

ORIGINAL RESEARCH

Mice population dynamics and structure over time and space after wildfires

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Keywords

Algerian mice; disturbance; recovery strategies; small-mammal population; wildfire; wood mice; habitat use; population dynamics.

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Abstract

Rodents respond quickly to changes in habitat structure after wildfires. They constitute important prey items for vertebrate predators and influence vegetation structure and regeneration. Assessing the population dynamics of rodents in burnt areas, whether individuals originate from in situ survival or from ex situ immigration, is therefore a key question in understanding the recovery of trophic networks after disturbance. This study aimed to identify the recovery strategies of rodent populations in recently burnt forests in the Mediterranean basin using body condition, reproductive output, sex ratios, and distance covered by wood mice and Algerian mice. Sampling stations were set up at increasing distances from the perimeter of recently burnt areas. Rodents were captured using Sherman traps and measured. Wood mice and Algerian mice lived syntopically within the recently burnt areas studied, the former species being more abundant and the second one selecting drier areas. Results indicated that time since fire, shrub cover, and distance to the perimeter of the burnt area influenced wood mice and Algerian mice population structures. Adult female wood mice mainly remained close to the burnt area perimeter, due to this species' matriarchal structure, while juvenile males dispersed farther into the burnt area. Adult females were also recaptured more frequently than other age and sex categories over time, whereas males covered greater distances. These findings suggest that the recovery strategy of these widespread Mediterranean rodents is mainly driven by ex situ immigration from unburnt areas. These results will be useful for post-fire management decisions such as non-intervention, salvage logging or the conservation of open areas, given that mice are a fundamental component of the ecosystem. Results also suggest that management should focus on maintaining good connectivity between burnt and adjacent unburnt areas to support mice populations and facilitate other longer-term conservation benefits.

Introduction

Rodent populations respond quickly to changes in habitat structure and composition caused by ecological disturbances, such as wildfires (Horncastle et al., 2019; Puig-Gironès et al., 2018). Rodents constitute a fundamental food source for vertebrate predators (Long & Smith, 2000) and influence vegetation structure and regeneration through seed predation and dispersal (Gordon & Letnic, 2019; Morán-López et al., 2022). Understanding the population dynamics of rodents in burnt areas, including surviving and immigrating animals after fire, is a key question for understanding the recovery of trophic networks after disturbances. Although some studies support the hypothesis that post-fire population is composed mainly of

local animals that survived the wildfire (in situ recovery) (Banks et al., 2011; Hale et al., 2021; Schwilk & Keeley, 1998), others argue that the population is mostly composed of immigrants from the surrounding unburnt areas (ex situ recovery) (Borchert & Borchert, 2013; Fons et al., 1993; Puig-Gironès et al., 2018; Rosário & Mathias, 2007; Simms et al., 2019). These two hypotheses are not mutually exclusive (Puig-Gironès et al., 2018) and their relative importance may vary due to numerous factors including species' life histories, fire recurrence and severity, and time since fire (TSF), which will all shape rodent communities over time and space.

Wood mice (*Apodemus sylvaticus* Linnaeus, 1758) and Algerian mice (*Mus spretus* Lataste, 1883) occur in recently burnt forests in the Mediterranean basin (Puig-Gironès et al., 2018;

Sainz-Elipse et al., 2012; Torre & Díaz, 2004). Despite its preference for high shrub cover (Torre et al., 2022), the wood mouse is a habitat generalist. Females exhibit strong nest site fidelity (Rosalino et al., 2011) and high breeding energy requirements (Montgomery et al., 1991). They also associate with maternal kin to increase their fitness (Gerlach & Bartmann, 2002). Polygynous males compete with females for food and with conspecifics for mating opportunities (Godsall et al., 2014; Montgomery et al., 1997). Intraspecific competition implies that seasonal changes in food abundance may lead to temporal changes in female abundance, but not in males (Sunyer et al., 2016). Males cover long distances during the breeding season (Godsall et al., 2014; Montgomery & Gurnell, 1985) and establish dominance-submission relationships. Juvenile males are more exposed to predators as they inhabit more open habitats (Dickman et al., 1991). Algerian mouse is well adapted to xeric environments due to its low water requirements (Pita et al., 2003). A monogamous mating system has been suggested for Algerian mouse (Cassaing & Isaac, 2007), whereby males also provide parental care for offspring (Cassaing et al., 2010). Older males are sedentary, suggesting territorial organization based on dominance hierarchies without exclusion of non-breeding younger males from territories (Palomo et al., 2009). Algerian mice dispersal has been linked to the presence of neighboring conspecifics (Gray et al., 1998). Similar responses have been found in fragmented forest surrounded by open habitats (Díaz et al., 1999; García et al., 1998).

Age and sex may influence the recovery strategies of these two mice species. We hypothesize that if in situ survival is dominant, the individual body condition (body mass index) and certain demographic parameters (sex ratio and the proportions of breeding actively and recently born individuals) will be similar throughout the burnt area, as colonization occurs independently of distance from unburnt areas. Nevertheless, if the ex situ immigration strategy drives recovery, breeding activity and body mass index will be higher near the burnt area's perimeter (close to both burnt and unburnt areas) where adults dominate, while juvenile males will be forced to roam within the burnt area. The mating system also plays a role, as in polygynous species, males are more likely to disperse, while in most monogamous species, both sexes have an equal likelihood of dispersing (Favre et al., 1997; Perrin & Mazalov, 2000).

In this study, we used the body condition, reproductive output, and sex ratios of wood and Algerian mice to investigate the recovery strategy of rodent populations in recently Mediterranean burnt forest, and to describe the rodent population structure after fire. Sampling was conducted in four recently burnt forests in Catalonia (NE Spain) to estimate the body condition, reproductive state, and distance covered by wood and Algerian mice populations. The different dispersal capabilities of these two species, along with their population structure, generate specific expectations given the recovery scenarios in the hypothetical framework that guided our study. Thus, the main questions addressed in this study were: (1) Is there differential space use between wood and Algerian mice populations after fire? If Algerian mice take advantage of open dry areas, the capture probability of this species will be greater in the burnt area; conversely, wood mice will be more abundant in

