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Effects of forest fragmentation on the winter body condition and population parameters of an habitat generalist, the wood mouse *Apodemus sylvaticus*: a test of hypotheses

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Abstract – Three main causal hypotheses have been proposed to explain the inverse relationships between habitat patch size and density of generalist mouse species in fragmented habitats: 1) enhanced habitat conditions as habitat patch size decreases; 2) inhibited emigration of excess individuals in small and isolated habitat patches; and 3) reduced territoriality in small patches because they are occupied temporarily by non-reproductive individuals. From the mechanism underlying each hypothesis, we derived predictions on the effects of fragment size on the body condition of individuals (measured both as absolute body size and as body mass relative to body size) and some demographic parameters of mouse populations related to reproductive output (sex-ratio and proportions of sexually active and recently-born individuals), and we tested such predictions with data from wood mice *Apodemus sylvaticus* wintering in three Spanish forest archipelagos in which the inverse relationship between forest patch size and mouse abundance had been previously proven. No differences in average body size or in average body mass relative to body size were detected among fragments. Mouse populations wintering in small fragments showed more male-biased sex-ratios, a larger proportion of sexually active adults and fewer juveniles as compared to mouse populations wintering in large fragments nearby. Results clearly rejected the third hypothesis and did not support the second one. It thus seemed that habitat conditions for mice improved as forest fragment size decreased, although the expected positive effects on individuals could have been prevented by relaxed territoriality and increased food resource depletion by denser mouse populations. Bearing in mind the negative effects of dense wood mice populations on the distribution, abundance and population dynamics of forest species, this apparent enhancement of habitat conditions for mice in small forest fragments could have far-reaching consequences for the long-term persistence of such fragments. © Elsevier, Paris

Body condition / body size / demography / forest fragmentation / population density / winter / wood mouse

1. INTRODUCTION

The fragmentation of forest areas is a widespread process in both temperate and tropical regions (see [25, 32] and references therein). The effects of fragmentation on the patterns of distribution and abundance of organisms appear to depend mainly on the degree of specialisation in forest exploitation of the species concerned (for a review, see [50]). Among small mammals, for instance, the responses of forest specialist species such as *Clethrionomys* voles are clearly opposite to the responses of some species of *Apodemus* and *Peromyscus* that are habitat generalists in that they exploit a wide range of habitat types apart from forests [34]. *Clethrionomys* voles show reduced abundance and range in fragmented forests [33, 57], whereas the densities of *Apodemus sylvaticus* and *Peromyscus leucopus* are greatly enhanced by forest fragmentation, in such a way that the abundance in small forest fragments can be one or two orders of magnitude larger than in large forest tracts ([16, 18, 38, 55] and references therein). Similar results have been found for other species of *Peromyscus* living in experimentally fragmented old-field habitats [7, 9, 14].

Most work performed to date on the responses of organisms to forest fragmentation has focused on forest specialists, largely neglecting habitat generalists (for review, see [39, 50, 51]). This situation contrasts with the key role of generalist species in some of the processes that are responsible for the negative effects of fragmentation on forest specialists, such as increased predation and/or parasitism rates or decreased food availability within fragments (e.g. [28, 29, 43, 55]). Further, some generalist species may even be able to modify the dynamics of the whole forest habitat through direct effects on their regenera-

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tive capability, thus being potential keystone species [41] in fragmented forests.

The wood mouse *Apodemus sylvaticus* appears to be one such key species in Spanish forest archipelagos during winter. Mouse populations show marked and consistent increases in abundance as fragment size decreases [16, 55], as well as greater abundances in forest edges as compared to forest interior [17]. Wintering mice prey heavily upon the seeds and fruits produced by forest trees in autumn [47, 48, 55]. Such predation appears to be strong enough to affect negatively the winter distributions of some frugivorous bird species through exploitative competition [48], and even to reduce drastically tree recruitment within fragments [47, 48].

