



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 Council Centre for Environmental Decisions, National Environmental Research Program, The Australian National University, Canberra, ACT 0200, Australia

ARTICLE INFO

Article history:

Received 16 October 2014

Accepted 21 December 2014

Handled by Raquel Monclús

Available online 30 December 2014

Keywords:

Coppice

Demography

Rodents

Survival

Timber production

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 a 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; Spiecker, 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.,

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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 avellanus*), 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 effects 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

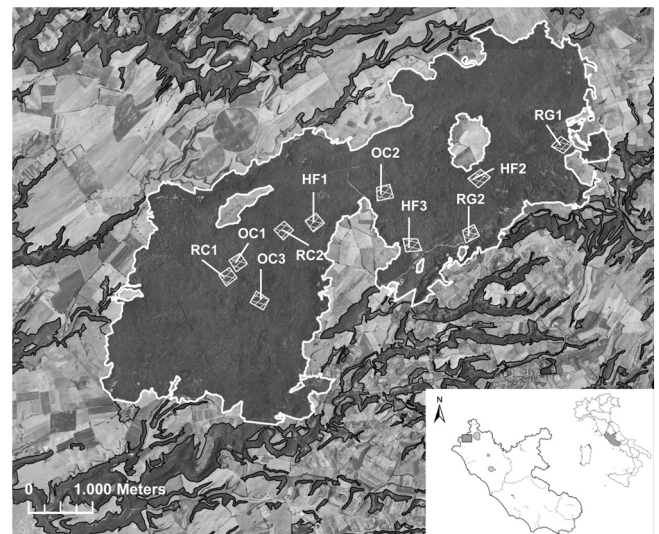


Fig. 1. Aerial photo of the study area: the “Selva del Lamone” nature Reserve in central Italy. The labels locate the position of each sampling grid; RC = recent coppice; RG = regrowing forest; HF = high forest; OC = old coppice.

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

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).

Collection of data on hazel dormice

We conducted a total of 14,328 nest-box inspections, including 42 sampling sessions to 10 grids composed by 36 nest-boxes each, with the exception of the two recently coppiced grids which had only 31 sampling sessions.

The study was conducted from May 2010 to December 2012; sampling of grids RC1 and RC2 started in April 2011 due to logistical constraints; between January and March of each year the sampling was interrupted because of hibernation of the hazel dormouse. Nest-boxes were inspected once per month in the period May 2010–December 2010. In 2011 and 2012, on alternate months, we added a second and third visit respectively after 4 and 8 days after the first (e.g. three visits in May, one in June, three in July, etc.). This increase of sampling effort was necessary to provide additional data for supporting Capture–Mark–Recapture model parameterization.

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

Microhabitat and resources assessment

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

Microhabitat structure was evaluated at tree and shrub layers using the variables detailed in Table 1. Resource abundance was quantified by means of shrub cover as we were not able to measure directly the biomass of shrub fruits and seeds. However, a previous pilot survey on a similar area in central Italy established that fruit biomass was correlated with shrub cover (Bartolommei, unpublished data: Spearman's $\rho = 0.606$, $p < 0.001$), therefore we are confident in using shrub cover as the best available proxy for resource abundance. Cover of each shrub species was categorized in five classes (0%; 0.1–25%; 25–50%; 50–75%; 75–100%). We calculated an abundance index of shrubs by summing cover of all shrub species; we also calculated a partial abundance index for preferred shrub species by including only a set of key shrubs species that hazel dormouse is known to use as sources of food, shelter and nesting sites. Set of preferred species mostly included species with big seeds (e.g. *Corylus avellana*), fleshy fruits (e.g. *Rosa canina*, *Crataegus* spp., *Prunus spinosa*), edible leaves, or providing structural features (e.g. *Hedera helix*) (Amori et al., 2008a; Juškaitis, 2008) and are detailed in Table 1. Data from 2011 and 2012 were averaged as the analysis of inter-annual vegetation differences was not among our aims.

