treatment. To maximize the independence between treatments we
115 made sure that each area had been managed (e.g. coppiced) independently from the others. To
116 minimize spatial correlation and the movement of individuals between grids we selected sites 300-
117 1300 m apart. The only exception were grids RC1 and OC1 (Fig. 1), which were 30 m apart, in two
118 adjacent stands independently managed (i.e. coppiced in different occasions) and separated by a
119 country road not representing a barrier for dormice. No inter-grid movements were observed during
120 the entire study period even between the two adjacent stands. We sampled a total of ten sites with
121 different management regimes: regrowing stands (hereafter RG; 2 grids: RG1, RG2), recently
122 coppiced stands (hereafter RC; 2 grids: RC1, RC2), old coppice stands (hereafter OC; 3 grids: RC1,
123 RC2, RC3) and high forest (hereafter HF; 3 grids: HF1, HF2, HF3). RG sites are formerly
124 cultivated and/or grazed areas which have been left unmanaged for the last 20 years; they are

125 characterized by a high density of young trees and shrubs. Coppiced areas are managed for timber
126 production; recent coppices were logged 1-5 years ago and are characterized by a very low tree
127 density with regrowing shrubs; old coppices are more mature stages (logged 20-30 years ago) with
128 a higher tree density. High forest stands are the most mature areas, they have no longer been used
129 for timber production for the past 35-40 years and are dominated by high, old trees (most of them
130 older than 50 years) scattered at low density. More quantitative measurements on the characteristics
131 of the different stands are provided as part of results.

132 Dormice were captured by using wooden nest-boxes (average size 18x21x10 cm) placed on trees at
133 a height of 1.5-2 m, with the entrance hole (3 cm of diameter) pointed towards the trunk (Morris et
134 al., 1990). Nest-boxes were placed in 4 ha grids, composed by 36 nest-boxes (6 x 6 lines) spaced 40
135 m. The distance between nest-boxes was comparable to other studies on this species (Juškaitis,
136 2006). Given the home-range size of the hazel dormouse (up to 1 ha; Juškaitis, 2008) it is expected
137 that several nest-boxes may be included in an individual home-range (Amori et al., 2008a),
138 increasing the chance of individual recapture. Grids with a higher density of nest-boxes may have
139 an effect on population parameters and are thus not recommended for population ecology studies
140 (Juškaitis, 2006).

141

142 *Collection of data on hazel dormice*

143 We conducted a total of 14328 nest-box inspections, including 42 sampling sessions to 10 grids
144 composed by 36 nest-boxes each, with the exception of the two recently coppiced grids which had
145 only 31 sampling sessions.

146 The study was conducted from May 2010 to December 2012; sampling of grids RC1 and RC2
147 started in April 2011 due to logistical constraints; between January and March of each year the
148 sampling was interrupted because of hibernation of the hazel dormouse. Nest-boxes were inspected
149 once per month in the period May 2010 - December 2010. In 2011 and 2012, on alternate months,
150 we added a second and third visit respectively after 4 and 8 days after the first (e.g. three visits in

151 May, one in June, three in July, etc). This increase of sampling effort was necessary to provide
152 additional data for supporting Capture-Mark-Recapture model parameterization.

153 Individuals found in the nest-boxes were captured, weighed, sexed, assigned to an age-class (adult
154 or juvenile, based on weight and fur characteristics) and individually marked by means of PIT tags
155 (2010) or ear tags (2011-2012). In order to minimize disturbance, females with litter were not
156 handled and marked. Pups were counted, weighed and immediately released with the mother in the
157 nest-box.

158

159 *Microhabitat and resources assessment*

160 We assessed microhabitat structure and abundance of resources in each grid through vegetation
161 sampling in 10x10m quadrats. Quadrats were selected following a systematic random sampling
162 approach. Following a pilot study, we found that the variability in vegetation structure differed
163 between grids. Therefore, in order to make our plots more representative of the variability of each
164 site, we increased the number of quadrats (range: 8-25) to sample according to the variability of
165 vegetation structure in each grid (Elzinga et al., 2001). Data from quadrats were averaged to obtain
166 single values for each grid. Vegetation sampling was conducted in spring 2011 and 2012.

