

1 Title: First estimates of survival and densities of invasive alien Eastern cottontail (*Sylvilagus*  
2 *floridanus*) in Italy: a capture-recapture approach.

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5 **Authors:** Cerri J.<sup>1</sup>, Gola L.<sup>2</sup>, Perrone A.<sup>3</sup>, Bertolino S.<sup>4</sup>

6  
7 **Affiliations:**

8 1. Istituto Superiore per la Protezione e la Ricerca Ambientale, Via del Cedro 38, 57122,  
9 Livorno, Italy; email: [jacopo.cerri@isprambiente.it](mailto:jacopo.cerri@isprambiente.it)

10 2. Ente di gestione delle aree protette del Po vercellese-alessandrino, Viale Lungo Po Antonio  
11 Gramsci 8/10, 15033, Casale Monferrato, Italy; email: [laura.gola@parcodelpo-vcal.it](mailto:laura.gola@parcodelpo-vcal.it)

12 3. Wildlife Science, Via Cossolo, 68/A, 10029 Villastellone (TO); email:  
13 [perrone.aurelio@libero.it](mailto:perrone.aurelio@libero.it)

14 4. Università degli Studi di Torino, Dipartimento di Scienze della Vita e Biologia dei Sistemi,  
15 Via Accademia Albertina 13, 10123, Torino, Italy; email: [sandro.bertolino@unito.it](mailto:sandro.bertolino@unito.it)

16  
17 **Corresponding author:** Jacopo Cerri, Istituto Superiore per la Protezione e la Ricerca Ambientale,  
18 Via del Cedro 38, 57122, Livorno, Italy; email: [jacopo.cerri@isprambiente.it](mailto:jacopo.cerri@isprambiente.it); mobile: (+39)  
19 3395692346;

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24 invasive;

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27 **Abstract**

28 The Eastern cottontail (*Sylvilagus floridanus*) has become invasive in Central and Northern Italy,  
29 where it affects prey-predator dynamics between native species. Although many different studies  
30 explored survival rates and the density of cottontails in North America, no information is available  
31 for its invasive range. Between December 2003 and October 2005, a capture-recapture scheme for  
32 Eastern cottontails was enforced on the Orba River, Italy. We fitted an open-population Cormack-  
33 Jolly-Seber model to estimate survival of adult individuals ( $n=258$ ) and their density in the study  
34 area. Adult cottontails showed a constant survival ( $\phi = 0.84 \pm 0.02$ ) across the various sessions, as  
35 well as between individuals of different sexes. Capture probabilities and densities varied seasonally,  
36 with densities ranging between  $2.06 \pm 1.24$  and  $8.00 \pm 4.60$  cottontails/hectare, with an average of  
37  $4.72$  individuals/hectare.

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

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52 **Introduction**

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

62 Due to multiple legal and illegal introductions, cottontails managed to colonize a significant portion  
63 of the Po plain, as well as many different croplands and riparian ecosystems of Central Italy (Dori et  
64 al., 2019). Cottontails have complex interactions with native species and their introduction  
65 ecosystems. Although they do not directly compete for habitat or food with native European hares  
66 (*Lepus europaeus*; Bertolino et al., 2011a,b, 2013; Vidus-Rosin et al., 2008, 2010, 2011), they seem  
67 to negatively affect them through apparent competition, by modifying prey-predator dynamics with  
68 native red foxes (*Vulpes vulpes*, Cerri et al., 2017). Moreover, the role of cottontails in the  
69 transmission of lagoviruses is still unclear (Lavazza et al., 2015; D'Angelo et al., 2018), although  
70 they are major vectors for many zoonoses and wildlife diseases (Bertolino et al., 2010; Gallo et al.,  
71 2005; Tizzani et al., 2014; Zanet et al., 2013).