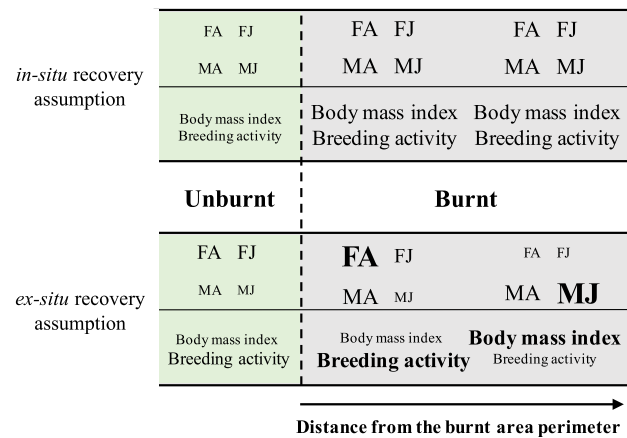


Figure 1 Conceptual diagram showing the two hypotheses of rodent population recovery after fire, where: (1) In situ survival-driven recovery in which population structure, breeding activity, and body mass index area unrelated to the distance from the perimeter of the burnt area. (2) Ex situ immigration, in which a higher abundance of sub-adult and juvenile males far from the perimeter of the burned area and a higher proportion of breeding activity near the perimeter are associated with a higher abundance of breeding females. Font size and bold type represents higher abundances of rodents (the sex and age combination), breeding activity, and body mass index.

regions with denser vegetative cover. (2) Are populations in the recently burnt area derived from survival or immigration from surrounding unburnt areas? If the main mechanism for recovery is immigration, we would expect greater abundances of juvenile males far from the burnt area perimeter and a greater proportion of breeding activity close to the burnt area perimeter associated with the higher abundance of reproductive females. However, if recovery is driven by in situ survivors, population structure, breeding activity and the body mass index will be unrelated to the distance from the burnt area perimeter (Fig. 1). (3) Does habitat structure affect population structure? If it does, we would expect to capture more adult females and adult males in areas with more plant cover given their roles as dominant individuals, and so juveniles will be more exposed to predation. (4) Are there sex and age differences in the distance covered by individuals? If there are, we would expect to detect (a) large daily movements within burnt areas by juvenile males, because adults are generally dominant and expulse juveniles and (b) more captures of females at the same locations given their nest site fidelity during the breeding season.

Materials and methods

Study area

Four large areas (over 200 ha each), recently (<6 months) and severely burnt in Catalonia (NE Spain; Fig. 2) were studied. Catalonia is characterized by high environmental heterogeneity, with sharp climatic and geological gradients, varying rainfall (from 350 to 1200 mm) and elevation (from 0 to 3143 m a.s.l.), and increasing aridity from North to South and East to West.

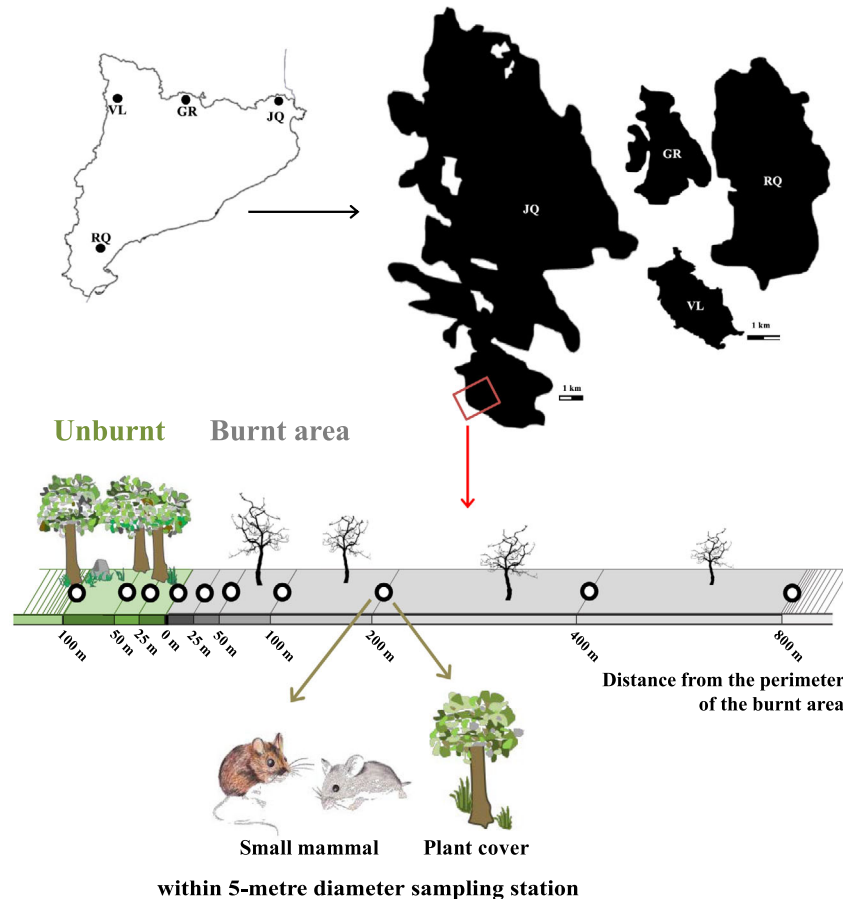


Figure 2 Location and schematic sampling design. Location of the four burnt study areas in Catalonia (NE Iberian Peninsula) and their size and shape, in black. Schematic representation of sampling transects, which contained ten 5-metre diameter sampling stations, three placed in the unburnt area (25, 50 and 100 m from the burnt area perimeter, approximate distances), one on the burnt area perimeter (0 m) and six in the burnt area (25, 50, 100, 200, 400 and 800 m from the burnt area perimeter, approximate distances). Each sampling station held a Sherman trap and was the sampling unit for plant cover variables.

Human presence since pre-historical times has led to changes in plant composition and distribution. According to Gracia et al. (2004), current land cover consists of 31% forests, 29% shrublands, and 33% agricultural land. Fire is a significant landscape driver in the region, with 25% of land being burnt between 1975 and 2010 (González & Pukkala, 2007). Two of our study areas were located in lowlands with Mediterranean climate, whereas the other two were in the Pyrenees where a humid mountain climate predominates (Table 1).

Sampling design

In each study area, we established linear transects, perpendicular to the section of the burnt area perimeter where the transect was located, across straight borders to avoid perimeter geometry effects (Fernández et al., 2002) and in places of high fire severity. Transects were ~ 900 m in length and separated from one another by at least 140 m at their closest points; with 61% separated by at least 500 m. The number of transects

varied by area, from five to 17, according to the size. Each transect contained 10 sampling stations, three in the unburnt area (at ~ 25, 50 and 100 m from the perimeter of the burnt area), one on the perimeter and six in the burnt area (at ~ 25, 50, 100, 200, 400 and 800 m; Fig. 2). The minimum distance between the inner-most stations of each transect and the opposite side of the perimeter of the burnt area was 1200 m. Sampling frequency decreased with TSF at La Jonquera and Ger, being monthly in the first 6 months, bi-monthly for months 7–24, and every 3 months thereafter until 30 months after fire (Table 1). Ger sampling was started 1 week after fire, while La Jonquera started 2 weeks after. Rasquera and Viu de Llevata were regularly sampled every 3 months from 18 and 23 weeks after fire, respectively. To avoid possible interference between wood management and vegetation recovery, and rodent behavior, we discarded the data from areas subject to salvage logging (see Puig-Gironès et al. (2020)).

