
Edge-Core Effects and the Effectiveness of Traditional Reserves in Conservation: Eurasian Badgers in Doñana National Park

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Abstract: High rates of human-mediated mortality on animals are frequently reported inside protected areas, especially near their borders, so the overall effect of reserves on animal conservation is not usually known. To determine the effect of a traditional reserve (Doñana National Park, southwestern Spain) on the Eurasian badger (*Meles meles*), a medium sized carnivore, we studied mortality causes and rates, with the aid of radiotelemetry, in two populations inside the reserve, one closer to the border than the other. Human-related mortality (poaching and road kills) was by far the most common cause of mortality (85% of deaths recorded). The average annual mortality rate due to poaching was high (0.48 ± 0.08) for the population close to the border of the park, whereas none of the radiomarked badgers in the core of the reserve died during the study period. A logistic model that included distance from the border of the park, sampling effort, and the local area (i.e., edge and core populations) indicated that the difference between both sites was due to the effect of distance from the border on survival probability. On a regional scale, badger density at the core of the park was 3.16 times higher than outside. Overall, the effect of the reserve was positive, but edge effects reduced reserve effectiveness by 36%. Edge effects in close proximity of the border were strong, reducing badger density even below the expected density outside the reserve. Edge effects should be considered carefully when reserves are implemented because they can greatly reduce reserve effectiveness and influence the viability of the populations inside. Enlargement of reserves and control of human activities that promote edge effects, both inside and outside the reserve, are the two management actions that can most effectively mitigate edge effects.

Efectos de Borde-Núcleo y la Efectividad de las Reservas Tradicionales en la Conservación: el Tejón Eurasiático en el Parque Nacional Doñana

Resumen: Dentro de las áreas protegidas y en la proximidad de su borde se registran frecuentemente elevadas tasas de mortalidad, y por ello, el efecto global de los espacios protegidos en la conservación de muchas especies es desconocido. Para definir el efecto de una reserva tradicional (Parque Nacional Doñana, sudoeste de España) en un carnívoro mediano, el tejón eurasiático (*Meles meles*), hemos estudiado las causas y tasas de mortalidad con la ayuda de radiotelemedría, en dos poblaciones dentro de esta reserva (una más cercana al borde que la otra). Las causas de muerte debidas a humanos (caza furtiva y atropellos) fueron, con diferencia, las más frecuentes (85% de los casos). La tasa de mortalidad media anual debida a la caza furtiva fue alta (0.48 ± 0.08) para la población cercana al borde, mientras que ninguno de los animales marcados en el núcleo del parque murió durante el seguimiento. Un modelo logístico que incluyó la distancia al borde del parque, el esfuerzo de muestreo y la población, indicó que la diferencia entre las dos poblaciones fue debida al efecto de la primera variable en la probabilidad de supervivencia. A escala regional, la densidad relativa de tejones en el núcleo del parque fue 3.16 veces mayor que fuera. El efecto total de la reserva fue positivo pero la existencia de efectos de borde redujo su efectividad en un 36%. Los efectos de borde en las cercanías

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del límite del parque fueron elevados, reduciendo la densidad de tejones incluso por debajo de la esperada fuera de la reserva. Los efectos de borde deben ser cuidadosamente considerados cuando se implementa una reserva dado que pueden reducir en gran medida su efectividad y afectar la viabilidad de las poblaciones que se incluyen en ella. El incremento en el tamaño de la reserva y el control tanto dentro, como fuera de la reserva, de las actividades humanas que causan el efecto de borde, son dos acciones de manejo no excluyentes que pueden mitigar los efectos de borde.

Introduction

Edge effects can be important in the dynamic of populations living in fragmented landscapes because they may affect key population parameters, such as survival and reproduction (Yahner 1988; Saunders et al. 1991; Murcia 1995; Noss & Csuti 1997). Edge effects frequently occur at the borders between different habitat types, especially between forested and cleared areas (Murcia 1995), but they also occur at the administrative borders of reserves (Woodroffe & Ginsberg 1998).

Because of their large spatial requirements and low densities, carnivores are especially sensitive to edge effects related to human-induced mortality (Schonewald-Cox et al. 1991; Clark et al. 1996; Woodroffe & Ginsberg 1998), and adult mortality rate is a key factor in the viability of small populations of carnivores either fragmented or at low density (e.g., Gaona et al. 1997; Wiegand et al. 1998). Carnivore mortality can be accidental, as in road kills and nonselective trapping, or intentional, as in hunting and poaching. Accidental killing in traps set for other species is a main concern in the conservation of small- and medium-sized carnivores, especially if the target species is common and a rare carnivore is taken (Schreiber et al. 1989), whereas for larger species direct hunting and poaching are the main problem (McLellan 1989; Powell et al. 1996; Beringer et al. 1998; Seidensticker et al. 1999). This human-mediated mortality is frequently reported at administrative borders of reserves for local populations. There are few cases, however, when the expected edge effects are clearly identified on a broader scale such as the reserve as a whole. Thus, the overall effect of reserves on the conservation of carnivores is not usually known.

