Animal Conservation
Animal Conservation. Print ISSN 1367-9430

Conditioned odor aversion as a tool for reducing post-release predation during animal translocations

J. Tobajas[1], E. Descalzo[1], R. Villafuerte[2], J. Jimenez[1], R. Mateo[1] & P. Ferreras[1]

1 Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM, Ronda de Toledo 12, Ciudad Real, 13071, Spain
2 Instituto de Estudios Sociales Avanzados (IESA-CSIC), Campo Santo de los Mártires 7, Córdoba, 14004, Spain

Keywords
BACI; conditioned odor aversion; conditioned taste aversion; post-release survival; predation; predator–prey relationship; reintroductions; translocations.

Correspondence
Jorge Tobajas, Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM, Ronda de Toledo 12, Ciudad Real, 13071, Spain.
Email: jtobajas47@gmail.com

Editor: John Ewen
Associate Editor: Carolyn Hogg

Received 22 November 2019; accepted 25 August 2020

doi:10.1111/acv.12643

Abstract

Predation is a key factor in prey population dynamics and could impact population recovery. One common means employed to recover prey populations is that of translocations, but most fail owing to high predation during the early stages. We tested whether conditioned odor aversion can reduce predation during animal translocations by using the predation of the European rabbit *Oryctolagus cuniculus* by the red fox *Vulpes vulpes* as a case study. Following a before-after control-impact design (BACI), we deployed bait stations monitored using camera-traps in two zones to which rabbits were translocated. One week before the rabbits were released, microencapsulated levamisole was added to rabbit baits located in the treatment zones, along with vanilla essence as an odor cue. A total of 148 rabbits were distributed in artificial warrens with the odor cue and 68 of them were fitted with radio collars in order to determine their survival rates. The response to the treatment and translocation as regards subsequent rabbit abundance was evaluated using N-mixture models, while rabbit establishment was evaluated using a warren use index (WUI). The treatment decreased the proportion of baits consumed by foxes, but this decrease was partially compensated by other predators. WUI and rabbit population growth increased significantly more after translocations in the treatment zones than in the control zones. The short-term survival of translocated rabbits was also higher in the treatment zones than in the control zones. Our study showed that conditioned odor aversion reduced rabbit predation by foxes, and had a positive effect on rabbit population growth after translocation, since there was an increase in rabbit survival and warren establishment. This method could be used as a non-lethal tool for the recovery of a key prey when carrying out programs concerning the reintroduction of endangered predators or for other vulnerable species requiring translocations.

Introduction

Interpreting predation effects on prey populations is difficult because prey survival and reproduction are driven by a variety of other factors (e.g. habitat quality, disease) (Norbury & Jones, 2015). However, it is known that prey abundance and population growth can be regulated by predation (Sinclair *et al*., 1998; Delibes-Mateos, Ferreras & Villafuerte, 2008*a*), particularly in the case of low prey abundances (Fernandez-de-Simon *et al*., 2015; Norbury & Jones, 2015). Moreover, high predation pressure can limit the prey's recovery after severe declines (Sinclair *et al*., 1998; Delibes-Mateos, Ferreras & Villafuerte, 2009). Predator control, together with other management techniques, such as habitat improvement or translocations, have, therefore, been applied in an attempt to restore prey populations (Moreno & Villafuerte, 1995; Sinclair *et al*., 1998; Banks, 2000; Calvete & Estrada, 2004; Delibes-Mateos *et al*., 2009).

Translocation is defined as the human-mediated movement of living organisms from one area with release in another (IUCN/SCC, 2013). Translocations are a common practice in conservation biology and wildlife management for conservation purposes (Seddon, Strauss & Innes, 2012; Carro, Ortega & Soriguer, 2019). With regard to the maintenance of ecological systems, a sufficient number of individuals is required, not only to prevent species extinction, but also to perform ecological roles (Gaston, 2010). This is the case of those keystone species that function as key prey or ecosystem engineers (Delibes-Mateos *et al*., 2007; Swaisgood *et al*., 2019), which may be pests in some regions and ecologically important species as regards re-establishing ecosystem functions in others (Delibes-Mateos *et al*., 2008*a*; Swaisgood *et al*., 2019). One example of these species is the European rabbit *Oryctolagus cuniculus*, thousands of which have been translocated onto hunting estates and into conservation areas in order to reinforce the populations of this key species as a prey for several endangered species, such as the Iberian lynx *Lynx pardinus* or the imperial eagle *Aquila adalberti* (Delibes-Mateos *et al*., 2008*b*; Carro *et al*., 2019). These translocations have been necessary owing to the sharp decline in rabbit populations in the Iberian Peninsula, principally as a result of the arrival of two viral diseases: myxomatosis in the 1950s (Villafuerte *et al*., 2017) and the rabbit hemorrhagic disease (RHD) in the late 1980s (Delibes-Mateos *et al*., 2008*a*). The expansion of rabbits into Mediterranean woodland has subsequently been very limited in comparison with what has occurred in open areas (Delibes-Mateos *et al*., 2008*a*), which has led to a mismatch between the distribution of endangered predators and their main prey (Real *et al*., 2009). The reinforcement of rabbit populations in the expansion areas and future reintroduction areas of these endangered species is, therefore, necessary (Moreno *et al*., 2004; Ferreira & Delibes-Mateos, 2010).

Although the science of translocation biology has advanced rapidly in recent decades, there has been no increase in the proportion of translocation studies that directly test alternative management actions (Taylor *et al*., 2017), and new approaches with which to meet translocation challenges, such as the post-release effects of predation, are, therefore, required (Berger-Tal, Blumstein & Swaisgood, 2019). The traditional methods employed to translocate rabbits have had negligible success (Calvete *et al*., 1997; Calvete & Estrada, 2004). Capture and handling, the novelty of the environment, social disturbance and induced stress may affect the short-term survival of the released rabbits (Letty *et al*., 2003; Cabezas, Calvete & Moreno, 2011; Ruiz-Aizpurua & Tortosa, 2018), but predation has been shown to be the most important factor in the failure of rabbit translocations (Calvete *et al*., 1997; Letty *et al*., 2002; Calvete & Estrada, 2004). Experimental translocation research has demonstrated that high mortality of rabbits occurs due to predation by carnivores during the first days after release, especially by red foxes *Vulpes vulpes*, causing 65–75% of rabbit mortality (Calvete *et al*., 1997; Letty *et al*., 2002; Calvete & Estrada, 2004; Moreno *et al*., 2004). Traditional predator control is carried out to reduce this high mortality resulting from carnivore predation (Reynolds & Tapper, 1996; Virgós & Travaini, 2005). Several studies have shown that predator removal could be a successful management strategy by which to increase rabbit numbers in areas into which rabbits have been introduced (Trout & Tittensor, 1989; Banks, 2000). These studies have also shown that rabbit populations could be regulated at low abundance by predator pressure, especially after sharp population drops. This effect is known as the 'Predator-Pit' (Trout & Tittensor, 1989). The effectiveness of this traditional predator control practice has not been tested in Mediterranean areas, where there is a diverse predator community (Delibes-Mateos *et al*., 2009). However, a higher rabbit population recovery rate was reported for areas in which predator control, and particularly the removal of red foxes, was a common practice (Delibes-Mateos *et al*., 2008*a*). However, rabbit population trends are not correlated with the fox abundance index in north-eastern Spain (Williams *et al*., 2007), and the potential positive effect of predator control on rabbit recovery in the Iberian Peninsula is, therefore, still controversial (Delibes-Mateos *et al*., 2009). In the case of rabbit translocations, experimental attempts to reduce predation after release have employed predator exclusion fences, electric fences, and the selective night shooting of foxes and feral dogs during the first days after release (Calvete *et al*., 1997; Calvete & Estrada, 2004; Cabezas *et al*., 2011). Although these methods have reduced the predation in the short term, the lack of a long-term effect and their high cost prevent their general use for rabbit translocations (Rouco *et al*., 2008; Cabezas *et al*., 2011). There is, moreover, an increasing public demand for non-lethal approaches for wildlife conflict reduction (Cowan, Reynolds & Gill, 2000; van Eeden *et al*., 2019).