72 In North America, various studies explored the survival of cottontails in captivity, as well as in the  
73 wild. Overall, cottontails are characterized by heterogeneous survival rates, which might vary  
74 substantially between the breeding and the non-breeding season, and between protected and non-  
75 protected areas. It is worth noticing that most studies estimated the survival of cottontails without  
76 assigning them to different age classes, a practice that could certainly have caused such  
77 heterogeneity. Cottontail densities are also extremely variable, both across different habitats and  
78 between different seasons. In suitable conditions, like enclosures or islands, with few or no

79 predators, cottontails were found to reach very high densities, up to 20 individuals/hectare. A  
80 complete overview of existing studies about survival and densities of cottontails in North America  
81 are available in Table 1.

82 To the best of our knowledge, no study measured cottontail survival in their introduction range, in  
83 Europe and, although they were widely studied in North America, few information is available  
84 about cottontail densities in their introduction range. For example, in Central Italy cottontails were  
85 found to reach densities ranging between  $7.29 \pm 0.99$  and  $71.60 \pm 12.98$  individuals/km<sup>2</sup> (Cerri et al.,  
86 2014). In Northern Italy higher densities were reported, between 4.40 and 110.41 individuals/km<sup>2</sup>  
87 (Bertolino et al., 2011), between 4.3 and 27 individuals/km<sup>2</sup> (Silvano et al., 2000) or between 47.3  
88 and 61.5 individuals/km<sup>2</sup> (Vidus-Rosin et al., 2010). These studies estimated cottontail densities  
89 mostly through nocturnal spotlight transects, with and without distance sampling. Considered that  
90 cottontails at night forage mostly near to permanent cover (Bertolino et al., 2011, 2013; Vidus-  
91 Rosin et al., 2008, 2010, 2011), which might decrease their detectability, these studies were likely to  
92 underestimate the real density of the species. Obtaining this information would be extremely  
93 important to understand how the species adapted in the introduced range, to design effective control  
94 schemes, which rely on the efforts of voluntary hunters (Cerri et al., 2018), and for epidemiological  
95 modeling (Salvioli et al., 2017). Moreover, to the best of our knowledge, no study explored  
96 cottontail survival in their introduction range. Obtaining some baseline information about this  
97 biological parameter can be extremely important for invasion ecology, for example to correctly  
98 parameterize matrix-based population models (Sakai et al., 2001).

99 In this research we aim to partially fill these two gaps by estimating the survival and the densities of  
100 adult cottontails in Northern Italy, from capture-recapture data. Capture-recapture methods are a  
101 valuable tool to achieve these two goals, as they enable researchers to estimate both survival and the  
102 number of individuals in a certain geographical area (Nichols, 1992; Schwartz and Seber, 1999;  
103 Sutherland, 2006). Notably, capture-recapture models proved themselves to be the gold standard for

104 the robust estimation of the densities of elusive nocturnal mammals, such as many lagomorphs  
105 (Langbein et al., 1999).

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## 107 **Materials and methods**

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

116 Cottontails were trapped with cage traps (double entry traps, “100 × 40 × 40  
117 cm, S. 237 Gibis”, France) every other month for two years. Traps were set in  
118 the field, baited with carrots and lettuce, and checked at sunset and after dawn  
119 for 5-7 days. Trapped animals were marked with ear-tags (a Monel No. 3,  
120 National Band and Tag Co., USA and a coloured tag with number). Cottontails  
121 were sexed through the visual inspection of genitalia, then operators measure  
122 their weight and the length of their rear foot.

