Demographic parameters of sexes in an elusive insect: Implications for monitoring methods

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Abstract

Estimating demographic parameters in rare species is challenging because of the low number of individuals and their cryptic behaviour. One way to address this challenge is to gather data from several regions or years through mark-release-recapture (MRR) and radio-tracking monitoring. However, the comparison of demographic estimates obtained using these methods has rarely been investigated. Using five years of intensive MRR and radio-tracking surveys of an elusive and endangered saproxylic insect, the hermit beetle (*Osmoderma eremita*), in two regions of France, we aimed to estimate population size at the adult stage for each sex separately and to assess differences in demographic parameter estimates between survey methods. We found that males were approximately three times more likely to be recaptured than females. Taking this into account, we determined that the sex ratio was male-biased in almost all populations, except in *Malus* trees, where it was female-biased. Temporal fluctuations of sex ratios were also detected in one region. The radio-tracking transmitter (450 mg) allowed only the largest individuals (> 2 g) to be targeted. However, we found that, among non-equipped individuals, the larger males survived better than the smaller males. We also confirmed that transmitter-equipped individuals survived approximately 25 % better than non-equipped individuals. Extrapolating the estimates from radio-tracking surveys to the population scale may result in overly optimistic population projections. Our results revealed large temporal and spatial variations in population size and sex ratios. This knowledge is crucial for predicting the persistence of small populations in fragmented landscapes. This study also questioned the representativeness of radio-tracking surveys for insect species in estimating demographic

parameters at the population scale.

Keywords:

Insect conservation • Mark-release-recapture • Microhabitat quality • *Osmoderma eremita* •

Radio-tracking • Sex ratio

Introduction

Stochastic fluctuations of the operational sex ratio in a small population could lead to high extinction probability (Legendre et al. 1999). These fluctuations could affect the effective population size by increasing reproductive variance among individuals (Anthony and Blumstein 2000). Biased sex ratios may also cause an Allee effect, mostly because of limited mate finding (Engen et al. 2003). Reliable methods for estimating population sizes of males and females and their variation over time are thus critical for the success of effective management. This issue is particularly challenging when the managed species are rare or elusive (Mackenzie et al. 2005). Indeed, for those species, data are often sparse, and estimates of demographic parameters often rely solely on assumptions of population dynamics. For example, with no information on mating systems, a balanced sex ratio would be assumed (Seger and Stubblefield 2002). Moreover, for rare or elusive species, a low detection probability of individuals leads to bias in population size estimates if only counts of individuals are used (Pollock et al. 2004). Furthermore, bias in the estimation of male and female population sizes can arise if sexes have different probabilities of recapture due to systematic differences in their behaviour (Conn et al. 2004; White 2005), if sex biases in survival and dispersal occur (Julliard 2000), and if these sex variations are ignored in estimation models. To limit the uncertainty of inferences drawn from studies of rare species, Mackenzie et al. (2005) proposed, when appropriate, to borrow information regarding detectability and other demographic parameters from various times or locations. The mark-release-recapture approach (MRR) is commonly used to estimate animal population sizes, including those of insects (Drag et al. 2011). MRR data are analysed with

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models that correct for the imperfect detection probability of individuals. Techniques such as radio-tracking avoid bias due to imperfect detectability but impose constraints on the size of monitored individuals (Boiteau and Colpitts 2001). Radio-tracking is also costlier in money and time than classical MRR techniques. Comparing the efficiency of survey methods is quite easy if large numbers of individuals are sampled, but this comparison is often neglected for rare and elusive species. For example, Soisalo and Cavalcanti (2006) compared jaguar (*Panthera onca*) density estimates obtained using MRR methods with those obtained by GPS monitoring and noted that MRR methods overestimated the population size, with potential consequences for the time taken to initiate conservation actions. Therefore, the assessment of method biases on demographic estimates is crucial. For example, if one method is biased towards monitoring the largest individuals, and if body size influences demographic parameters, the reliability of the method must then be questioned. Comparing characteristics of individuals monitored with different methods and testing the effect of these characteristics on demographic parameters could allow method-based bias to be detected.

We addressed issues regarding male and female population size estimates for the rare and elusive saproxylic insect *Osmoderma eremita* (Coleoptera: Cetoniidae) using intensive MRR and radio-tracking surveys during a five-year period in two study areas. Based on temporal fluctuations in the size of populations and in groups of populations (Ranius 2001), the neighbouring populations of *O. eremita* are considered to be organised as a metapopulation, with each tree regarded as a habitat patch hosting a single local population (Ranius 2007). In addition, a low dispersal rate was revealed (15 % of the adults of *O. eremita* leave their natal local population; Ranius and Hedin 2001), as well as a short

dispersal range (less than 200 m; Hedin et al. 2008). Combining all trees and years of surveys, Ranius (2001) found a balanced sex ratio and used this assumption to estimate population size per tree and year but did not take into account differential survival or dispersal between sexes in population size estimations. However, highly biased sex ratios are likely in rare and poor habitats and when habitat quality varies largely in space but moderately in time (Julliard 2000), such as the habitat of some saproxylic insects.