We studied the effect of a traditional reserve, Doñana National Park, on the conservation of a medium-sized carnivore, the Eurasian badger (*Meles meles*). Doñana National Park is one of the most important reserves in Europe because of its high biological diversity and its strategic situation between Europe and Africa and between the Atlantic Ocean and the Mediterranean Sea (Fernández-Delgado 1997). Its use as a game area has preserved Doñana from human development for centuries. Badgers inhabit Mediterranean scrubland of the park and surrounding areas, forming a population isolated from

the northern range of the species in Sierra Morena mountains. They are not the target of any specific management or conservation action. Eurasian badgers are not threatened at a continental scale, but they are thought to be declining in Mediterranean areas, especially where they live at low densities as in Doñana (Griffiths & Thomas 1997; Revilla et al. 1999).

We measured causes and rates of mortality at the population level in two areas inside the park, one closer to the border than the other. We expected that mortality inside the reserve would be higher in the proximity of the edge than at the core. This information, however, does not indicate whether the park supports badger conservation on a regional scale. To determine the extent of edge effects, we studied the effect of the reserve on badger abundance on a landscape scale using structural equation modeling and path analysis, which control for the ecological variables that may affect badger survival probability and density. In this way we were able to isolate and estimate edge effects and determine whether they are counterbalanced by core effects, thus determining how the reserve is affecting the conservation of badgers in Doñana.

Methods

Study Area and Badger Natural History

We conducted our study in the Doñana region of southwestern Spain, an area of approximately 2750 km². The eastern, southern and southwestern boundaries of this large area are delimited by the Guadalquivir River and the Atlantic Ocean, and the north and northwest boundaries by the alluvial plain of the Tinto River and the intensively cultivated high ground of the Aljarafe (Fig. 1). It is a flat region with sandy soils, except in the eastern part, which is marshland (Fig. 1). Croplands cover 43% of the region. The remaining vegetation is dominated by Mediterranean scrubland (*Halimium* spp., *Cistus* spp., and *Pistacia lentiscus*) and by pine (*Pinus pinea*) and eucalyptus (*Eucalyptus* sp.) plantations. Doñana National Park (the reserve) is at the core of this region. The park occupies about 550 km², of which 240 km² is Mediterranean scrubland and pine plantations with undergrowth, habitat

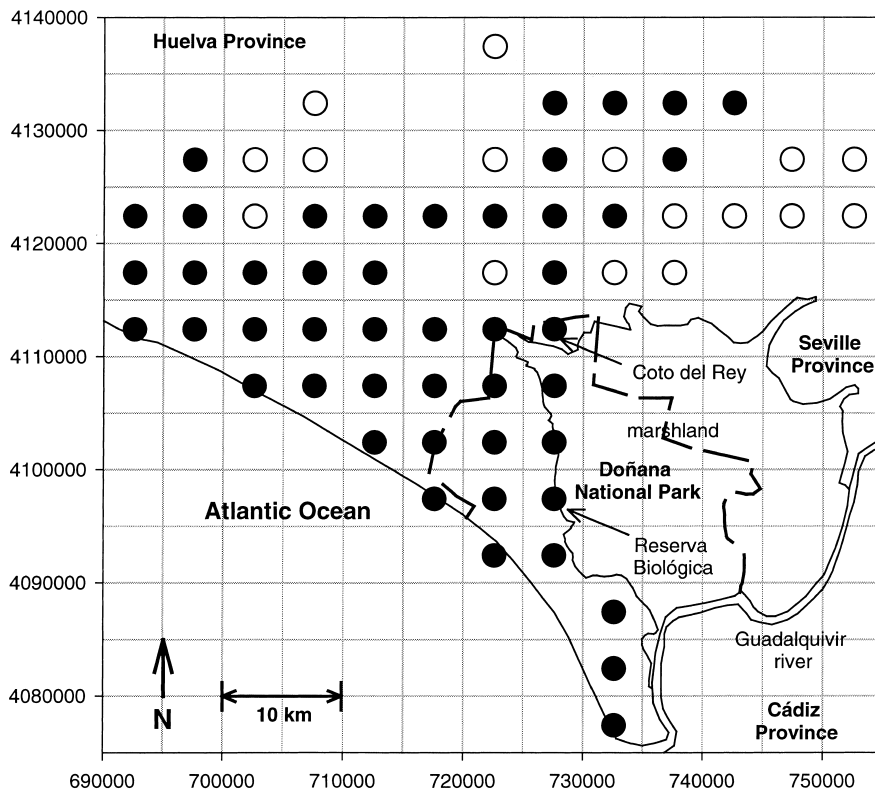


Figure 1. Map of the study area showing the Doñana region in southwestern Spain. Circles represent the 5×5 km squares where we searched for badger tracks (filled circles, badgers present; open circles, badgers absent). The center of the two "local populations" where badgers were radiomarked (Coto del Rey and Reserva Biológica) are also shown. Solid lines show the Atlantic coast, the Guadalquivir River, and the marshland. Dashed line shows the border of Doñana National Park. Reference system is Universal Transverse Mercator.

suitable for the Eurasian badger. The remainder is mostly marshland (Fig. 1; Fernández-Delgado 1997). The park is fenced, and free access is forbidden to people. Human activities are restricted to traditional, nonintensive use such as extensive grazing of cattle or pinecone harvesting. Tourism is limited to focal points. Wild ungulates reach high densities inside the park (up to 54, 48, and 22 individuals per square kilometer, respectively, for red deer [*Cervus elaphus*], wild boar [*Sus scrofa*], and fallow deer [*Dama dama*]) (Braza et al. 1984).