One potential non-lethal approach that can be used to reduce predation is conditioned food aversion (CFA). CFA involves the avoidance of a certain food following a period of illness after consuming that food (Garcia, Hankins & Rusiniak, 1974). Animals associate the taste and characteristics of a particular food with negative symptoms caused by a toxic substance, mainly nausea, sickness or vomiting. CFA can be induced deliberately by adding a chemical substance to the food or prey desired to be protected from predation in order to produce rejection by the predator (Gustavson *et al*., 1974; Cowan *et al*., 2000; O'Donnell, Webb & Shine, 2010). Recent studies carried out with captive dogs *Canis familiaris* and Iberian wolves *Canis lupus signatus* have shown the possibility of creating aversion by adding an artificial odor cue during conditioning (Tobajas *et al*., 2019*a*; Tobajas *et al*., unpublished data), thus, creating an enhanced aversion to that odor rather than to the food itself (Tobajas *et al*., 2019*b*). This enables the predator to detect that a prey is noxious at a distance (Rusiniak *et al*., 1979), and makes it possible to employ this disruptive effect caused by the odor aversion to stop predation during predatory behavior (Tobajas *et al*., 2019*b*; Tobajas *et al*., unpublished data). As a model with which to improve translocations, we aimed to evaluate CFA plus an artificial odor cue as a tool to reduce rabbit predation by red foxes after translocations to areas in which the abundance of rabbit populations is low and needs to be reinforced in order to allow the establishment of endangered predators. We achieved this by inducing aversion to predators using rabbit meat baits containing levamisole plus vanilla odor. This was done to protect the zones into which rabbits would be released in order to reduce their predation during the first period, when they are more vulnerable. Our hypothesis is that the use of this technique will improve rabbit survival during translocations, and that this may, therefore, alter the population dynamics by increasing rabbit abundance in the treatment areas.

Materials and methods

Study area

The study was carried out in four zones with similar habitat characteristics in one locality (Picón, 4° 5'0" W, 39° 5' 0"

N) in Ciudad Real province (Central Spain) (Fig. 1). The study plots are distributed on private properties, and are occupied by a mixture of Mediterranean scrubland and sparse patches of holm oak *Quercus ilex subsp. rotundifolia*, with olive trees and cereal fields. The study area had a low rabbit abundance owing to the aforementioned diseases (with the greatest decline in the 1990s) and predation pressure. Long before the study took place, some rabbit translocations were carried out by the local hunting associations between 2001 and 2010 (involving ca. 500 rabbits) in an attempt to improve the rabbit population, but without any significant success. Predator control was not performed during the study period.

Experimental design

In order to evaluate the treatment effect (CFA plus odor cue) on rabbit predation (by the red fox and other predators) and rabbit population response, we performed a Before-After Control-Impact (BACI) experiment. During the first year of study, we performed the experiments simultaneously in four zones, which were initially defined and randomly assigned as two control and two treatment areas. During the second year, the treatment and control areas were interchanged in order to control the site effects. The design of BACI makes it possible to distinguish the treatment effects from background time effects shared by all areas and from background differences between control and treatment areas (Popescu *et al*., 2012). BACI approaches are analyzed using generalized linear mixed models (McDonald, Erickson & McDonald, 2000), in which a significant interaction between treatment area (control − treatment) × time (before − after) indicates an effect of the experimental treatment.

The experiment was performed in three phases: (1) preconditioning (only bait (rabbit meat), 5 weeks); (2) conditioning (bait + aversive agent (microencapsulated levamisole) + odor (vanilla essence) in treatment spots, only bait in control spots, 2 weeks) and (3) post-conditioning (bait + odor in treatment spots, only bait in control spots, 15 weeks) phases. We compared the pre- and post-conditioning bait intake of untreated baits (with neither an aversive agent nor an odor cue) by foxes and other predators between the control and treatment areas as a measure of CFA response. Levamisole hydrochloride is an imidazothiazole derivative that has been used as a broad-spectrum anthelmintic in different species, and has also been used in previous