Increased abundance of forest generalist in fragmented forests is generally attributed to the fact that such species are positively affected by edge effects, as generalist habits allow animals to exploit both the forest and the surrounding habitats thus permitting greater abundances at forest edges (see [16] and references therein) and the relative amount of edge increases with decreasing forest patch size for basic geometrical reasons. However, this 'explanation' does not address the biological causes of such distributions. Three main causal hypotheses have been proposed to explain the inverse relationships between abundance and habitat patch size in generalist mouse species. First, habitat conditions within patches could be improved as patch size decreases, either because of area-related changes in vegetation structure and productivity and/or because of reductions in the populations of competitors and predators [9, 38]. Second, mouse populations in small forest fragments could grow to abnormally high densities if the dispersion of the excess individuals was prevented by bad habitat conditions in the matrix surrounding the fragments (the so-called 'fence effect' by Krebs et al. [31]; for a review, see [40]). Finally, a third hypothesis postulates that small patches could sustain high population densities because they are temporarily used by non-territorial individuals, whereas large patches are permanently occupied by individuals that hold territories. The time scales for this temporal occupation could vary from truly transient individuals that visit patches without staying [7, 14] to seasonal movements in which mice concentrate in the fragmented habitat mainly during the non-breeding season [55].

The processes underlying the above hypotheses should have strong effects on the body condition of individuals and on some demographic traits of mouse populations living in fragmented habitats. Under the first hypothesis, it can be expected that the body condition and/or the reproductive output would be enhanced in small fragments as compared to large forest tracts because of the improved habitat conditions experienced by individuals [38]. Contrary to this, the second hypothesis implies some degree of habitat impoverishment caused by overpopulation, so that negative effects on the body condition and/or the reproductive output of mouse populations are expected in small fragments ([31]; however, see [40]). The third hypothesis predicts that populations living in small fragments should be mainly composed of non-reproductive individuals with reduced (or suppressed) territoriality [7, 14, 55]. No clear predictions regarding the body condition of individuals can be derived from this hypotheses, since such condition will also be affected by the dispersal strategy of the species (see e.g. [52]).

In this paper, we address whether the body condition of individual mice and the reproductive output of their populations are affected by forest fragmentation, in an attempt to elucidate the proximate causes of the observed positive relationships between forest fragment size and mouse abundance. To achieve this goal, we obtained estimates of the body condition and reproductive state of individuals caught in three independent studies carried out in central Spain which successfully tested the expected inverse relationship between forest fragment size and wood mice abundance [16, 55]. While the assessment of the sex, age and reproductive state of individuals is generally straightforward (see references below for the case of the wood mouse), it is much more difficult to obtain unbiased and unambiguous estimates of their body condition (see [4] and references therein). However, we have previously shown [1] that the body size (measured as skeletal size) and the body mass relative to body size of wood mice populations wintering in central Spain were positively affected by habitat quality. This relationship, however purely empirical, suggested to us to use these morphological variables as estimates of the body condition of individuals. On these bases, we will specifically analyse whether the body size and the body mass relative to the body size of individual mice and the reproductive activity and sex-ratio of mouse populations wintering in three Spanish fragmented forests varied consistently with forest fragment size and mouse population abundance, as predicted by the hypotheses outlined above.

2. MATERIALS AND METHODS

2.1. Study areas and species

Field work was carried out independently in three separate study areas located near the localities of Lerma (Burgos province; 42°02' N 3°46' W, 800 m a.s.l.), Santa Elena de Jamuz-La Bañeza (León province; 42°15' N 5°52' W, 750–900 m a.s.l.), and Villatobas-Corral de Almaguer (Toledo province; 39°50' N 3°10' W, 700–730 m a.s.l.; *figure 1*). They are flat areas devoted mainly to extensive cereal cultivation (barley and wheat). Remnants of the original holm oak, *Quercus ilex*, forest of a variety of sizes are interspersed among cultivated fields. Apart from dominant holm oaks, some Pyrenean *Q. pyrenaica* and Lusitanian *Q. faginea* oaks and Spanish junipers *Juniperus thurifera* in Lerma and Jamuz, and Kermes oaks *Q. coccifera* in Villatobas, can be found. The main understorey shrub species (apart from tree saplings) are *Cistus laurifolius*, *Erica* spp. and *Genista* spp. in Lerma and Jamuz, and *C. ladanifer*, *Thymus* spp. and *Lavandula* spp. in Villatobas. These vegetation traits, as well as the climatic characteristics of the study areas (mild summers and cold wet winters in the two northern areas, and hot dry summers and mild winters in the southern one [11]), are representatives of the supramediterranean and mesomediterranean bioclimatic stages of the Iberian Peninsula ([42]; *figure 1*).