The aim of this study was first 1) to study sex differences in demographical parameters of *O. eremita*. To improve the accuracy of estimates, both recaptures and recoveries were used, and the effects of sex, study area and year on survival rate and probability of recapture were tested (1.i). As advised by Mackenzie et al. (2005), a hierarchical method was used to obtain a maximal number of marked individuals. We then used the best estimates of demographic parameters to estimate population size of males and females with a Burnham-Jolly-Seber model (Burnham 1991) to test the year, region and tree species effects (1.ii). This hierarchical approach allowed us to estimate the sex ratio of *O. eremita* and to study fluctuations of male and female population sizes between years. We were also interested in 2) assessing the reliability of radio-tracking to estimate demographic parameters. Consequently, we measured and compared the biometrics of individuals equipped and not equipped with a transmitter (2.i), and we tested whether those characteristics had an effect on demographic parameters using advances in including individual covariates in Burnham joint live and dead encounter MRR models (2.ii).

Materials and methods

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Study species and study sites

The hermit beetle (*Osmoderma eremita*) is a strict saproxylophagous and cavicolous beetle (Bouget et al. 2005) of western Europe (Audisio et al. 2008). Its life cycle is long, with a 2-3 year sedentary larval stage in the cavity of tree hollows (Ranius et al. 2005). The adult life span of *O. eremita* is limited to approximately 1-2 months, and adults can be observed in northwestern Europe with a maximum probability in July and August (Ranius et al. 2005). The dispersal of *O. eremita* occurs in the adult stage (Ranius et al. 2005), 1-2 months after emergence. The study sites were located in the French departments of Orne (48°45'N 0°18'E) and Sarthe (47°41'N 0°21'E) and were described in Dubois and Vignon (2008) and Dubois et al. (2009) (see pictures of habitat types in S1 in Electronic Supplementary Material EMS).

Monitoring

The survey was conducted over five years (2004-2008) in the two study sites. Each year, it started presumably before first emergence or when the very first adults had emerged (at the beginning of July) and ended when the daily total number of captures fell below one capture per day (at the end of August). Adults of *O. eremita* were captured using one or two pitfall traps per tree (Dubois and Vignon 2008) in 35 hollow trees (20 in Orne and 15 in Sarthe). Adults were also searched for in tree hollows and on trunks during the standardised time of trap visits. Each adult was individually numbered by marking the elytra with a drill (Dubois and Vignon 2008, see picture S1 in EMS). Adults were then released on the

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surface of the wood mould where they usually dug down. Dead individuals were opportunistically reported.

We equipped some individuals in Sarthe with radio-transmitters, as in Dubois and Vignon (2008) (see picture S1 in EMS). The decision to equip an individual was made if the operator found that the individuals had a sufficient size and mass to be equipped, as described in Hedin and Ranius (2002).

Estimation of survival and recapture rates

Survival and recapture models were computed with a capture resighting approach (Lebreton et al. 1992) using the program MARK (White and Burnham 1999). Within each season of mark-release-recapture (MRR), we considered a time step of three days in which all trees were visited at least once. Incorporating information on recoveries into MRR models may lead to improved estimate precision (Barker 1997). This information was available in our study and was used in all analyses. Data from radio tracking was included in the MRR analyses only when testing for a difference in survival rate between transmitter-equipped and non-equipped individuals.

We used models including information on recaptures and recoveries. Those models were based on the formalism of Burnham (1993) and included survival rate (S), recapture probability (p), recovery probability (r, the probability that a dead individual is reported) and fidelity (F, the probability that an individual remains alive in the study site) parameters. We used Akaike's procedure (Burnham and Anderson 1998), which allows for comparisons of non-nested models according to their Akaike information criterion corrected for

overdispersion and sample size (QAIC$_c$). The criterion was calculated as QAIC$_c$ = -2log(L)/ĉ+2np+ 2np(np + 1)/(n-ess - np - 1), with L being the likelihood of the considered model, ĉ being a measure of overdispersion, np being the number of parameters of the model and n-ess being the effective sample size. The model that has the lowest QAIC$_c$ value is considered as the best approximating model (Symonds and Moussalli 2011). Goodness-of-fit tests were performed and we computed the variance inflation factor, $ĉ$, to scale the deviance of fitted models (see S2 in EMS).

First, 20 groups were distinguished in the analysis according to sex (n = 2), region (n = 2), and year of monitoring (n = 5). We assessed potential differences in parameters by comparing different models, some of which separately modelled the effect of each group, while others considered the groups as a common pool.