167 Microhabitat structure was evaluated at tree and shrub layers using the variables detailed in Table 1.
168 Resource abundance was quantified by means of shrub cover as we were not able to measure
169 directly the biomass of shrub fruits and seeds. However, a previous pilot survey on a similar area in
170 central Italy established that fruit biomass was correlated with shrub cover (Bartolommei,
171 unpublished data: Spearman's rho = 0.606, $p < 0.001$), therefore we are confident in using shrub
172 cover as the best available proxy for resource abundance. Cover of each shrub species was
173 categorized in five classes (0%; 0.1-25%; 25-50%; 50-75%; 75-100%). We calculated an abundance
174 index of shrubs by summing cover of all shrub species; we also calculated a partial abundance index
175 for preferred shrub species by including only a set of key shrubs species that hazel dormouse is
176 known to use as sources of food, shelter and nesting sites. Set of preferred species mostly included

177 species with big seeds (e.g. *Corylus avellana*), fleshy fruits (e.g. *Rosa canina*, *Crataegus* spp., *Prunus*
178 *spinosa*), edible leaves, or providing structural features (e.g. *Hedera helix*) (Amori et al., 2008a; Juškaitis,
179 2008) and are detailed in Table 1. Data from 2011 and 2012 were averaged as the analysis of inter-
180 annual vegetation differences was not among our aims.

181

182 *Data analysis*

183 To confirm differences in the forest structure and resource abundance between grids characterized
184 by different types of forest management, we conducted an ANOVA for the 20 target variables listed
185 in Table 1.

186 We then tested the effect of forest management on population abundance, individual survival and
187 litter size. We structured the modeling phase in two **distinct** and **sequential** steps:

188 **step 1)** we tested whether management regimes had an effect on the target ecological variables
189 (survival, fertility and density) by including them as predictor categorical covariates;

190 **step 2)** we tested the effect of covariates quantifying habitat structure, resources abundance and
191 resource diversity in order to identify the most likely proximate causes of the differences found in
192 the step 1.

193 Details on the specific analyses carried out on each parameter are provided in the corresponding
194 paragraphs.

195

196 *Individual survival*

197 We fitted Cormack-Jolly-Seber models for open populations (software MARK; (White and
198 Burnham, 1999) on the capture history data, taking into account variation in sampling periods. The
199 variation in sampling periods between grids and over the duration of the study was dealt by
200 specifying the missing visits in the encounter history file and with the function "Set Time Intervals"
201 implemented in MARK.

202 First, we modeled recapture probability (p) as a function of season (warm season - August and July
203 - versus the rest of the year) to take into account seasonality in dormice activity and obtain more
204 reliable estimates of survival probability (ϕ). We then modeled survival probability by including
205 management type (**step 1**) or habitat/resources variables (**step 2**) as covariates. Management types
206 were treated as 4 different categories. We further pooled these categories in groups in order to
207 evaluate their relative differences (e.g. old coppices versus the other categories pooled together). In
208 this way we could compare each management type with each of the other three. Mean body weight
209 of each individual was also included as a covariate to take into account variability in survival due to
210 possible individual differences (fat accumulation is very important for dormice survival; (Juškaitis,
211 2008), as well as in interaction with the habitat variables, if applicable.

212 We adopted the Information Theoretic Approach to evaluate the relative importance of models and
213 variables (Burnham and Anderson, 2002). Models were ranked according to the Akaike Information
214 Criterion corrected for small sample-size (AICc). Models within $2\Delta AICc$ were included in the top
215 model set. The goodness-of-fit (GOF) of the most general Cormack-Jolly-Seber model
216 ($\phi(\cdot)p(\text{season})$) fitted to the data was estimated using software RELEASE, implemented in
217 program MARK. Since the estimate of \hat{c} was <1 we corrected it to 1, as suggested by (Cooch
218 and White, 2013).