Data analysis

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

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

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

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

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

Individual survival

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

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

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

Abundance

The time-series of monthly abundance (count of individuals actually captured) in each grid were modeled by fitting GLMMs (Generalized Linear Mixed Models) with a Poisson distribution and a logarithmic link (Bolker et al., 2009). Our dependent variable should therefore be considered an index of population abundance rather than an estimate (i.e. what would have been obtained by fitting CMR models). We followed this approach to keep the CMR analyses the least parameterized as possible. For months with three

Table 1

Description of the tested habitat variables. Variables were calculated as the mean values 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	<i>Ligustrum vulgare</i>
Lon.spp	<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 europaeus</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

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 GLMM's 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).

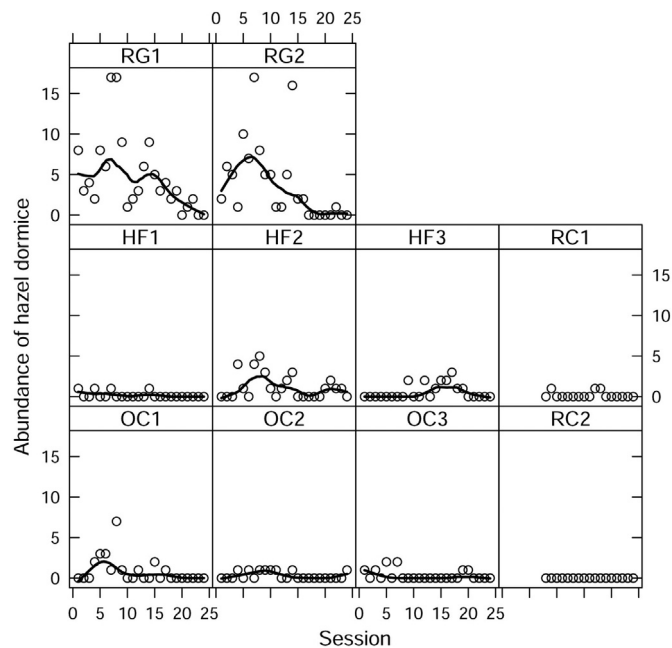


Fig. 2. Time series of abundance of hazel dormice in each sampling grid. RC = recent coppice; RG = regrowing forest; HF = high forest; OC = old coppice. A smoothing line was added to facilitate interpretation. Numbers on the x-axis represent monthly sessions in the three years of the study: from 1 to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

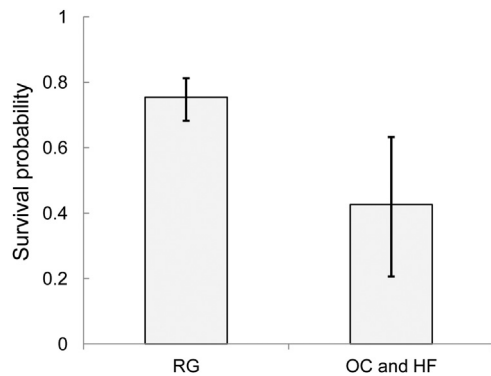


Fig. 3. Estimated monthly survival probability (with 95% confidence intervals) in different management regimes for individuals with average value of body weight. RG = regrowing forest; HF = high forest; OC = old coppice.

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).

