

Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models



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ABSTRACT

Road mortality affects natural populations worldwide. Although the effects of road mortality are often documented, studies assessing the impact of road mortality on the viability of the affected populations are not so common. In fact, road mortality data are often limited to a small number of years from which it is difficult to build statistical models to assess the impact of road mortality on population trends, including the probability of extinction. In the last decades several studies have reported a considerable decline in barn owl (*Tyto alba*) populations attributed mainly to land use change and to the expansion of the road network to accommodate traffic growth. For instance, road monitoring programs show high road mortality rates ranging from 0.07 owls/km/year to 2.61 owls/km/year. We developed a stochastic, age-structured model to evaluate the impact of road-kills on barn owl populations and their risk of extinction. Using this model we identified the range of parameters that are most likely to apply to a population in southern Portugal and assessed how road mortality has affected this population. Three important results are: the number of individuals of the barn owl population exhibits high intra and inter-annual variability, even an annual road mortality rate of 5% reduces barn owl populations to half of their original size, and probability of extinction increases dramatically when annual road mortality exceeds 30% and it is largely independent of the original population size. Although simulations seem to show that road mortality is still below the values for which there is risk of extinction, we recommend authorities to closely monitor the owls' numbers temporal trends and to take the necessary measures to reduce road mortality.

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1. Introduction

There is growing evidence of the negative impacts of roads on wildlife and ecosystems, suggesting that these infrastructures represent a driving factor of biodiversity loss (Forman et al., 2003). In fact, roads represent an important source of mortality for many species (e.g. Gunson et al., 2011) and road mortality can contribute significantly to the background mortality rate altering the populations' demographics and increasing their extinction risk (Beaudry et al., 2008; Row et al., 2007; Jackson and Fahrig, 2011). A number of studies has estimated road mortality rates and modeled the factors that promote mortality risk in order to identify the most appropriate measures to minimize the effects of this source of mortality on populations (e.g. Gomes et al., 2009; Grilo et al., 2012; Langen et al., 2012). Although such studies have provided important information to road managers on where and when to apply mitigation measures, the consequences of road mortality to population viability are still

poorly understood. Indeed, as observed by Roedenbeck et al. (2007) only a few studies have analyzed the impact of road mortality on the affected populations viability (but see Fahrig and Rytwinski, 2009). Here we study via computer simulations the impact of road mortality on the viability of populations of barn owls (*Tyto alba*) in the south of Portugal by developing an age-structured model.

Barn owls are found on all continents, except Antarctica, mainly in habitats characterized by open countryside, such as, grassland, pastures and agricultural fields (König and Weick, 2008). However, in the last decades several authors have reported a considerable decline in barn owl populations: e.g. Colvin (1985) for Utah, Fajardo (2001) and references therein for Spain, and Ramsden (2003) for the United Kingdom. Two hypotheses, not mutually exclusive, have emerged to explain such decline: land use change (Hindmarch et al., 2012), and mortality due to the expansion of the road network to accommodate traffic growth. In fact, barn owls have the highest road mortality rates among raptors (e.g. Ramsden, 2003; Gomes et al., 2009; Boves and Belthoff, 2012), with estimates ranging from 0.07 owls/km/year (Illner, 1992) to 2.61 owls/km/year (Boves and Belthoff, 2012). For the southern Portuguese barn owl population Silva et al. (2008) and Gomes et al. (2009) estimate that the

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road mortality is approximately 0.49 owls/km/year. However, how much this mortality rate affects the population, and, hence, what the risk of extinction is, still remains unanswered.

A variety of modeling approaches have been used to assess the impact of road traffic in wild populations. For instance, Row et al. (2007) used the software package VORTEX (Lacy and Pollak, 2013) to study the impact of road mortality in black rat snakes (*Elaphe obsoleta*), Beaudry et al. (2008) developed a gravity model (e.g. Isard, 1975) and used the software package RAMAS (Akçakaya and Root, 2002) to assess road mortality threats to spotted (*Clemmys guttata*) and Blanding’s (*Emydoidea blandingii*) turtles, and Jackson and Fahrig (2011) used the package SIMCOAL (Laval and Excoffier, 2004) to simulate the effects of barrier and depletion caused by roads on population genetic diversity. Here we developed a space implicit, age-structured, stochastic model implemented in R (RCORE Team 2012) to assess the impact of road mortality on animal populations that takes into account (i) the specificities of the barn owl life history (e.g. two broods per year), (ii) the different impact of road mortality at different stages of development of the owls (juveniles are the age class most affected), and (iii) the temporal variability of road mortality over the year (mortality is higher in the autumn and winter). Although the model was devised to implement the life history of barn owls, it can easily be adapted to describe species with other life histories or other sources of mortality.

Our study proceeded along the following lines. We first studied the general characteristics of the time evolution of the population with and without road mortality, and then we estimated the decline of the population, including its probability of extinction, for different road mortality rates and carrying capacities. Finally, we compared the results of the simulations with data collected in the south of Portugal on the number of barn owls killed by collision with vehicles during a five year period, from 2004 to 2008, to assess the impact of road mortality on the population.

2. Methods

2.1. The model

In our model the population is controlled by mortality, Z , age of first breed, A_b , and recruitment, R . Mortality consists of natural, M , and road, C , mortalities, that is, $Z = M + C$. The population is divided into n age classes ($n = 9$ in our simulations), aged between 0 and $n - 1$ years old, and, based on the barn owls life-history (e.g. König and Weick, 2008), there are two broods per year at times T_{recr1} and T_{recr2} , where a number of juveniles $R(T_{recr1})$ and $R(T_{recr2})$ enters the population.