Eurasian badgers are medium-sized nocturnal carnivores (6–7 kg in Doñana; Revilla et al. 1999) that live in territories occupied by at least one female and one male (Woodroffe & Macdonald 1993). They eat a wide range of foods (Roper & Mickevicius 1995; Neal & Cheeseman 1996), but in Mediterranean areas they feed on European rabbits (*Oryctolagus cuniculus*) when rabbits are abundant (Martín et al. 1995; Fedriani et al. 1998; Revilla 1998). When rabbit densities are high, more badgers join territories and form social groups (Woodroffe & Macdonald 1993; Revilla 1998). Badgers in general show a strong preference for areas with high ground cover (Lüps & Wandeler 1993; Neal & Cheeseman 1996), such as Mediterranean scrubland in the Doñana area (Revilla 1998; Fedriani et al. 1999). Badger density in Doñana ranges between 0.2 and 0.7 badgers per square kilometer (Revilla et al. 1999). Density depends on territory size and on the existence of social groups (Woodroffe &

Macdonald 1993; Revilla 1998), which in turn depend on the presence of scrubland and abundant food resources.

Badger Populations at the Local Scale

We studied causes of mortality and rates of survival and mortality at two locations in Doñana National Park. The first, Coto del Rey, is situated at the northern border; the second, Reserva Biológica, is close to the center of the park (Fig. 1). We used radiotracking to determine the fate of individuals. Badgers were captured, anesthetized, individually marked with a microchip, fitted with a radio collar (with activity and mortality switch), and released at the point of capture (Cheeseman & Mallinson 1980; Travaini et al. 1994; Revilla 1998). In Coto del Rey we marked 24 individuals between 1994 and 1997 which belonged to five different territories. In Reserva Biológica we tagged 6 badgers in 1985 and 1986 (Rodríguez et al. 1995) and 3 more in 1997, for a total of six different territories. We located radiomarked badgers daily in Coto del Rey and two or three times per week in Reserva Biológica. We also recorded any dead unmarked badger found between 1994 and 1997.

We calculated survival and mortality rates with the Trent-Rongstad maximum likelihood estimator, following the methods of Heisey and Fuller (1985). We used MICROMORT software (Heisey & Fuller 1985; Heisey

1995), which estimates the probability of survival for a time interval as the product of daily survival rates. The main assumption of this method is that intervals must be defined as having constant daily survival rates (i.e., the hazard function is constant over the interval chosen; White & Garrott 1990). We selected years and seasons as intervals because they cover a complete reproductive cycle and changes in habitat preferences and space use (Revilla 1998). We performed comparisons between rate estimates using z statistics (Heisey 1995).

To quantify the effect of distance from the border of the reserve on survival rate, we estimated survival probability using logistic regression. We used as predictors distance from the border of the park, local area (i.e., Coto del Rey or Reserva Biologica), and sampling effort (measured as the number of weeks that every animal was monitored). We did not include censored individuals, those with an uncertain cause of end of tracking, in the analysis. We considered a badger to be alive after a period of monitoring if the end of the period was due either to transmitter failure or to the predetermined end of monitoring. Correlation between predictors was low (0.01–0.15), so we fitted the complete model. We used procedure LOGISTIC in the SAS software package (SAS Institute 1990a). We evaluated goodness of fit using $-2\log$ -likelihood estimator, which has a chi-square distribution under the null hypothesis (all the explanatory variables in the model are zero), based on the predicted and observed associated probabilities for each case (SAS Institute 1990a).

Badger Populations at a Regional Scale

We analyzed the effect of the park on badger abundance for the entire Doñana area by means of structural equation modeling and path analysis (Kingsolver & Schemske 1991; Mitchell 1992; Smith et al. 1997; Palomares et al. 1998). Path analysis permits the partitioning of the correlation among variables, accounting for both direct and indirect effects. It is based on a priori knowledge of causal relationships between variables, which are represented with a path diagram showing the working hypotheses. Relationships between variables are unidirectionally causal (indicated by single-headed arrows on path diagrams), residual correlations (double-headed arrows), or residual unexplained variances (arrows originating in U on path diagrams). The magnitude of a path coefficient (standardized regression coefficient) indicates the degree to which predictor variables directly influence the dependent variable when all other variables are held constant (for more information see Kingsolver & Schemske 1991; Mitchell 1992; Sokal & Rohlf 1995; Palomares et al. 1998).