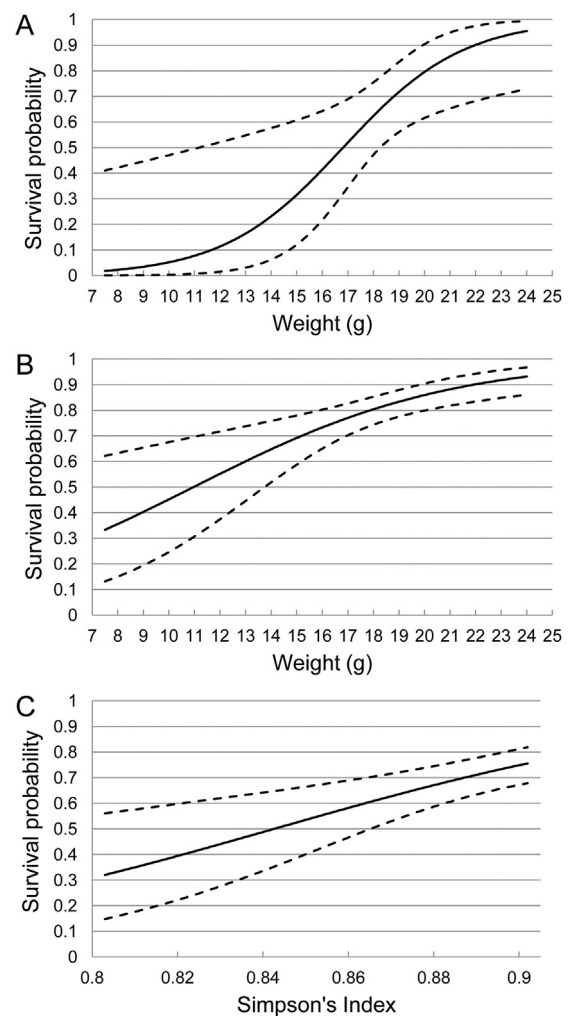


Fig. 4. Monthly survival probability of dormice as estimated through the top ranking CJS model. Dashed lines represent 95% confidence intervals. Panel A represents the relationships between survival and body weight in high forest and old coppice stands. Panel B represents the relationship between survival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

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.

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

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). ϕ = survival probability, p = recapture probability, AICc = Akaike's Information Criterion, AICc wgt = Akaike's weight, Num. Par = number of estimated parameters.

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

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.

Random effects				
Term	Variance		Standard deviation	
Session	0.73		0.85	
Grid	0.22		0.47	
Fixed effects				
Term	β	SE	Wald's test <i>Z</i>	Significance <i>p</i>
<i>RC as reference category</i>				
(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
<i>RG as reference category</i>				
(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
<i>OC as reference category</i>				
(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

Step 2: the top model set included two models within 2Δ AICc (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).

Population abundance

Step 1: the abundance of dormice was influenced by forest management, with dormice numbers being significantly higher in RG forest, OC and HF when compared to RC forest (Fig. 2 and Table 4). We found significant differences between all other comparisons;

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	SE	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

the only non-significant difference that we found was between OC and HF (i.e. OC and HF had similar abundance; Fig. 2 and Table 4). **Step 2:** five variables resulted to have a significant effect on the abundance of dormice (betas of all significant variables are provided in Table 5); numbers of dormice occurred in grids with higher cover of shrubs (single species or total shrubs). Detailed results of all models, including random and fixed term estimates, are provided in Appendix D.

Litter size

Step 1 and Step 2. We found 7 litters in HF, 12 litters in OC and 23 litters in RG. Mean litter size ($\pm$ 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 $p > 0.05$).

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 affected 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 an 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.

Acknowledgements

Dormice were captured and handled with permit number PNM 0024822 granted to A.M. by the Ministry of Environment, Rome, Italy. The following students assisted the field component of this study: Cristina Cervone, Stefano Fagiani, Lorenzo Mastrofini, Martina Scacco and Luca Santarelli. Thanks to Luciana Carotenuto (!), Pietro Politi, and all the staff of the Riserva Naturale Selva del Lamone for helping us to complete this project; to Dario Capizzi and Giovanni Amori for support and advice. This study was funded by WWF “Biodiversamente” and “Brusarosco” grants to A.M. Further funding was provided by: Riserva Naturale Selva del Lamone, University of Rome “La Sapienza”, private funds.

