First estimates of survival and densities of invasive alien Eastern cottontail (*Sylvilagus floridanus*) in Italy: a Bayesian robust design approach

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Abstract

The Eastern cottontail (Sylvilagus floridanus) has become invasive in Central and Northern Italy, where it affects prey-predator dynamics between native species. Although many different studies explored survival rates and the density of cottontails in North America, no information is available for its invasive range. Between December 2003 and October 2005, a capture-recapture scheme for Eastern cottontails was enforced on the Orba River, Italy. We fitted a Bayesian version of the Pollock's Closed Robust Design to estimate the survival of adult male and female cottontails (n=258) and their density in the study area. Adult cottontails showed minor seasonal differences in survival, with no clear differences between males and females. Densities varied seasonally, with females having higher densities (min = 80 individuals/km^2; max = 553 individuals/km^2) than males (min = 56 individuals/km^2; max = 337 individuals/km^2).

Eastern cottontails are characterized by high survival and high densities, at least when adults, in their invaded range in Italy. Although densities are comparable to those reported in North America, our analysis focused on adult cottontails only and overall densities are certainly higher. Moreover, our estimates, obtained through a capture-recapture approach, were higher than those reported in previous studies from Italy based on nocturnal spotlight censuses. Spotlight transects are likely to underestimate cottontail densities, due to nocturnal habitat selection of cottontails, which might decrease their detectability.

Introduction

The Eastern cottontail (*Sylvilagus floridanus*) is North American lagomorph, whose geographical range spans from Canada to Venezuela and Colombia (Nielsen Lanier 2019). The species includes 18 subspecies and it is a major game in Canada and the US. Its importance for recreational hunters caused the species to be translocated at many sites in North America and to be introduced in Cuba, where it successfully established and became invasive (Mancina et al., 2015). In the 1960s the species was also introduced in various European countries, including France, Spain, Switzerland and Italy (Barbar et al., 2018). While introductions were not successful in France and Spain, where cottontails are not reported anymore (Delibes-Mateos et al., 2018), the species became a successful invader in Italy (Bertolino et al. 2011b; Dori et al. 2019).

Due to multiple legal and illegal introductions, cottontails managed to colonize a significant portion of the Po plain, as well as many different croplands and riparian ecosystems of Central Italy (Dori et al., 2019). Cottontails have complex interactions with native species and their introduction ecosystems. Although they do not directly compete for habitat or food with native European hares (*Lepus europaeus*; Bertolino et al., 2011a,b, 2013; Vidus-Rosin et al., 2008, 2010, 2011), they seem to negatively affect them through apparent competition, by modifying prey-predator dynamics with native red foxes (*Vulpes vulpes*, Cerri et al., 2017). Moreover, the role of cottontails in the transmission of lagoviruses is still unclear (Lavazza et al., 2015; D'Angelo et al., 2018), although they are major vectors for many zoonoses and wildlife diseases (Bertolino et al., 2010; Gallo et al., 2005; Tizzani et al., 2014; Zanet et al., 2013).

In North America, various studies explored the survival of cottontails in captivity, as well as in the wild. Overall, cottontails are characterized by heterogeneous survival rates, which might vary substantially between the breeding and the non-breeding season, and between protected and non-protected areas. It is worth noticing that most studies estimated the survival of cottontails without assigning them to different age classes, a practice that could certainly have caused such heterogeneity. Cottontail densities are also extremely variable, both across different habitats and between different seasons. In suitable conditions, like enclosures or islands, with few or no predators, cottontails were found to reach very high densities, up to 20 individuals/hectare. A complete overview of existing studies about survival and densities of cottontails in North America are available in Table 1.