One year has time length T , and the time of first recruitment, T_{recr1} , defines the instant when a cohort in age class m moves to an older age class $m + 1$. We discretized time into δt units smaller than one year ($\delta t = T/12$ – one month in our simulations) and assumed that the mortality Z_m affecting age class m is constant during δt (the survival rates for different age classes are listed in Table 1).

Table 1
Tyto alba life history parameters after Altwegg et al. (2003, 2007).

Parameter	Mean	Standard deviation
Clutch size	5.972	0.306
Probability of producing a second clutch (logit scale)	-3.149	2.173
Proportion breeding as yearlings	0.693	0.275
Juvenile survival rate	0.18	0.045
Yearling survival rate	0.543	0.116
Adult survival rate	0.768	0.044

Therefore, the number of individuals in age class m from time t_1 , $N_m(t_1)$, to time $t_1 + \delta t$ is

$$N_m(t_1 + \delta t) = N_m(t_1)e^{-Z_m\delta t}.$$

If $t_1 + \delta t$ coincides with the first recruitment event, then the surviving individuals from cohort m move to cohort $m + 1$,

$$N_{m+1}(t_1 + \delta t) = N_m(t_1)e^{-Z_m\delta t}$$

and cohort N_0 is initialized with the first brood

$$N_0(t_1 + \delta t) = R(T_{recr1}).$$

If $t_1 + \delta t$ coincides with the second recruitment event, then the recruitments of the second brood enter cohort N_0

$$N_0(t_1 + \delta t) = N_0(t_1)e^{-Z_0\delta t} + R(T_{recr2}).$$

Notice that not all individuals in age class 0 (the juveniles) have the same age because individuals in the second recruitment are $T_{recr2} - T_{recr1}$ younger than the ones in the first. However, we consider that the approximation of the juveniles having all the same age is reasonable as long as the two recruitment times are not too far apart; in our simulation the month of first recruitment is June and the second is August, that is, they are two months apart. We estimated the times for the introduction of the recruits based on the beginning of the breeding season, March and April (Roque and Tomé, 2004), and the typical time for young to leave the nest, 60 days (König and Weick, 2008); the time for the introduction of the second clutch was based on the results by Frey et al. (2011) and on our personal observations.

The number of juveniles, R , at time T_{recr} is a function of the number of eggs, E , laid by the mature females alive at that time, $N(T_{recr})/2$; we assumed that females made up half of the population. For each female alive at T_{recr} of age equal or older than the age of first breed, A_b , the number of eggs laid, L , is obtained from a normal distribution (“clutch size” parameters in Table 1), hence, the total number of eggs is

$$E(T_{recr1}) = \sum_{j \geq A_b} \sum_{i=1}^{N_j(T_{recr1})/2} L_i.$$

In the simulations $A_b = 1$, that is, yearlings reproduce, but only a fraction, thus, we introduce a variable sampled from a beta distribution, p (“proportion breeding as yearlings” in Table 1), that reduces the number of female yearlings reproducing, N'_{Ab} , becoming then $N'_{Ab} = p0.5N_{Ab}$.

There are fewer pairs producing a second clutch, hence the number of juveniles in the second pulse is typically smaller than that of the first (Altwegg et al., 2007), therefore only a fraction s of the mature animals contribute to the second recruitment and the above formula becomes

$$E(T_{recr2}) = \sum_{j \geq A_b} \sum_{i=1}^{sN_j(T_{recr2})/2} L_i,$$

where s is sampled each year from a normal distribution assuming a logit scale (“probability of producing a second clutch” in Table 1, and see also Appendix C).

Density dependence is introduced in the model through the relationship between the number of juveniles, R , and the number of eggs, E . As Beverton and Holt (1957) showed, the relationship between R and E cannot be linear, otherwise a decrease, or increase, in the number of recruits in one year leads to a geometric series in the subsequent years resulting in the extinction, or growth without limits, of the population. Because we introduced the density dependence between the number of recruits, R , and the number of

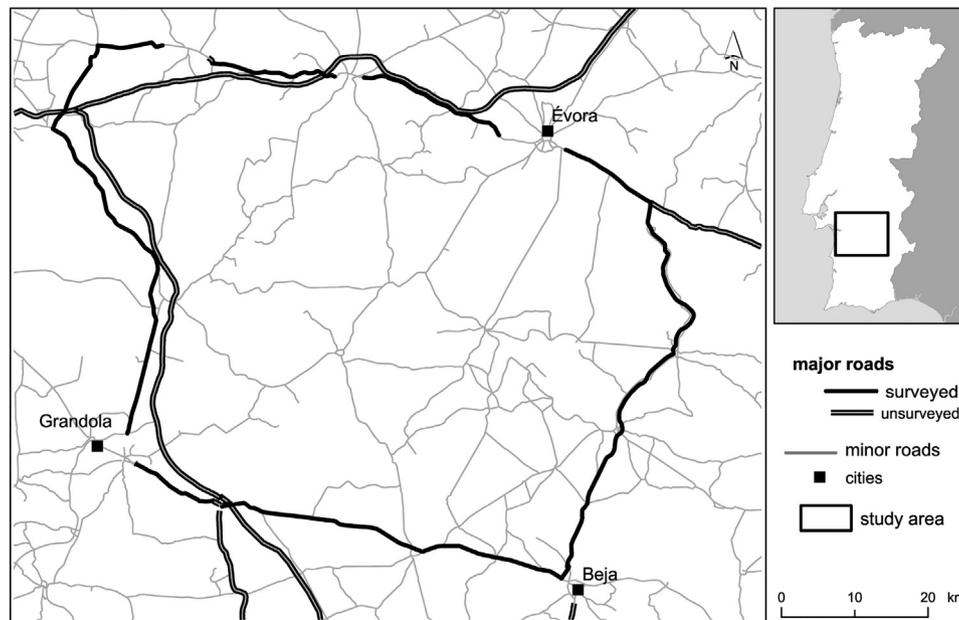


Fig. 1. Study region in southern Portugal showing the roads surveyed.

eggs, E , the former has to be smaller than the latter. We used the Beverton–Holt relationship

$$R = \frac{aE}{b + E}, \quad (1)$$

choosing a and b such that the number of recruits is always smaller than the number of eggs (e.g. $a \leq b$).