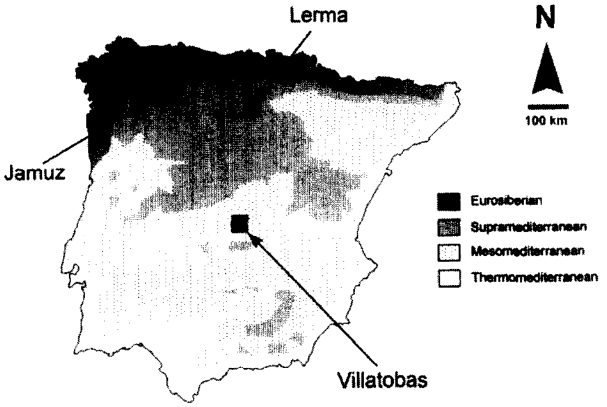

Figure 1. Map showing the location of the study areas. The main bioclimatic regions of the Iberian Peninsula are also depicted (the Eurosiberian region, and the supramediterranean, mesomediterranean and thermomediterranean stages forming the Mediterranean region [42]).

The wood mouse is the most common small mammal inhabiting these fragmented forests [16, 55]. This species is also dominant in the cereal crop landscapes of mid-Spain [56], where it shows a pattern of habitat selection which is markedly seasonal. Wood mice forage and reproduce across the whole agricultural landscape during summer whereas in winter, they concentrate in the uncultivated patches interspersed among fields, apparently because of their need for stable refuges and safe foraging places at that time of the year [2, 5, 56]. Winter concentrations in unploughed habitats are also evident in fragmented forests surrounded by croplands, where mice are found only occasionally in the agricultural matrix [16, 55]. Wood mouse densities are larger at forest edges and in fragments than in forest interior, and there is evidence that mice exploit to some extent the agricultural matrix close to fragment edges [17]. These patterns are in close agreement with results obtained for other European agricultural landscapes (see [18, 20, 26, 35, 36, 44, 45, 58] and references therein).

2.2. Sampling design

We selected the forest fragments studied in such a way that their range of sizes (measured on aerial photographs) were representative for each study area. In each fragment, we established six to 49 trapping points according to a size-logarithmic scale to ensure that the trapping effort was as homogeneous as possible among different-sized fragments. We used snap-traps in Lerma and pitfall traps (9 cm in diameter, 29 cm in depth) in Jamuz and Villatobas, since in the first area, we focused our study on wood mice populations only [55] and in the other two, we aimed to study the whole small mammal community ([16]; for a comparative study of both trapping methods, see Tellería et al. [54]). This latter fact, as well as the wide geographic range covered in that study, made the use of live traps logistically unfeasible. We placed two snap-traps at each trapping point to prevent trap saturation, whereas we located pitfall traps singly since they are not affected by this factor [53]. Pitfalls were half-filled with water supersaturated with salt to avoid freezing. All these trapping schemes were fully allowed by the corresponding Spanish authorities and strictly controlled by us, so that they did not suppose any threat to the populations of the studied species.

Trapping was conducted during two consecutive new moon nights in March 1989 at Lerma, and during a whole moon cycle (28 nights) in February–March 1995 at Jamuz and Villatobas. We checked snap-traps early in the morning, while pitfall traps were checked at 2–5-d intervals. The rationale for this schedule was to compensate for differences in effectiveness between trap types (see [54]) while avoiding moonlight effects on the mobility and trappability of small mammals [30]. Visual inspection of plots of the cumulative number of captures against time for each forest fragment showed that captures reached asymptotic values for most fragments, thus indicating both exhaustive capture of mice populations inhabiting each fragment and low incidence of dispersal between fragments. Hence, we estimated the density of wood mice in each forest fragment as the number of individuals caught per 100 traps-night of total trapping effort.

Different trapping methods and years of study in Lerma as compared to Villatobas and Jamuz precluded direct comparisons of population densities between areas [54]. However, methods were homogeneous in each study area thus allowing for proper within-area comparisons of densities and population parameters among different-sized forest fragments. The results obtained for each study area were then combined to analyse their consistency.