To sample rodent populations, we used Sherman live trap (Sherman, Tallahassee, US) set in the center of a 5-m-diameter

Table 1 Characteristics of the four burnt areas

Wildfire	La Jonquera	Rasquera	Ger	Viu de Llevata
Region	Mediterranean	Mediterranean	Pyrenees	Pyrenees
Bioclimate	Subhumid Mediterranean	Dry continental Mediterranean	Humid Mediterranean mountain	Humid Mediterranean mountain
Elevation min/average/max (m)	90/263/574	317/348/409	1461/1672/1893	1180/1300/1510
Burnt area (ha)	13 088	3082	250	214
Date of fire	July 2012	May 2012	August 2012	March 2012
Time after fire in first sampling (weeks)	2	18	1	23
Last sampling week	117	138	118	141
Pre-fire habitat	Oak, pine and shrubland	Pine and shrubland	Pine and shrubland	Oak, pine and shrubland
Number of transects	9	5	11	5
Sampling occasions	15	7	16	8
Number of stations				
Unburnt	27	15	33	15
Burnt (including perimeter)	63	35	77	35

Description of the four burnt areas sampled for 2.5 years. The number of burnt stations includes the station located on the burnt area perimeter (for more information see Puig-Gironès et al. (2018)).

station. Sherman traps ($5.1 \times 6.4 \times 22.3$ cm) were baited with a mixture of tuna, flour, oil and apple (Torre et al., 2004) and were active for 24 h before being checked. Traps were checked daily, early in the morning, for three consecutive nights. The utilization of a single trap per station, deviating from the conventional methodology of utilizing multiple traps, may pose limitations in capturing all individuals present in the area sampled by each trap (trap saturation), but this was mitigated by the short interval between trapping periods, increasing the likelihood of capturing individuals that may have evaded capture during the initial trapping period. The utilization of a single trap may reduce the potential for trap-induced wariness or trap-fatigue, increasing trapping efficacy. Cotton wool was used to minimize thermal variation in traps to protect captured individuals and minimize mortality. Our recorded mortality was 1.4% of total, significantly lower than that reported by the Spanish and Andorran small-mammal monitoring programs (Torre et al., 2016, 2018).

Data on demographic parameters

Small-mammals were identified by species, sexed, weighed (± 1 g), measured (body, tail and right hind-foot, ± 1 mm), and ear-tagged for tracking (National Band & Tag Company, Newport, US). All the sampling procedures, as well as the research on live animals, met the American Society of Mammalogists Care & Use Guidelines and followed ethical guidelines (Sikes et al., 2011; Sikes & The Animal Care & Use Committee of the American Society of Mammalogists, 2016).

We differentiated two age classes based on weight measurements and reproductive activity. Juvenile wood mice were classified if weighing < 15 g (Díaz et al., 2010; Fernández et al., 1996), and Algerian mice if weighing < 7 g (Cassaing & Croset, 1985); but we classified them as adults if they show active reproduction signs. Breeding activity was determined visually, with *actively breeding* females having vaginal perforation, pregnancy, lactation or enlarged nipples, and *active* males

having descended testicles. We calculated the *body condition index (BMI)* using the formula described by Peig and Green (2009):

$$\text{Scaled mass index} : \hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$$

where M_i and L_i are the body mass and linear body measurement of individual i , respectively; b_{SMA} is the scaling exponent estimated by the standardized major axis (SMA) regression of $\ln M$ on $\ln L$; L_0 is an arbitrary value of L (arithmetic mean value for the study population); and \hat{M}_i is the predicted body mass for individual i when the linear body measure is standardized to L_0 (Peig & Green, 2009, 2010).

Recaptured individuals were used to collect information on survival and movements within the study area. First, the *total distance covered* (m) was calculated as the sum of the distances between different traps in which an individual was recaptured. *Time since the first capture* corresponded to the days elapsed from the first capture to the latest capture. The *relative distance covered* (m/day) was calculated by dividing the total distance covered (m) by the time elapsed since the first capture (days). Two recaptured individuals out of a total of 176 were recaptured on neighboring transects. The remaining individuals were all recaptured on the same transect.

Environmental and spatial variables

Sampling season was used to take into account seasonal effects on rodent abundance (Díaz et al., 2010; Palomo et al., 2009). TSF, the number of weeks elapsed since fire, ranged from 1 to 141 (first week = 1 and so on). Distance from burn perimeter was measured from the center of the station to the closest point of the perimeter using a topographic digital map and UTM coordinates. The perimeter was defined visually on-site as the border between unburnt and totally or partially burnt vegetation. Negative values were assigned to stations in the

unburnt area, and positive values indicated distances within the burnt area. The exact distances (mean \pm SE) of consecutive stations in the transects were: -96 ± 16 , -57 ± 9 and -26 ± 7 m for unburnt areas, 0 ± 0 m for stations on the perimeter, and 27 ± 6 , 55 ± 10 , 107 ± 20 , 219 ± 39 , 385 ± 56 and 717 ± 78 m for burnt areas.

We used a series of variables related to vegetation structure to characterize the habitat in an area of 5-m diameter surrounding the sampling station. Foliage cover (%), an indicator of vegetation recovery, was estimated using a reference chart for six virtual vegetation height layers: 0–0.25, 0.25–0.5, 0.50–1, 1–2, 2–4 and over 4 m (Prodon & Lebreton, 1981). A principal component analysis (PCA) was used to summarize the information obtained from the six variables after arcsine transformation. The first component (PC1, *plant cover*) corresponded to the extent of plant cover, while the second (PC2, *height of vegetation*) placed stations in order in terms of the height of the dominant vegetation layers (see Puig-Gironès et al. (2018)). We also estimated the percentage covers of woody species at three height layers: 0–0.25, 0.25–0.5 and 0.50–1 m, which was the inverse of the percent of herbaceous cover. A PCA was used to summarize the information, where the first component (PC1, *shrub cover*) corresponded to the extent of shrub foliage cover (Figure S1). These three components of the habitat structure were used as independent variables in the analyses.