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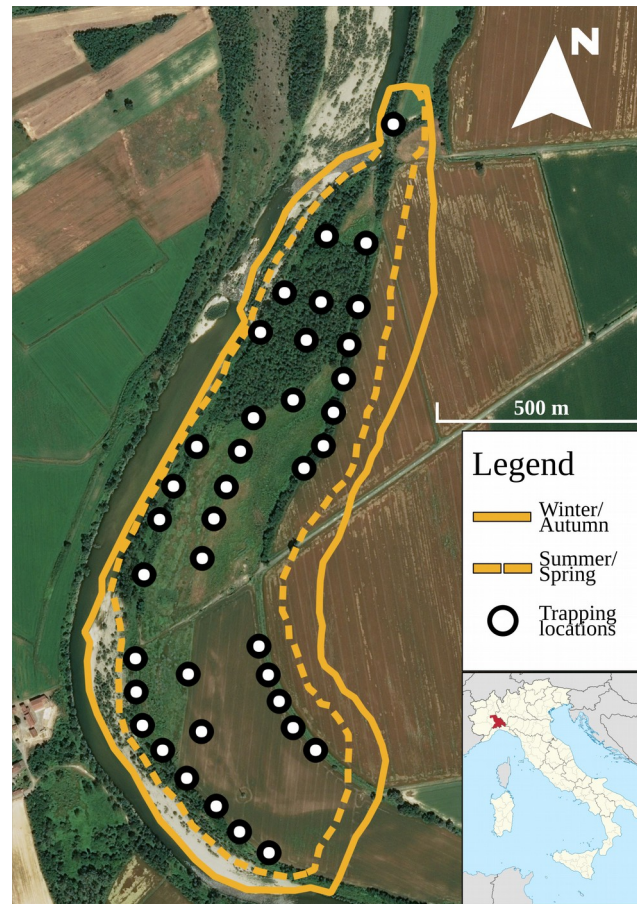


Fig. 1. Map of the study area: limits during winter/ autumn (continuous line) and in summer/spring (dashed line), altogether with trapping sites (dots). Study area was evaluated by considering a buffer around traps of about 64 m (winter/autumn) and 87 m (summer/spring).

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

156 survival and capture probabilities, as well as for multi-state models. Originally, our sampling was  
157 based on the robust design, with primary and secondary trapping periods. However, our data were  
158 too unbalanced, with unequal sampling intervals and we opted for modeling capture histories from  
159 primary periods only.

160 We fit an open-population Cormack-Jolly-Seber model (CJS, McCrea and Morgan, 2014), to  
161 estimate recapture and survival probabilities, as well as the number of animals in the study area  
162 through the Horovitz-Thompson estimator. We compared a set of models, with the full model  
163 accounting for time and sex as covariates for survival and recapture probabilities. Goodness-of-Fit  
164 testing was adopted, to compare the full model with a saturated one, through chi-squared testing.  
165 Then, model selection was based on information criteria, log likelihood function and deviance. The  
166 CJS model was estimated with the package ‘mra’ on the statistical software R (R Core Team 2019).  
167 Density was obtained by dividing the estimated number of animals by the  
168 effective trapping area which was calculated by adding a boundary strip  
169 (Flowerdew, 1986), equal to the radius of the average home ranges evaluated on the same animals  
170 (Bertolino et al., 2013) and considered to be circular. The size of the home ranges can in theory  
171 change for males and females and according to the season. However, we did not find significant  
172 differences in the home-ranges of males and females, as well as between the spring and summer  
173 seasons and between autumn and winter. We then calculated the radius of an average home-range  
174 for the cottontail in autumn-winter (64 m) and spring-summer (87 m), and used these measures to  
175 expand the capture area to 35.80 ha in autumn-winter and 39.98 ha in spring-summer.