We measured the fresh body mass (to the nearest 0.5 g) of snap-trapped mice during the early-morning visits to traps. This measure was impossible to obtain for pitfall-trapped individuals. Every individual caught was preserved for laboratory assessment of its condilobasal length (CBL), sex, and reproductive condition. We measured CBL from the outer basis of the occipital condiles to the outermost point of the upper mandible (marked by the root of the incisor teeth) with a vernier caliper (intrinsic error: 0.1 mm). We considered males as sexually active if they had descended testicles, and females if they were pregnant, lactating, or had enlarged nipples. We were able to differentiate two age classes from CBL measurements and reproductive activity scores: recently-born individuals (less than 4–5-weeks-old), with CBL < 21.0 mm (none of which was sexually active), and adults, larger in size and comprising a variable proportion of sexually active individuals [22, 46]. Finally, we measured the body mass relative to the body size of mice snap-trapped in Lerma as the residuals from the regression equation relating fresh body mass to CBL for this population (see [1] for a similar procedure).

2.3. Data analysis

We analysed the relationships between body size (measured as CBL) or body mass relative to body size of wintering mice and the size of forest fragments by means of regression analysis between the log-transformed area of fragments (independent variable) and either the average CBL or the average body mass relative to body size of the adult mice caught in each fragment (dependent variable). We performed regressions separately for each sex since male wood mice are larger than females [1, 3] and, hence, the average values for each forest fragment would have otherwise been affected by sex-ratios. Recently-born mice were excluded from these analysis for similar reasons.

Although fragment size was closely related to population abundance in each study area, there was a large dispersion of individual values, especially for the smallest fragments, a fact that has been attributed to chance effects during the retreat of the mouse populations breeding in the agricultural matrix into the forest patches at the beginning of winter [16, 55]. As the second hypothesis (inhibited emigration) is based on the effects of overpopulation on the body condition of individual mice, we tested the effect of density values by means of correlations between the residuals of the above regressions and the index of population density for each fragment. Multiple regressions with fragment size and population abundance as independent variables cannot be performed properly because both variables were highly correlated [37].

We analysed categorical variables (sex-ratio, proportion of sexually active adults and proportion of recently-born individuals) by means of the fit of log-linear models to the four-way contingency table generated by the factors fragment size, sex/age, reproductive condition and presence/absence of capture, taking into account the structural zeros of the cells corresponding to sexually active x recently-born mice [12]. This procedure is analogous to an analysis of variance in that total variance of frequency data is partitioned into different factors and factor interactions, hence permitting a test of the significance of their effects [12]. We grouped captures into three fragment size categories (< 10, 10–100 and > 100 ha) because the number of captures in each fragment was too low to estimate accurately the proportions of individuals of each sex, age and reproductive condition. This fact, together with the chance effects associated to the early winter occupation of forest fragments (see above), precluded the application of more powerful statistical tests such as multiple logistic regressions, since these methods would have to consider each forest fragment as an independent observation [27]. The size categories of forest fragments were established for consistency with previous studies [16, 55].

3. RESULTS

We sampled 17, 27 and 26 forest fragments in the study areas of Lerma, Jamuz and Villatobas, respectively, ranging in size from 0.06 to 280 ha (*appendix*). Overall, we caught 592 wood mice with a total trapping effort of 21 865 traps-night. The skulls of 45 individuals were broken by snap-traps (Lerma) or during laboratory manipulations (Villatobas); hence, we could not measure the CBL (nor the age) of such individuals (*appendix*).

The distributions of the sizes of forest fragments (log-transformed), mouse densities, average body sizes, and average body reserves of mice, did not differ from normality for any sex or study area (Kolmogorov-Smirnov test: $DN = 0.104–0.234$, $P = 0.345–0.996$, $n = 14–25$ [59]). Males were larger than females irrespective of fragment size and study area, hence supporting our separate analysis for each sex ($F_{1.111} = 16.46$, $P = 0.0001$ for the effect of sex in an ANCOVA analysis using average CBL as the dependent variable, the log-transformed size of fragments as the covariate, and sex and study area as classification factors; $F_{1.111} = 1.01$, $P = 0.317$ for the effect of fragment size, $F_{2.111} = 2.57$, $P = 0.081$ for the effect of the study area, and $F_{2.111} = 0.668$, $P = 0.516$ for the interaction between sex and study area).