Based on local-scale results, we hypothesized that the border of the park has a negative effect on badger abundance. Our proposed path diagrams considered two sets of variables (Fig. 2). The first included the most important ecological predictors of badger abundance, rabbit density and scrubland cover. The other set of variables, management variables, included distance from the border of the park, the variable of interest and the presence

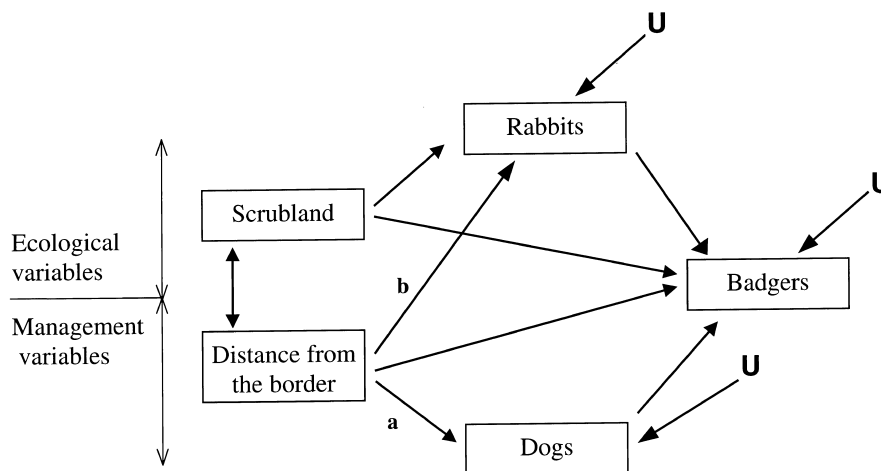


Figure 2. Path diagrams of the four alternative models proposed for explaining the relationship among badger and dog track numbers, rabbit abundance, ground cover by scrubland, and distance from the border of Doñana National Park in the Doñana region in southwestern Spain. Model 1 considers the effect of distance from the border on dogs and rabbits (paths labeled a and b, respectively); model 2 considers the effect of distance from the border only on dogs (path a); model 3 considers the effect of distance from the border only on rabbits (path b); and model 4 does not consider paths a and b. Unidirectional relationships between variables are indicated by single-headed arrows (“paths”). Double-headed arrows indicate residual correlation (accounted for, but the direction of the effect is unknown). Arrows originating in U represent the unexplained variances of dependent variables.

of dogs. Dogs were included in the model because they kill badgers (Neal & Cheeseman 1996) and are a good indicator of human interference (Aaris-Sorensen 1987; Jenkinson & Wheater 1998). We proposed four alternative nested models representing the working hypothesis (models 1–4, Fig. 2).

We fitted these models using the data obtained in a carnivore track survey conducted during the winter of 1992–1993 over the entire Doñana region (Fig. 1; for a complete explanation of field sampling procedures, see Palomares et al. 1998). We divided the study area into squares of 5×5 km and searched for badger and dog tracks in sandy roads and firebreaks in suitable badger habitat (i.e., scrubland). We carried out the surveys at least 3 days after any rainfall. Tracks clearly produced by the same individual were counted only once. The sampling of each square lasted at least 50 minutes, the time needed to detect 95% of the squares where badgers were present (E.R., unpublished analysis). Number of badger and dog tracks was expressed as number of tracks per hour of search and was considered a relative approximation of the actual density of the square.

We estimated a score of the abundance of scrubland and a score of rabbit abundance in the places we searched for tracks. Scrub cover was scored at six levels (from 1 to 6 respectively for 0, 1–20, 21–40, 41–60, 61–80, and 81–100%). Rabbit abundance was determined by individuals seen and rabbit signs detected (warrens, latrines, and tracks) and scored as scarce, 1; medium, 2; and abundant, 3. Distance from the border of the park to survey sites was measured as the distance to the closest administrative border in kilometers (without considering the border with the marsh and the Atlantic ocean). Distance was set to zero when samples were taken from unprotected areas. With this design we aimed to detect any overall reserve effect and any effect of distance from the border of the reserve on badger abundance. Distance from the border and badger and dog tracks per hour were transformed as natural $\log(x + 0.001)$.

We tested the proposed hypothesis and the strength of the interactions between the variables involved with the CALIS procedure in SAS (SAS Institute 1990b). Goodness of fit of the alternative models was examined by chi-square test and Bentler's comparative fit index (CFI). A nonsignificant chi-square result means the analyzed model does not significantly depart from the data, whereas CFI values over 0.9 (they range from 0–1) indicate an acceptable fit of the model to data (Bollen 1989; Hatcher 1994; Palomares et al. 1998). The CFI is a reliable index with small sample sizes (Bollen 1989; Hatcher 1994). The final decision between models was based on parsimony, as shown by the lowest values of Akaike information criterion (AIC) and Schwarz's Bayesian criterion (SBC; SAS Institute 1990b).

We tested the significance of individual path coefficients (i.e., the probability of being different from zero)

using accelerated bootstrap (this technique adjusts for potential bias and skewness of the bootstrap distribution; Dixon 1993; Manly 1997). We calculated the approximate bootstrap distribution after performing 10,000 bootstrap replicates and then the 95% confidence intervals for each path coefficient. A path coefficient was considered significant when 95% confidence intervals did not include zero (Manly 1997; Palomares et al. 1998).

Results

Local Scale

During the study we recorded 20 dead Eurasian badgers in the Doñana area; the majority of deaths were due to human activities such as road kills or poaching (15% and 70% of the casualties, respectively). Poachers go inside the park with hounds at night; their targets are wild ungulates, such as red deer, fallow deer, and wild boar. Occasionally, badgers were captured by hounds and killed by the poacher. Poachers rarely took badgers as trophies, leaving most of the casualties in the field. All poached badgers were killed in habitats lacking scrubland cover. Eighty percent of the poached badgers were killed inside Doñana National Park, and the remaining were killed outside at <2 km from the border. Only one of the animals found dead inside the protected area was in the core of the park (at the Biological Reserve).