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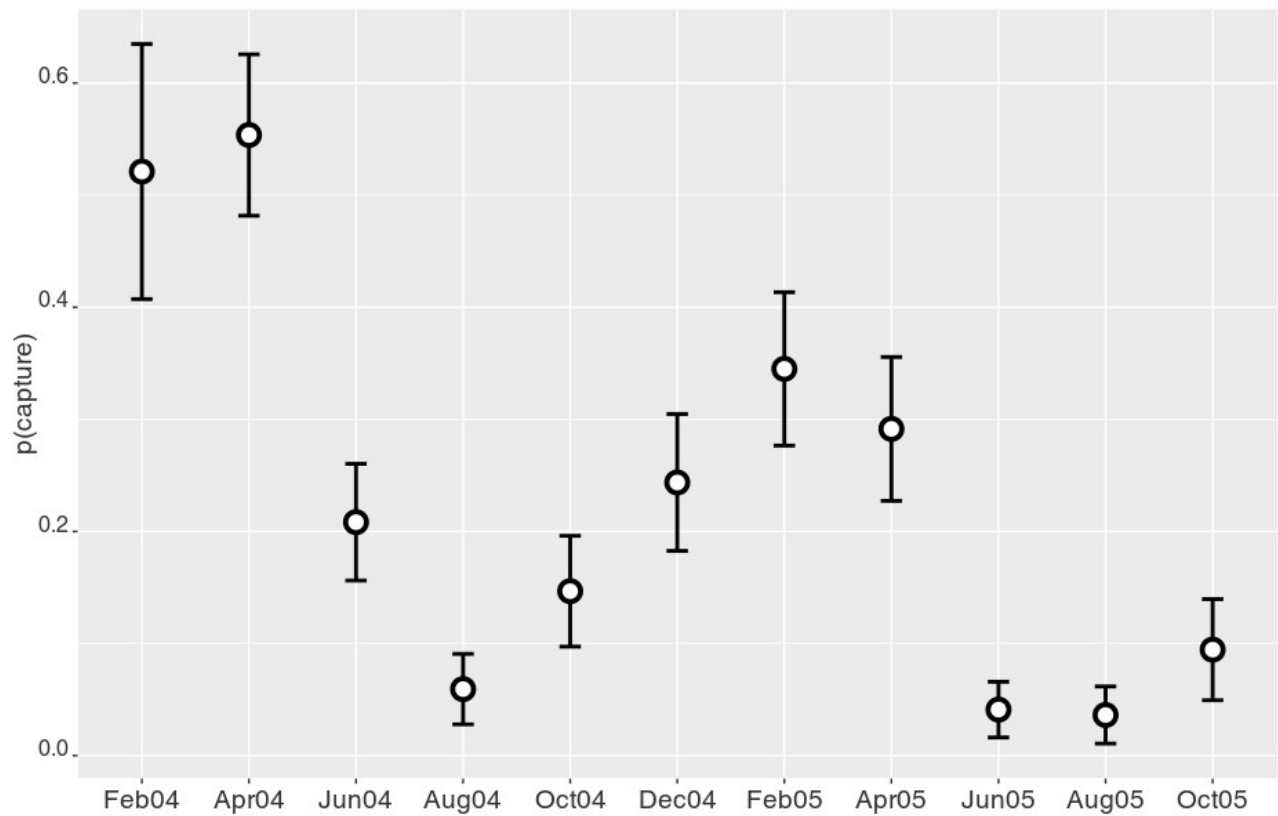
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## 178 **Results**

179 Our initial model showed a good fit to the data (Osjus-Rojek chi-squared:  $\chi^2 = 76.99$ ,  $df = 84$ ,  $p =$   
180  $0.85$ ; Hosmer-Lemeshow chi-squared:  $\chi^2 = 2.22$ ,  $df = 7$ ,  $p = 0.94$ ; mark-recaptureR chi-squared:  $\chi^2 =$   
181  $1953.81$ ,  $df = 1978$ ,  $p = 0.64$ ; ROC = 0.81), while our best candidate model was accounted for fixed

182 survival ( $0.84 \pm 0.03$ ) and time-varying capture-recapture probabilities, without any difference  
 183 between male and female cottontails (Table 2).  
 184 Capture probabilities were higher during the first two trapping sessions, then they declined.  
 185 However, recapture probabilities were higher in February and April, for both years, and reached  
 186 their minimum between June and September (Fig. 2).

187



188 Fig. 2. Recapture probabilities of adult cottontails between seasons.

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190 The estimated number of cottontails ranged between  $74.04 \pm 44.25$  in October 2005 (density =  $2.06$   
 191  $\pm 1.24$  cottontails/hectare) and  $320.15 \pm 184.02$  in August 2004 (density =  $8.00 \pm 4.60$   
 192 cottontails/hectare) (Fig. 3). The average density, over the entire period, was  $4.72$   
 193 cottontails/hectare.