219

220 *Abundance*

221 The time-series of monthly abundance (count of individuals actually captured) in each grid were
222 modeled by fitting GLMMs (Generalized Linear Mixed Models) with a Poisson distribution and a
223 logarithmic link (Bolker et al., 2009). Our dependent variable should therefore be considered an
224 index of population abundance rather than an estimate (i.e. what would have been obtained by
225 fitting CMR models). We followed this approach to keep the CMR analyses the least parameterized
226 as possible. For months with three visits, we only used count data from the first visit so that
227 sampling effort was homogeneous and the abundance index was consistent across the years. We

228 stress that the abundance index here considered is conceptually analogous to a density index
229 because the size of sampled grids was constant. We used GLMM's so that we could take into
230 account temporal autocorrelation in the data by using sampling grid and sampling session as
231 random effects. As AIC values for model comparison are not reliable with GLMM (Müller et al.,
232 2013), we used Wald's tests to evaluate the significance of each variable (Bolker et al., 2009). As
233 the variable "Management" is a categorical variable, to evaluate all possible comparisons between
234 the four management types we run the analyses with RC (recently coppiced), then RG (regrowing
235 forest) and finally OC (old coppices) as reference category (**step 1**). Continuous variables (**step 2**)
236 were standardized so that we could compare the betas of different variables. To keep our models as
237 simple as possible, avoiding over-parameterization and collinearity issues, we individually tested all
238 the variables listed in Table 1 (univariate models) and applied the Benjamini and Hochberg (1995)
239 correction on p-values. The aim of running univariate models was to evaluate the significance of
240 each variable and to provide support for the importance of several aspects of habitat quality. Models
241 were fitted by using package lme4 (Bates et al., 2011) for R.

242

243 *Litter size*

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

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

256

257 Results

258

259 *Characterization of sites*

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

267

268 *Dormouse population dynamics*

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

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

274

275 *Individual Survival*

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

278 **Step 1:** the top model set (Table 2) included two models within $2\Delta AICc$. Recapture probability was
279 influenced by season, being lower in warm months (July and August) than in the rest of the year
280 (Appendix B).

281 Forest management influenced individual survival. Individuals in RG forest had the highest
282 survival, whereas the survival of individuals in OC and HF stands was significantly lower (Fig. 3,
283 Appendix B). Other models including different parameterizations of forest management had
284 considerable less support according the adopted model selection criteria (Burnham and Anderson,
285 2002).

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

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

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

304

305 *Population Abundance*

306 **Step 1:** the abundance of dormice was influenced by forest management, with dormice numbers
307 being significantly higher in RG forest, OC and HF when compared to RC forest (Fig. 2 and Table
308 4). We found significant differences between all other comparisons; the only non-significant
309 difference that we found was between OC and HF (i.e. OC and HF had similar abundance; Fig. 2
310 and Table 4).

311 **Step 2:** five variables resulted to have a significant effect on the abundance of dormice (betas of all
312 significant variables are provided in Table 5): numbers of dormice occurred in grids with higher
313 cover of shrubs (single species or total shrubs). Detailed results of all models, including random and
314 fixed term estimates, are provided in Appendix D.

315

316 *Litter size*

317 **Step 1 and Step 2.** We found 7 litters in HF, 12 litters in OC and 23 litters in RG. Mean litter size
318 (\pm standard deviation) was 4.3 (\pm 2.0), 4.8 (\pm 1.3), 4.5 (\pm 1.8) respectively in HF, OC and RG. Litter
319 size was not influenced by forest management (GLM analyses with management categories, all
320 $p > 0.5$) or by the habitat variables (GLM analyses with variables listed in Table 1, all $p > 0.05$).

321

322 Discussion

323

324 Our study showed a strong effect of forest management on a hazel dormouse population in central
325 Italy. We found that the effect of management was acting at different ecological scales: the
326 individual-level (direct effect on individual survival) and the population level (abundance of
327 individuals). Forest management affects key variables (e.g. abundance and diversity of resources)
328 which in turn affect individual and population variables of the hazel dormouse. We found that the
329 regrowing forest was the most suitable stand for hazel dormice. Regrowing stands are characterized

330 by a high density of young trees and abundant and diverse shrubs (Appendix A) which provide a
331 high amount and diversity of food resources, as well as protection from predators and nesting sites
332 (Berg, 1996; Juškaitis, 2008).