Of 33 badgers radiomarked between 1985 and 1997, 13 died, 5 were still alive at the end of the study, 13 were lost due to transmitter failures or collar loss, and 2 disappeared for unknown reasons. Poaching was the cause of death of 45.8% of the badgers marked in Coto del Rey area. There, all but one of the poached animals were adults (>2 years old). Other causes of mortality in radiomarked badgers included intraguild predation (one subadult badger was killed by a red fox [*Vulpes vulpes*]) and unknown causes. None of the nine marked badgers in the Reserva Biologica died during our monitoring period.

The average annual survival rate (\pm SD) in Coto del Rey was 0.44 ± 0.09 (range 0.22–0.60; Table 1). Average annual mortality rate due to poaching was 0.48 ± 0.08 (range, 0.29–0.64; Table 1), whereas other causes of mortality accounted for only 0.09 ± 0.05 (range, 0.00–0.20). There was no significant difference between years in survival and mortality rates ($z < 1.57$, $p > 0.05$, in all cases, and $z < 1.42$, $p > 0.05$, in all cases, respectively). Seasonal survival rate was 0.80 ± 0.04 (range, 0.55–1.0), and seasonal mortality rate due to poaching was 0.17 ± 0.04 (range, 0.00–0.45). There was no seasonal pattern to survival and poaching mortality rates. Because none of the nine radiomarked badgers in the Reserva Biologica died during the study, survival rate was considered to be 1.

Table 1. Annual rates of survival and mortality due to poaching of Eurasian badgers (*Meles meles*) radiomarked in Coto del Rey (Doñana, Spain).*

Years	Sampling effort (radio-days)	Number of radiomarked animals (estimated population size)	Number of dead animals (poached)	Interval survival rate (95% confidence interval)	Interval mortality rate for poaching (95% confidence interval)
1994	952	8 (15)	4 (3)	0.22 (0.05–0.97)	0.59 (0.18–1.00)
1995	1936	10 (12)	3 (2)	0.57 (0.30–1.00)	0.29 (0.00–0.62)
1996	1434	9 (10)	4 (4)	0.36 (0.13–0.98)	0.64 (0.29–0.99)
1997	722	3 (9)	1 (1)	0.60 (0.22–1.00)	0.40 (0.00–0.99)

*We also monitored nine badgers in Reserva Biologica (six individuals marked in 1985–1986 and three more in 1999, located for a total of 1589 radio-days), but none of them died during their monitoring.

Distance between the center of the home ranges of marked badgers and the border of the park in Coto del Rey and Reserva Biologica averaged 1.22 ± 0.13 km (range, 0.2–1.85) and 6.56 ± 0.69 km (range, 1.5–9.0), respectively. The logistic model was significant ($\chi^2 = 28.63$, $df = 3$, $p = 0.0001$). Associations of predicted probabilities were 97% concordant and 3% discordant. Distance from the border was significant in the model (Wald $\chi^2 = 5.54$, $df = 1$, $p = 0.01$), but the area (i.e., Coto del Rey or Reserva Biologica) and sampling effort were not (Wald $\chi^2 < 1.10$, $df = 1$, $p > 0.29$). Fitting the logistic model to the mean of the sampling effort (28 weeks) and for Coto del Rey (i.e., where we detected dead animals), we predicted that at 1.75 km away from the border survival probability was 95%, increasing up to 100% at 3.5 km from the border (Fig. 3). These results indicate that the distance to the administrative border strongly affects survival probability, at least for the badger population in Coto del Rey.

Regional Scale

Badgers and dogs were present at 74.6% and 77.7% of the sampled squares ($n = 63$), respectively. Badgers were present in all the squares containing badger habitat

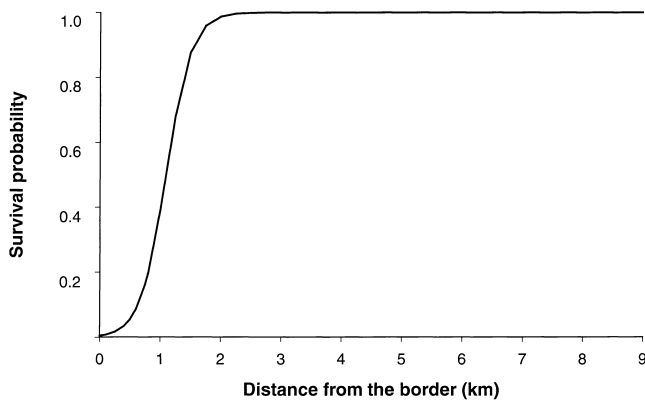


Figure 3. Survival probability predicted by the logistic model for badgers living in Coto del Rey (close to the border of the park) after 28 weeks of monitoring, as a function of the distance of the center of their territories from the border of the national park.

situated inside the park ($n = 14$), whereas dogs were present at 64.3%. Mean number of badger and dog tracks per hour was 4.01 ± 0.69 (range, 0.00–26.70) and 4.68 ± 0.59 (range, 0.00–21.10), respectively. Badger tracks were significantly more abundant inside the national park than outside, even when we considered only those squares outside the park where badgers were present (3.40 ± 0.52 and 10.02 ± 2.02 for outside and inside the park, respectively; $t = 4.35$, $df = 45$, $p < 0.001$). Correlations between variables ranged between -0.34 for distance from the border and dog tracks and 0.39 for distance from the border and badger tracks.