Average body sizes of adult mice were not related to fragment size for any sex or study area (*table I*), and the residuals from these regressions were not related to

Table I. Relationships between the average body size of adult mice (Y, measured as the condilo-basal length, in mm) and the size of forest fragments (X, in ha, log-transformed). Results are shown separately for each sex and study area.

	Model	F	df	*P*	r^2
Lerma, males	$Y = 23.60 - 0.054 \cdot X$	1.84	1,14	0.197	11.59 %
Lerma, females	$Y = 23.03 - 0.045 \cdot X$	0.58	1,12	0.460	4.62 %
Jamuz, males	$Y = 23.43 - 0.068 \cdot X$	3.40	1,22	0.080	14.54 %
Jamuz, females	$Y = 23.18 - 0.140 \cdot X$	1.90	1,13	0.190	11.93 %
Villatobas, males	$Y = 22.96 + 0.132 \cdot X$	4.22	1,23	0.051	15.52 %
Villatobas, females	$Y = 22.84 + 0.014 \cdot X$	0.06	1,23	0.807	0.26 %

Table II. Relationships between the average body mass relative to body size of male and female adult mice caught in Lerma (Y) and the size of forest fragments (X, in ha, log-transformed). Body mass relative to body size was estimated as the residuals from the alometric equation $W = 0.000167 \cdot CBL^{3.7384}$ (W: fresh body mass in g; CBL: condilo-basal length in mm; $F_{1,99} = 148.24$, $P = 0.000$, $r^2 = 59.96$ %, $n = 101$ wood mice wintering in Lerma [1]).

	Model	F	df	*P*	r^2
Males	$Y = 0.014 - 0.008 \cdot X$	0.81	1,14	0.382	5.49 %
Females	$Y = -0.025 + 0.014 \cdot X$	4.45	1,12	0.051	27.07 %

the indices of abundance of mouse populations wintering in each forest fragment either ($-0.504 < r < 0.351$, $0.061 < P < 0.763$). The average body reserves of male and female mice in Lerma were not related to forest fragment size (*table II*), and the residuals from these regressions were not related to the indices of abundance of mice wintering in each forest fragment either ($r = 0.066$, $P = 0.807$ and $r = -0.235$, $P = 0.419$ for males and females, respectively).

The three mouse populations studied showed male-biased sex-ratios and variable proportions of sexually active adults and recently-born individuals (*figure* 2). Also, overall mouse abundance varied among forest fragment sizes, as shown by the highly significant effects of activity, sex/age and fragment size on mouse density (*table III*), thus supporting previous results [16, 55]. There was also a strong effect of study area on mouse abundance, but this result was most likely due to the different trapping methods in Lerma as compared to Jamuz and Villatobas. All two-way interactions were significant. The proportion of sexually active adults was greater for males than for females, also differing among study areas and among fragment sizes. The sex-ratio and the proportion of recently-born individuals varied among study areas and among fragment sizes. Finally, the effect of fragment size on mouse abundance varied among study areas (stronger in Lerma than in Jamuz and Villatobas). There were only one three-way and no four-way significant interactions (*table III*). The differences in activity between sexes differed between study areas, being greater in Lerma, where no females were sexually active, and smaller in Villatobas. This between-area difference was not affected by between-area differences in fragment sizes. There were no between-area differences in the effects of fragment size on sexual activity, sex-ratio or their interaction. In summary, in spite of the strong between-area differences in overall sex-ratio and amount of sexual activity, mouse populations wintering in large forest fragments showed reduced den-

Table III. Results of the fit of log-linear models to the five-way contingency table generated by the factors study area (Lerma, Jamuz or Villatobas), fragment size (< 10, 10–100 or > 100 ha), sex/age (male, female, or recently-born individuals), reproductive activity (sexually active or inactive) and presence/absence of capture. The analysis takes into account that, by definition, no sexually active individuals can be found among recently-born mice, so that the corresponding cell values were defined as structural zeros [12].