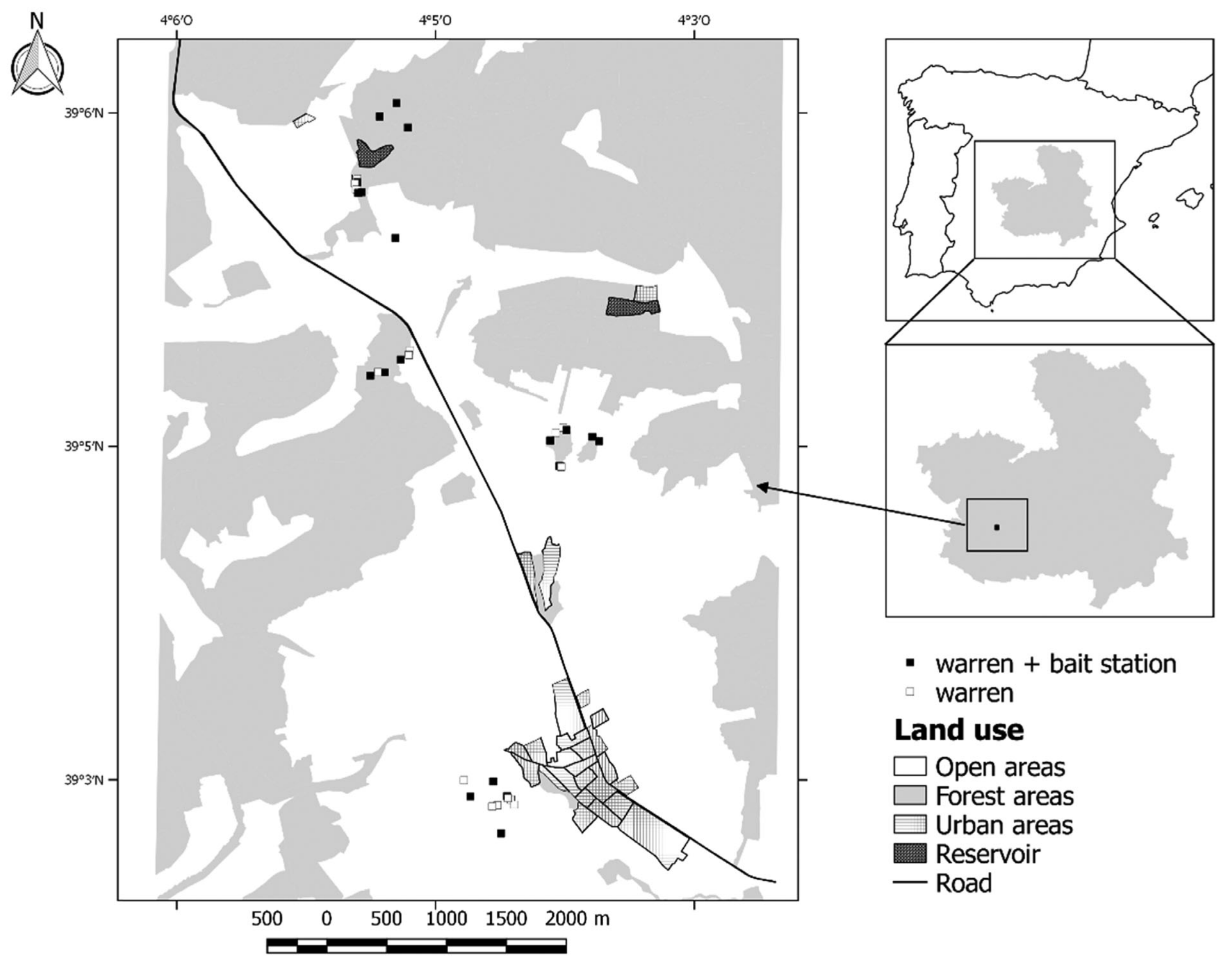

Figure 1 Locations of the warrens and bait stations in the study area in Castilla La Mancha (Spain).

conditioned food aversion studies on dogs, as it causes digestive symptoms (vomiting, nausea and/or diarrhea) without severe adverse health effects (Tobajas *et al*., 2019*b*, *c*).

Moreover, the treatment effect on predation was also studied with rabbits experimentally translocated in each of the study years (2016 and 2017) to artificial warrens (stones covered by soil). These artificial warrens were built for the previous rabbit translocations undertaken in the period 2001–2010 and had a low or no rabbit occupation. The conditioning phase started 1 week before the rabbit translocation in order to induce aversion in foxes and other predators before the rabbits were released, thus, improving their chances of survival. The evolution of the rabbit translocation and the differences between study plots were assessed through the use of rabbit abundance estimation and index of artificial warrens use (see below). Rabbit abundance was assessed by employing open N-mixture models for spatially replicated repeated count data (Royle, 2004; Dail & Madsen, 2011), obtained from camera-trap data (see Section 2.4). The use of artificial warrens was monitored using a relative warren use index (WUI) created from the observation of several indirect signs (i.e. scrapes, pellet counts) that make it possible to estimate rabbit population trends (Palomares, 2001; Delibes-Mateos *et al*., 2008*a*; Fernandez-de-Simon *et al*., 2011). The abundance activity of red foxes and other terrestrial predators on the study plots was estimated using a relative abundance index (RAI), which accounts for species independent records divided by the sampling effort obtained by the camera-traps (O'Brien, Kinnaird & Wibisono, 2003). We compared the pre- and post-release values of the relative abundance indices in order to assess the CFA treatment effect as a measure of the predator's response in relation to avoiding the prey (i.e. foxes not eating rabbits).

Finally, during the second year of the experiment, a sample of the translocated rabbits was tagged with VHF collars to estimate survival rates. We compared the survival rates between the control and treatment areas in order to assess the effect of CFA on rabbit survivorship.

Bait station monitoring

A total of 13-14 bait stations monitored by a camera-trap were placed near (1.5–2 m) the warrens into which the rabbits would be released: 7 bait stations on the treatment plots and 6 on the control plots during 2016, and 7 on each during 2017. Additionally, 14 bait stations without a camera-trap were employed during the conditioning period in 2017 so as to increase the probability of the predator species being conditioned. A bait station consisted of an infrared camera-trap (Spartan SR1-BK® HCO Outdoor Products, Norcross, Georgia, USA) situated in front of a wooden stake to which a piece of wild rabbit meat (around 200 g) and a 30 ml glass bottle with a diffusing wick containing vanilla essence were tied (see Supporting Information S1). During the conditioning phase (2 weeks), two gelatin capsules (17 mm long), each of which contained 175 mg of microencapsulated levamisole, were placed inside the meat on the treatment plots. The intended dose of levamisole was 70 mg/kg body weight based on previous studies with wild foxes (Massei, Lyon & Cowan, 2003; Nielsen *et al*., 2015). The bait stations were active 24 h/day during the 22 weeks of the study period and were visited approximately every 7 days for rebaiting, camera-trap maintenance and data download (see Data S1).

Rabbit translocation and radio-tracking

Two experimental translocations were carried out with adult wild rabbits in the autumn of 2016 and 2017. Wild rabbits (72 in 2016 and 76 in 2017) were released into 15–18 artificial warrens distributed in the four experimental zones. The rabbits were ferreted and caught with nets at the warren entrances on donor sites and were transported immediately after capture and released in the study area (see Data S2). In the first translocation (2016), 4 rabbits were released into each artificial warren (treatment = 11; control = 7), while during the second, (2017) 4–5 rabbits were released into each artificial warren (treatment = 8; control = 7). Rabbits from the same social group were released into the same warren or in nearby warrens of the same plot (see Data S2). After the rabbit translocation, all the entrances of the warrens on the treatment plots were sprayed each week with the same vanilla solution used at the bait stations. Before the experiment, we confirmed that the used vanilla essence did not have any effect on the rabbits' behavior, such as space avoidance or feeding behavior (see Data S3).