Statistical analysis

Capture likelihood of mouse species

Generalized additive mixed models (GAMM) with a binomial response and a logit link function were used to compare the probability of capturing a wood mice (as opposed to an Algerian mice) in Mediterranean sites (no Algerian mice were found in the two Pyrenean study areas). Season, TSF, distance from burn perimeter, plant cover, height of vegetation and shrub cover were used as explanatory variables. GAMM are a powerful and flexible way of performing regression analyses (Wood, 2017) and consist of Generalized Linear Mixed Models (GLMM) with smoothed splines fitted to the explanatory variables rather than to the original values of the variables. *Transect* was used as a random factor to control site-based differences. TSF, distance from burn perimeter, plant cover, height of vegetation and shrub cover were treated as smoothed variables.

Sex and age ratios

To understand the impact of environmental variables on rodent population structure, we used multinomial logistic regression (MNL) to calculate the likelihood of capturing each sex-age combination. The response variable had four categories: adult female, adult male, juvenile female and juvenile male. Environmental variables included TSF, distance from burn perimeter, plant cover, height of vegetation and shrub cover. The Adult male category was used as the reference level, i.e. the probability of capturing each of the other three sex-age combinations

were compared with the adult male probability. We also analyzed how environmental variables affected the presence of the four sex-age combinations for each species immediately after fire using four binomial GAMMs, with season, TSF, distance from burn perimeter, plant cover, height of vegetation and shrub cover as explanatory variables. We did not analyze age ratios for Algerian mice as only one juvenile was captured.

Breeding activity

A binomial GAMM was used to detect differences in the breeding activity of both species. Explanatory variables included sex, age, season, TSF, distance from burn perimeter, plant cover, height of vegetation and shrub cover.

Body mass index

A negative binomial GAMM was used to test the variation in the body mass index of both species, with sex, age, season, TSF, distance from burn perimeter, plant cover, height of vegetation and shrub cover used as explanatory variables.

Movements

We used negative binomial GLMM and logit link function to evaluate mouse movements (total and relative distances covered) and estimate survival (time since first capture). The models included sex, age and body mass indices as explanatory variables. Rodent trappability may be influenced by multiple factors including sex, trap or season (Byers et al., 2019; Tanton, 1965; Torre et al., 2016). Male wood mice are more likely to enter a trap, as they are more active and more attracted to the scent of attractants used in traps. Contrarily, females tend to be more cautious and less likely to enter a trap to avoid potential danger (Tanton, 1965; Unnsteinsdóttir, 2014). Furthermore, in social groups comprising males and females, females were more likely to exhibit trap-prone or trap-shy behavior, with more males being caught than females (Crowcroft & Jeffers, 1961). However, these relations may change in burnt areas due to sex and age relative abundances over time and space.

Our model selection approach used all possible sub-models derived from a set of explanatory variables, which limits model selection bias and provides a relative measure of the importance (weight of evidence) of each predictor. All possible models were ranked according to their Akaike Information Criteria corrected for small samples (AICc) (Burnham & Anderson, 2002). We analyzed the diagnostic plots of the fitted values, residuals and the fitted splines for each term of each model to assess their goodness of fit. We quantified generalized variance-inflation factors (GVIF) to check for collinearity and dropped any factors with high GVIF values (arbitrary threshold of ≤ 2.5) (Fox & Monette, 1992; Zuur et al., 2010). We calculated AIC weight (AIC ω) for each model (total AIC ω adds 1) (Wagenmakers & Farrell, 2004). If there was no clear most-parsimonious model (AIC difference of less than two from the best model), we estimated the average final model of all these models (Burnham & Anderson, 2002). To interpret the

magnitude of each variable in the average final model, the relative importance of each variable (RIV) was weighted based on the sum of ω_i for each variable (Table S1). The RIV ranged from 0 to 1 and the explanatory variable was considered robust if it had an RIV >0.9 , a moderate between 0.6 and 0.9, weak between 0.5 and 0.6, and no effect below 0.5 (Chiaradia et al., 2016; Kennedy et al., 2013). To perform these analyses, we used R software (R Development Core Team, 2017) with the *nnet* (Venables & Ripley, 2002), *car* (Fox & Weisberg, 2011), *gam4* (Wood & Scheipl, 2014), *lme4* (Bates et al., 2015), *MuMIn* (Bartoń, 2016) and *ggplot2* (Wickham, 2009) packages.

Results

We captured 1065 rodents over 16 430 traps nights (calculated as the sum of the number of nights multiplied by the number of traps used) over a 2.5 years period, resulting in a capture rate of 6.48 individuals/100 adjusted trap nights. In all, 904 wood mice and 161 Algerian mice were captured. Of the total captures, 175 were recaptures (16.4%), 141 of which were

wood mice (80.6%) and 34 were Algerian mice (19.4%). Although one mouse was captured seven times, most individuals were captured only twice (77.2%) or three times (19.2%).

Modeling using GAMM revealed that TSF and summer season increased the likelihoods of capturing an Algerian mouse (Table S2). The distance from burn perimeter also had a positive effect on capturing Algerian mice, while wood mice were more likely to be captured closer to the perimeter (Fig. 3).

Our analysis using a multinomial logistic regression (MNL) showed that, in terms of sex and age, the likelihood of capturing a rodent mainly depends on TSF, distance from burn perimeter and shrub cover. Adult females were more likely to be captured closer to the perimeter and in places with high grass cover than adult males (Table 2). Juvenile females were more likely to be captured with increasing TSF, closer to the perimeter and in stations with higher shrub cover than adult males. The probability of capturing a juvenile male was greater with more TSF and in places with higher shrub cover than adult males.

Adult and juvenile male wood mice (Table S2) were more frequent within the burnt area and farther from the perimeter