Effect	df	G^2	*P*
Activity	1	19.64	0.000
Sex/age	2	49.84	0.000
Fragment size	2	96.65	0.000
Study area	2	508.80	0.000
Activity × sex/age	1	206.18	0.000
Activity × f. size	2	6.65	0.036
Activity × s. area	2	40.01	0.000
Sex/age × f. size	4	10.06	0.039
Sex/age × s. area	4	68.81	0.000
F. size × s. area	4	14.92	0.005
Activity × sex/age × f. size	1	0.51	0.474
Activity × sex/age × s. area	1	8.09	0.004
Activity × f. size × s. area	4	2.63	0.621
Sex/age × f. size × s. area	8	3.36	0.909
Activity × sex/age × f. size × s. area	6	2.83	0.829

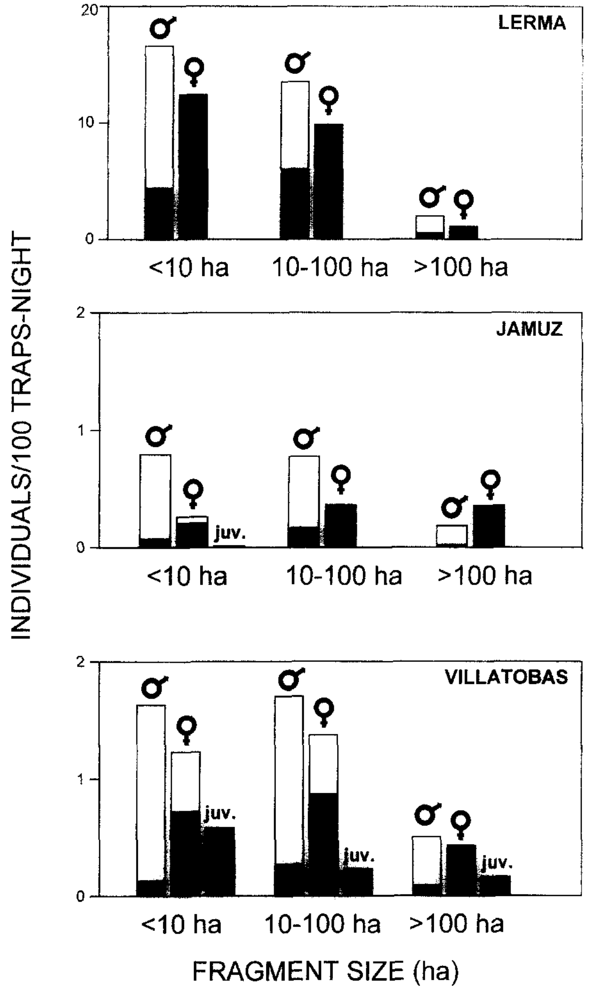

Figure 2. Mouse densities according to fragment size, sex and age (adult males, adult females, and juveniles), and reproductive condition (closed bars: sexually inactive; open bars: sexually active). Results are shown separately for each study area.

sities, more balanced sex-ratios, a smaller proportion of sexually active adults and a larger proportion of recently-born individuals than mouse populations wintering in smaller fragments nearby (*figure* 2).

4. DISCUSSION

In spite of the range of forest fragment sizes and mouse population abundances covered in this study, we did not find any evidence of either positive or negative effects of fragment size on the body condition of individual mice. The inverse relationships between fragment size and body size or body mass relative to body size that would have been expected if habitat conditions were improved by forest fragmentation [38] were not found. The positive relationships that would have been expected if enclosed mouse populations had significantly depleted their food sources within fragments [40] were not found either. Further, we did not find differences in body size among study areas, in spite of likely between-area differences in habitat quality as indicated by the overall reproductive activity of mouse populations (winter reproduction in wood mice is related to adequacy of environmental conditions [24] and such conditions improve southwards in the Iberian Peninsula [42]). These results contrast with previous findings on the significant relationships between fragment size [38] or gross habitat quality [1] and the body mass, body size or body mass relative to body size of individual mice.

Although forest fragment size did not appear to affect the body condition of individual wood mice, we found a strong effect of fragment size on the structure of their winter populations. Mouse populations wintering in small forest fragments showed larger proportions of sexually active adults, fewer recently-born individuals, and more male-biased sex ratios as compared to mouse populations wintering in large forest fragments nearby. These patterns were consistent among study areas in spite of between-area differences in overall reproductive activity of mouse populations (*figure* 2).