Due to the large number of potential models (> 20 000 if all combinations of time, age, sex, region and year of monitoring on S, p, r and F were tested), we first studied the sex effect, and we then examined region and year effects for each parameter of the best sex model (Fig. 1). Only models that tested explicit hypotheses regarding the biology and the monitoring of *O. eremita* were run (n = 54 models). The sequential steps of the analysis are presented in Fig. 1 and detailed below.

We combined data from the two study areas for all years. The survey duration varied between years and regions (from 14 to 19 occasions). Therefore, we fixed p and r to 0 for missing occasions. We first looked for the best model by starting with the least constrained model and simplifying it by first considering nuisance parameters (r and p), followed by fidelity (F) and survival parameters (S). For each parameter, we tested the effect of sex, time and age with two age classes and interaction based on an *a priori* set of pre-defined

models for each demographic parameter (Table S3 in EMS). According to the results of sex

effect analysis, we examined the effect of region and years for each parameter of the best

model selected in the previous step. As mentioned previously, we sequentially tested the

effects of time, age, region and year on the demographic parameters (Table S4 in EMS).

We considered an effect to be significant when it was supported by the best selected model.

Sequential strategies of model selection procedures may affect parameter estimates

(Doherty et al. 2012). To limit bias due to our selection approach, we estimated the

parameters using model averaging over the models that had a $QAIC_c$ weight higher than 1

%.

Population size estimates

We estimated population size at first capture and tested the effects of sex, year and habitat

type (tree species) with the Burnham-Jolly-Seber method (implemented in MARK;

Burnham 1991) in each region. As mentioned previously, we considered a time step of

three days in which all trees were visited at least once. We used an open model, as dispersal

and mortality could occur during the monitoring session. The use of the Burnham-Jolly-

Seber model necessitated that the study area remains a consistent size, and that, at each

sampling occasion, the probability of recapture of an unmarked individual should be the

same as a marked individual. We considered that our data fulfilled these two conditions

because the study area did not change from 2004 to 2008, and we did not consider

transmitter-equipped individuals in population size estimates.

We constrained the model structure of survival rate and recapture probability to the best

model selected above (Fig. 1). In both regions, two tree species were monitored: *Castanea sativa* and *Quercus robur* in Sarthe and *Malus domestica* and *Q. robur* in Orne. Therefore, in each region, 20 groups were considered according to sex ($n = 2$), year ($n = 5$) and tree species ($n = 2$). We tested whether population size and recruitment rates differed between sexes, years and tree species with the model selection approach in AIC_c. We used a logit link function and computed profile likelihood confidence using simulated annealing to assess convergence of the models. The best selected models for each step were run with three initial different values to check for parameter convergence. Only models that converged were used for the model averaging analyses (number of models in Sarthe = 15, in Orne = 8).

Assessing sampling bias in radio-tracking surveys

Right elytron length, body mass and body condition were measured in 294 individuals (141 individuals captured in 2007 and 2008 in Orne and 153 captured from 2005 to 2008 in Sarthe). Right elytron length was measured using the longest length from the humeral callus to the apex with a digital calliper (precision of 0.01 mm). Body mass was measured at first capture with a portable electronic balance (precision of 0.01 g; Dubois and Vignon 2008). We used a residual body condition index which was independent from body size to enable comparison of body condition across individuals as shown in Dubois et al. (2010). We compared biometric measurements of marked and transmitter-equipped individuals using a linear model (Gaussian family, normal error), which included the fixed effects of year, region and sex. We then included the three biometrical measurements as individual

covariates in the best MRR models selected with all individuals (see above) to test if the covariates influenced survival rates and recapture probabilities of sexes (only two groups in analyses). Site and year effect were not studied. In total, 111 combinations of effects of covariate on survival rates and recapture probabilities were tested, and four more combinations including second order relationships were tested with the best model selected (Table S6 in EMS).

We also built a data set pooling equipped and non-equipped individuals from Sarthe (the only region were individuals were radio tracked) and compared survival rate of equipped and non-equipped individuals using the Burnham joint live and dead recoveries model. We used the model structure of the best model selected when we tested sex, year and regional effects (Fig. 1) and model selection was based on $QAIC_c$ (five models considered). The recapture and recovery probabilities for transmitter-equipped individuals were fixed to 1.

Ethics statement

Permission for the monitoring of hermit beetle populations at each site was given by the prefectural office of the Orne and Sarthe departments. All landowners where the monitoring occurred (DIREN Pays-de-la-Loire, General Council of Sarthe department, Cofiroute company and other private owners) gave their permission to conduct the study.

Results

In total, 426 individuals were marked in five years in the two study areas (Table 1). We

performed 1 056 captures, recaptures, and recoveries (i.e., individuals found dead, $n = 48$) (Table 1). In total, 41 individuals (20 males and 21 females) from Sarthe were equipped with radio-transmitters.

Survival and recapture estimates

All models run when testing for sex, region and year effects are presented in Tables S3 and S4 in EMS.