A likelihood ratio test and CFI showed that none of the four alternative nested models (Fig. 2) significantly departed from the observed data (Table 2). Chi-square tests did not detect significant differences between models ($\chi^2 < 0.34$, $p > 0.75$, in all comparisons). We kept model 2 (Fig. 4) as the best fit to the observed data, given its lower Akaike information criterion and Schwarz’s Bayesian criterion (Table 2).

Accelerated bootstrap showed significant direct effects of paths from distance from the border to badgers and from distance from the border to dogs (Table 3; Fig. 4). Distance from the border had a positive effect on badgers and a negative effect on dogs. Scrub through rabbits and protection through dogs had a weak positive indirect effect on badgers (indirect effects, Table 3). The

Table 2. Results of path analysis for the four proposed models explaining the relationships on a regional scale (Doñana, Spain) among badger and dog track numbers, distance from the border of the national park, rabbit abundance, and scrub cover (see Fig. 2).

Model	χ^2	df	p^a	CFI ^b	AIC ^c	SBC ^d
1	2.85	2	0.2405	0.96	-1.15	-5.44
2	2.91	3	0.4052	1	-3.09	-9.52
3	2.57	1	0.1089	0.93	0.57	-1.57
4	2.63	2	0.2681	0.97	-1.38	-5.65

^aNonsignificant results indicate an adequate fit of the models to data.

^bBentler’s comparative fit index; values closer to 1 indicate better models.

^cAkaike information criterion; lower values indicate a more parsimonious model.

^dSchwarz’s bayesian criterion; lower values indicate a more parsimonious model.

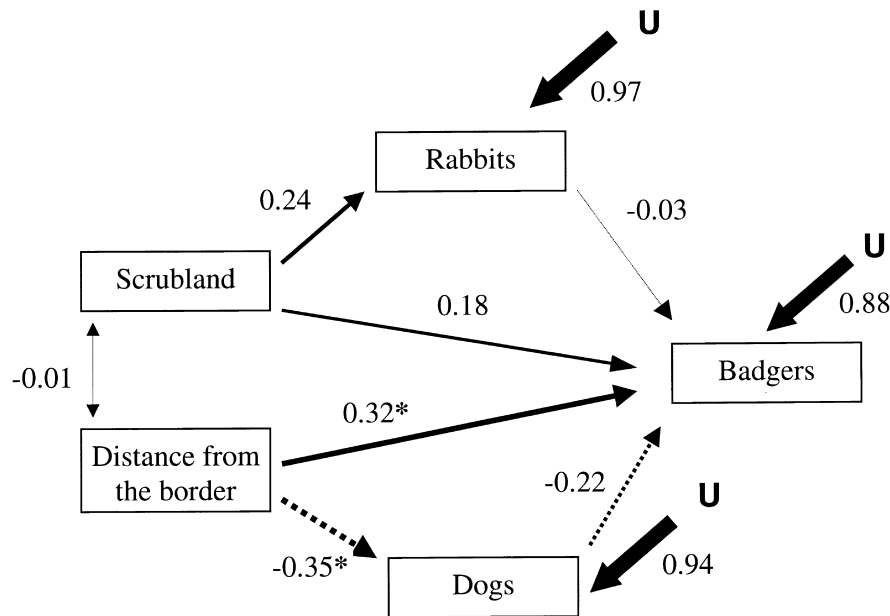


Figure 4. Solved path diagram of model 2 (Fig. 2) explaining the relationship among badger and dog track numbers, rabbit abundance, ground cover by scrubland, and distance from the border of Doñana National Park in the Doñana region of southwestern Spain. Solid lines represent positive effects; dashed lines represent negative effects. Width of line (arrow weight) is proportional to the strength of each path, and numbers are standardized path coefficient values that indicate the degree to which predictor variables directly influence the affected variable, with all other variables held constant. Paths significantly different from zero are indicated with an asterisk. Model explanation provided in legend of Fig. 2.

total effect of distance from the border on badger abundance was the strongest of the model, with a positive value of 0.40; in other words, inside the reserve with all else being held constant, badger density was expected to increase with distance from the border (Table 3).