Each simulation consists of two parts. The first part was used to establish the probability of extinction without road mortality. We initialized all age classes with the same number of individuals, and though this was unrealistic, we observed that the population quickly converged to a stable proportion of individuals among age classes; to guarantee that this transient did not interfere with the simulation results we ran a burn in period of 20 years. In the second part, we introduced road mortality resulting in an abrupt decay of the population size, which led to the population extinction or to the population settling around a lower range of number of individuals. In cases where the population did not go extinct, and in order to obtain population statistics, we ignored the iterations during the abrupt decay transition, which typically lasted less than 50 years.

We implemented road mortality by removing every year a fraction, f , of the population in the month of the first recruitment, June. The number of individuals killed was spread over the year following the mortality per month and per age class as observed in the data, and as discussed below.

2.2. Life-history parameters

We parameterize our model with the estimates of Altwegg et al. (2003, 2007) for a population of barn owls in the Payerne region of western Switzerland (Table 1). We used these estimates because the Swiss owl population are within the typical range of the parameters listed for this species (e.g. König and Weick, 2008; Elphick Jr. et al., 2001) and they correspond to a population in a northern hemisphere temperate region, thus with a similar life-history of those of southern Portugal. We modeled with beta distributions the parameters that are necessarily between 0 and 1, such survival rates and proportions. Notice that we use the true survival rates, instead of the local ones, because the latter underestimate the true

survival rate by not taking into account birds that immigrate into the study region (Altwegg et al., 2003, 2007).

2.3. Study area and data collection

Our study region was in southern Portugal ($8^{\circ}49'N$, $38^{\circ}46'E$), comprising a total area of 8589 km^2 (Fig. 1). The road density is $0.27 \text{ km roads/km}^2$ and we can find two types of roads: major roads with traffic intensity between 1000 and 5000 vehicles/night, comprising 462 km, and minor road segments with less than 1000 vehicles/night, comprising 1947 km. The climate is Mediterranean and its land cover comprises cork and holm woodlands (40%), extensive agriculture (crop fields: 28%), intensive agriculture (orchards, vineyards and olive tree groves: 13%), forest plantations of *Eucalyptus* spp. and *Pinus pinaster* (11%) and urban areas (8%). Topographically, plains with altitudes ranging from 200 to 400 m characterize the region. Human population density is approximately $43 \text{ inhabitants/km}^2$.

We used data on road kills collected twice a month from January 2004 to December 2008 on 247 km of 462 km of major roads. Once a carcass was found we recorded its geographical location, removed it to avoid double counting and, when possible, identified its gender and age. The number of owls killed per month varied considerably over the year, with the maximum in the winter and the minimum in the summer (Fig. 2). Although this pattern was consistent across years, the total number of carcasses found per year changed considerably; the largest number was 176 in 2005 and the minimum 37 in 2006 (Fig. 2). In accordance with other studies (e.g. Massemín et al., 1998), 68% of the casualties were females. The majority of carcasses, 66%, were of juveniles, probably reflecting the abundance of juveniles in the population, their propensity to disperse more than adults which increases the risk of collisions with vehicles (e.g. Boves and Belthoff, 2012), as well as the tendency of the adults to avoid busy roads (Grilo et al., 2012).

Since we only surveyed 233 km of a total of 462 km of the major roads, we had to extrapolate the number of carcasses found to the entire length of the major roads. Previous studies have shown that both the type of the road and the land cover category determine the probability of collision with vehicles (Gomes et al., 2009). Therefore, using the Corine Land Cover 2006

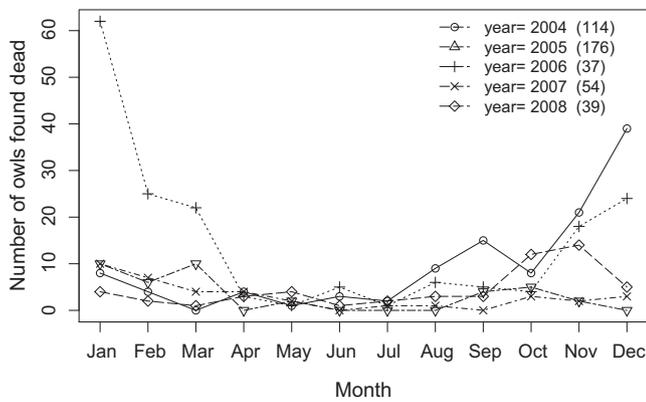


Fig. 2. Number of barn owls found dead per month from 2004 to 2008 in the roads surveyed. The numbers in brackets in the plot legend correspond to the total number of owls found in the corresponding year.