We found evidence for sex and regional differences for the probability of recapture (Table 2). The year effect was not significant. The probability of recapture varied with age for females: the probability of recapture for the first occasion was higher than for the latter occasions (Table 2, $p_{fa1} = 0.11 - 0.20$, $p_{fa2} = 0.06 - 0.17$). For males, the probability of recapture was constant in time (in Sarthe $p_m = 0.34$, in Orne $p_m = 0.46$) and was approximately three times higher for males than for females. The probability of recapture for males in Orne was higher than in Sarthe, whereas the inverse trend was observed for females (Table 2).

Survival rates depended on age for both sexes with no significant differences found between males and females, regions or years. Survival rate for both sexes after the first occasion of capture was lower than the "long term" survival rates (i.e., after the second capture) ($S_{a1} = 0.59$-0.67, $S_{a2} = 0.77$-0.78, Table 2). According to survival estimates, the expected adult life span was approximately 60 days (time for which cumulative survival < 0.5 %).

Population size estimates

All models run for population estimates in each region are presented in Table S5 in EMS.

At both study sites, population size estimates varied significantly between sexes and tree

species (Fig. 2). In Sarthe, an additional year effect was detected (Fig. 2). The results of the

z-test to compare males' and females' average numbers indicated a significant male-biased

sex ratio except in the Sarthe-2008-*Castanea* group (no difference) and in the Orne-*Malus*

group (significant female-biased sex ratio). In Sarthe, the fluctuations between years for

each sex were not correlated with the tree species group (Spearman test, $P > 0.1$). This

resulted in the sex ratio varying from 1 to 5.8 in the *Castanea* group and from 2.7 to 6.9 in

the *Quercus* group in Sarthe. The linear model (Gaussian family) explaining the variation

of sex ratio with year and tree species as fixed effects explained 78 % of the total variation

(R^2 adjusted = 0.78, $F_{2,6}$ = 15.08, P = 0.0045). A negative linear trend was significantly

detected between sex ratio and year (β =-0.99, $F_{1,6}$ = 20.52, P = 0.0039). The sex ratio in

Quercus species was significantly higher than in *Castanea* species ($F_{1,6}$ = 12.1, P = 0.01).

In Orne, the sex ratio varied from 0.79 in the *Malus* group to 3.69 in the *Quercus* group

without fluctuation between years.

Representativeness of radio-tracking

For both sexes, the biometrics were highest for transmitter-equipped individuals than the

other captured individuals (all linear model tests, $P < 0.01$; Fig. 3).

In total, 82 covariate models of 115 (Table S6 in EMS) were better than the models without covariates. The best model was the one assuming that survival rate after first capture and probability of recapture of males varied with the individual mass, that long term survival rates of males varied with length of elytra and that long term survival rates of females varied with their body condition index (Table S7 in EMS). The survival rate of individuals after their first capture increased significantly with their mass (β = 1.05, 95 % CI [0.41, 1.70] %). The long term survival rate of males also increased significantly with the length of their elytra (β = 0.45, 95 % CI [0.08, 0.81] %), whereas the relationship between the long term survival rate of females and their body condition was not significant (β = 1.47, 95 % CI [-0.03, 2.98] %, Δ QAIC$_c$ = 1.94). Heavy males were captured less often than light males (β = -0.68, 95 % CI [-0.96, -0.39] %).

When directly testing the difference in survival rates of transmitter-equipped and non-equipped individuals, the best selected model assumed that the survival rate of transmitter-equipped individuals was constant and different from the model of non-equipped individuals. The survival rate of transmitter-equipped individuals was approximately 25 % higher than the survival rate of non-equipped individuals (model averaged estimates of survival rate of transmitter-equipped individuals = 0.97, sSE = 0.01, non-equipped in Table 2).

Discussion

Sex-biased capture and survival rates

The recapture probability was approximately 35 % higher for males than for females. This finding is consistent with another study on this species in which catchability was the highest for males (Ranius 2001). Females were more often re-encountered immediately after the first capture than at other times. This result may be due to a temporal change of female behaviour: after mating, which would occur mainly at emergence and at wood mould surface, they would behave in a more cryptic way by frequenting the bottom of the wood mould for egg laying (Hedin et al. 2008). The additional regional effects on recapture rate that we found in both sexes may be ascribable to differences in trap efficiency between study sites as a result of architectural differences in tree hollows between tree species, for example, or to microclimatic differences that might affect behaviour in the species (Oleksa and Gawronski 2008).

Survival rate was lower for both sexes after first capture than after all other occasions. The adult lifespan calculated using survival estimates (two months) was consistent with previous observations conducted in the laboratory (Luce 1995; Schaffrath 2003; Tauzin 2005). The low survival rate after first capture may be linked to several factors. We could exclude extra mortality due to the marking method, as previous studies suggested that elytron piercing, potentially resulting in abdomen injury, has little or no effect on survival (Ranius 2001). Moreover, this effect was not detected for transmitter-equipped individuals, for which manipulation was higher. The lower survival rate may be due to the dispersal of individuals from the tree where they were observed. We did not observe desertions from trees due to manipulation itself, and individuals usually dug down into the wood mould immediately after we released them. Our results reveal that maximum dispersal activity occurs immediately after emergence in the species. This finding is in accordance with

previous results of an independent tethered flight experiment, showing that flying males are the ones with the best body condition and likely the youngest (Dubois et al. 2010).