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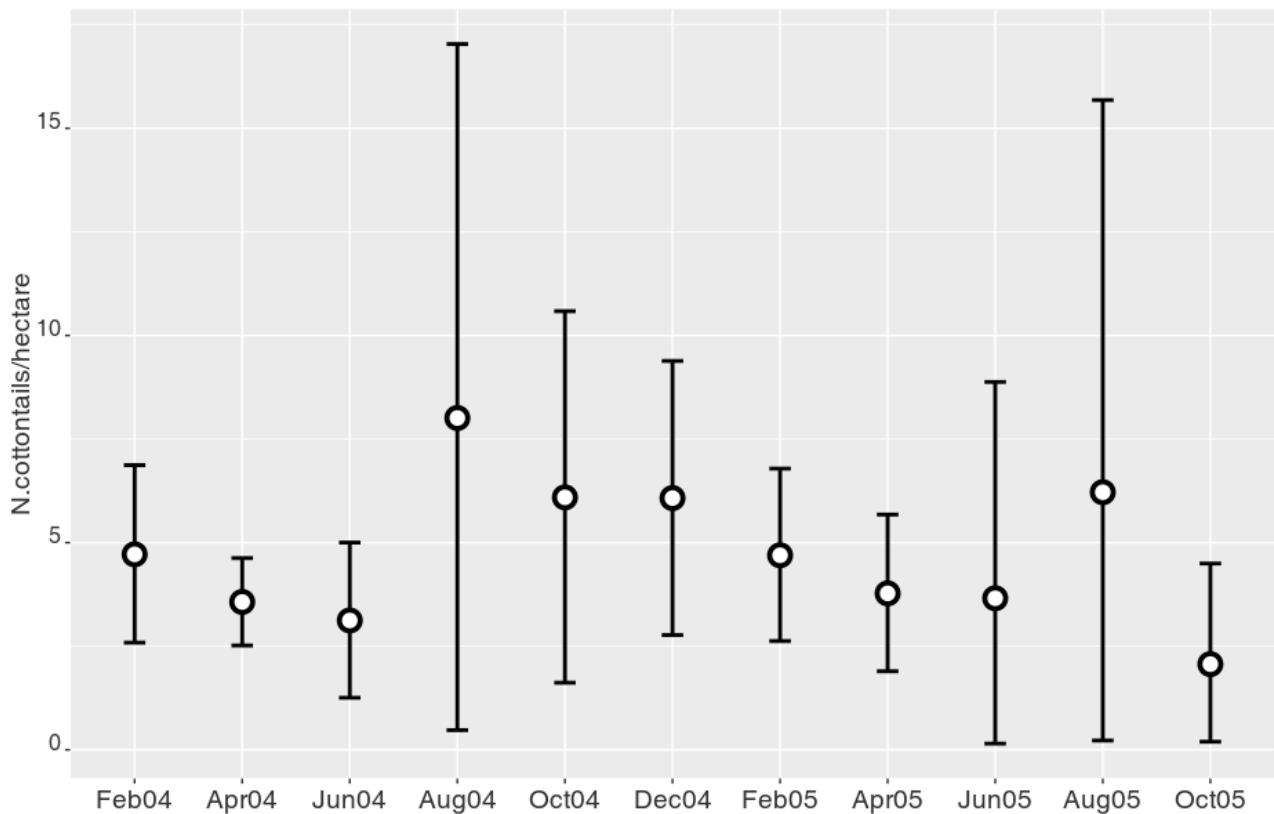


Fig. 3. Density of adult cottontails (individuals/hectare) between seasons.

## Discussion

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 between seasons and different years, which can remain relatively constant across seasons. This picture is different from the studies that had been conducted in 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 mixed 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