To better understand the relationship between distance from the border and badger density, we fitted model 2 to a gradient of distances from the border of the park (i.e., representing a cross-section of the study area; Fig. 5). Ecological variables were set to overall means. Density of dog tracks was set as the mean outside and in-

side the park for predicting density of badger tracks outside and inside the park, respectively. Under these conditions, the model predicted a density of badger tracks at the core of the park (10 km from the border) 3.16 times higher than outside the reserve (Fig. 5). Badger density increased with increasing distance from the border of the reserve (Fig. 5). There was an overall positive effect—core effect—of the reserve on badger abundance. This is shown by a 1.38-fold increase in density compared with the density in the unprotected surroundings. The extent of edge effect can be measured as the

Table 3. Results of the path analysis for model 2 (Figs. 2 & 4) representing the relationship among badger and dog track numbers, distance from the border of the national park, rabbit abundance, and scrub cover in the Doñana region of Spain.*

	Effects on badgers			Effects on dogs			Effects on rabbits		
	DE	IE	TE	DE	IE	TE	DE	IE	TE
Effect from rabbits	-0.03	—	-0.03	—	—	—	—	—	—
Effect from scrubland	0.18	-0.01	0.18	—	—	—	0.24	—	0.24
Effect from dogs	-0.22	—	-0.22	—	—	—	-0.12/0.51	—	—
Effect from distance to border	0.32	0.08	0.40	-0.35	—	-0.35	—	—	—
r^2	0.23			0.12			0.06		

*Values are the observed standardized path coefficients and the lower and upper 95% confidence limits for the bootstrap distribution (if zero is not included within those limits the paths are considered significantly different from zero) for direct (DE), indirect (IE), and total effects (TE). Badger and dog tracks are log-natural-transformed; r^2 is the amount of the variance of each variable explained by the model.

difference between the maximum expected badger density, fixed as the maximum density reached at the core of the park, and the actual estimate of badger density (Fig. 5), accounting for 36% of the maximum expected density. The edge effect in the proximity of the reserve boundary was strong (Fig. 5), reducing badger density even below that outside the park (in the example of Fig. 5, it is 5.7 times lower inside the park close to the border than outside). This reduction in density is only 1% of the core effect observed in the example.

Discussion

Local Scale: Badger Mortality and Edge Effects

Human activity was the most significant cause of mortality among badgers in the Doñana region. This finding is in contrast with that of high-density badger populations in, for example, England, where road accidents are the

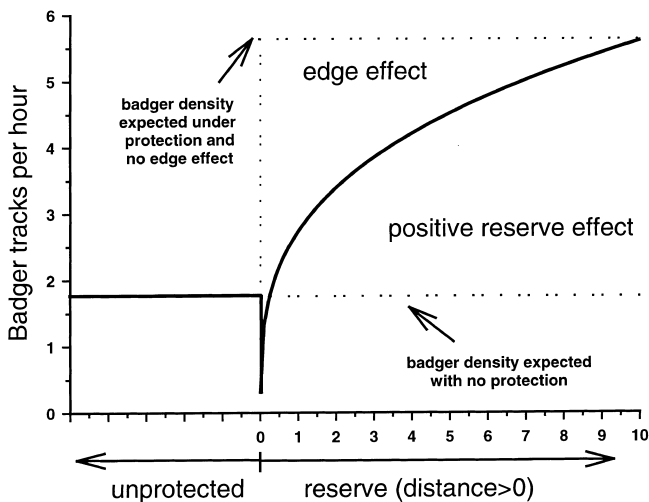


Figure 5. Relationship between badger relative abundance and distance from the border of Doñana National Park (distance of zero indicates locations outside the reserve [unprotected], and positive values indicate locations inside the reserve) predicted by model 2 (Table 3; Fig. 4) in the Doñana region of southwestern Spain. Ecological predictors—rabbit abundance and scrubland cover—were set to overall means. Number of dog tracks was set as the mean outside and inside the reserve, respectively. The extent of edge effects can be measured as the surface enclosed by the maximum badger density expected under no edge effects (upper and left dotted lines) and the badger density predicted inside the reserve. The extent of core effects can be measured as the surface enclosed between the badger density expected with no protection (lower dotted line) and the badger density predicted inside the reserve.

main cause of mortality and accounting for up to 67% of all fatalities (15% in Doñana), and where only 9% of badgers are killed by people (at least 70% in Doñana area; Rogers et al. 1997; Clarke et al. 1998). In these high-density badger populations, annual mortality rates of adult badgers are lower than in Coto del Rey (21–34% vs. 54% in Coto del Rey; Cheeseman et al. 1987; Harris & Cresswell 1987; Rogers et al. 1997).

In Doñana National Park, interaction with humans is also the most important cause of mortality among other carnivores, such as the endangered Iberian lynx (*Lynx pardinus*; 70.8% of all deaths; Ferreras et al. 1992) and the large grey mongoose (*Herpestes ichneumon*; in one study at least 56.3% of all radiomarked mongooses were illegally hunted; Palomares 1992). Many other species of carnivores living in reserves around the world are also affected by interactions with humans (reviewed by Woodroffe & Ginsberg 1998).

The high mortality rates in Coto del Rey contrast with the fact that no radiomarked badger was killed in Reserva Biologica. Nevertheless, poaching also occurred in the core of the park, where we found an unmarked poached badger. Results from the logistic regression show that distance from the border was the only variable that significantly affected badger survival probability, so we can ignore any negative effect of habitat quality on survival probability. The effect of edge on survival probability went as far as 3.5 km inside the park in Coto del Rey and affected one or two territories (average maximum territory axis in Coto del Rey is 2.8 km; Revilla 1998).