(<http://sniamb.apambiente.pt/clc/frm/>) we obtained the total road length in each main land cover categories in the region, including the fraction surveyed: cork oak and holm woodlands (242 km; surveyed 109 km), intensive agriculture (61 km; surveyed 48 km) and extensive agriculture (145 km; surveyed 76 km). Then, based on the number of carcasses found in our surveys in each land cover category, we extrapolated these values for the entire region assuming a linear relationship (Table 2). In addition, because a fraction of the owls killed goes undetected (Santos et al., 2011), we corrected for detectability bias using a method by Guinard et al. (2012) as explained in Appendix A of the Supporting Material, with the corrected values listed in the last row of Table 2.

3. Results

3.1. General characteristics of the population time evolution

In order to show a typical time evolution of a simulated population we use road mortality $f=0.1$, and $a=b=10,000$ for the Beverton–Holt recruitment relationship, Eq. (1), because this set of parameters reproduces closely the values observed in the data collected in southern Portugal, as we will show later. Since the density

Table 2

The observed number of barn owls killed in roads per habitat type, the extrapolated number for the entire major roads in the studied region, and the corrected number taking into account detectability bias. We extrapolated the observed number of owls by assuming a linear relationship of the number of carcasses found, the length of the roads and the associated land cover (total road length (surveyed length): cork oak and holm woodlands 242 km (109 km), intensive agriculture 61 km (48 km), extensive agriculture 145 km (76 km)). These estimates were further corrected taking into account the probability of detection using the method and values of Guinard et al. (2012), as detailed in the Supplementary Material (Appendix A).

	Year				
	2004	2005	2006	2007	2008
Observed					
Woodlands	31	65	15	9	15
Intensive agriculture	13	26	6	13	9
Extensive agriculture	66	78	14	31	14
Other	4	7	2	1	1
Total	114	176	37	54	39
Extrapolated					
Woodlands	68.8	144.3	33.3	20.0	33.3
Intensive agriculture	16.5	33.0	7.6	16.5	11.4
Extensive agriculture	125.9	148.8	26.7	59.1	26.7
Other	4	15	2	1	1
Total	215.3	333.2	69.6	96.6	72.4
Corrected					
	322	498	104	144	108

of birds is usually provided in terms of breeding pairs we show the time evolution of the population size using the numbers of individuals in May, the month when all birds are mature according to the model; the population exhibits similar patterns for other months. As expected, there are two distinct regimes, one before road mortality is applied and another after, with the latter characterized by a smaller number of individuals (Fig. 3a). Notice that both regimes exhibit large fluctuations in the number of individuals.

In addition to the inter-annual variability there is also intra-annual variability in the number of individuals (Fig. 3b). The peaks in the number of owls in June and August correspond to the two pulses of juveniles, and the reduction observed in the other months is due to the natural and road mortalities. In contrast to the inter and intra-annual oscillations, the relative number of individuals among age classes is very stable, and the convergence to this fixed proportion from the initial condition happens in fewer than 20 years (Fig. 3c).

The large inter-annual variability in the number of owls has implications for the number of casualties per year, which we show in a histogram (Fig. 4a). A cursory inspection reveals that the histogram has a large (fat) right tail, implying that some years have a disproportionately large number of road killings. This observation is reinforced if we use double logarithmic scales in Fig. 4b, where one can see that the right tail is approximately linear. The large variability in the number of road casualties, having an almost erratic behavior from year to year, analogous of that in Fig. 3a, is one of the most important insights from the simulations, with consequences for analyses of real data.

3.2. Time evolution under different population sizes and road mortality rates

We now consider the time evolution of populations with different sizes before application of road mortality (as controlled by the parameter a of the Beverton–Holt relationship and, as before, $a=b$), and several values of road mortality, f . Before proceeding, however, two caveats are in order. First, because the probability of a population becoming extinct increases with time, in order to obtain results that were meaningful for conservation policies, we assumed a period of 50 years after road mortality was applied to assess whether a population became extinct, or not. Second, we use the median and the maximum and minimum values of the number of individuals because the histogram of Fig. 4 revealed a fat tail, a situation where the mean and standard deviation may be misleading statistics.

As expected, the number of individuals decreases when road mortality, f , increases (Fig. 5a). Such decrease can be important even for small values of f . For instance, when $f=0.05$, the median population size is about half of the value without road mortality. When f is larger than 0.4 the populations become extinct. Observe that when $f>0.1$ the curves of different original population sizes (different a) converge. The maximum number of individuals killed occurred for $f\cong 0.05$ (Fig. 5b). The maximum occurs for intermediate values of f because after a certain threshold, here $f\cong 0.05$, the population becomes so depleted (the abrupt reduction in the number of individuals observed in Fig. 3a) that the absolute number of individuals killed is correspondingly small.

As observed in Fig. 5a, for large values of f the number of animals killed is similar and independent of the original population size. This, in turn, implies that the probability of extinction is also largely independent of the original population size (Fig. 5c). The probability of extinction is equal to zero up to a value of f of onset, f_{onset} , approximately equal to 0.3, rising then fast and it is virtually equal to 1 for $f>0.4$. On the other hand, and not surprisingly, the time to extinction decreases when f increases (Fig. 5d). For example, when $f\sim 0.4$ the time to extinction is approximately 28 years, and for the