To the best of our knowledge, no study measured cottontail survival in their introduction range, in Europe and, although they were widely studied in North America, few information is available about cottontail densities in their introduction range. For example, in Central Italy cottontails were found to reach densities ranging between 7.29 ± 0.99 and 71.60 ± 12.98 individuals/km^2 (Cerri et al., 2014). In Northern Italy higher densities were reported, between 4.40 and 110.41 individuals/km^2 (Bertolino et al., 2011), between 4.3 and 27 individuals/km^2 (Silvano et al., 2000) or between 47.3 and 61.5 individuals/km^2(Vidus-Rosin et al., 2010). These studies estimated cottontail densities mostly through nocturnal spotlight transects, with and without distance sampling. Considered that cottontails at night forage mostly near to permanent cover (Bertolino et al., 2011, 2013; Vidus-Rosin et al., 2008, 2010, 2011), which might decrease their detectability, these studies were likely to underestimate the real density of the species. Obtaining this information would be extremely important to understand how the species adapted in the introduced range, to design effective control schemes, which rely on the efforts of voluntary hunters (Cerri et al., 2018), and for epidemiological modeling (Salvioli et al., 2017). Moreover, to the best of our knowledge, no study explored cottontail survival in their introduction range. Obtaining some baseline information about this biological parameter can be extremely important for invasion ecology, for example to correctly parameterize matrix-based population models (Sakai et al., 2001).

In this research we aim to partially fill these two gaps by estimating the survival and the densities of adult cottontails in Northern Italy, from a capture-recapture scheme based on the robust design. Capture-recapture methods can estimate both the survival and the number of individuals in a certain geographical area (Nichols, 1992; Schwartz and Seber, 1999; Sutherland, 2006) and they are the gold standard for the robust estimation of the densities of elusive nocturnal mammals, such as many lagomorphs (Langbein et al., 1999). Notably, in this study we adopted the robust design, which is the best capture-recapture approach to estimate population size and survival correctly, without making some strong assumptions characterizing other models (Kendall and Pollock, 1992).

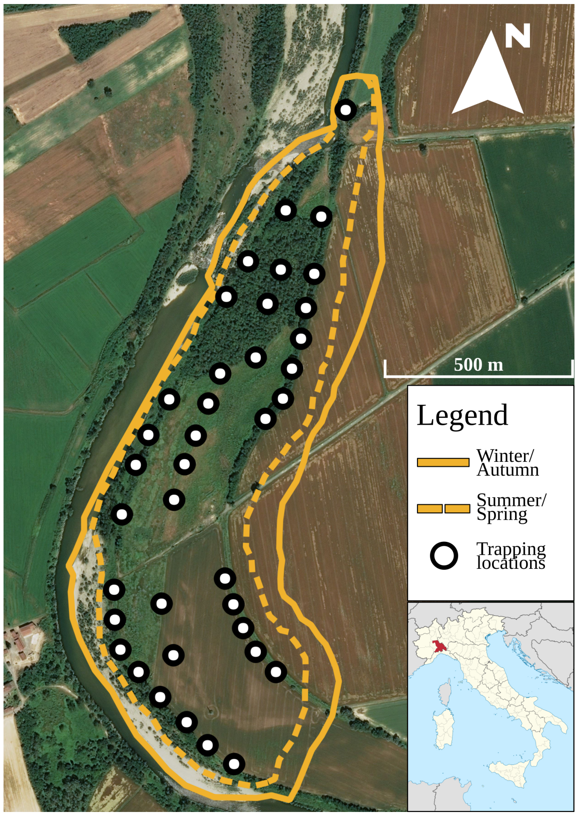

Figure 1 | Map of the study area: limits during winter/ autumn (continuous line) and in summer/spring (dashed line), altogether with trapping sites (dots). Study area was evaluated by considering a buffer around traps of about 64 m (winter/autumn) and 87 m (summer/spring).

Methods

Study area

From December 2003 to October 2005, cottontails were trapped in a capture-recapture scheme, in a study area located on the right bank (Piedmont, Northern Italy; Fig. 1) of the Orba River. The study area was a natural reserve, adjacent to a game reserve where hunting was also prohibited. The landscape was composed by a narrow shore, partially covered with shrubs and low trees, mainly willows (*Salix* sp.), a small woodland mainly with black locust (*Robinia pseudoacacia*) and common oak (*Quercus robur*), with a rich understory, and a shrubby area that bordered with fallow lands and field crops.