Population size and sex ratio fluctuations

Our hierarchical approach enabled us to estimate the initial population size of each sex and to test year, region and tree species effect. The average population size estimates per group of trees and per year are consistent with estimates by Ranius (2001) in Sweden. In particular, our mean population size estimates for *Q. robur* (8.8 adults tree^{-1} year^{-1} in Sarthe and 11.2 adults tree^{-1} year^{-1} in Orne) are very similar to the estimates of Ranius (2001), measured in *Q. robur* (11 adults tree^{-1} year^{-1}) using Jolly-Seber's and Craig's methods. In Sarthe, by contrast, we found temporal fluctuations of population sizes unlike the populations studied in Sweden (Ranius 2001). The factors influencing *O. eremita* population size are poorly known. Ranius et al. (2009) showed that population sizes of *O. eremita* inhabiting hollow oaks are positively correlated with the volume of wood mould, but this factor is unlikely to fluctuate widely from one year to the next. Spatio-temporal fluctuations of population size in *O. eremita* may also be explained by the dynamics of predators of its larvae, such as some Elateridae (Coleoptera; Svensson et al. 2004), which would imply a plurispecific survey of trees. In our study, we estimated the population size at emergence; thus, the variation of this population size may reflect fluctuating climatic conditions influencing the larval development of the species, which lasts approximately three years. In that case, these fluctuations would have differentially impacted the male and female larvae and would have been habitat specific, as we found no temporal correlation

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between male and female population sizes or between the population sizes of each tree species. Unfortunately, studies on the factors affecting reproduction and larval development of the study species are scarce.

The current study noted that an unbalanced sex ratio occurs in *O. eremita*. Several authors previously reported field observations suggesting the existence of a female-biased sex ratio in the species (Paulian and Baraud 1982; Vignon et al. 2005), but there were no corrections for unequal catchability of sexes. Using corrections, we found that unbalanced sex ratios, mostly male-biased, could occur in *O. eremita* populations. The sex ratio fluctuated from 0.78 to 6.9. These stochastic fluctuations of sex ratio may enhance extinction risk (Legendre et al. 1999), especially in small population sizes. These fluctuations may be the consequence of different emergence times between sexes inducing different recruitment between sexes (Schtickzelle et al. 2002). The sex-biased dispersal capacity described for *O. eremita* (Dubois et al. 2010) may induce unbalanced sex ratio as a result of differential adult dispersal strategies. A biased operational sex ratio could also be due to a biased sex ratio at birth in the tree hollow, or to a sex-biased mortality at the larval stage. Although larvae can be sexed on the basis of an external morphological criterion in *O. eremita* (Dubois 2009), no studies on larval sexing in the field or laboratory has been published to our knowledge.

Further, an unbalanced operational sex ratio may have an adaptive value in *O. eremita*. Indeed, theory predicts that if dispersal rate is sex-biased and reproductive success varies between habitat patches, it is adaptive to produce more offspring of the most dispersing (vs. the most philopatric) sex in low-quality (vs. high-quality) habitat patches (Julliard 2000). According to this theory, as it was previously reported that females have higher dispersal

capacity than males (Dubois et al. 2010), female-biased sex ratios should be detected in low-quality habitats. A female-biased sex ratio has been revealed in *Malus* trees. In our study sites, *Malus* trees are known to have smaller tree hollows than *Quercus* and *Castanea* trees, which may be an indicator of poor habitat because the volume of the tree hollow positively influences the population size (Ranius et al. 2009).

Implications for methods of estimating demographic parameters in elusive species

The combination of different methods to estimate demographic parameters is thought to be the most efficient approach (Ranius 2006). Various advanced technological methods (e.g., radio-tracking) are used by conservation biologists, whereas more classical methods may be more appropriate. Within the framework of conservation and societal expectations, a cost-profit trade-off of the methodology should be found, taking into account data robustness, financial and time costs, as well as the complexity of the selected methodology.