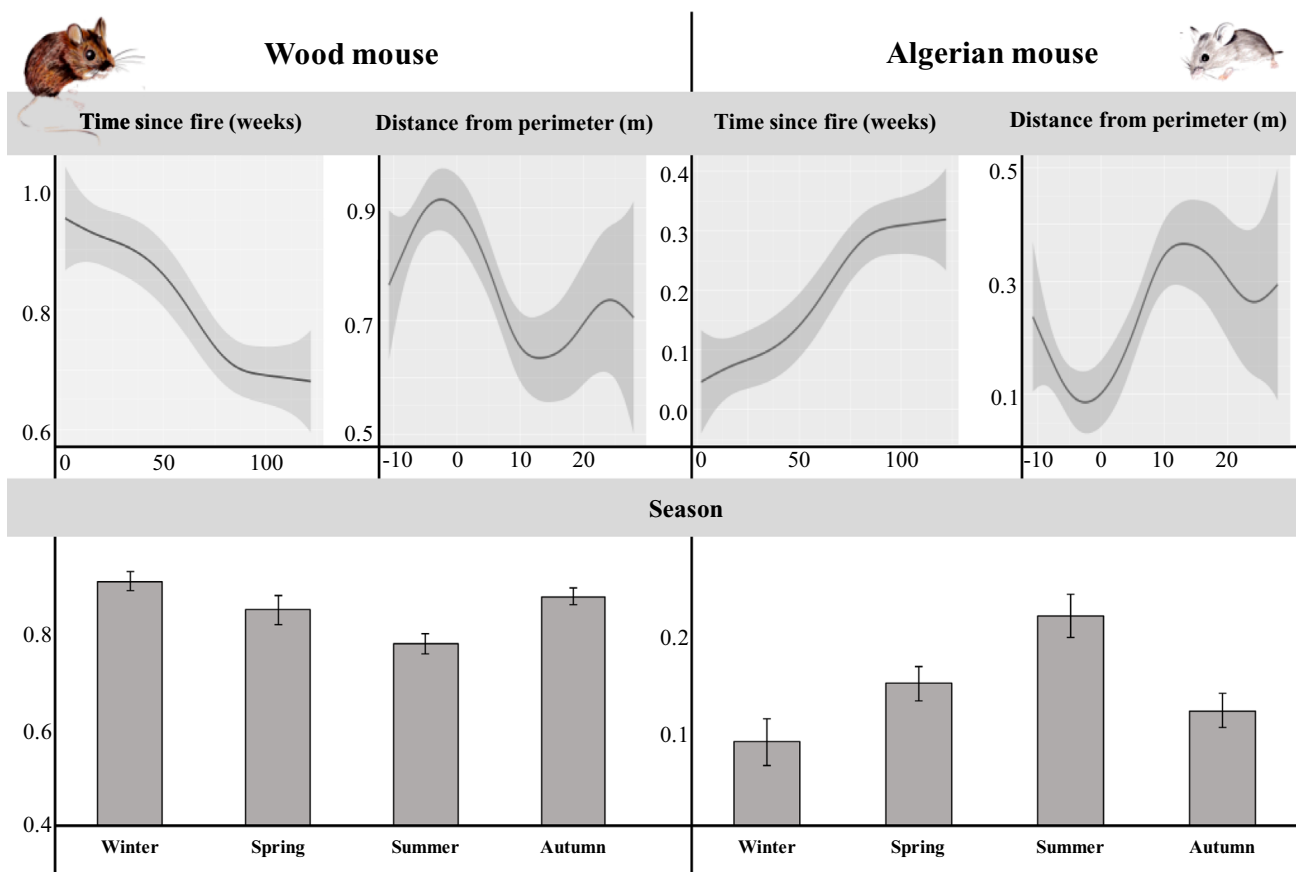


Figure 3 Capture probability model for two rodent species. Probability of capturing a wood mouse in relation to the probability of capturing an Algerian mouse, as a function of the time since fire, distance from burnt area perimeter and season is shown. Time and distance marginal effects (that measure the instantaneous rate of change) are extracted from generalized additive mixed models (GAMM). Trend line and standard error (shaded areas) shown in upper plots were obtained from GAMM estimates. Standard error bars are shown in the bottom plots.

Table 2 Multinomial model of rodent responses after fire

	RVI	Adult female		Juvenile female		Juvenile male	
		Estimate ± SE	<i>P</i> value	Estimate ± SE	<i>P</i> value	Estimate ± SE	<i>P</i> value
Intercept		-0.28 ± 0.16	0.08	-3.07 ± 0.39	< 0.001	-2.7 ± 0.32	< 0.001
Time since fire	1.0	0.001 ± 0.002	0.57	0.01 ± 0.004	0.01	0.01 ± 0.003	< 0.001
Distance from burn perimeter	1.0	-0.04 ± 0.009	< 0.001	-0.08 ± 0.02	< 0.001	-0.02 ± 0.01	0.12
Height of vegetation	0.43	0.14 ± 0.10	0.15	-0.18 ± 0.23	0.44	-0.22 ± 0.19	0.25
Shrub cover	1.0	-0.12 ± 0.05	0.02	0.28 ± 0.10	0.008	0.13 ± 0.08	0.09

Parameter estimates of the multinomial logistic regression (MNL) model on mice grouped by sex and age. The table shows the model parameter coefficient, its standard error (±SE) and the associated *P* values.

Relative importance of each variable (RVI) was weighted based on the sum of ω_i for each variable (Table S1).

Values in bold correspond to significant parameters ($P < 0.05$).

than females (Fig. 4). TSF and shrub cover increased the likelihood of capturing juvenile wood mice. Adult female wood mice, however, preferred stations with greater grass cover near the perimeter. Wood mice body mass index was better in individuals within the burnt area than outside (ANOVA $F = 25.56$, $P < 0.001$), and increased over time and in spring. Although not significantly, the body mass index was worse in juvenile females (ANOVA $F = 1.34$, $P = 0.26$). Male Algerian mice were captured more frequently in autumn and spring and farther from the perimeter (Fig. 5). The breeding activity of this mouse species was higher in places with tallest vegetation and its body mass index was worse in places with little plant cover (Table S2). No differences in body mass index were found between Algerian mice captured inside and outside the burnt area (ANOVA $F = 0.02$, $P = 0.90$) nor between sexes (ANOVA $F = 0.25$, $P = 0.62$).

GAMM showed that adult and juvenile male wood mice covered longer distances than female wood mice (Fig. 6; Table S3). Adult female wood mice were more likely to be recaptured over time. Male Algerian mice also covered larger distances than females, although the distance covered per day was related to a better body mass index. Male Algerian mice with better body mass index was more often captured over time than females (Figure S2).

Discussion

Our results show how TSF, seasonality and habitat complexity affected differently the probability of capturing Algerian mice versus wood mice immediately after fire. TSF and the summer period increased the probability of capturing an Algerian mouse, whereas the wood mice were more frequent close to the burnt perimeter where the habitat was more complex. Despite living syntopically in the study area, wood mice were more abundant than Algerian mice in all the studied burnt areas. This dominance – as previously reported – is attributed to the higher competitive ability of wood mice linked to its larger body size. However, it is also possible that this dominance was a result of the wood mouse's polygamous behavior, while the Algerian mouse is monogamous (Cassaing & Isaac, 2007; Montgomery & Gurnell, 1985). Life expectancy for wood mice is 12 months (Niethammer & Krapp, 1978) and for Algerian mice 4 months (Cassaing & Croset, 1985), allowing for more dispersing wood mice juveniles to

spread widely in the burnt area. However, Algerian mice can thrive in dry areas with poor shrubby regeneration (Fuentes et al., 1998) where they may outcompete wood mice (Grant, 1972). Nonetheless, other key aspects as fecundity or age at sexual maturation should be considered in future studies.