Cottontails were trapped with cage traps (double entry traps, “100 × 40 × 40 cm, S. 237 Gibis”, France) every other month for two years. Traps were set in the field, baited with carrots and lettuce. The sampling was based on the robust design approach, which includes primary periods, where traps are closed and the population is assumed to be open, and short secondary periods, where traps are active and the population is assumed to be closed (Williams et al., 2002). In the sampling design, primary periods lasted about 5 weeks and secondary periods 5-7 days, when traps were opened and checked at sunset and after dawn. Trapped animals were marked with ear-tags (a Monel No. 3, National Band and Tag Co., USA and a coloured tag with number). Cottontails were sexed through the visual inspection of genitalia, then operators measure their weight and the length of their rear foot.

Totally 310 cottontails were trapped. Most individuals (n=258) were adults, older than 2 years, while fewer of them were individuals from the year (n=32) or individuals between 1 and 2 years of age (n=20). In this study we focused on adult cottontails only (n=258, 46.6% males), for multiple reasons. First, our sampling was clearly unbalanced, hardly representative of the whole target population, with too many adults than the typical age-structure of a cottontail population (Chapman and Litvaitis, 2003). Second, the number of juveniles was too low for modeling age-specific survival and capture probabilities, as well as for multi-state models.

To estimate the number of adult cottontails in the study area, as well as their survival between secondary periods, we fitted a Bayesian implementation of the Pollock’s Closed Robust Design allowing for individual heterogeneity of detection probabilities (Rankin et al., 2016). As our robust design model does not allow for individual covariates, we fit two models for males and females, and we used posterior predictive checks for inspecting convergence and assess the estimation of model parameters, in place of goodness of fit testing, which is not available for the PCRD model (White and Burnham, 1999). The PCRD model estimated the following parameters: *i*) the total number of cottontails that were available for capture in each primary period, *ii*) the total number of cottontails that were alive in the population, *iii*) the probability that an animal outside of the study area at time t-1 remained outside it at time t, being unavailable for capture, *iv*) the probability of temporary emigration, notably that an animal inside the study area at t-1 emigrated temporarily and was unavailable at time t, *v*) the apparent survival between two consecutive secondary periods, which included real survival and the lack of permanent emigration, *vi*) the probability of detecting an animal in a secondary period s within each primary period t, *vii*) transition probabilities between four states describing a recruitment parameter combining birth permanent immigration and mark accumulation, *viii*) random effects governing individual heterogeneity in capture probabilities for secondary periods, overall capture probabilities, survival, lacked immigration and temporary emigration. For sake of simplicity, in this study we will comment only findings about the three parameters of interest, namely the apparent survival, the number of individuals in the study area that were available for capture and the probability of temporary emigration. A complete overview of model outputs is available in the Supplementary Information. For further details about the mathematical structure of the adopted model, we encourage you to read Rankin et al. (2016).

Density was obtained by dividing the estimated number of animals by the effective trapping area which was calculated by adding a boundary strip (Flowerdew, 1986), equal to the radius of the average home ranges evaluated on the same animals (Bertolino et al., 2013) and considered to be circular. The size of the home ranges can in theory change for males and females and according to the season. However, we did not find significant differences in the home-ranges of males and females, as well as between the spring and summer seasons and between autumn and winter. We then calculated the radius of an average home-range for the cottontail in autumn-winter (64 m) and spring-summer (87 m), and used these measures to expand the capture area to 35.80 ha in autumn-winter and 39.98 ha in spring-summer.

Statistical analyses were carried out with the statistical software R (R Core Team, 2020) and the model was fitted with JAGS, following the supplementary materials provided by Rankin et al. (2016). A reproducible software code, altogether with the dataset and with a graphical summary of Markov-Chain-Monte-Carlo (MCMC) convergence and posterior checks, is available in the Supplementary Information.