333 Other studies have previously shown that intermediate successional stages of vegetation are the
334 most suitable for this species (Berg, 1996; Bright and Morris, 1990; Capizzi et al., 2002; Juškaitis,
335 2008; Vilhelmsen, 2003). We add to existing knowledge by showing that two different aspects of
336 shrub resources were important and each acted at a different ecological scale (individual survival
337 and population abundance) in determining the observed effect of habitat management. 1) A higher
338 abundance of shrubs, which meant an overall higher amount of food resources (especially fruits),
339 led to a higher abundance of individuals, most likely because it increased the habitat carrying
340 capacity. 2) The diversity of resources, instead, played a role in increasing individual survival:
341 survival in the most diverse stands was twice as high as survival in the least diverse stands (Fig.
342 4C). A higher diversity of shrub species with different phenology may in fact provide a longer
343 availability of different sources of food throughout the year (Bright and Morris, 1996).

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

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

356 both cases, however, the presence of dormice is clearly ephemeral and cannot be considered as part
357 of a stable population.

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

361

362 *Demographic mechanisms*

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

375 Our preliminary results suggest that management practices do not significantly affect the
376 reproductive success of hazel dormice. We acknowledge, however, that litter size is just one of the
377 components of reproductive success (including, as an example, the percentage of reproducing
378 individuals, the number of litters/year and the survival of newborns (Büchner et al., 2003; Juškaitis,
379 2008; Naim et al., 2011). Further empirical evidence is required to confirm our findings on
380 reproductive success.

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

387

388 *Conclusions*

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

401

402 *Acknowledgements*

403

404 Dormice were captured and handled with permit number PNM 0024822 granted to A.M. by the
405 Ministry of Environment, Rome, Italy. The following students assisted the field component of this
406 study: Cristina Cervone, Stefano Fagiani, Lorenzo Mastrofina, Martina Scacco and Luca Santarelli.

407 Thanks to Luciana Carotenuto (!), Pietro Politi, and all the staff of the Riserva Naturale Selva del
408 Lamone for helping us to complete this project; to Dario Capizzi and Giovanni Amori for support
409 and advice. This study was funded by WWF “Biodiversamente” and “Brusarosco” grants to A.M..
410 Further funding was provided by: Riserva Naturale Selva del Lamone, University of Rome “La
411 Sapienza”, private funds.

412

413

414 References

- 415 Amori, G., Contoli, L., Nappi, A., 2008a. Fauna d’Italia: Mammalia II. Edizioni Calderini de Il Sole
416 24 ORE Edagricole, Bologna, Italy.
- 417 Amori, G., Hutterer, R., Kryštufek, B., Yigit, N., Mitsain, G., Meinig, H., Juškaitis, R., 2008b.
418 *Muscardinus avellanarius* [WWW Document]. IUCN 2013. IUCN Red List Threat. Species.
419 Version 2013.2. URL www.iucnredlist.org (accessed 5.16.14).
- 420 Bates, D., Maechler, M., Bolker, B., 2011. lme4: Linear mixed-effects models using S4 classes.
- 421 Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem
422 function and management of European forests. *For. Ecol. Manage.* 132, 39–50.
- 423 Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful
424 approach to multiple testing. *J. R. Stat. Soc. Ser. B* 57, 289–300.
- 425 Berg, L., 1996. Small-scale changes in the distribution of the dormouse *Muscardinus avellanarius*
426 (Rodentia, Myoxidae) in relation to vegetation changes. *Mammalia* 60, 211–216.
- 427 Bogdziewicz, M., Zwolak, R., 2014. Responses of small mammals to clear-cutting in temperate and
428 boreal forests of Europe: a meta-analysis and review. *Eur. J. For. Res.* 133, 1–11.
- 429 Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-
430 S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution.
431 *Trends Ecol. Evol.* 24, 127–35.
- 432 Bowman, J., Forbes, G., Dilworth, T., 2001. Landscape context and small-mammal abundance in a
433 managed forest. *For. Ecol. Manage.* 140, 249–255.
- 434 Bright, P.W., Morris, P.A., 1990. Habitat Requirements of Dormice *Muscardinus avellanarius* in
435 Relation to Woodland Management in Southwest England. *Biol. Conserv.* 54, 307–326.
- 436 Bright, P.W., Morris, P.A., 1996. Why are Dormice rare ? A case study in conservation biology.
437 *Mamm. Rev.* 26, 157–187.