Identifying spatial variation in resilient populations after disturbances facilitates predictions of future recovery mechanisms and patterns (Franklin et al., 2000) and can help forecast which species – as well as their age and sex structure – will occur. Our results support the importance of surrounding population sources in the recovery of burnt areas (Borchert & Borchert, 2013; Fons et al., 1993; Puig-Gironès et al., 2018; Rosário & Mathias, 2007; Simms et al., 2019) by Mediterranean wood mice and Algerian mice. Life-history traits play a role in species' responses to fire (Kelly et al., 2010). Immediately after fire, we were more likely to capture a territorial and active breeding adult female close to unburnt areas. Males, instead, were captured more frequently far from the burnt perimeter. As TSF increases, we found an increase in juveniles in the burnt area, as other authors have also found (Fons et al., 1988). Algerian mice showed spatial segregation, with males captured farther from the burnt perimeter than females. This suggests that the recovery of these rodent populations is mainly driven by immigration from unburnt areas. Our findings confirm that wood mice females can establish themselves in areas with few females and become reproductively active, while males tend to move towards areas that offer the greatest opportunity for copulation (Montgomery et al., 1997).

As previously reported (Clarke, 1985), wood mice in the Mediterranean Basin breed in autumn and spring with a period of latency in winter. However, we found no clear winter break, which may be an opportunistic breeding strategy (Massoud et al., 2021) and/or a response to resource availability (Díaz & Alonso, 2003) in burnt areas. Intrinsic demographic regulatory mechanisms, such as segregation and competition for food, territories, natal dispersal and reproductive suppression (Godsall et al., 2014; Montgomery et al., 1997; Sunyer et al., 2016; Wolff, 1997), regulate population growth. Experimental removal of adult male wood mice resulted in an increase in adult females, although lack of females led to immigration and enhanced reproductive success in female immigrants (Montgomery et al., 1997). Subsequently, spatial density-dependent breeding inhibition in females regulates population increases

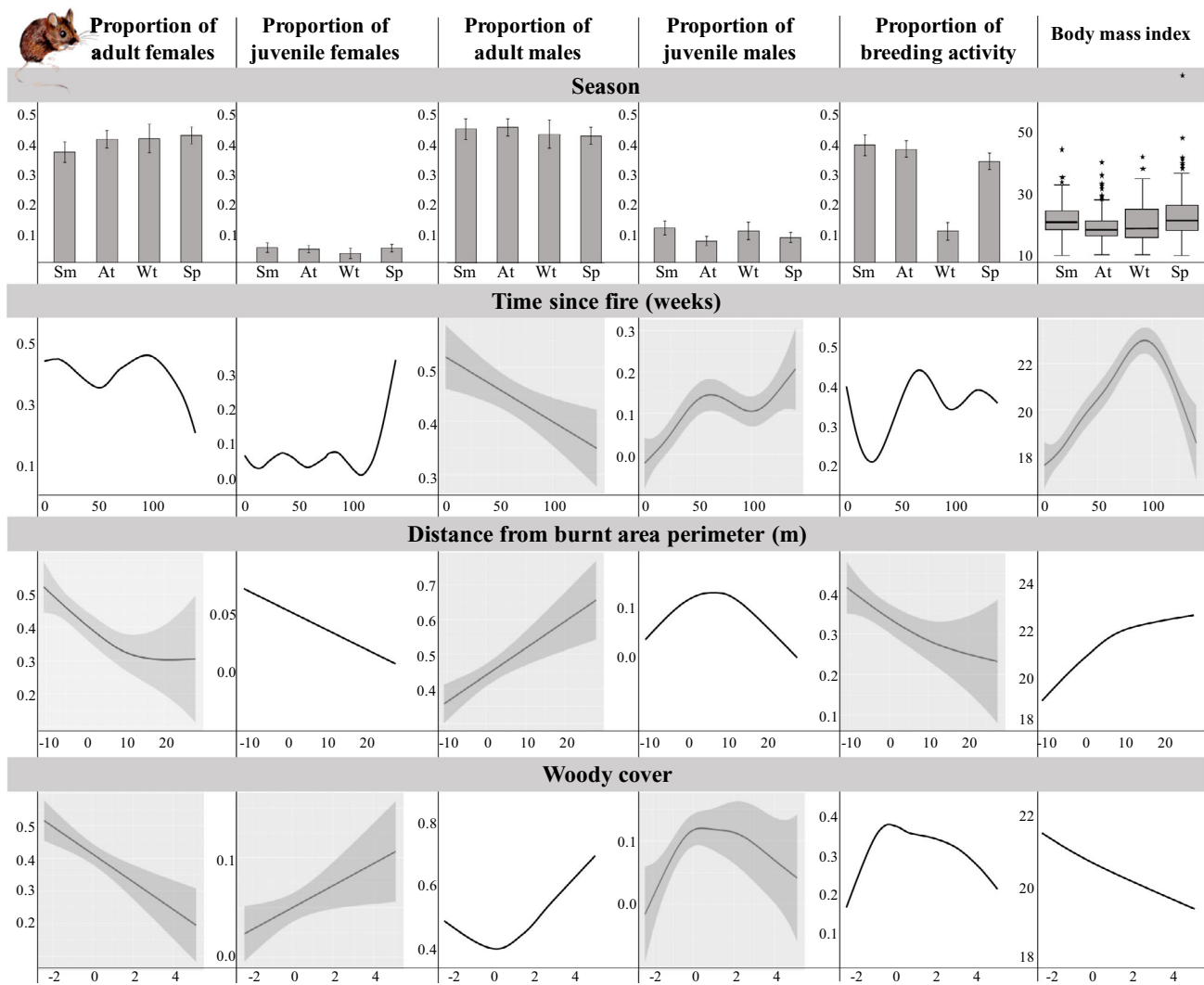


Figure 4 Model predictions for wood mice. The proportion of wood mice adult and juvenile, female and male, breeding activity and body mass index as a function of season, time since fire, distance from burnt area perimeter and shrub cover are shown. Time and distance marginal effects (measure the instantaneous rate of change) are extracted from generalized additive mixed models (GAMM). Trend lines and standard errors were obtained from GAMM estimates. Lines without shaded areas indicate non-significant relationships or low weight in the final model. Standard error bars are shown for the sampling season factor. SM, Summer; AT, Autumn; WT, Winter, and SP, Spring.