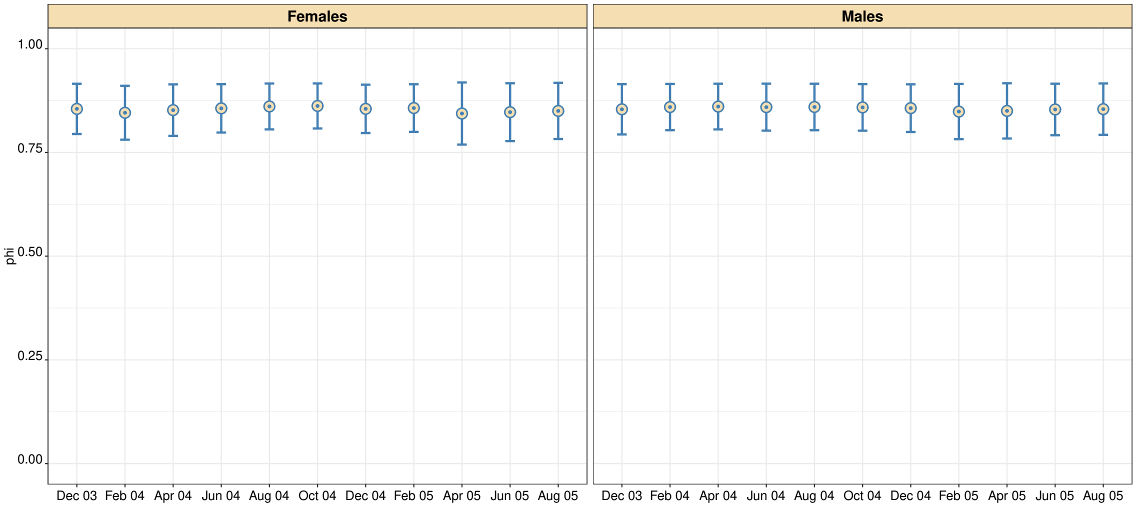

Figure 2 | Survival of female and mail cottontails, between secondary periods.

Results

Although no formal goodness-of-fit test is available, our model showed a good convergence of MCMC chains and estimated the posterior distribution of model parameters, both for male and female cottontails (see the Supplementary Information).

Male and female cottontails had similar probabilities of survival between consecutive primary periods, with values that were generally high, between 80% and 90% (Table 1, Fig. 2). Both male and female cottontails also had relatively low probabilities of temporary migration, which means that relatively few individuals were assumed to move out from the study area between consecutive primary periods. Indeed, females had slightly higher values than males (Table 1, Fig. 3). We did not detect any change in survival or temporary emigration, throughout the whole sampling period. Cottontail densities were higher for females than for males (Table 1, Fig. 4), with an average sex ratio of 1.42 females per males. The estimated density of female cottontails ranged between 53.19 ± 24.55 individuals (density = 79 -217 individuals/km^2) in October 2005 and 158.43 ± 39.56 individuals (density = 332 – 552 individuals/km^2) in October 2004 , while the estimated number of male cottontails ranged between 35.20 ± 14.99 individuals in October 2005 (density = 56 – 140 individuals/km^2) and 96.52 ± 28.55 individuals (density = 188 – 329 individuals/km^2) in August 2004.

The average overall density of cottontails in the study area, throughout the entire period was 279 female cottontails/km^2 and 196 male cottontails/km^2, so 475 individuals/km^2. Overall, during the period when cottontails were less abundant, in late summer 2005, densities of adult cottontails ranged between 135 and 357 individuals/km^2, while during the period of maximum abundance in late summer 2004, cottontail densities ranged between 520 and 881 individuals/km^2. We noticed that mean density of adult cottontails in 2005 was 39.01% lower than density in 2004.