We randomly selected 68 (28 males and 40 females) of the 76 adult rabbits released in 2017 for survival monitoring during the post-conditioning phase (126 days). Each rabbit was weighed, ear-marked with a numbered metal tag (model #1005-3; National Band and Tag Company, Newport, KY, USA) and fitted with a VHF radio collar (22 g, BIOTRACK, Wareham UK). All the collars incorporated a mortality sensor, which generates a different pulse-rate after 4 h of inactivity. All the tagged rabbits were tracked daily during the whole post-conditioning phase (126 days) to determine whether they were dead or alive.

Rabbit and predator abundance

Repeated count data from camera-traps were used to estimate rabbit abundance and population trends using a dynamic N-mixture model, which is a robust design generalized form of N-mixture models for open populations (Royle, 2004; Dail & Madsen, 2011). In order to avoid duplicate counts of the same individual rabbit, we used the maximum number of individuals observed in the same independent event, which allowed us to obtain a minimum rabbit count each day on each site. We compared treatment and control using the *pcountOpen* function from the unmarked package (Fiske & Chandler, 2011) in R 3.5.1 (R Core Team, 2018), with the treatment, phase and the "treatment × phase" interaction as covariates to examine the effect of the treatment on rabbit population growth (see Data S4).

The RAI of red fox and other predators was calculated weekly by dividing the number of independent capture events of each species on each camera-trap site by the sampling effort (trap-nights) on that site and expressed as integer records per 100 trap nights (O'Brien *et al.*, 2003). Consecutive images of the same species within 30 min intervals were considered as the same event unless different individuals could be recognized (O'Brien *et al.*, 2003), whereas those separated by longer intervals were interpreted as independent events.

Rabbit warren use

A relative warren use index (WUI) was obtained in order to evaluate the change in use of release warrens by the rabbits. We recorded four indirect signs related to the rabbits' use of warrens (Palomares, 2001; Delibes-Mateos *et al.*, 2008*a*; Fernandez-de-Simon *et al.*, 2011): percentage of active entrances and numbers of pellets, rabbit scrapes and rabbit latrines within 2 m surrounding each warren. Each year, these signs were sampled five times during the experiment, before the rabbits were released (week 4), throughout the post-conditioning period (week 8, 13 and 18), and at the end of the experiment (week 22). We considered an entrance to be active when it showed signs of regular use, with fresh pellets and trampled runs (Parer & Wood, 1986). A latrine was defined as a group of at least 20 pellets within an area of 200×300 mm (Virgós *et al.*, 2003). The WUI was obtained as the first axis score from a Principal Component Analysis (PCA) of the four variables that were highly correlated.

Statistical analysis

We assessed whether levamisole plus the odor cue-induced CFA in the rabbit bait consumed by red fox and the other predators by performing a Generalized Linear Mixed Model (GLMM) with binomial error and logit link function. The effect of the experimental treatment on bait intake by red fox was analyzed by including treatment, phase, year, zone, bait intake by other predators (binomial) and the "treatment × phase" interaction as fixed factors. The bait station was included as a random factor. A similar model was run to analyze the experimental treatment effect on the bait intake by other predators, grouping all these intake events into a single category. Furthermore, we fitted a GLMM using the WUI as a response variable to test whether warren use by translocated rabbits was related to the following factors and covariates: treatment, phase, year, zone, fox RAI, other predators RAI and WUI value at the moment of rabbit release (indicating the degree of warren use before release), and the "treatment × phase" interaction. The warren was introduced as a random factor in the WUI model. We used a repeated measure analysis, including an autocorrelation structure, in order to take into account the fact that repeated measures were obtained at the same bait station and in the same warren (Mangiafico, 2016).

The GLMM models were compared using the Akaike Information Criteria (AIC) for model selection, during which a backward deletion stepwise procedure was employed. Covariates were examined for co-linearity using Pearson correlation coefficients, and co-linear variables ($r > 0.7$) were excluded from the model. According to the BACI design, a significant interaction between "treatment × phase" indicates that the dependent variable changes among phases that differ among experimental treatments. The statistical analyses were carried out using the nlme and rcompanion package with the R software version 3.5.1 (R Core Team, 2018).

We examined differences in the survival rate of the radio-collared rabbits between the treatment and control areas using Kaplan–Meier survival analyses with the survival package of the R software version 3.5.1 (R Core Team, 2018). We compared survival distributions over two time periods, the first 21 days after release, when the rabbits are more vulnerable (Calvete *et al.*, 1997; Letty *et al.*, 2002), and throughout the 126 days after release, which correspond to the whole post-conditioning period.

Results

Bait intake

We placed a total number of 584 baits during the 2 years of study (2016: 238, 40.75%; 2017: 346, 59.25%). The proportion of mean bait intake during the pre-conditioning phase was 0.60 (±0.055 SE) in the treatment areas and 0.66 (±0.063 SE) in the control areas, while during the post-conditioning phase it was 0.69 (±0.039 SE) and 0.94 (±0.021 SE), respectively. The principal bait consumers in the study area were the red fox, Egyptian mongoose *Herpestes ichneumon*, stone marten *Martes foina* and European badger *Meles meles* (Fig. 2, Data S5).

The model for red fox bait intake showed a significant effect of the interaction "treatment × phase" ($F_{1,339} = 11.52$, $P < 0.001$), with a decrease in the proportion of bait consumed by red foxes in the post-conditioning phase from 0.225 (±0.047 SE) to 0.007 (±0.007 SE) as regards to the treatment when compared to the control (from 0.246 (±0.058 SE) to 0.14 (±0.033 SE)) (Fig. 2). However, the model also showed a significant effect of the other predators ($F_{1,339} = 75.23$, $P < 0.001$), which increased the amount of bait intake in the post-conditioning phase from 0.363 (±0.054 SE) to 0.60 (±0.042 SE) as regards to the treatment (Fig. 2). The model for bait intake by red fox also showed differences according to zones ($F_{3,339} = 7.21$, $P < 0.001$) and year ($F_{1,339} = 16.57$, $P < 0.001$). No significant effect of the interaction "treatment × phase" was, however, found for the bait intake by other predators in the corresponding model ($F_{1,339} = 3.66$, $P > 0.05$), which was influenced only by the intake of the red fox ($F_{1,339} = 64.37$, $P < 0.001$) as the main competitor as regards bait intake in the study area.