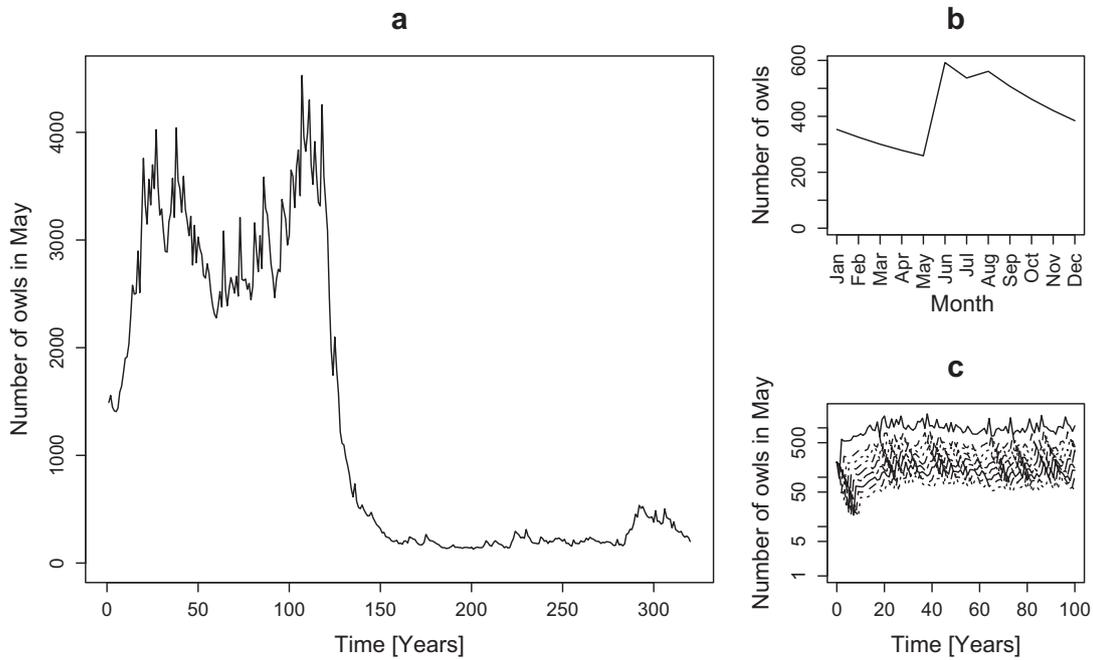


Fig. 3. Plot a: Time evolution of the simulated number of owls in May during 320 years. We observe two regimes, one up to year 120, before road mortality is applied, and another once road mortality is applied. Notice the large oscillations in both regimes and the fast decline in the number of individuals due to road mortality. Plot b: Mean number of individuals per month. Observe that the number of individuals changes considerably from month to month. Plot c: Time evolution of the age classes toward a fixed proportion of individuals among age classes. Juveniles, age 0, correspond to the most abundant class (top line), followed by yearlings, age 1, down to the owls aged 8 years old, bottom line.

largest values of f it tends to 10 years. Again, we observe that the time to extinction is largely unaffected by the original population size.

We also assessed the sensitivity of the median population size to changes in the central tendency values of the simulation parameters. The results in Appendix B show that the juvenile survival rate is the parameter with the largest impact on the population size, as expected, given the large proportion of birds in this age class. For instance, a reduction of 30% in the survival rate of juveniles leads to approximately a decrease of f_{onset} from 0.32 to 0.25, and an increase of 30% in the proportion of owls killed being juveniles led to f_{onset} to drop to 0.27.

3.3. Population size and extinction risk for barn owls in southern Portugal

We assessed the magnitude of the impact of road mortality on the southern Portuguese barn owl population using the insights provided by the simulations. The estimated number of individuals killed shows a large variability, from 104 individuals in 2006 to 498 in 2005 (Table 2). This wide range of values is in accordance with the results of the simulations (e.g. Fig. 3a) and can be accommodated with the parameters listed in Table 1. For example, if we assume that the population is described by the black lines in Fig. 5, which corresponds to a population with median

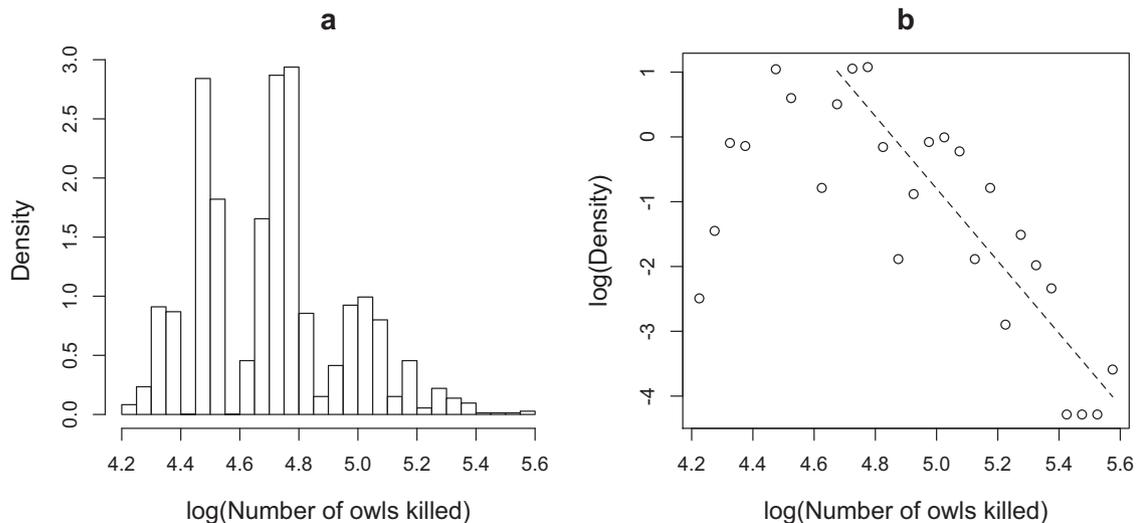


Fig. 4. Plot a is the histogram of the logarithm of the simulated number of individuals killed per year during the road mortality regime, and plot b shows the same data but in double logarithmic scales. Notice in plot b that the right tail of the distribution is approximately linear.