As in many radio-tracking surveys, we experienced an operator-biased survey towards the largest and heaviest individuals of the species for size and load reasons (Hedin and Ranius 2002). We further revealed that the largest and heaviest individuals survived better, especially in males, and detected that transmitter-equipped individuals survived up to 25 % better than non-equipped individuals. As a result, a radio-tracking survey with 450 mg transmitters (current study; Hedin and Ranius 2002; Dubois and Vignon 2008) may reveal inaccurate dispersal rate and range patterns in *O. eremita*, especially regarding the influence of body condition on dispersal capacity in the species (Dubois et al. 2010). Such biases may also occur for other large and endangered insect species such as *Lucanus cervus*

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(Coleoptera: Lucanidae; Rink and Sinsch 2007), in which the smallest individuals cannot be equipped with radio transmitters. Diodes used with harmonic radar are smaller than transmitters, but their localisation is less efficient in dense vegetation than that of transmitters (Boiteau et al. 2009). Moreover, Coleoptera species have a wide body size range, and only a small number are large enough (Ulrich 2007); thus, interspecific comparative studies are limited. To study dispersal, flight mill experiments could be less expensive and might provide more powerful data for comparative studies. Controlling dispersal factors with flight mill experiments may help to measure dispersal capacities of a species (Dubois et al. 2010) and to discuss the scale at which it uses its environment (Dubois et al. 2009).

Conclusions

Our study highlighted methods to improve parameter estimates in elusive species by: (*i*) long term studies and the choice of an adequate spatial scale to address inter-site and temporal variability; (*ii*) the use of a hierarchical approach to estimate population size to separate sexes, region and time effects. We revealed that sex ratios showed large fluctuations from one year to the next and depended on habitat quality. Understanding such fluctuations is crucial for predicting and managing the persistence of small populations in fragmented landscapes.

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Table 1: Numbers of individuals captured, re-encountered alive at least once and re-encountered dead per year and region. M = male, F = female; Numbers concern individuals from trees that were trapped five years or less.

Region	Year	Number of occasions	Number captured		Number re-encountered alive at least once		Number re-encountered dead	
			M	F	M	F	M	F
Orne	2004	14	30	11	20	2	4	0
	2005	14	26	13	9	0	3	3
	2006	15	23	17	10	1	4	0
	2007	16	60	31	31	3	4	0
	2008	14	29	10	9	5	3	1
Sarthe	2004	14	13	7	4	0	0	0
	2005	19	9	7	4	0	4	1
	2006	19	30	13	20	5	9	1
	2007	18	31	22	15	7	2	4
	2008	17	34	10	15	2	3	1

Table 2: Model averaged estimates of survival over 3 days and recapture rates (computed

for models with Δ QAIC$_c$ $>>1$ % see Table S4 in EMS).

Parameters	Model averaged estimates (SE)
Probability of recapture	
Females	
after first year of recapture in Orne	0.110 (0.007)
after first year of recapture in Sarthe - 2004	0.163 (0.022)
after first year of recapture in Sarthe - 2005	0.203 (0.044)
after first year of recapture in Sarthe - 2006	0.191 (0.025)
after first year of recapture in Sarthe - 2007	0.184 (0.015)
after first year of recapture in Sarthe - 2008	0.163 (0.022)
from second year of recapture in Orne	0.062 (0.005)
from second year of recapture in Sarthe - 2004	0.101 (0.014)
from second year of recapture in Sarthe - 2005	0.177 (0.007)
from second year of recapture in Sarthe - 2006	0.116 (0.013)
from second year of recapture in Sarthe - 2007	0.109 (0.006)
from second year of recapture in Sarthe - 2008	0.109 (0.006)
Males	
in Orne - 2004	0.460 (0.011)
in Orne - 2005	0.451 (0.009)
in Orne - 2006	0.453 (0.008)
in Orne - 2007	0.447 (0.011)
in Orne - 2008	0.464 (0.014)
in Sarthe - 2004	0.361 (0.012)
in Sarthe - 2005	0.341 (0.018)
in Sarthe - 2006	0.360 (0.011)

in Sarthe - 2007	0.357 (0.010)
in Sarthe - 2008	0.343 (0.016)