Rabbit abundance response

We found differences in rabbit population dynamics between the treatment and control areas after the rabbit translocation (Fig. 3). The rabbit abundance on the treatment plots increased from 0.52 (±0.14 SE) rabbits/site at week 6 to 1.6 (±0.42 SE) rabbits/site at week 22. However, the increase in

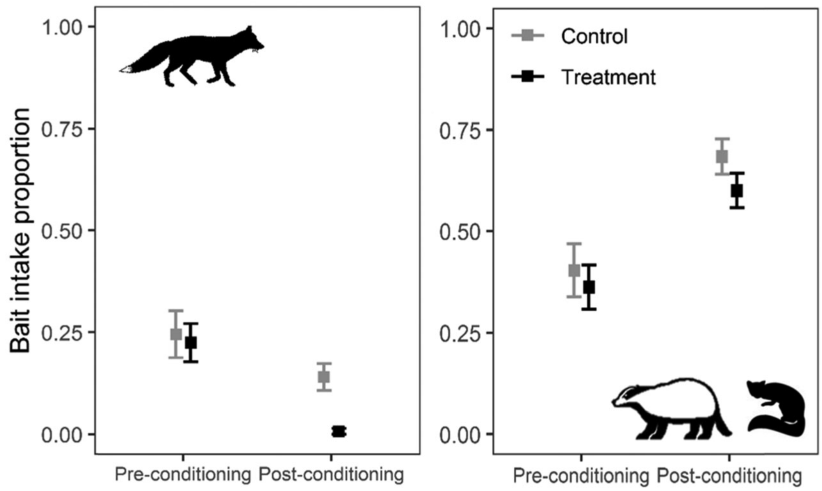

Figure 2 Proportion of bait (±SE) consumed by red fox and other predators during the two experimental phases (Pre-conditioning; Post-conditioning) and treatment areas.

rabbit abundance on the control plots was very slight: from 0.33 (±0.10 SE) rabbits/site at week 6 to 0.44 (±0.11 SE) rabbits/site at week 22 (Fig. 3). The best-fitted model (ΔAIC < 2) for rabbit population growth was constant (Data S6), with an interaction between treatment and phase, showing a positive effect of the treatment on rabbit population growth when compared to the control areas (Fig. 3, Data S7). The goodness of fit of the model showed an adequate fit to the data (Data S8).

WUI explained 69% of the variance of the warren use variables. As occurred with rabbit abundance, the use of warrens by rabbits (WUI) increased more on the treatment plots than on the control plots (Fig. 4). The model showed a "treatment × phase" interaction ($F_{1,147}$ = 39.99, P < 0.001), indicating that the use of warrens after the translocation increased on the treatment plots when compared with the control plots (Fig. 4). The model showed that zone ($F_{3,147}$ = 15.01, P < 0.001), year ($F_{1,147}$ = 6.39, P < 0.013) and the initial WUI ($F_{1,147}$ = 63.59, P < 0.001) had significant effects on the WUI response, showing a negative effect of the initial WUI on the rabbit response after translocation.

Rabbit survival

Although the trend toward rabbit survival was higher in the treatment zone than in the control zone (Fig. 5), differences between treatments were significant neither in the first 21 days post-release (X^2 = 2.2, d.f. = 1, P = 0.1) nor throughout the entire study period (X^2 = 0.6, d.f. = 1, P = 0.45) (Fig. 5).

Discussion

Our study provides one of the first pieces of evidence that CFA may be a useful management tool by which to reduce fox predation and may increase the success of prey translocations (O'Donnell *et al.*, 2010). The combination of levamisole plus vanilla odor causes red foxes to experience an aversion to untreated rabbit meat in the presence of vanilla odor. The treatment additionally appears to reduce the risk of rabbit predation after their translocation, thus, improving their short-term survival (although not significantly) and consequently improving the translocation success when compared with untreated zones. The observed decrease in the bait intake could be attributed to the CFA induced in those foxes that consumed the rabbit baits with vanilla odor, and subsequent changes in the foxes' use of space, since they may keep to their own territory and use the areas with the odor cue to a lesser extent (Tobajas *et al.*, 2020). However, the data showed no effect of the treatment on the bait intake by other predators (mainly mustelids: the stone marten and the European badger), thus, showing a trend towards bait intake compensation by scavenging. Compensatory predation has been reported in other CFA studies of red foxes (Tobajas *et al.*, 2020) and also in predator control studies (Holt *et al.*, 2008; Beggs *et al.*, 2019*a*), but in our case these species are mainly scavengers and rarely prey on adult rabbits. However, compensatory predation could be a limitation as regards employing the CFA technique in situations in which there are more than one predator species. Moreover, a scenario in which there is a high abundance and diversity of predators and scavengers could require a greater effort to conditioning the target predators owing to competition for baits. However, the total bait intake during the post-conditioning phase was lower in the treatment zones than in the control zones, thus, indicating the importance of the red fox as a rabbit predator and scavenger in Mediterranean habitats (Diaz-Ruiz *et al.*, 2013; Fernandez-de-Simon *et al.*, 2015). The red fox has been described as the main predator during rabbit translocations in the Iberian Peninsula (Calvete *et al.*, 1997; Moreno *et al.*, 2004), predating up to 65–72% of the translocated rabbits in the first few weeks after release (Calvete *et al.*, 1997; Letty *et al.*, 2002; Calvete & Estrada, 2004).