(Montgomery et al., 1997). Nevertheless, this mechanism may be overridden by greater food availability and lack of competition in recently burnt areas (Puig-Gironès et al., 2018; Puig-Gironès & Pons, 2020). Self-regulation is more expected in polygynous species with territorial females (Wolff, 1997). Algerian mice did not show any reduction in breeding individuals throughout the year, although the percentage was slightly lower in winter, as is usual (Vargas et al., 1991). This is supported by a moderate testis reduction in winter (Massoud et al., 2021) and is considered a response to resource availability. Wood mice body condition – related to an animal’s health and fitness – increased with TSF but decreased 2 years after fire, possibly due to an increase in juvenile females with poorer body condition in burnt areas.

Tall plant cover provides small-mammals with protection against predators and food resources (Torre & Díaz, 2004) and allows rodents safer foraging and eating (Manson & Stiles, 1998; Muñoz et al., 2009). However, cover selection varies by species, sex, and age. For example, adult females were more often captured in places with taller grass cover, and shrub cover, used as shelter, increased wood mice abundance in the burnt area (Díaz, 1992; Puig-Gironès et al., 2020). Algerian mice did not show any sex-dependent habitat preferences, but taller vegetation and lower plant cover did favor breeding and body mass condition, respectively. In general, our study indicated that habitat structure was crucial, and dispersing wood mice take advantage of empty habitats with sufficient resources (shelter and food), while open habitats favor Algerian mice.

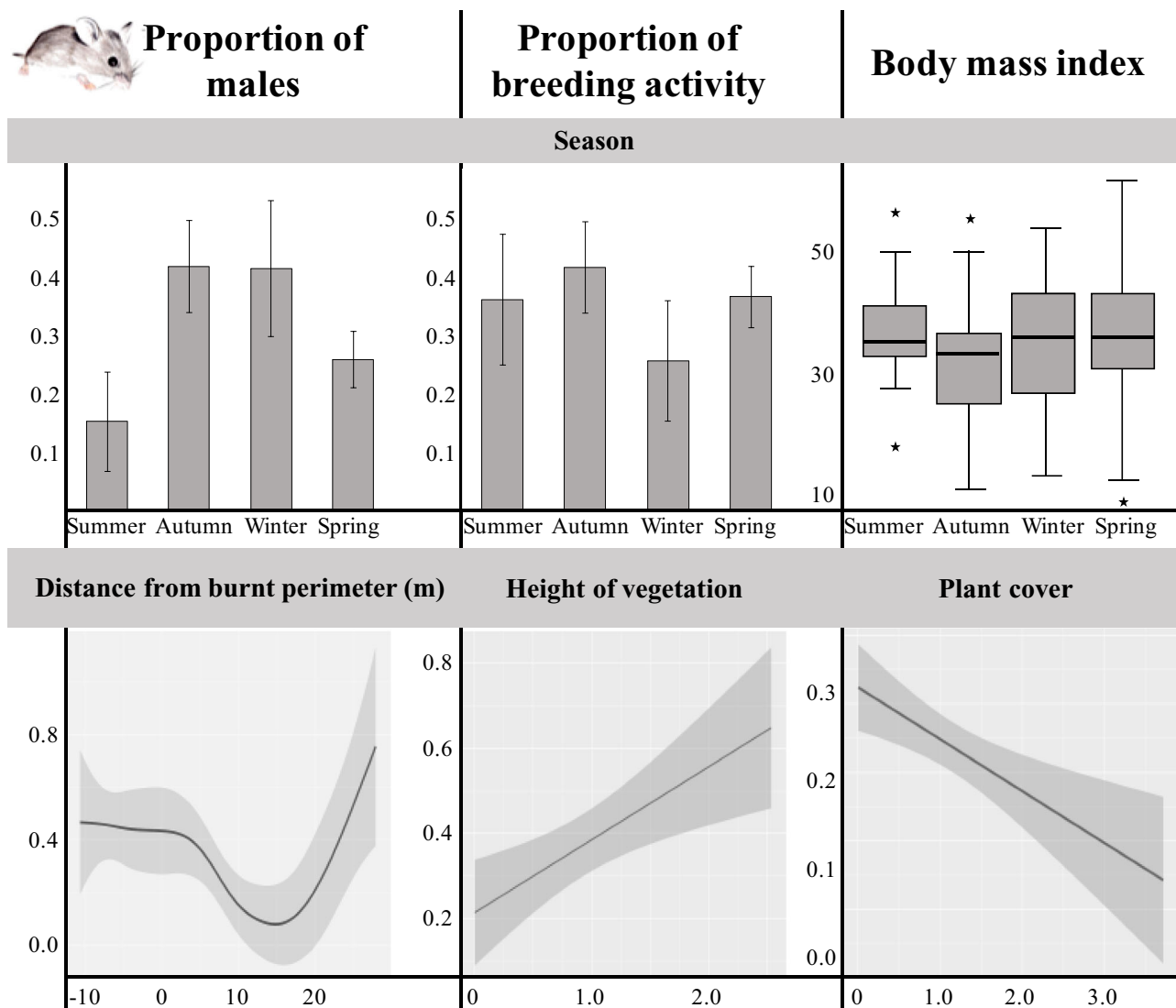


Figure 5 Model predictions for Algerian mice. The proportion of Algerian mice males (in relation to the total number of captured female individuals), breeding activity and body mass index as a function of season and generalized additive mixed models (GAMM) significant relationships are shown. Trend lines and standard errors (bars shown for the sampling season factor) were obtained from GAMM estimates.

Understanding animal movement patterns is important for understanding how populations connected through dispersal. Movements are a species-specific trait with implications for the species population dynamics and the structuring of communities (Gentile & Cerqueira, 1995). Differences found in mobility were probably the consequence the reproductive strategies. Wood mice females moved little, were captured repeatedly, and showed nest site fidelity (Rosalino et al., 2011). Juvenile males, instead, moved more and were captured less, covering greater distances (around 20 m/day) over short periods of time (Dickman et al., 1991; Montgomery & Gurnell, 1985). Although it is known that wood mice can travel many meters in a few hours or return home from distances as far as 500 m (Bovet, 1978), dispersal is dependent on habitat quality, in

which food availability and vegetation cover are fundamental factors (Montgomery et al., 1991). Male Algerian mice covered greater distances and were captured more often than females. Cassaing and Croset (1985) and Gray et al. (1998) found that Algerian mice moved between 13 and 55 m in a few days. Our results seem to coincide with previous studies; nevertheless, our live-trap method has limitations and may underestimate animal movements as we only have information from the stations at which they were trapped, and do not know how animals behaved while moving between points. Additionally, animals may become accustomed to traps and be caught regularly. Consequently, we also assume that inter-individual differences in capture probability may affect these results (Byers et al., 2019).