- 438 Büchner, S., Stubbe, M., Striese, D., 2003. Breeding and biological data for the common dormouse
 439 (*Muscardinus avellanarius*) in eastern Saxony (Germany). *Acta Zool. Acad. Sci. Hungaricae*
 440 49, 19–26.
- 441 Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: A practical
 442 information-theoretic approach, 2nd ed. Springer-Verlag.
- 443 Capizzi, D., Battistini, M., Amori, G., 2002. Analysis of the hazel dormouse, *Muscardinus*
 444 *avellanarius*, distribution in a Mediterranean fragmented woodland. *Ital. J. Zool.* 69, 25–31.
- 445 Capizzi, D., Battistini, M., Amori, G., 2003. Effects of habitat fragmentation and forest
 446 management on the distribution of the edible dormouse *Glis glis*. *Acta Theriol.* 48, 359–371.
- 447 Carey, A.B., Harrington, C.A., 2001. Small mammals in young forests: implications for
 448 management for sustainability. *For. Ecol. Manage.* 154, 289–309.
- 449 Carey, A.B., Kershner, J., Biswell, B., De Toledo, L.D., 1999. Ecological scale and forest
 450 development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests.
 451 *Wildl. Monogr.* 142.
- 452 Cooch, E.G., White, G.C., 2013. Program MARK - A gentle introduction, Edition 13. ed.
- 453 Ecke, F., Löfgren, O.L.A., Sörlin, D., 2002. Population dynamics of small mammals in relation to
 454 forest age and structural habitat factors in northern Sweden. *J. Appl. Ecol.* 39, 781–792.
- 455 Elzinga, C.L., Salzer, D.W., Willoughby, J.W., Gibbs, J.P., 2001. *Monitoring Plant and Animal*
 456 *Populations*. Blackwell, Oxford.
- 457 Etcheverry, P., Ouellet, J., Crête, M., 2005. Response of small mammals to clear-cutting and
 458 precommercial thinning in mixed forests of southeastern Quebec. *Can. J. For. Res.* 35, 2813–
 459 2822.
- 460 FAO, 2010. *Global forest resources assessment 2010 - Main report*. Rome.
- 461 Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the
 462 North American boreal forest. *Mamm. Rev.* 35, 51–81.
- 463 Gorini, L., Linnell, J.D.C., Boitani, L., Hauptmann, U., Odden, M., Wegge, P., Nilsen, E.B., 2011.
 464 Guild composition and habitat use of voles in 2 forest landscapes in south-eastern Norway.
 465 *Integr. Zool.* 6, 299–310.
- 466 Juškaitis, R., 2003. Abundance dynamics and reproduction success in the common dormouse,
 467 *Muscardinus avellanarius*. *Folia Zool.* 52, 239–248.
- 468 Juškaitis, R., 2006. Nestbox grids in population studies of the common dormouse (*Muscardinus*
 469 *avellanarius* L.): methodological aspects. *Polish J. Ecol.* 54, 351–358.
- 470 Juškaitis, R., 2008. *The common dormouse Muscardinus avellanarius: Ecology, population*
 471 *structure and dynamics*. Institute of Ecology of Vilnius University Publishers, Vilnius.