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

- Amori, G., Contoli, L., Nappi, A., 2008a. *Fauna d'Italia: Mammalia II. Edizioni Calderini de Il Sole 24 ORE Edagricole, Bologna, Italy.*
- Amori, G., Hutterer, R., Kryštufek, B., Yigit, N., Mitsain, G., Meinig, H., Juškaitis, R., 2008b. *Muscardinus avellanarius* [WWW Document]. IUCN 2013. The IUCN Red List Threatened Species. Version 2013.2, URL: www.iucnredlist.org (accessed 16.05.14).
- Bates, D., Maechler, M., Bolker, B., 2011. *lme4: Linear mixed-effects models using Eigen and Eigen++*.
- Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manage.* 132, 39–50.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B* 57, 289–300.
- Berg, L., 1996. Small-scale changes in the distribution of the dormouse *Muscardinus avellanarius* (Rodentia, Myoxidae) in relation to vegetation changes. *Mammalia* 60, 211–216.
- Bogdziewicz, M., Zwolak, R., 2014. Responses of small mammals to clear-cutting in temperate and boreal forests of Europe: a meta-analysis and review. *Eur. J. For. Res.* 133, 1–11.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135.

- Bowman, J., Forbes, G., Dilworth, T., 2001. Landscape context and small-mammal abundance in a managed forest. *For. Ecol. Manage.* 140, 249–255.
- Bright, P.W., Morris, P.A., 1990. Habitat requirements of dormice *Muscardinus avellanarius* in relation to woodland management in southwest England. *Biol. Conserv.* 54, 307–326.
- Bright, P.W., Morris, P.A., 1996. Why are Dormice rare? A case study in conservation biology. *Mamm. Rev.* 26, 157–187.
- Büchner, S., Stubbe, M., Striese, D., 2003. Breeding and biological data for the common dormouse (*Muscardinus avellanarius*) in eastern Saxony (Germany). *Acta Zool. Acad. Sci. Hung.* 49, 19–26.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer-Verlag.
- Capizzi, D., Battistini, M., Amori, G., 2002. Analysis of the hazel dormouse, *Muscardinus avellanarius*, distribution in a Mediterranean fragmented woodland. *Ital. J. Zool.* 69, 25–31.
- Capizzi, D., Battistini, M., Amori, G., 2003. Effects of habitat fragmentation and forest management on the distribution of the edible dormouse *Glis glis*. *Acta Theriol.* 48, 359–371.
- Carey, A.B., Harrington, C.A., 2001. Small mammals in young forests: implications for management for sustainability. *For. Ecol. Manage.* 154, 289–309.
- Carey, A.B., Kershner, J., Biswell, B., De Toledo, L.D., 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildl. Monogr.*, 142.
- Cooch, E.G., White, G.C., 2013. Program MARK – A Gentle Introduction, 13th ed.
- Ecke, F., Löfgren, O.L.A., Sörlin, D., 2002. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. *J. Appl. Ecol.* 39, 781–792.
- Elzinga, C.L., Salzer, D.W., Willoughby, J.W., Gibbs, J.P., 2001. *Monitoring Plant and Animal Populations*. Blackwell, Oxford.
- Etcheverry, P., Ouellet, J., Crête, M., 2005. Response of small mammals to clear-cutting and precommercial thinning in mixed forests of southeastern Quebec. *Can. J. For. Res.* 35, 2813–2822.
- FAO, 2010. *Global Forest Resources Assessment 2010 – Main Report*. FAO, Rome.
- Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mamm. Rev.* 35, 51–81.
- Gorini, L., Linnell, J.D.C., Boitani, L., Hauptmann, U., Odden, M., Wegge, P., Nilsen, E.B., 2011. Guild composition and habitat use of voles in 2 forest landscapes in south-eastern Norway. *Integr. Zool.* 6, 299–310.
- Juškaitis, R., 2003. Abundance dynamics and reproduction success in the common dormouse, *Muscardinus avellanarius*. *Folia Zool.* 52, 239–248.
- Juškaitis, R., 2006. Nestbox grids in population studies of the common dormouse (*Muscardinus avellanarius* L.): methodological aspects. *Polish J. Ecol.* 54, 351–358.