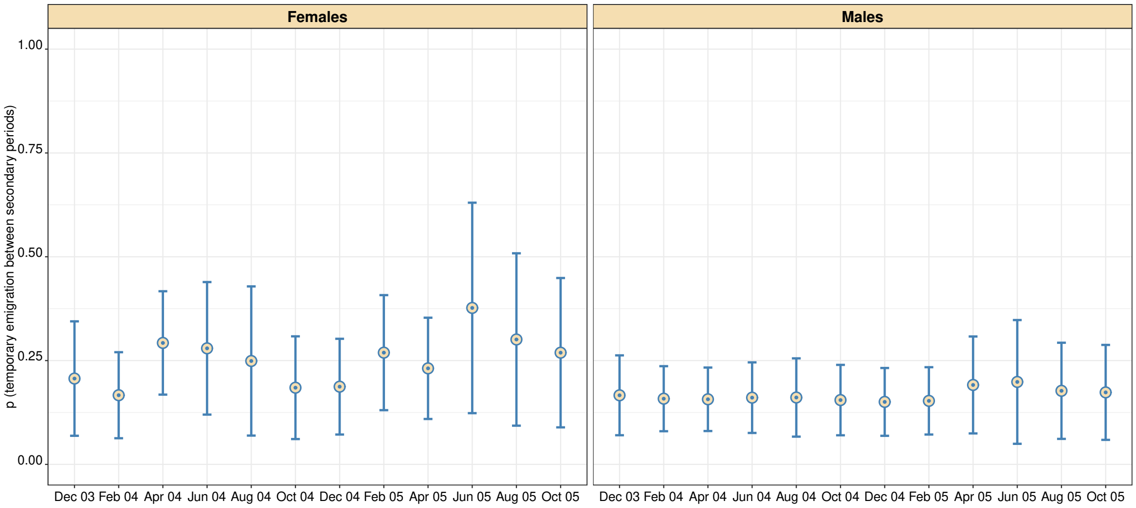

Figure 3 | Probability of temporary emigration between secondary periods.

Discussion and conclusion

Our findings are arguably the first about the survival rate of adult invasive Eastern cottontails in their invasive range in Italy. We found that adult cottontails have a high survival, which can remain relatively constant across seasons, differently than previous studies from North America, where survival was generally lower and where seasonal fluctuations were recorded. As we mentioned above, our survival was probably higher due to the fact that we focused on adult individuals only, discarding juveniles which typically have much higher mortality. Most studies that were carried out in the native range of the species were based on mixes samples, where individuals had not been aged, and they modeled the overall mortality of adult and juvenile cottontails. On the other hand, the lack of strong seasonal effects was surprising. Even adult cottontails are susceptible to harsh and prolonged winter times, especially when trophic resources are scarce and coccidiosis strongly affect cottontail health (Dorney, 1962; Weidman and Litvaitis, 2011), or to dry summers (Havera, 1972). The study area is characterized by a continental climate (average temperature = 12.5 °C, variation between average temperatures = 19.7 °C, rainfalls = 960mm) with dry summer times (June-September: average temperature = 20.9 °C; average minimum temperature = 15.9 °C; average maximum temperature = 25.9 °C; rainfalls: 256 mm) and relatively hard winters (December-March: average temperature = 5. °C; average minimum temperature = 1.4 °C; average maximum temperature = 8.9 °C; rainfalls: 313 mm), therefore we expected at least some sort of seasonal variation, which was absent. This constant survival might suggest two different points, that need further research. First, cottontails that were introduced in Piedmont, might belong to a subspecies which is native of geographical areas with more continental climates than the rest of the native range. To date, no genetic study about invasive cottontails in Italy was carried out and we believe they might be fundamental to better understand whether one, or more, subspecies were introduced. Characterizing the taxonomy of invasive cottontails could also help understanding whether they hybridized or not between different subspecies, and if this hybridization facilitated their invasion dynamic. Moreover, constant survival of adult cottontails seems to indicate a scarce role of parasites, food availability and native predators over cottontail survival. Cerri et al. (2017) found that cottontails influenced fox populations, in a geographical area close to that of this study, by acting as a prey and it is known that cottontail could become a focal prey for foxes (Balestrieri et al., 2005) However it is unclear whether this predation involved young or adult cottontails. Future studies should clarify this point, to avoid cascade effects during management interventions, which might negatively affect native mammals, like the European hare. It is important to note that our PCRD model estimated apparent survival, hence it did not distinguish between individuals that survived between primary periods and individuals that did not emigrate outside of the study area. However, we believe adult cottontails to have a relatively high survival, because available literature indicates that immigration in Eastern cottontails involves mostly young individuals and because adult cottontails are relatively sedentary, as confirmed by previous telemetry studies (Chapman and Litvaitis, 2003) and by our low estimated temporary emigration.