- 472 Kirkland, G.L.J., 1990. Patterns of initial small mammal community change after clearcutting of
473 temperate North American forests. *Oikos* 59, 313–320.
- 474 Kirkland, G.L.J., 1997. Responses of small mammals to the clearcutting of northern Appalachian
475 forests. *J. Mammal.* 58, 600–609.
- 476 Lidicker, W., 1988. The synergistic effects of reductionist and holistic approaches in animal
477 ecology. *Oikos* 53, 278–281.
- 478 Morris, P.A., Bright, P.W., Woods, D., 1990. Use of nestboxes by the Dormouse *Muscardinus*
479 *avellanarius*. *Biol. Conserv.* 51, 1–13.
- 480 Mortelliti, A., Amori, G., Capizzi, D., Cervone, C., Fagiani, S., Pollini, B., Boitani, L., 2011.
481 Independent effects of habitat loss, habitat fragmentation and structural connectivity on the
482 distribution of two arboreal rodents. *J. Appl. Ecol.* 48, 153–162.
- 483 Mortelliti, A., Amori, G., Capizzi, D., Rondinini, C., Boitani, L., 2010. Experimental design and
484 taxonomic scope of fragmentation studies on European mammals: current status and future
485 priorities. *Mamm. Rev.* 40, 125–154.
- 486 Mortelliti, A., Santarelli, L., Sozio, G., Fagiani, S., Boitani, L., 2013. Long distance field crossings
487 by hazel dormice (*Muscardinus avellanarius*) in fragmented landscapes. *Mamm. Biol.* 78,
488 309–312.
- 489 Mortelliti, A., Santulli Sanzo, G., Boitani, L., 2008. Species' surrogacy for conservation planning:
490 caveats from comparing the response of three arboreal rodents to habitat loss and
491 fragmentation. *Biodivers. Conserv.* 18, 1131–1145.
- 492 Mortelliti A, Sozio G., Driscoll D.A, Bani L., Boitani L., Lindenmayer D.B. 2014. Population and
493 individual-scale responses to patch size, isolation and quality in the hazel dormouse. *Ecosphere*
494 5(9): art107. <http://dx.doi.org/10.1890/ES14-00115.1>
- 495 Müller, S., Scaely, J.L., Welsh, A.H., 2013. Model selection in linear mixed models. *Stat. Sci.* 28,
496 135–167.
- 497 Naim, D., Telfer, S., Sanderson, S., Kemp, S.J., Watts, P.C., 2011. Prevalence of multiple mating
498 by female common dormice, *Muscardinus avellanarius*. *Conserv. Genet.* 12, 971–979.
- 499 Paillet, Y., Bergès, L., Hjältén, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J.,
500 De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz,
501 S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A.,
502 Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and
503 unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* 24, 101–112.
- 504 Panzacchi, M., Linnell, J.D.C., Melis, C., Odden, M., Odden, J., Gorini, L., Andersen, R., 2010.
505 Effect of land-use on small mammal abundance and diversity in a forest–farmland mosaic
506 landscape in south-eastern Norway. *For. Ecol. Manage.* 259, 1536–1545.
- 507 R Core Team, 2013. R: A language and environment for statistical computing.

- 508 Savola, S., Henttonen, H., Lindén, H., 2013. Vole population dynamics during the succession of a
509 commercial forest in northern Finland. *Ann. Zool. Fenn.* 50 50, 79–88.
- 510 Spiecker, H., 2003. Silvicultural management in maintaining biodiversity and resistance of forests
511 in Europe - temperate zone. *J. Environ. Manage.* 67, 55–65.
- 512 Sullivan, T.P., Sullivan, D.S., 2001. Influence of variable retention harvests on forest ecosystems.
513 II. Diversity and population dynamics of small mammals. *J. Appl. Ecol.* 38, 1234–1252.
- 514 Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2009. Stand structure and the
515 abundance and diversity of plants and small mammals in natural and intensively managed
516 forests. *For. Ecol. Manage.* 258S, S127–S141.
- 517 Sutherland, W., Freckleton, R., 2013. Identification of 100 fundamental ecological questions. *J.*
518 *Ecol.* 58–67.
- 519 Van Horne, B., 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47,
520 893–901.
- 521 Vilhelmsen, H., 2003. Status of Dormice (*Muscardinus avellanarius*) in Denmark. *Acta Zool. Acad.*
522 *Sci. Hungaricae* 49, 139–145.
- 523 Wauters, L.A., Gurnell, J., Currado, I., Mazzoglio, P.J., 1997. Grey squirrel *Sciurus carolinensis*
524 management in Italy - squirrel distribution in a highly fragmented landscape. *Wildlife Biol.* 3,
525 117–124.
- 526 White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of
527 marked animals. *Bird Study* 46, S120–S139.
- 528
- 529