Survival rates

|	
after first year of recapture in Orne - 2004	0.675 (0.028)
after first year of recapture in Orne - 2005	0.587 (0.022)
after first year of recapture in Orne - 2006	0.608 (0.011)
after first year of recapture in Orne - 2007	0.621 (0.005)
after first year of recapture in Orne - 2008	0.656 (0.017)
after first year of recapture in Sarthe	0.657 (0.012)
from second year of recapture in Orne - 2004	0.783 (0.006)
from second year of recapture in Orne - 2005	0.781 (0.004)
from second year of recapture in Orne - 2006	0.770 (0.002)
from second year of recapture in Orne - 2007	0.768 (0.003)
from second year of recapture in Orne - 2008	0.777 (0.002)
from second year of recapture in Sarthe	0.770 (0.001)
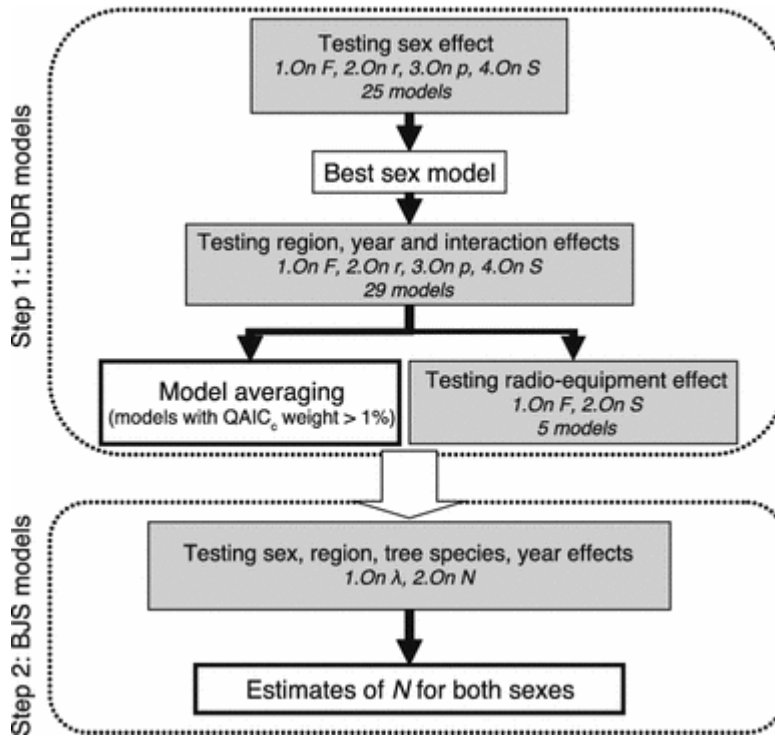
Figure 1: Hierarchical approach for estimating population size of *O. eremita* for both

sexes. LRDR: live recapture dead recoveries models, BJS: Burnham-Jolly-Seber models, *F*:

fidelity rate, *r*: recovery rate, *p*: probability of observation *S*: survival rate, λ: population