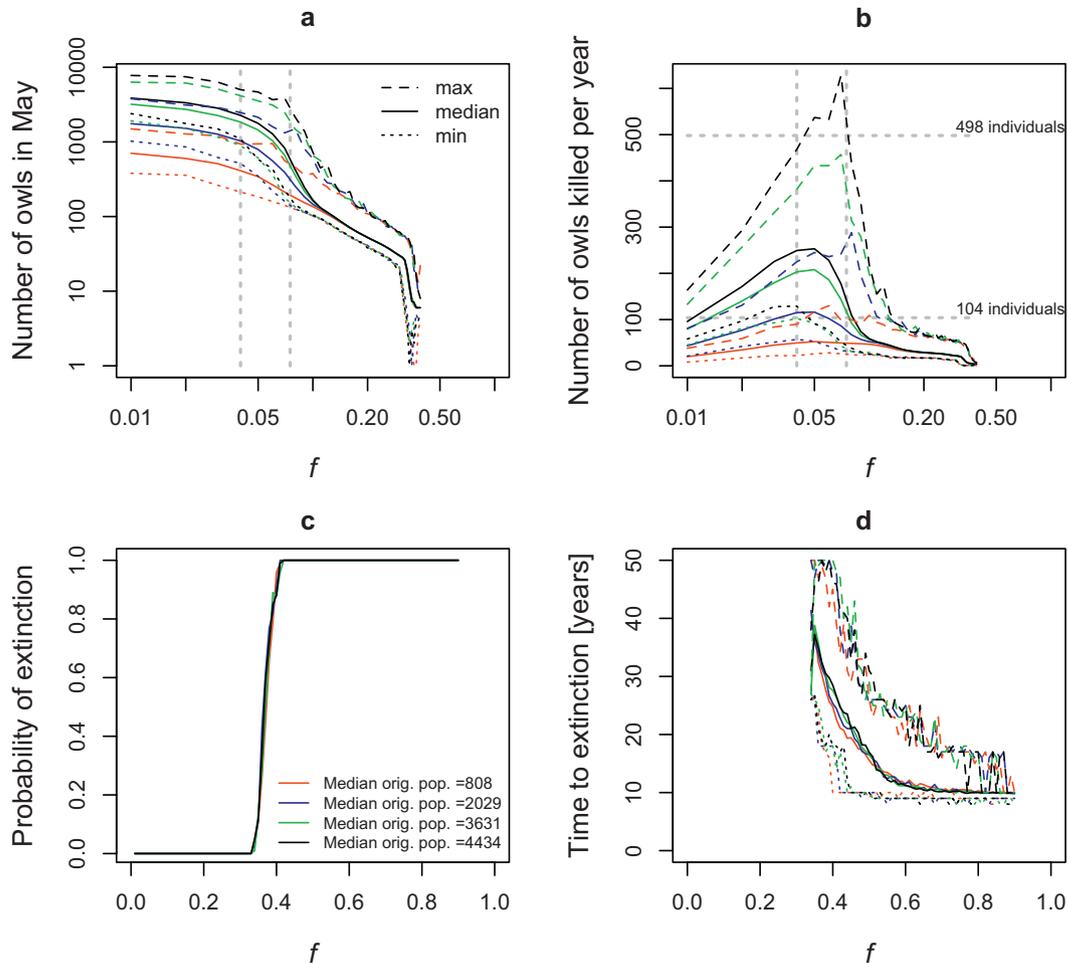


Fig. 5. Results of the simulations for four different values of $\alpha = 3000$ (red), 7500 (blue), 13,500 (green), 19,500 (black), and several values of f . The full lines correspond to the mean of the median, the dotted lines to the minima and the dashed lines the maxima of the values observed in 100 repetitions. Plot a shows the number of owls in May, plot b the number of owls killed per year, plot c the probability of extinction, and plot d the time to extinction. To avoid cluttering of the figures we show only in plot a the line types for the maximum, minimum and median, and only in plot c the colors corresponding to the carrying capacity, defined as the median size of the populations before application of road mortality.

size of pre-road mortality of 4400 individuals, then the vertical dashed gray lines in Fig. 5b show that the interval $0.04 < f < 0.075$ encompasses the largest number of animals killed in one year (498). Using now these values ($f = 0.04$ and $f = 0.075$), from Fig. 5a we conclude that the median population densities are in the range of 0.08 individuals/km² (670 individuals) to 0.27 individuals/km² (2360 individuals).

However, we know that our data collection coincided with an exceptional severe drought (García-Herrera et al., 2007). This drought may have reduced the vegetation growth, leading to a decrease in the number of rodents (Taylor, 1994), the main food source of barn owls, which may have then affected the owl population in at least two ways. By forcing the owls to travel longer distances when looking for prey (Taylor, 1994), increasing the risk of collision with vehicles, or by leading to birds in poorer shape thus less able to escape traffic. These hypotheses are not mutually exclusive, but we favor the former given the absence of relationship between bird condition and the number of casualties observed in other studies (e.g. Bujoczek et al., 2011, but see Massemín et al., 1998). The data can then be interpreted as revealing very high levels of mortality in 2004 and 2005 that led to a considerable decline in the population size, thus the lower number of owls killed by road accidents in 2006, followed by a recovery of the population in the next years. If we assume that the number of casualties in