- Juškaitis, R., 2008. The common dormouse *Muscardinus avellanarius*: ecology, population structure and dynamics. Institute of Ecology of Vilnius University Publishers, Vilnius.
- Kirkland, G.L.J., 1990. Patterns of initial small mammal community change after clearcutting of temperate North American forests. *Oikos* 59, 313–320.
- Kirkland, G.L.J., 1997. Responses of small mammals to the clearcutting of northern Appalachian forests. *J. Mammal.* 58, 600–609.
- Lidicker, W., 1988. The synergistic effects of reductionist and holistic approaches in animal ecology. *Oikos* 53, 278–281.
- Morris, P.A., Bright, P.W., Woods, D., 1990. Use of nestboxes by the Dormouse *Muscardinus avellanarius*. *Biol. Conserv.* 51, 1–13.
- Mortelliti, A., Amori, G., Capizzi, D., Cervone, C., Fagiani, S., Pollini, B., Boitani, L., 2011. Independent effects of habitat loss, habitat fragmentation and structural connectivity on the distribution of two arboreal rodents. *J. Appl. Ecol.* 48, 153–162.
- Mortelliti, A., Amori, G., Capizzi, D., Rondinini, C., Boitani, L., 2010. Experimental design and taxonomic scope of fragmentation studies on European mammals: current status and future priorities. *Mamm. Rev.* 40, 125–154.
- Mortelliti, A., Santarelli, L., Sozio, G., Fagiani, S., Boitani, L., 2013. Long distance field crossings by hazel dormice (*Muscardinus avellanarius*) in fragmented landscapes. *Mamm. Biol.* 78, 309–312.
- Mortelliti, A., Santulli Sanzo, G., Boitani, L., 2008. Species' surrogacy for conservation planning: caveats from comparing the response of three arboreal rodents to habitat loss and fragmentation. *Biodivers. Conserv.* 18, 1131–1145.
- Mortelliti, A., Sozio, G., Driscoll, D.A., Bani, L., Boitani, L., Lindenmayer, D.B., 2014. Population and individual-scale responses to patch size, isolation and quality in the hazel dormouse. *Ecosphere* 5 (9), <http://dx.doi.org/10.1890/ES14-00115.1> (art107).
- Müller, S., Sealey, J.L., Welsh, A.H., 2013. Model selection in linear mixed models. *Stat. Sci.* 28, 135–167.
- Naim, D., Telfer, S., Sanderson, S., Kemp, S.J., Watts, P.C., 2011. Prevalence of multiple mating by female common dormice, *Muscardinus avellanarius*. *Conserv. Genet.* 12, 971–979.
- Paillet, Y., Bergès, L., Hjaltn, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* 24, 101–112.
- Panzacchi, M., Linnell, J.D.C., Melis, C., Odden, M., Odden, J., Gorini, L., Andersen, R., 2010. Effect of land-use on small mammal abundance and diversity in a forest–farmland mosaic landscape in south-eastern Norway. *For. Ecol. Manage.* 259, 1536–1545.
- R Core Team, 2013. *R: A Language and Environment for Statistical Computing*.
- Savola, S., Henttonen, H., Lindén, H., 2013. Vole population dynamics during the succession of a commercial forest in northern Finland. *Ann. Zool. Fenn.* 50 (50), 79–88.
- Spiecker, H., 2003. Silvicultural management in maintaining biodiversity and resistance of forests in Europe – temperate zone. *J. Environ. Manage.* 67, 55–65.
- Sullivan, T.P., Sullivan, D.S., 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. *J. Appl. Ecol.* 38, 1234–1252.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2009. Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests. *For. Ecol. Manage.* 258S, S127–S141.
- Sutherland, W., Freckleton, R., 2013. Identification of 100 fundamental ecological questions. *J. Ecol.*, 58–67.
- Van Horne, B., 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47, 893–901.
- Vilhelmsen, H., 2003. Status of Dormice (*Muscardinus avellanarius*) in Denmark. *Acta Zool. Acad. Sci. Hung.* 49, 139–145.
- Wauters, L.A., Gurnell, J., Currado, I., Mazzogio, P.J., 1997. Grey squirrel *Sciurus carolinensis* management in Italy – squirrel distribution in a highly fragmented landscape. *Wildl. Biol.* 3, 117–124.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, S120–S139.