Regional Scale: Edge Effects and Reserve Effectiveness

Human interference can have a negative effect on badger density, depending on how far it spreads inside the reserve and whether it occurs along the entire border. This negative effect may be counterbalanced by any positive numerical response (depending on reserve size and physiognomy) at the core of the protected area. We considered these possibilities through structural equation modeling and path analysis (Mitchell 1992; Wootton 1994).

Our sampling design minimized the effects of habitat quality on badger abundance at a large scale because we sampled only those squares containing badger habitat and, within those squares, only badger habitat. Our analysis was also designed to control the effect of ecological variables on a local scale because we controlled for the effect of vegetation cover and rabbit abundance at each sampled point and thus isolated the effects of management variables. Structural-equation modeling showed that model 2 was a good description of data but explained a relatively small amount of variance (Table 3). This is not rare in ecological studies (Mitchell 1993; Palomares et al. 1998) and can be caused by unmeasured factors

not considered in the model and by natural random variations (Mitchell 1993). Given the sampling design, we expected low and nonsignificant effects in paths from scrubland to badgers and from rabbits to badgers (i.e., those explaining badger ecology).

Path analysis showed that distance from the border had a significant effect on the relative abundance of dogs and badgers. Furthermore, the total effect of distance to border on badger abundance was the largest in the model. The overall effect of protection on badger density was positive (Fig. 5), as expected from the significant difference between number of badger tracks found per hour outside and inside the reserve, although edge effects were present along the entire border of the reserve. Edge effects, however, greatly diminished overall reserve effectiveness (36% reduction in relative badger abundance in Fig. 5), which depends on badger density outside the reserve (as a function of dog density and habitat quality). This relationship needs to be controlled before the question of reserve effectiveness can be considered. It is also interesting that inside the reserve densities in the proximity of the border fell below even the expected density outside (Fig. 5). Again, the extent of this "negative reserve effect" is related to badger density outside the reserve. This low density of badgers inside the reserve is most likely caused by a high mortality rate (as in Coto del Rey) that cannot be counterbalanced by reproduction and dispersal fast enough to avoid the density reduction. This sink at the border of the park can produce local extinction, as reported in 1996 in Los Sotos, an area on the border of the park (E.R., unpublished data), and may increase the probability of badger extinction on a regional scale (as for many other carnivores; Woodroffe & Ginsberg 1998).

The presence of strong edge effects for species also present outside the reserve (usually of no conservation concern) may lead to protection having a neutral or even negative effect overall. On the other hand, if the effects of edge on survival probability are present far inside the reserve, the population may face a strong density reduction. The threat of extinction may then appear if there are no sources outside the reserve to counterbalance mortality. Edge effects may reach the core of the park when reserve size is too small in relation to the scale of the species' movement, or when populations are too small to compensate for mortality at the administrative border.

High mortality produces empty areas of good habitat where dispersing individuals tend to settle. Thus, those areas can be considered to be an attractive sink generated by the high mortality produced by the population's interaction with people at the border. This conservation paradox poses a question about the effect of reserves in carnivore conservation, a question of scales: the effectiveness of a reserve for any given species depends on species scale, defined by its ranging behavior (e.g., home

range or territory size); on reserve scale, defined by reserve size and physiognomy (e.g., relationship between area and perimeter); and on human-activities scale, defined by the spatial needs of human activities that occur in the same landscape as the population (including the reserve) and that interfere negatively with the species (e.g., how far poachers go inside the reserve).

The closer the species scale is to the human-activity scale, the worse the conservation scenario for the species will be. Reserves will be successful only when their scale is larger than the scales of both human activities and species of concern. Unfortunately, the solution of increasing reserve size often is not possible because it is frequently the most difficult variable to manage. Thus, the best alternative may be implementation of transborder conservation measures at both sides of the administrative edge. To preserve species with large spatial requirements that interfere with human activities (such as trophy or subsistence hunting, competing for prey, or killing cattle or even people), it is necessary to manage human activities inside and outside protected areas so as to reduce edge effects.

Badger Conservation in Doñana

The Eurasian badger is not a target species either for conservation policies or for poachers and hunters. Poachers are attracted to the reserve by high and unnatural densities of ungulates created by lack of both natural predators (only the Iberian lynx occasionally preys on fallow deer) and human control of ungulates inside the park. This situation is the result of the application of a management model similar to the one used in wild areas of Africa or North America but does not account for the fact that the landscape in Europe has been managed by people for thousands of years (Fernández-Delgado 1997; Schröder 1998). High densities of fearless game attract poachers but rarely subsistence hunters. Thus, a species such as the badger that is not of conservation concern but is sensitive to high mortality rates can be affected negatively by the implementation of a reserve; the consequences for the future viability of the Doñana population, which is isolated due to habitat loss, are unknown.

Overgrazing by wild and domestic ungulates is one of the major problems of the park (Fernández-Delgado 1997). Human intervention is needed to maintain diversity and ecosystem processes in areas historically managed by people. To improve the effectiveness of Doñana National Park for the conservation of badgers and other carnivores, managers need to be able to control poaching. The inefficiency of the actual management system, despite the large number of wardens working in the park (Fernández-Delgado 1997), indicates a complex sociological problem. The solution will be not only a reinforcement of control policies but also an education cam-

paign aimed at improving the image of the reserve among local people, together with better management of ungulate densities.

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