211 cottontails are susceptible to harsh and prolonged winter times, especially when trophic resources  
212 are scarce and coccidiosis strongly affect cottontail health (Dorney, 1962; Weidman and Litvaitis,  
213 2011), or to dry summers (Havera, 1972). The study area is characterized by a continental climate  
214 (average temperature = 12.5 °C, variation between average temperatures = 19.7 °C, rainfalls =  
215 960mm) with dry summer times (June-September: average temperature = 20.9 °C; average  
216 minimum temperature = 15.9 °C; average maximum temperature = 25.9 °C; rainfalls: 256 mm) and  
217 relatively hard winters (December-March: average temperature = 5. °C; average minimum  
218 temperature = 1.4 °C; average maximum temperature = 8.9 °C; rainfalls: 313 mm), therefore we  
219 expected at least some sort of seasonal variation, which was absent. This constant survival might  
220 suggest two different points, that need further research. First, cottontails that were introduced in  
221 Piedmont, might belong to a subspecies which is native of geographical areas with more continental  
222 climates than the rest of the native range. To date, no genetic study about invasive cottontails in  
223 Italy was carried out and we believe they might be fundamental to better understand whether one, or  
224 more, subspecies were introduced. Characterizing the taxonomy of invasive cottontails could also  
225 help understanding whether they hybridized or not between different subspecies, and if this  
226 hybridization facilitated their invasion dynamic. Moreover, constant survival of adult cottontails  
227 seems to indicate a scarce role of parasites, food availability and native predators over cottontail  
228 survival. Cerri et al. (2017) found that cottontails influenced fox populations, in a geographical area  
229 close to that of this study, by acting as a prey and it is known that cottontail could become a focal  
230 prey for foxes (Balestrieri et al., 2005) However it is unclear whether this predation involved young  
231 or adult cottontails. Future studies should clarify this point, to avoid cascade effects during  
232 management interventions, which might negatively affect native mammals, like the European hare.  
233 This study also shows that invasive cottontails can reach extremely high densities in their invasion  
234 range in Italy, comparable to those reported for populations in North America. Cottontail densities  
235 reached their maximum in late summer, during the last part of the breeding season, although their  
236 variation was less dramatic than that reported by other authors in North America. Taken together,

237 these two points indicate that adult cottontails are not subjected to strong mortality caused by  
238 competition, predation and diseases and that juveniles might be a considerable proportion of  
239 cottontail populations. Cottontails often become adults, and start breeding, even just after 12-13  
240 months. Although our sample focused on adult cottontails, it was hard to exactly determine the age  
241 of cottontails. This is why we discarded yearlings and individuals of unclear age. Indeed, our  
242 cottontails could have included individuals with 12-16 months. We believe that future studies,  
243 accounting for juveniles, might estimate much higher values of cottontail densities. In turn, these  
244 high densities and survival, might partially explain the huge spread of cottontails across Italy.  
245 Although the species is actively dispersed by hunters, through illegal restocking as a game, it was  
246 also characterized by a very rapid local dispersal (Bertolino et al. 2011b), which enabled it to  
247 colonize entire regions between introduction hotspots. To date, this fact sounded surprising, given  
248 the limited home range of Eastern cottontails in Northern Italy (Bertolino et al., 2013). However,  
249 given these unexpected population densities, it would not be surprising if cottontails in Italy were  
250 characterized by high dispersal and emigration.

251 Finally, it is worth noticing that our densities, although involving only adult cottontails, were much  
252 higher than those reported in Italian studies adopting nocturnal spotlight censuses. We believe our  
253 findings to be more robust than spotlight counts, due to the habitat preferences of the species, which  
254 might strongly limit its visual detectability. For instance, in our study area a density of only  $12.82 \pm$   
255  $4.97 \text{ ind./km}^2$  was estimated through nocturnal spotlight censuses just the winter before we started  
256 trapping (Bertolino et al., 2011). Future studies exploring population dynamics of invasive  
257 cottontails should therefore prefer capture-recapture approaches to visual censuses. These methods,  
258 though very demanding, will provide researchers and managers with more realistic estimates of  
259 cottontail populations, which might be useful for evaluating the effort required by control  
260 operations and for epidemiological modeling. Future studies should also involve young cottontails  
261 and model their survival, to improve population estimates. As cottontails have a flexible sexual

262 maturity, which might occur between 9 and 24 months, multistate capture-recapture models might  
263 be useful for this task (Pradel, 2005).