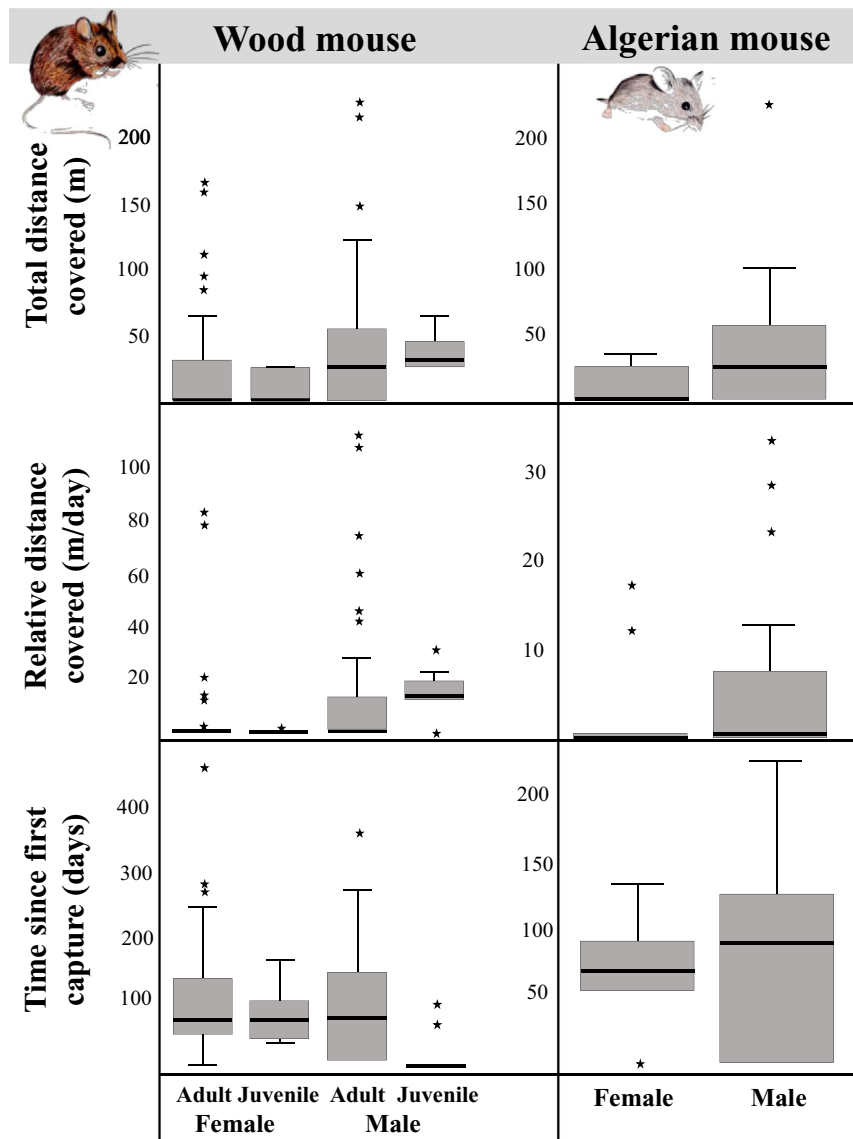


Figure 6 Distance covered by rodents and time since first capture. The rates of movement of sex (both species) and age (wood mice only) categories of mice captured within the burnt area as a function of total (m) and relative distance covered by individuals (m/day) and time since the first capture (days) are shown.

Conclusions and conservation implications

Our results suggest that ex situ immigration is the main mechanism of recovery for wood mice and Algerian mice (Borchert & Borchert, 2013; Fons et al., 1993; Puig-Gironès et al., 2018; Rosário & Mathias, 2007; Simms et al., 2019) in wildfires in the Mediterranean Basin. However, recovery by immigrants may mask recovery by internal survivors. Mice displayed distance segregation within the burnt area, with males and juveniles captured farther from the burnt perimeter than females. Furthermore, establishment of reproductive immigrant females in the burnt area ensure the reoccupation. Both species also showed space segregation, with Algerian mice using dry areas

with poor and late shrub regeneration, where they are probably more competitive than wood mice. However, the total number of wood mice was higher in the burnt area, and as woody vegetation encroaches over time, it is expected to become more favorable for wood mice due to their preference for dense shrublands and/or open forests.

Identifying spatial drivers after disturbance is crucial in decision-making for post-fire planning and management. In this sense, alternative strategies, such as non-intervention, immediate salvage logging, or conservation of open areas to favor threatened species should be considered. In our non-intervention burnt areas, rodents mainly recovered from the perimeter by dispersing juveniles. However, in the long term,

non-intervention will allow succession to produce woody encroachment, and the attendant collapse of open-habitat small-mammals (Puig-Gironès et al., 2022; Torre & Díaz, 2004), and will likely increase the fire risk (Brotons et al., 2013; Duane et al., 2021). If salvage logging is chosen, based on our results, maintaining good connectivity between burnt and adjacent unburnt areas is crucial. This may be achieved through wood debris piles, which provide shelter, reduce erosion, and benefit plant regeneration and animal presence (Mauri & Pons, 2019; Puig-Gironès et al., 2020; Sullivan et al., 2012). For open-habitat maintenance, management should begin 5 years after fire, when the habitat is no longer optimal for open-habitat specialists (Puig-Gironès et al., 2022) and mice have likely recovered (Torre & Díaz, 2004). This may benefit Algerian mice, an open-habitat specialist, which is undergoing a moderate-to-serious population decline in our study area (Torre et al., 2018). Furthermore, owing to the great adaptability of rodents and their ability to recovery, no negative impact on populations would be expected. However, the maintenance of open habitats should include scattered shrub-like wildlife shelters (Morán-López et al., 2016). These three management options are not mutually exclusive and it would be interesting to manage by generating a landscape matrix with different successional stages to enhance diversity and resilience of organisms.

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Data Availability Statement

The datasets generated during and/or analyzed during the current study are available upon request.

Author contributions

RPG conceived the ideas; RPG and PP designed methodology; RPG collected the data and analyzed the data; RPG and PP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Principal component analysis (PCA) of the shrub cover.

Figure S2. Number of captures and recaptures of the wood mouse among sex and ages categories.

Table S1. Selected models and criteria.

Table S2. Effect of environmental variables on rodents.

Table S3. Effect of environmental variables on rodents.