growth, N population size.
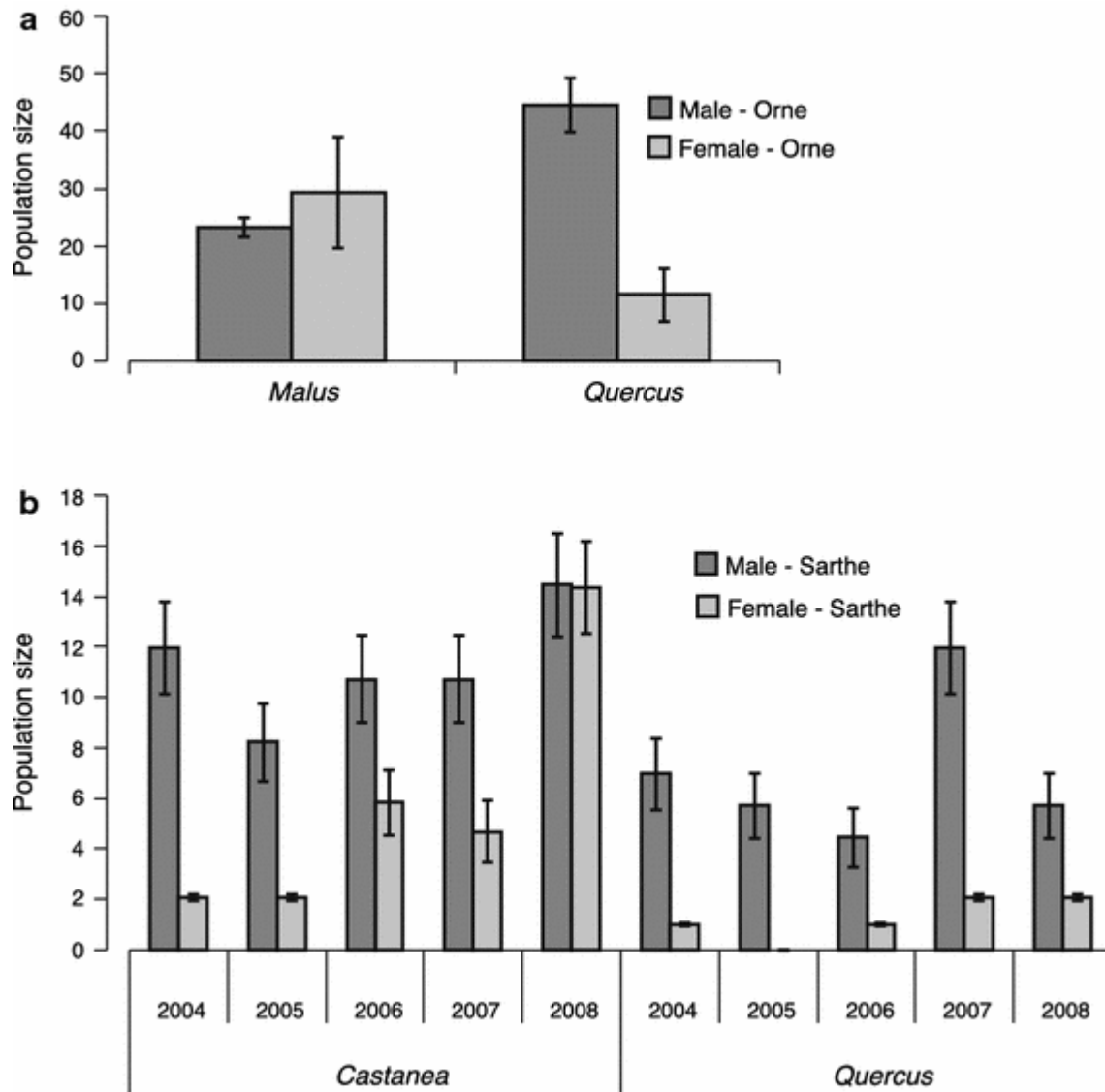
Figure 2: Model averaged population size estimates in Orne (a) and Sarthe (b) for males (black bars) and females (grey bars).
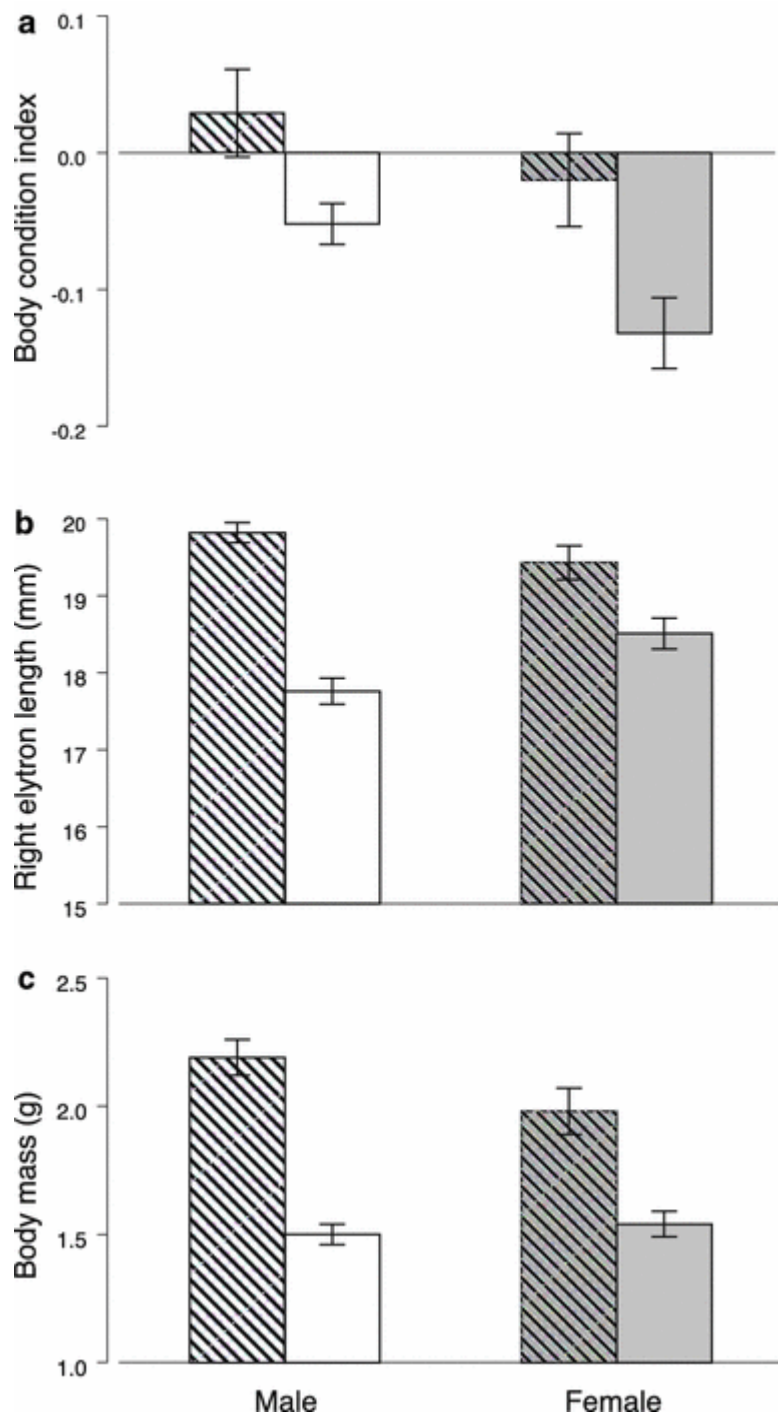
Figure 3: Average values of body condition index (a), right elytron length (in mm); b) and body mass (in g); c) for males (white bar) and females (grey bar) that were transmitter

equipped (shaded) or non-equipped (not shaded). Equipped males: $n = 19$; non-equipped

males: $n = 83$; equipped females: $n = 20$; non-equipped females: $n = 31$. Standard errors are

represented.