Widespread reproduction in small forest fragments did not support the idea that populations inhabiting such fragments were transient assemblages of non-territorial individuals, so that suppressed territoriality cannot account for increased mouse densities in such fragments [14]. Winter reproduction in small forest fragments did not support either the idea that dense mouse populations could have sufficiently reduced their food resources. Moreover, we found no evidence of population traits characteristic of enclosed rodent populations such as reduced reproduction or age-structure highly skewed towards juveniles [19, 38]. The only evidence for impoverished habitat conditions in small fragments was that reproduction seemed to be slightly delayed in such fragments, as indicated by the smaller proportions of recently-born individuals found in small fragments as compared with larger forest tracts [13]. Hence, results did not support inhibited dispersal as the main cause for increased mouse densities in forest fragments. In fact, wood mouse populations wintering in Spanish forest archipelagos could not be considered as totally closed, since wood mice occupy the whole agricultural landscape outside the winter season [2, 5].

Winter reproduction and larger proportions of sexually active adults in the smaller fragments supported the hypothesis of an improvement of habitat conditions for mice in fragmented forests. However, this conclusion is in contradiction with the apparent impoverishment of food conditions in small fragments caused by the strong depletion of tree crops by mice [47, 48, 55], as well as with the lack of positive effects of fragment size on the body condition of individual mice found in this study.

Concerning food availability, depletion of tree crops could have been compensated if individual mice had a better foraging access to alternative food sources, such as the seed banks accumulated in the agricultural land surrounding forest fragments (e.g. [55]). This agricultural matrix seemed easier to exploit from forest refuges as fragment size decreased due to more favourable perimeter-to-area relationships [17], and perhaps to relaxed predation risk (there is some evidence that mammalian carnivores and owls were negatively affected by forests fragmentation in the study areas [49]). However, data on the movements of marked individuals are required to test this hypothesis.

The lack of effects of habitat conditions on the condition of individuals may have been caused by changes in the structure of mouse populations. The effects of improved habitat conditions on individuals appear to be mediated by the social system of the species [10, 23]. If intraspecific agonistic behaviour is greater at high densities or in more favourable habitats, then better body condition and reproduction would be expected in the best habitats (Fretwell's 'ideal-despotic' scenario [15]). Alternatively, if there was a decrease in agonistic behaviours as food conditions improved, no differences in condition and demography among fragment sizes would be expected, since the increased population densities resulting from relaxed territoriality would compensate for differences in habitat quality (Fretwell's 'ideal-free' scenario [15]). We found that sex-ratios of mouse populations were more male-biased as fragment size decreases, and this result was consistent among study areas (*figure 2*). Since dominant *Apodemus* males usually exclude juvenile ones [8, 21], this result indicates a decrease in agonistic interactions in small fragments that would have allowed for the density compensation of improved habitat quality expected under 'ideal-free' conditions [10, 15].

In summary, the observed patterns of body condition of individuals, sex-ratio and reproductive output of populations indicate that winter habitat conditions for wood mice were improved by forest fragmentation. This generalist species appeared to take advantage of better habitat conditions by means of population responses (advanced reproduction and relaxed territoriality) rather than by responses of individuals, a fact that has been recently confirmed by experimental manipulation of the food resources available to populations of wood mice wintering in small forest fragments in central Spain (Alonso and Díaz, pers. obs.). This demographic flexibility [6] can explain both high population densities in small fragments and the lack of changes in the body condition of individual mice. On the other hand, the lack of negative effects of high winter densities on mice populations inhabiting small forest fragments implies that the negative effects of such dense populations on the distribution, abundance and population dynamics of forest species [47, 48] would be enhanced rather than attenuated as forest fragmentation advanced, a fact that could contribute to further accelerate the degradation of fragmented forests.

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Appendix. Size of the forest fragments studied and number of individuals captured in each (males, females, recently-born individuals – 'born' – and individuals whose condilo-basal length, fresh mass, or both, could not be measured accurately – 'unm.'). The trapping effort (number of traps-night) applied to each fragment and the corresponding index of mouse abundance (number of individuals/100 traps-night) are also shown.