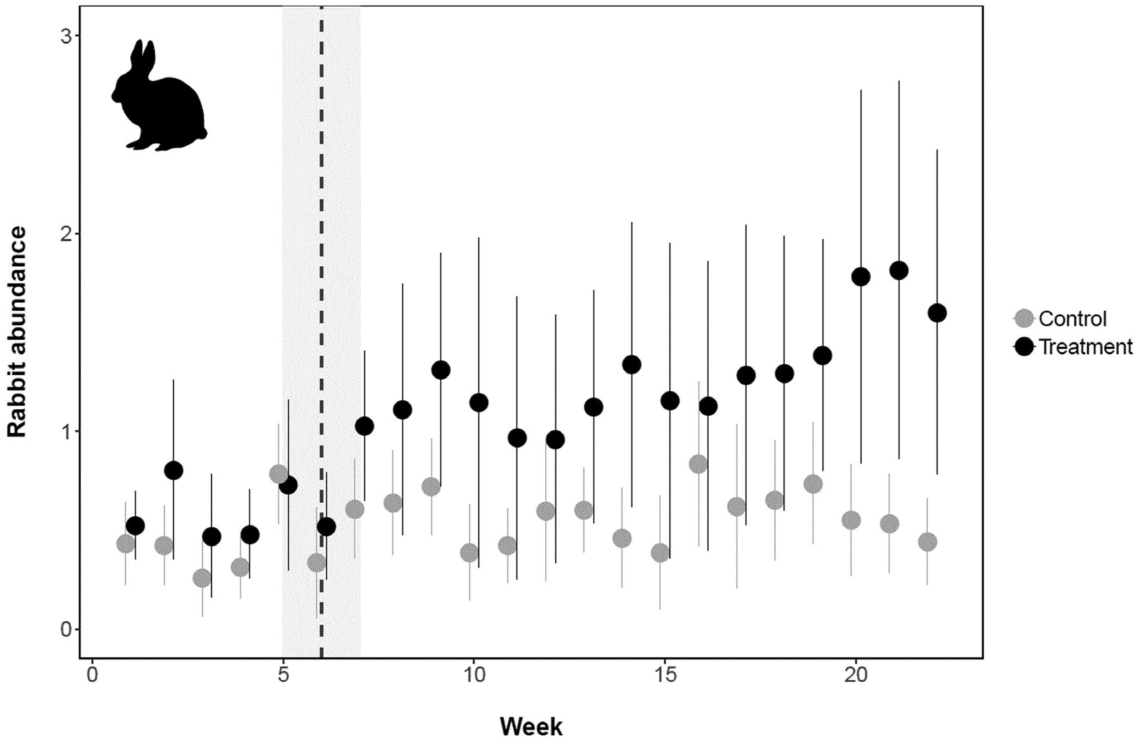

Figure 3 Weekly rabbit abundance (mean and 90% CI) obtained from camera-trap data throughout the study period in the treatment and control areas using N-mixture models. The shaded area represents the conditioning period, while the dashed line represents the date of rabbit translocation.

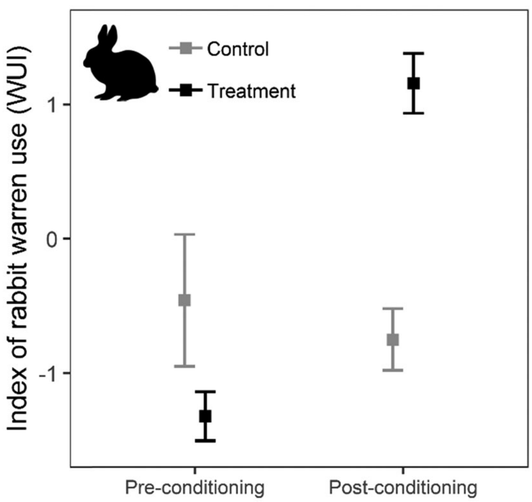

Figure 4 Mean Index of rabbit warren use (WUI) (±SE) during the two experimental phases (Pre-conditioning; Post-conditioning) in the treatment and control areas.

The experimental treatment improved rabbit abundance and WUI. The rabbit abundance model showed the positive effect of the treatment and rabbit translocation when compared to the control. Rabbit survival improved in the short term after release in the treatment zones when compared with the control zones (although not significantly), and rabbit population growth differed among zones, with a higher increase in rabbit abundance in the treatment than in the control zones (Fig. 3). The rabbit abundance in the study area was probably in a predator-pit situation (Trout & Tittensor, 1989; Banks, 2000), which prevents the recovery of rabbit populations (Delibes-Mateos *et al*., 2008*a*; Norbury & Jones, 2015). In this situation, the conditioning of red foxes during rabbit translocation allows the rabbit population in the treatment zones to overcome this situation of low rabbit abundance in the short term. Moreover, the sudden increase in numbers of recently translocated rabbits may attract non-conditioned predators to the release areas (Calvete & Estrada, 2004), which could entail a negative effect on the population growth in the long term.

The CFA treatment similarly had a positive effect on the WUI after the translocation. This could be owing to an increase in rabbit survival after the translocation, thus, allowing the establishment of a greater number of rabbits in the release warrens. Moreover, a lower activity of red fox would allow the rabbits to settle faster (Moreno *et al*., 2004; Rouco *et al*., 2008). The WUI model also showed the negative effect of the initial warren use on establishment and subsequent warren use by the rabbits, which indicates that releasing rabbits into warrens that were previously occupied is not recommended (Moreno *et al*., 2004; Ruiz-Aizpurua & Tortosa, 2018) because the translocated rabbits may be expelled by resident rabbits (Monclús, Saavedra & de Miguel, 2014; Ruiz-Aizpurua & Tortosa, 2018). The WUI model also

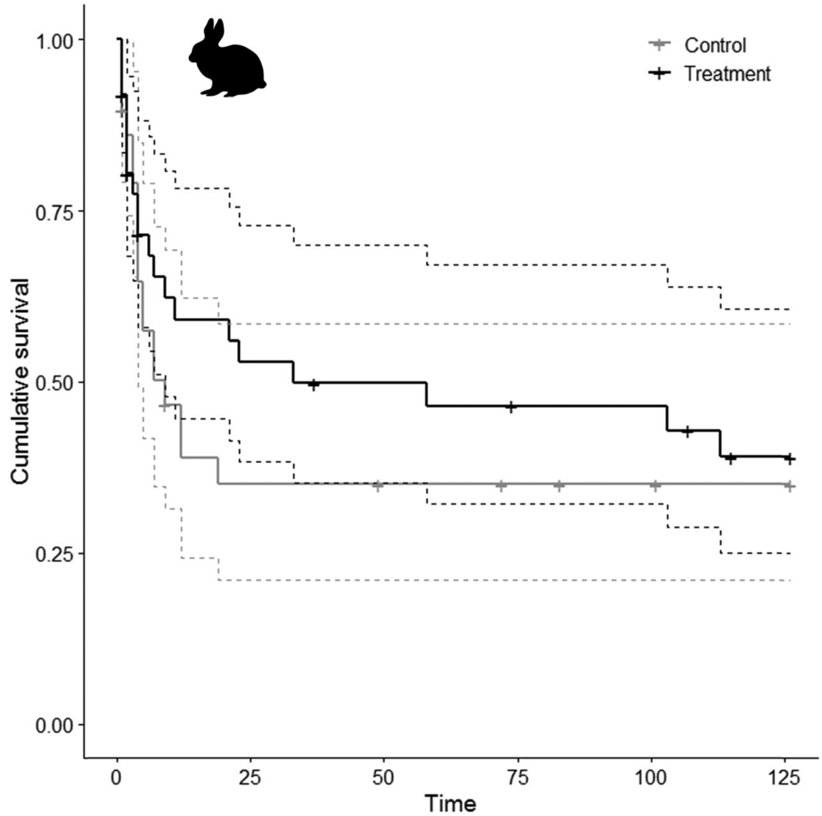

Figure 5 Distribution of survival of radio-collared rabbits in both treatment areas over the 126-day study period. Dashed lines represent the 95% confidence interval.

showed significant differences between years, with the warrens being less occupied during the post-conditioning in the second year. This may be for two reasons. Firstly, in the second year, some rabbits were translocated to warrens in which other rabbits had been translocated and established in the previous year (Ruiz-Aizpurua & Tortosa, 2018). Rabbit translocations are not, therefore, recommended in consecutive years in the same areas (Cabezas & Moreno, 2007; Ruiz-Aizpurua & Tortosa, 2018). This procedure has, however, been recommended for other similar ecosystem engineer species such as ground squirrels (Swaisgood *et al*., 2019). Secondly, the study area suffered from a severe drought during the fall of 2017, with a water deficit of 51.2 mm, in contrast to the excess of water of 79.4 mm in 2016 (SIAR, 2019). This could have forced some of the rabbits to search for optimal areas with more food resources (McNamara & Houston, 1987; Moreno *et al*., 2004), thus, leading to a lower establishment and reproduction of translocated rabbits in the release warrens when compared to the first year (Calvete *et al*., 1997). The post-release dispersal from the release point reduces the chances of establishing a unified breeding population and has been shown to be a key factor in the success of animal translocations (Armstrong & Seddon, 2008; Berger-Tal *et al*., 2019). Furthermore, climatic factors have been shown to determine the breeding success of wild rabbits (Martins *et al*., 2003; Cabezas & Moreno, 2007).