2005 was truly abnormal and we ignore this year, then the range of killed animals can also be described by the green line in Fig. 5b, which corresponds to a population with median size of pre-road mortality of 3630 individuals, with a range of $0.03 < f < 0.08$. From Fig. 5a we estimate the corresponding population size with median size ranging to be between 0.05 individuals/km² (430 individuals) and 0.27 individuals/km² (2360 individuals). This interval for the number of individuals and the one estimated in the previous paragraph are in accordance with estimates of barn owl breeding pairs densities in several regions of Portugal and in two regions in the United Kingdom, as listed in Table 3; notice that, although we do not know the traffic intensity in these regions, it is likely that their populations also suffer from road mortality. São Mañços, 0.04 individuals/km², and Ciborro, 0.14 individuals/km², are in the study region and the latter value is clearly within our range of possible population densities.

The probability of producing a second brood is the one of the simulation parameters on which there is more uncertainty and that can affect our results. Taylor (1994) mentions that second broods are more common among central than west and southern European barn owl populations. However, Martínez and Lopéz (1999) reported that 1/3 of the females of a population in Spain produce a second clutch, a value similar to those reported by Taylor for central Europe, therefore, if the Spanish populations are

Table 3

Compilation of the number of barn owls densities from several sources; partially based on Table 1 of Roque and Tomé (2004).

Location	Pairs/km ²	Individuals/8589 km ²
Devon (UK)	0.053–0.08	910–1202
Cornwall (UK)	0.086–0.115	1477–1975
Aveiro	0.01	172
Parque Natural de São Mamede	0.02	344
Ponta de Erva	0.16	2748
Reserva Natural do Estuário do Tejo	0.03	515
Ciborro, Montemor-o-Novo	0.07	1202
São Manços, Évora	0.02	344
Nordeste Algarvio	0.01	172
Parque Natural do Nordeste Algarvio e Sudoeste Alentejano	0.01	172
Coruche, Santarém	0.07	1202

similar to the Portuguese ones then the values we used based on Altwegg et al. (2007), with linear mean equal to 13%, are conservative. In Appendix C we show how the probability of having a second clutch affects the total number of individuals, and that a population with no second clutches could not have possibly sustained the mortality levels observed in 2004 and 2005, but that an increase of the probability to twice the values reported by Altwegg et al. (2007) and, thus closer to the ones mention by Martínez and Lopéz (1999) could easily sustain such levels of mortality.

In conclusion, a plausible scenario is that the southern Portuguese barn owl population suffers a road mortality $f < 0.1$, having median population sizes between 400 and 2300 individuals. This suggests that the road mortality, f , is below the threshold of $f_{onset} = 0.3$, the value above which the probability of extinction for the next 50 years is different from zero. However, values of f between 0.03 and 0.1 imply that the population has already suffered a considerable decline, with the number of individuals around or below 50% of its original, pre-road mortality, density.

4. Discussion

We developed an age-structured model to analyze the impact of man made structures on wild animal populations and applied it to the study of the viability of a barn owl population in southern Portugal. Comparison of the simulations with data revealed that the extinction risk of this barn owl population due to road mortality is likely to be low. However, several caveats apply to this finding. (i) We used parameters from a Swiss barn owl population, as the life-history parameters of the southern Portuguese population are not well known; notice, however, that we expect the Swiss population to have a similar life history to that of the Portuguese one, and that our sensitivity analyses (Appendix B of the Supplementary Material) did not reveal significant differences from the results presented here. (ii) Prey dynamics influence the predator dynamics, and while the main prey of Central European barn owls populations are *Microtus* species, which are highly cyclic, southern European populations depend largely on the wood mouse (*Apodemus sylvaticus*) and the greater white-toothed shrew (*Crocidura russula*) species, which are more stable (Martínez and Lopéz, 1999). Therefore, due to predator–prey interactions we expect central European populations to exhibit even larger fluctuations than the southern ones, and because larger fluctuations are more likely to put species at risk of extinction, the parameters of the Swiss barn owl population may tend to predict a large number of extinctions and correspond, then, to a worse case scenario to the Portuguese population. (iii) Simulations showed that even low mortality rates caused a considerable reduction in population size, and this has potential consequences for the functional roles played by this species in the ecosystem, such as rodent population

regulation. (iv) Given the propensity of the population to exhibit large temporal oscillations, stress factors other than road mortality, such as severe droughts, may reduce the population to sizes placing it at risk of extinction; recall that, according to the simulations, large oscillations are to be expected based solely in the internal dynamics of the population even without extreme environmental events. (v) It was implicit in our analyses that the parameters remain stable over large periods of time, which is unlikely to be the case for real populations due to, for instance, land use changes, climate change, or diseases that could wipe out a large percentage of the population.

The independence of the probability of extinction and of the time to extinction from the original population size, for the range of population sizes analyzed, is an important feature of our model. This happens because when $f > 0.1$ the population declines very rapidly to low numbers, and when the number of adults is small so is the number of eggs laid, E , therefore the denominator of the Beverton–Holt relationship, Eq. (1), $E + b$, is approximately equal to b , and Eq. (1) can be approximated by $R \sim aE/b$, and because $a = b$, then $R \sim E$. That is, when the population reaches small sizes, the number of recruits is largely independent of the parameters determining the carrying capacity, or the size of the population before road mortality, and the populations behave identically. In those simulations where $a/b \neq 1$, populations did not behave identically in the limit of very small number of individuals, but for values of a and b that led to realistic results, their behavior was very similar to the ones described above.