264

## 265 **Conclusion**

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

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

Density		
Study	Country	Value (and habitat)
Hunt et al. (2014)	US (Chicago)	9.4-16.3 ind./ha (urban park)
Scribner and Warren (1990)	US (Texas)	8.2-28.4 ind./ha (lake playa)
Chapman and Litvaitis (2003)	US	10-15 ind./hectare unspecified
Chapman (2003)	US (-)	Up to 20 ind./ha, in enclosures or islands (unspecified)
Chapman et al., 1982	US (Ohio)	3.1 ind./ha (free ranging population)
Leite, 1965	US (Ohio)	14.9 ind./ha (enclosed wildlife area)
Bittner and Chapman	US (St. Clemens Island, Maryland)	10.2 ind./ha (island)
Cerri, 2014	Italy (Tuscany)	7.29±0.99 and 71.60±12.98 ind./km <sup>2</sup> (free ranging population)
Bertolino et al., 2011	Italy (Piedmont)	4.40 and 110.41 ind./km <sup>2</sup> (free ranging population)
Silvano et al., 2000	Italy (Piedmont)	4.3 and 27 ind./km <sup>2</sup> (free ranging population)
Vidus-Rosin et al. 2010	Italy (Lombardy)	47.3–61.5 ind./km <sup>2</sup> (free ranging population)
Survival rate		
Trent and Rongstand (1974)	US (Wisconsin)	0.15-0.20 (annual survival, free ranging population) 0.34 (nonbreeding season)- 0.54 (breeding season)
Bond et al. (2001)	US (Mississippi)	0.18 (breeding season) – 0.70 (nonbreeding season) (free-ranging population)
Medve (1987)	US (Illinois)	0.56 (breeding season) - 0.72 (nonbreeding 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 (nonbreeding 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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277 Table 2. Model structure, information criteria, loglikelihood of the likelihood function and deviance of the Cormack-Jolly-Seber models

Structure	AIC	AICc	QAIC	QAICc	loglikelihood	deviance
$\Phi (\sim 1) p (\sim \text{time})$	1050.934	1052.426	735.2332	736.7250	-512.4669	1024.934
$\Phi (\sim \text{sex}) p (\sim \text{time})$	1051.698	1053.426	736.3780	738.1064	-511.8490	1023.698
$\Phi (\sim 1) p (\sim \text{time} + \text{sex})$	1054.494	1056.477	738.9287	740.9121	-512.2468	1024.494
$\Phi (\sim \text{sex}) p (\sim \text{time} + \text{sex})$	1055.698	1057.955	740.3780	742.6353	1023.6978	1023.698
$\Phi (\sim \text{time}) p (\sim \text{time})$	1060.136	1064.052	746.5296	750.4448	-509.0682	1018.136
$\Phi (\sim \text{time} + \text{sex}) p (\sim \text{time})$	1064.010	1068.728	750.4421	755.1600	1018.0100	1018.010
$\Phi (\sim \text{time} + \text{sex}) p (\sim \text{time} + \text{sex})$	1066.377	1071.981	753.3124	758.9159	1016.3774	1016.377
$\Phi (\sim \text{time}) p (\sim \text{sex})$	1085.214	1085.940	756.4903	757.2161	-533.6070	1067.214
$\Phi (\sim \text{time}) p (\sim 1)$	1089.971	1091.045	761.0145	762.0876	-533.9857	1067.971
$\Phi (\sim \text{time} + \text{sex}) p (\sim \text{sex})$	1091.210	1092.483	762.4873	763.7608	1067.2097	1067.210
$\Phi (\sim \text{time} + \text{sex}) p (\sim 1)$	1151.544	1093.155	762.9523	764.2258	1067.8817	1067.882
$\Phi (\sim 1) p (\sim 1)$	1152.583	1151.591	798.0767	798.1237	-573.7718	1147.544
$\Phi (\sim \text{sex}) p (\sim 1)$	1152.583	1152.677	799.4117	799.5062	-573.2913	1146.583
$\Phi (\sim 1) p (\sim \text{sex})$	1153.216	1153.310	799.8498	799.9442	-573.6078	1147.216
$\Phi (\sim \text{sex}) p (\sim \text{sex})$	1154.579	1154.737	801.4090	801.5671	-573.2983	1146.579
$\Phi (\sim \text{time}) p (\sim \text{time} + \text{sex})$	NaN	NaN	NaN	NaN	NaN	NaN





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