530 Figure captions

531

532 Fig. 1. Aerial photo of the study area: the “Selva del Lamone” nature Reserve in central Italy. The
533 labels locate the position of each sampling grid; RC = recent coppice; RG = regrowing forest; HF =
534 high forest; OC = old coppice.

535

536 Fig. 2. Time series of abundance of hazel dormice in each sampling grid. RC = recent coppice; RG
537 = regrowing forest; HF = high forest; OC = old coppice. A smoothing line was added to facilitate
538 interpretation. Numbers on the x axis represent monthly sessions in the three years of the study:
539 from 1 to 7: May-November 2010; from 8 to 16: April-December 2011; from 17 to 25: April-
540 December 2012.

541

542 Fig. 3. Estimated monthly survival probability (with 95% confidence intervals) in different
543 management regimes for individuals with average value of body weight. RG = regrowing forest; HF
544 = high forest; OC = old coppice.

545

546 Fig. 4. Monthly survival probability of dormice as estimated through the top ranking CJS model.
547 Dashed lines represent 95% confidence intervals. Panel A represents the relationships between
548 survival and body weight in high forest and old coppice stands. Panel B represents the relationship
549 between survival and body weight in regrowing forest stands. In panel C survival is expressed as a
550 function of Simpson’s Index for shrub diversity (for average value of individual body weight).

551

552

553 Tables

554

555 Table 1. Description of the tested habitat variables. Variables were calculated as the mean values

556 of quadrats in each grid. See Material and Methods for further details.

Variable	Description	
N_trees	Number of trees	
Height_can	Height of canopy	
dbh_mean	Mean of diameters at breast height of trees	
dbh_devst	Standard deviation of diameters at breast height of trees; it represents a measure of variability in the age of the trees.	
Cor.ave		<i>Corylus avellana</i>
Cor.mas		<i>Cornus mas</i>
Cra.spp		<i>Crataegus</i> spp.
Euo.eur		<i>Euonymus europaeus</i>
Hed.hel		<i>Hedera helix</i>
Lig.vul	Percentage of shrub cover	<i>Ligustrum vulgare</i>
Lon.spp	of:	<i>Lonicera</i> spp.
Pru.spi		<i>Prunus spinosa</i>
Ros.can		<i>Rosa canina</i>
Rub.spp		<i>Rubus</i> spp.
Rus.acu		<i>Ruscus aculeatus</i>
Smi.asp		<i>Smilax aspera</i>

SHR_tot	Sum of the cover (%) of the following shrub species: <i>Crataegus</i> spp.*, <i>Corylus avellana</i> *, <i>Cornus mas</i> *, <i>Euonymus europeaus</i> *, <i>Hedera helix</i> *, <i>Ligustrum vulgare</i> *, <i>Lonicera</i> spp.*, <i>Prunus spinosa</i> *, <i>Rosa canina</i> *, <i>Rubus</i> spp.*, <i>Ruscus aculeatus</i> *, <i>Smilax aspera</i> *, <i>Paliurus spina-christi</i> , <i>Cytisus scoparius</i> , <i>Sambucus nigra</i> , <i>Pistacia lentiscus</i> , <i>Phillyrea</i> spp., <i>Ilex aquifolium</i> , <i>Rubia peregrina</i> , <i>Viburnum</i> spp., <i>Clematis vitalba</i> , <i>Coronilla emerus</i> , <i>Bryonia dioica</i> , <i>Mespilus germanica</i> , <i>Asparagus acutifolius</i> , <i>Prunus avium</i> , <i>Laurus nobilis</i>
SHR_sel	Sum of the cover (%) of the shrub species preferred by hazel dormice and marked with (*) in the list above
Richness	Number of shrub species
Simpson	Simpson's Index for shrub diversity