The rabbit survival studied in 2017 was higher (although not significantly) during the first 21 days after release in the treatment than in the control areas, which could facilitate rabbit establishment in treatment areas (Calvete *et al*., 1997; Letty *et al*., 2002). However, the rabbit survival in treatment areas decreased progressively after the 21 days, data that could be related to the dry weather and the importance of habitat quality (food) and diseases in the long-term population response to translocation observed by other authors (Cabezas & Moreno, 2007; Cabezas *et al*., 2011; Batson *et al*., 2015; Berger-Tal *et al*., 2019). The lack of statistical differences was likely related to the small sample size, particularly when considering the direct mortality owing to the stress of capture and release. This caused that the effective sample size to observe the treatment effect in long-term rabbit survival was reduced.

When some of the factors limiting animal population growth (food, shelter, disease and predation) are not improved beforehand, the translocations in themselves are ineffective (Short *et al*., 1992; Fischer & Lindenmayer, 2000; Batson *et al*., 2015; Berger-Tal *et al*., 2019). In this respect, the use of CFA plus an odor cue during rabbit translocations to artificial warrens could contribute to reducing predation by main predators and improving establishment during the first weeks after translocation, thus, increasing rabbit survival and allowing them to overcome the predator-pit effect (Banks, 2000; Moreno *et al*., 2004). The recovery of low-density rabbit populations in predator-pit situations would require combining several tools, such as translocations with CFA techniques, improving shelter (artificial warrens), food supplementation or habitat management. Translocations would, thus, enable rabbit densities to reach a point beyond which the predator-pit is overcome (Banks, 2000; Cabezas & Moreno, 2007). In other contexts with other species it is, therefore, necessary to assess the need for additional measures to reduce predation and improve the success of animal translocation (Baston *et al*., 2015; Moseby, Carthey & Schroeder, 2015).

Several methods, such as predator exclusion fences and predator control, have been used to reduce predation during translocations (Short *et al*., 1992; Baston *et al*., 2015; Moseby *et al*., 2015). Although these methods could reduce post-release mortality (Armstrong *et al*., 2006; Moseby *et al*., 2015), numerous studies have shown translocation failures owing to predation, although they included measures to control this impact (Short *et al*., 1992; Moseby *et al*., 2011; Berger-Tal *et al*., 2019). In those cases in which predation has been effectively reduced, it has been through the systematic use of poison and trapping over time and on a wide spatial scale (Short *et al*., 1992; Armstrong *et al*., 2006). The creation of fences for the exclusion of predators, and the use of poison or lethal control on a large scale and in a systematic manner, have high economic and ecological costs which prevent their extensive use (Short *et al*., 1992; Rouco *et al*., 2008; Lennox *et al*., 2018), signifying the need to explore other approaches (Moseby *et al*., 2015; Swaisgood *et al*., 2019).

CFA appears to be a more appropriate method than other traditional methods employed to reduce predation of the key predators, such as trapping or poisoning, which aim only to control the carnivore population numerically. CFA could be more effective for territorial predators such as foxes than lethal control (Newsome, Crowther & Dickman, 2014; Porteus Reynolds & McAllister, 2019; Tobajas *et al*., 2020) because, when using CFA, the predators maintain their territories and expel other conspecific predators, while conditioned predators avoid killing the prey toward which they are conditioned (Nicolaus, 1987; Cowan *et al*., 2000; Tobajas *et al*., 2020). The density-dependent compensation caused by the replacement of extracted predators by immigrants is simultaneously avoided (Newsome *et al*., 2014; Beggs *et al*., 2019*b*). Moreover, CFA improves the cost-efficiency of predator management in animal translocations, which is an important issue in conservation programs (Canessa *et al*., 2014; Berger-Tal *et al*., 2019), and may help discourage the illegal use of poison to kill predators (Mateo-Tomás *et al*., 2012). However, the application of CFA is difficult to implement on large scales, and it could, therefore, be implemented as a tool on local scales and focused on translocation zones and periods, without ignoring the possibility of maintaining it in these zones over time. Although its effect is very specific at the individual level, it may be more effective than traditional predator's management measures at the population level. In this respect, other studies in which predators are trapped in order to control their population have also shown a limited effect over time (Newsome *et al*., 2014; Porteus *et al*., 2019). Our study was limited to the duration of 4 months after release, signifying that it is necessary to study the possible effect of long-term application and at landscape scale.

Based on animal welfare and ethical principles, current predator management would be improved by using non-lethal effective methods such as CFA (Baker, Singleton & Smith, 2007), and could alleviate the current conflict between stakeholders that exists in many countries where predator control is employed (van Eeden *et al*., 2019). In this respect, more studies using the CFA plus odor cue are necessary with different predators and in different contexts, such as livestock predation, wildlife management or biodiversity conservation (Cowan *et al*., 2000; Nielsen *et al*., 2015; Tobajas *et al*., 2020), and with new potential chemical compounds for different species (Tobajas *et al*., 2019c).

The present study shows that the use of CFA plus an odor cue is a promising tool by which to reduce the adverse impact of fox predation during post-release acclimation, without the risks of the predator control methods affecting non-target and endangered predator species. The approach shown here could be used to improve future translocations of the European rabbit, which has recently been declared endangered by the IUCN (Villafuerte & Delibes-Mateos, 2019). The European rabbit needs to increase its populations in Mediterranean woodland in order to ensure its population viability and help the conservation of the Iberian lynx and imperial eagle (Moreno *et al*., 2004; Delibes-Mateos *et al*., 2007). The CFA technique could also be expanded as a wildlife management tool for other species and conservancy challenges (Baker *et al*., 2007; O'Donnell *et al*., 2010; Tobajas *et al*., 2020).