Although the Beverton–Holt relationship is being expressed in terms of the number of eggs and the number of recruits, it indirectly relates the number of recruits with that of adults since the latter determines the number of eggs laid. One can interpret the relative reduction in the number of fledgling birds when the number of adults increases, as expressed by the Beverton–Holt relationship, to be a consequence of the reduction in prey availability. Several studies, as reported by Taylor (1994), have concluded that prey availability is one of the most important determinants of barn owls abundance; the other being severe winters, but since the breeding period occurs in the spring and summer, we ignore this factor here. It then seems natural to consider that density dependence occurs in the population during the breeding period due to the availability of prey, although other factors, such as the availability of nesting places, could also play a role.

One could conjecture that the large number of road casualties in our study region could lead to a source–sink dynamics (e.g. Borda-de-Água et al., 2011) where barn owls from adjacent areas, presumably less affected by road mortality, would disperse into our study region. However, this is unlikely to be the case for the following two reasons. First, neighboring populations are likely to be affected by road mortality at similar rates because road density is similar (personal observation). Second, due to large extensive agriculture patches, the availability of roosting and nesting sites, and relatively low human density, south of Portugal has some of the best conditions in the country for the persistence of barn owls (Cтры et al., 2010), hence, it is safe to assume that our study area is more likely to behave as a source than as a sink. It is also possible that some of the owls killed are wintering birds from northern Iberia or France. We did not find any data from where we could infer the relative proportion of long distance migrating birds, however, Cтры et al. (2010) suggest that the number of wintering owls is likely to be insignificant. Therefore, there is a compelling argument to be very cautious about the state of this population, to minimize the factors that may negatively impact it, and pay close attention to its future trends.

Some of the results obtained with the simulations are general and apply to other barn owl populations or species undergoing similar dynamics. We highlight two results: first, the large inter-annual variability of the population size, and, secondly, the occurrence

of the maximum animals killed for intermediate values of road mortality. Concerning the first, fluctuations in the size of wild populations are well known (e.g. Begon et al., 1996) and are to be expected in stochastic simulations, and in some cases even in deterministic ones (May, 1976). However, the large fluctuations predicted by the simulations are noteworthy (Fig. 3a) especially if we take into account that according to Altwegg et al. (2003) the parameters' variances used in the simulations were estimated during a time interval that included only mild winters, being severe winters the main cause of crashes in their population. An implication of this result is that censuses of similar populations based only on a few years may lead to very misleading results on the abundances or temporal trends, even in the absence of extreme environmental events. Concerning the second, the maximum number of animals killed occurring for intermediate values of road mortality, a similar pattern relating catch and effort is well known in fisheries (e.g. Pitcher and Hart, 1982). However, it leads to some counterintuitive results. For instance, a small number of animals killed due to vehicle collisions may lead to the erroneous conclusion that road mortality does not have an important impact on the population while, in fact, road kills may have already depleted the population to very low numbers, hence the small number of casualties.

There are several ways in which our model can be improved, as we now list. (i) We assumed that males and females are equal, but this is not strictly true, for instance, we know that females suffer higher road mortality, hence future version can include differences between genders. (ii) In the present version of the model, the fraction of animals killed does not depend on the population density but this is unlikely to be the case. For example, we can conjecture that lower owl densities would preclude juveniles to disperse long distances, thus reducing the risk of road mortality. As it is, the model is likely to overestimate the number of animals being killed when densities are low; this, again, implies that we are being conservative in our estimates of how the population is being affected. (iii) We used the Beverton–Holt relationship to model the number of recruits as a function of the number of eggs, but in the future other relationships can be incorporated in the model. (iv) Some simulation parameters were randomly sampled from probabilistic distributions in each iteration, without taking into account the possibility of temporal correlation among consecutive values. However, it is likely that there is some degree of correlation in time, and such correlation, if known, can be included in the model. (v) The model does not take into account the dynamics of the prey but we know that the dynamics of some barn owl populations closely follow that of their prey. For instance, Taylor (1994) showed that in southern Scotland barn owls have three year cycle exactly as the vole population on which they prey. Therefore, future versions could use a multispecies approach once more information is known on the dynamics of the prey species of the southern Portuguese barn owl population. (vi) Last but not least, at present the model is spatially implicit. A spatially explicit version would allow a better description of dispersal, hence modeling source–sink dynamics in an effective way, and better understanding of the impact of the different habitats, including the microhabitats along the roads. However, inclusion of more detail, increasing the realism of the model is only desirable when the parameter values and their uncertainty can be better quantified. We plan to increase the number of features modeled as data allowing more realistic parameterization of the processes governing the barn owl population dynamics is gathered.

Wild animals suffer from numerous anthropogenic sources. Although these sources are well documented, quantifying their impact on the affected populations is a difficult problem (e.g. Loss et al., 2012). This is, in particular, the case with the impact of road mortality (Roedenbeck et al., 2007; Fahrig and Rytwinski, 2009). In

this work we developed a space implicit stochastic age-structured model to quantify the impact of road mortality on the viability of barn owl populations in the south of Portugal. However, the framework of the model is general, thus it is a tool that can be used with generality in conservation planning and management. It was implemented in R, an open source package that can be easily run in different operating systems and, with minor changes, it can be adapted to a wide range of species and impacts, such as those of wind turbines (Bernardino et al., 2013) or collisions with buildings (Klem, 1990). The code requires the knowledge of the life history parameters of the population but the amount of parameters used can change depending on their availability or the degree of complexity required, hence it can be easily adapted to other species with life-histories different from that of barn owls.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2013.12.022>.

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