557

558

559

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

Model rank	Model	Δ AICc	AICc wgt	Num. Par
1	phi(weight * [RG vs OC and HF]) p(season)	0.00	0.43	6
2	phi(weight + [RG vs OC and HF]) p(season)	0.75	0.30	5
3	phi(weight + [RG vs OC vs HF]) p(season)	2.37	0.13	6
4	phi(weight * [RG vs OC vs HF]) p(season)	2.48	0.13	8
5	phi(weight) p(season)	7.67	0.01	4

566

567

568 Table 3. Step 2 - Final set of Cormack-Jolly-Seber models ranked according to AICc, with
569 survival as a function of trophic resources and vegetation variables, and recapture probability as
570 a function of season (summer versus rest of the year). Covariates are represented in brackets (see
571 Table 1 for details on the covariates). Phi = survival probability, p = recapture probability, AICc
572 = Akaike's Information Criterion, AICc wgt = Akaike's weight, Num. Par = number of
573 estimated parameters.

Model rank	Model	Δ AICc	AICc wgt	Num. Par
1	phi(weight + Simpson) p(season)	0.00	0.41	5
2	phi(weight * Simpson) p(season)	0.55	0.31	6
3	phi(weight + Cra.spp) p(season)	3.11	0.09	5
4	phi(weight + Richness) p(season)	4.46	0.04	5
5	phi(weight + Ros.can) p(season)	4.51	0.04	5
6	phi(weight + Pru.spi) p(season)	6.45	0.02	5
7	phi(weight + Lon.spp) p(season)	8.07	0.01	5
8	phi(weight + Cor.mas) p(season)	9.11	0.00	5

574

575

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

Term	Wald's Test Significance			
<hr/>				
<i>Random effects:</i>	<i>Variance</i>	<i>Standard Deviation</i>		
Session	0.73	0.85		
Grid	0.22	0.47		
<i>Fixed effects:</i>	β	<i>SE</i>	<i>Z</i>	<i>p</i>
<u>RC as reference category</u>				
(Intercept)	-2.70	0.71	-3.80	< 0.001
Manag (RG)	3.82	0.77	4.98	< 0.001
Manag (OC)	1.60	0.76	2.11	< 0.05
Manag (HF)	1.77	0.76	2.33	< 0.05
<u>RG as reference category</u>				
(Intercept)	1.12	0.38	2.93	< 0.01
Manag (RC)	-3.82	0.77	-4.98	< 0.001
Manag (OC)	-2.22	0.46	-4.78	< 0.001
Manag (HF)	-2.05	0.46	-4.45	< 0.001
<u>OC as reference category</u>				
(Intercept)	-1.10	0.37	-3.00	< 0.01

Manag (RG)	2.22	0.46	4.78	< 0.001
Manag (RC)	-1.60	0.76	-2.11	< 0.05
Manag (HF)	0.17	0.45	0.38	0.71

583

584

Table 5. Step 2 – Habitat variables with a significant ($p < 0.05$) effect on dormouse abundance. β values and standard errors were estimated by fitting GLMM models with a Poisson distribution with logarithmic link; random factors: sampling session, sampling grid. Each variable was tested in a different model (details on all fitted models, including non significant variables, are provided in Appendix D). Significance was tested with a Wald test (N=240; 24 sampling occasions on 10 grids) and p-values were corrected with Benjamini-Hochberg correction.

Model	Tested variable	β estimate	st. err.	Z	p
a	Cra.spp	0.920	0.287	3.201	0.010
b	Pru.spi	0.843	0.281	2.999	0.020
c	Ros.can	0.967	0.263	3.677	0.000
d	SHR_tot	0.848	0.310	2.738	0.024
e	SHR_sel	0.913	0.314	2.907	0.020