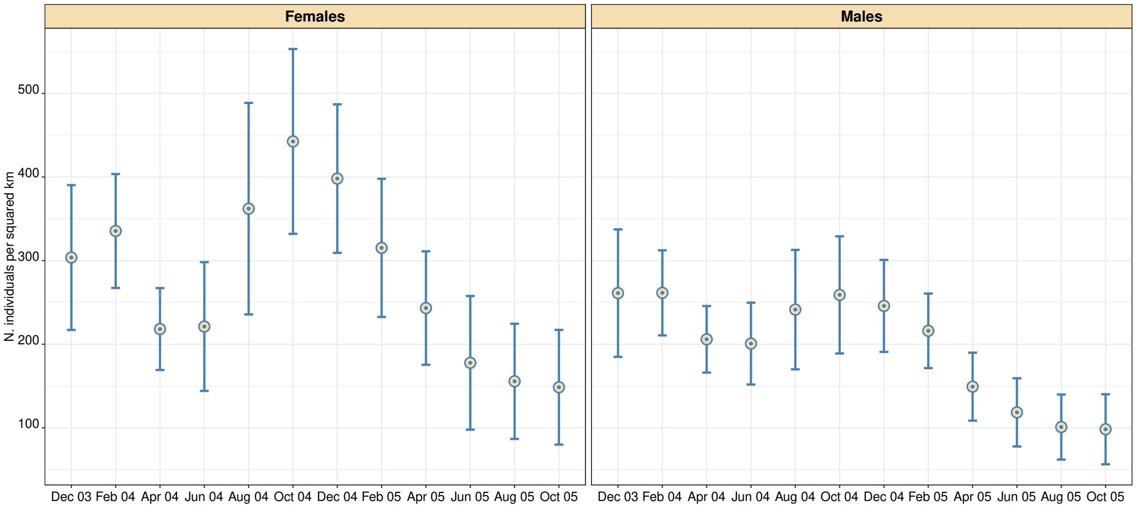

Figure 4 | Density of adult cottontails (individuals/km^2) between primary periods.

This study also shows that invasive cottontails can reach extremely high densities in their invasion range, comparable to those reported for populations in North America and much higher than those that had ever been provided for Italy. Even the lowest densities of adult cottontails that were estimated by our capture-recapture model, were much higher, and far less variable, than densities that had been estimated through nocturnal spotlight counts in Central and Northern Italy, which included juvenile individuals. For instance, in our study area a density of only 12.82 ± 4.97 ind./km^2 was estimated through nocturnal spotlight censuses just the winter before we started trapping (Bertolino et al., 2011), while we estimated a minimum of 135 adults/km^2 in October 2005. While our estimates were biologically plausible, as similar values were reported for North America (Table 1), they were previously unimaginable for Italy. Furthermore, we believe overall densities to be much higher, as we did not include juveniles, which are a considerable portion of cottontail populations. In facts, while we noticed that adult survival was generally high and did not change over time, we appreciated a 40% decline in cottontail numbers between 2004 and 2005. Considered that cottontails can reproduce at 12-13 months, this suggests that the recruitment of juveniles might involve a considerable number of individuals, so high that it affects the number of adult cottontails across consecutive years. These high densities might also explain two issues that emerged in observational studies about Eastern cottontails in Italy. First, they strongly support the idea that cottontails might interfere with prey-predator dynamics of native mammals (Cerri et al., 2017), as these densities of cottontails are likely to provide native predators with an endless amount of food resources, totally decoupling their population dynamics from those of native species. Moreover, these densities can explain the huge spread of cottontails across Italy. Although the species is actively dispersed by hunters, through illegal restocking as a game, it was also characterized by a very rapid local dispersal (Bertolino et al. 2011b), which enabled it to colonize entire regions between introduction hotspots. To date, this fact sounded surprising, given the limited home range of Eastern cottontails in Northern Italy (Bertolino et al., 2013). However, given these population densities, it would not be surprising if cottontails in Italy, especially juveniles, are characterized by high emigration in their first year. We believe that future capture-recapture and telemetry studies should broaden our findings, by estimating apparent survival and dispersal of cottontails during their first year of age. This information would be fundamental to accurately understand and model population dynamics of cottontails in Italy, and to better design control schemes for the species. In our opinion, capture-recapture studies should also replace spotlight counts in monitoring schemes for Eastern cottontails in Italy. Capture-recapture schemes, though very demanding, will provide researchers and managers with more realistic estimates of cottontail populations, which might otherwise be biased and severely underestimated if based on spotlight counts.