Fragment #	Size (ha)	Males	Females	Born	Unm	Total	Effort (traps-night)	Abundance (ind./100 traps-night)
Lerma								
1	0.10	2	2	0	4	8	12	66.67
2	0.30	2	1	0	1	4	24	16.67
3	0.30	2	0	0	1	3	24	12.50
4	0.30	5	2	0	5	12	24	50.00
5	0.30	3	2	0	3	8	24	33.33
6	0.30	0	0	0	1	1	24	4.17
7	0.60	4	4	0	0	8	24	33.33
8	0.70	4	0	0	1	5	24	20.83
9	0.70	3	2	0	2	7	24	29.17
10	0.80	2	1	0	4	7	24	29.17
11	1.20	3	4	0	1	8	24	33.33
12	1.30	5	2	0	3	10	24	41.67
13	2.00	2	3	0	1	6	24	25.00
14	12.00	11	7	0	1	19	88	21.59
15	16.00	7	6	0	11	24	96	25.00
16	150.00	3	1	0	0	4	196	2.04
17	280.00	4	2	0	2	8	196	4.08
Total		62	39	0	41	142	876	
Jamuz								
1	0.06	1	0	0	0	1	174	0.57
2	0.22	2	0	0	0	2	168	1.19
3	0.24	5	3	0	0	8	168	4.76
4	0.30	1	1	0	0	2	168	1.19
5	0.75	0	2	0	0	2	168	1.19
6	0.78	3	0	1	0	4	174	2.30
7	0.84	3	0	0	0	3	174	1.72
8	0.86	5	2	0	0	7	168	4.17
9	1.40	3	2	0	0	5	822	0.61
10	1.40	0	0	0	0	0	224	0.00
11	1.56	0	0	0	0	0	224	0.00
12	1.60	0	1	0	0	1	224	0.45
13	1.68	1	0	0	0	1	224	0.45
14	1.76	0	0	0	0	0	224	0.00
15	1.76	2	0	0	0	2	174	1.15
16	2.50	2	0	0	0	2	420	0.48
17	2.95	7	1	0	0	8	420	1.90
18	3.74	4	1	0	0	5	405	1.23
19	4.68	2	1	0	0	3	420	0.71
20	4.85	4	1	0	0	5	431	1.16
21	5.30	3	1	0	0	4	435	0.92
22	16.30	5	3	0	0	8	435	1.84
23	34.16	3	0	0	0	3	404	0.74
24	36.00	2	5	0	0	7	580	1.21
25	44.00	5	1	0	0	6	841	0.71
26	63.00	9	2	0	0	11	822	1.34
27	217.00	2	4	0	0	6	1 145	0.52
Total		74	31	1	0	106	10 236	

Appendix. (cont.).

Villatobas

Fragment #	Size (ha)	Males	Females	Born	Unm	Total	Effort (traps-night)	Abundance (ind./100 traps-night)
1	0.18	0	2	6	0	8	174	4.60
2	0.20	1	3	1	0	5	174	2.87
3	0.40	2	3	2	0	7	168	4.17
4	0.44	1	3	0	0	4	174	2.30
5	0.50	6	2	0	0	8	168	4.76
6	1.00	2	1	0	0	3	174	1.72
7	1.04	2	1	1	0	4	232	1.72
8	1.28	3	2	1	0	6	224	2.68
9	1.40	6	0	0	0	6	224	2.68
10	1.60	4	7	1	1	13	224	5.80
11	2.20	4	6	4	0	14	435	3.22
12	2.20	10	5	5	2	22	420	5.24
13	2.88	4	4	0	0	8	435	1.84
14	3.00	8	8	4	1	21	435	4.83
15	3.00	8	2	0	0	10	420	2.38
16	3.00	10	6	0	0	16	435	3.68
17	4.00	4	4	7	0	15	420	3.57
18	6.07	5	4	2	0	11	435	2.53
19	8.92	12	7	1	0	20	435	4.60
20	9.28	10	7	2	0	19	435	4.37
21	10.64	4	9	3	0	16	435	3.68
22	13.96	6	2	4	0	12	435	2.76
23	41.80	15	9	0	0	24	725	3.31
24	76.00	8	6	1	0	15	875	1.71
25	76.28	24	20	0	0	44	870	5.06
26	144.00	6	5	2	0	13	1 172	1.11
Total		165	128	47	4	344	10 753	