This study sheds light, through a robust capture-recapture approach, that invasive cottontails are successful invaders in Northern Italy. Adult cottontails are characterized by very high, and stable, survival, which might underlie a scarce effect of conventional limiting factors, such as climate, predators or parasites. Moreover, in the study area, cottontails were capable to reach very high densities, comparable to those reported for North America. Considered that our study dealt with adult cottontails only, real population densities might be even higher. Finally, we showed that capture-recapture methods provide higher values of cottontail density than nocturnal spotlight censuses, which are unlikely to underestimate cottontail populations, and should therefore be preferred for their monitoring.

Table 1. *Sylvilagus floridanus*: density and survival values reported in the literature

Density Study	Country	Value (and habitat)
Hunt et al. (2014)	US (Chicago)	940-1630 ind./km^2 (urban park)
Scribner and Warren (1990)	US (Texas)	820-2840 ind./km^2 (lake playa)
Chapman and Litvaitis (2003)	US (-)	1000-1500 ind./km^2 (unspecified)
Chapman et al., 1982	US (Ohio)	310 ind./km^2 (free ranging population)
Leite, 1965	US (Ohio)	3149 ind./km^2 (enclosed wildlife area))
Bittner and Chapman	US (St. Clemens Island, Maryland)	1020 ind./km^2 (island)
Cerri, 2014	Italy (Tuscany)	7.29 ± 0.99 and 71.60 ± 12.98 ind./km^2 (free ranging population)
Bertolino et al., 2011	Italy (Piedmont)	4.40 and 110.41 ind./km^2 (free ranging population)
Silvano et al., 2000	Italy (Piedmont)	4.3 and 27 ind./km^2 (free ranging population)
Vidus-Rosin et al. 2010	Italy (Lombardy)	47.3 and 61.5 ind./km^2 (free ranging population)
Survival rate		
Trent and Rongstand (1974)	US (Wisconsin)	0.15-0.20 (annual survival, free ranging population) 0.34 (non-breeding season) - 0.54 (breeding season)
Bond et al. (2001)	US (Mississipi)	0.18 (breeding season) – 0.70 (non-breeding season) (free-ranging population)
Medve (1987)	US (Illinois)	0.56 (breeding season) - 0.72 (non-breeding season)(free-ranging population)
Lewis (1972)	US (Wisconsin)	0.19 (nonbreeding season)(free-ranging population)
Matthews (1976)	US (South Carolina)	0.30 (breeding season) - 0.43 (non-breeding season)(free-ranging population))
Boland and Litvaitis (2008)	US (Cape Cod)	0.05 (hunted sites) – 0.19 (non-hunted sites)(free-ranging population)
Hunt et al. (2014)	US (Chicago)	0.30 ± 0.13 (annual survival)(free-ranging population in an urban park)
Keith and Bloomer (1993)	US (Wisconsin)	0.18 (mid-March) – 0.89 (October)

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