Acknowledgements

This study has been possible as a result of the CGL2013–40975-R and CGL2013-43197-R projects, from the I+D+I National Plan funded by the Spanish Ministry of Economy and Competitiveness. Jorge Tobajas is the recipient of an FPI PhD scholarship (BES-2014-068987) funded by the Spanish Ministry of Economy and Competitiveness. We would like to thank the members of the Picón hunting association for their help during the experiment. Thanks also go to José Manuel Usero, Jose Luis Garrido and Vicente Garrido (RIP) for their help capturing the rabbits. Thanks to Sally Newton for the English edition and the anonymous referees for improving the manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

References

Armstrong, D.P., Raeburn, E.H., Lewis, R.M. & Ravine, D.O.N. (2006). Estimating the viability of a reintroduced New Zealand robin population as a function of predator control. *J. Wildl. Manage.* **70**, 1020–1027.

Armstrong, D.P. & Seddon, P.J. (2008). Directions in reintroduction biology. *Trends Ecol. Evol.* **23**, 20–25. https://doi.org/10.1016/j.tree.2007.10.003

Baker, S.E., Singleton, G. & Smith, R. (2007). The nature of the beast: using biological processes in vertebrate pest management. In *Key topics in conservation biology*: 173–185. Macdonald, D.W. & Service, K. (Eds). Oxford, UK: Blackwell.

Banks, P.B. (2000). Can foxes regulate rabbit populations? *J. Wildl. Manage.* **64**, 401–406. https://doi.org/10.2307/3803238

Batson, W.G., Gordon, I.J., Fletcher, D.B. & Manning, A.D. (2015). Translocation tactics: a framework to support the IUCN Guidelines for wildlife translocations and improve the quality of applied methods. *J. Appl. Ecol.* **52**, 1598–1607. https://doi.org/10.1111/1365-2664.12498

Beggs, R., Pierson, J., Tulloch, A.I., Blanchard, W., Westgate, M.J. & Lindenmayer, D. (2019*a*). An experimental test of a compensatory nest predation model following lethal control of an overabundant native species. *Biol. Conserv.* **231**, 122–132. https://doi.org/10.1016/j.biocon.2019.01.003

Beggs, R., Tulloch, A.I., Pierson, J., Blanchard, W., Crane, M. & Lindenmayer, D. (2019*b*). Patch-scale culls of an overabundant bird defeated by immediate recolonization. *Ecol. Appl.* **29**, e01846. https://doi.org/10.1002/eap.1846

Berger-Tal, O., Blumstein, D.T. & Swaisgood, R.R. (2019). Conservation translocations: a review of common difficulties and promising directions. *Anim. Conserv.* **23**, 121–131. https://doi.org/10.1111/acv.12534

Cabezas, S., Calvete, C. & Moreno, S. (2011). Survival of translocated wild rabbits: importance of habitat, physiological and immune condition. *Anim. Conserv.* **14**, 665–675. https://doi.org/10.1111/j.1469-1795.2011.00472.x

Cabezas, S. & Moreno, S. (2007). An experimental study of translocation success and habitat improvement in wild rabbits. *Anim. Conserv.* **10**, 340–348. https://doi.org/10.1111/j.1469-1795.2007.00119.x

Calvete, C. & Estrada, R. (2004). Short-term survival and dispersal of translocated European wild rabbits. Improving the release protocol. *Biol. Conserv.* **120**, 507–516. https://doi.org/10.1016/j.biocon.2004.03.023

Calvete, C., Villafuerte, R., Lucientes, J. & Osacar, J.J. (1997). Effectiveness of traditional wild rabbit restocking in Spain. *J. Zool.* **241**, 271–277. https://doi.org/10.1111/j.1469-7998.1997.tb01957.x

Canessa, S., Hunter, D., McFadden, M., Marantelli, G. & McCarthy, M.A. (2014). Optimal release strategies for cost-effective reintroductions. *J. Appl. Ecol.* **51**, 1107–1115. https://doi.org/10.1111/1365-2664.12253

Carro, F., Ortega, M. & Soriguer, R.C. (2019). Is restocking a useful tool for increasing rabbit densities? *Glob. Ecol. Conserv.* **17**, e00560. https://doi.org/10.1016/j.gecco.2019.e00560

Cowan, D.P., Reynolds, J.C. & Gill, E.L. (2000). Reducing predation through conditioned taste aversion. In *Behaviour and conservation*: 281–299. Gosling, L.M. & Sutherland, W.J. (Eds). New York, NY: Cambridge University Press.

Dail, D. & Madsen, L. (2011). Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* **67**, 577–587. https://doi.org/10.1111/j.1541-0420.2010.01465.x

Delibes-Mateos, M., Ferreras, P. & Villafuerte, R. (2008*a*). Rabbit populations and game management: the situation after 15 years of rabbit haemorrhagic disease in central-southern Spain. *Biodivers. Conserv.* **17**, 559–574. https://doi.org/10.1007/s10531-007-9272-5

Delibes-Mateos, M., Ramírez, E., Ferreras, P. & Villafuerte, R. (2008*b*). Translocations as a risk for the conservation of European wild rabbit *Oryctolagus cuniculus* lineages. *Oryx* **42**, 259–264. https://doi.org/10.1017/s0030605308006984

Delibes-Mateos, M., Ferreras, P. & Villafuerte, R. (2009). European rabbit population trends and associated factors: a review of the situation in the Iberian Peninsula. *Mammal Rev.* **39**, 124–140. https://doi.org/10.1111/j.1365-2907.2009.00140.x.

Delibes-Mateos, M., Redpath, S.M., Angulo, E., Ferreras, P. & Villafuerte, R. (2007). Rabbits as a keystone species in southern Europe. *Biol. Conserv.* **137**, 149–156. https://doi.org/10.1016/j.biocon.2007.01.024

Díaz-Ruiz, F., Delibes-Mateos, M., García-Moreno, J.L., López-Martín, J.M., Ferreira, C. & Ferreras, P. (2013). Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula. *Mammal Rev.* **43**, 59–70. https://doi.org/10.1111/j.1365-2907.2011.00206.x

Fernandez-de-Simon, J., Díaz-Ruiz, F., Cirilli, F., Tortosa, F.S., Villafuerte, R., Delibes-Mateos, M. & Ferreras, P. (2011). Towards a standardized index of European rabbit abundance in Iberian Mediterranean habitats. *Eur. J. Wildl. Res.* **57**, 1091–1100. https://doi.org/10.1007/s10344-011-0524-z

Fernandez-de-Simon, J., Díaz-Ruiz, F., Rodríguez-de la Cruz, M., Delibes-Mateos, M., Villafuerte, R. & Ferreras, P. (2015). Can widespread generalist predators affect keystone prey? A case study with red foxes and European rabbits in their native range. *Popul. Ecol.* **57**, 591–599. https://doi.org/10.1007/s10144-015-0510-5

Ferreira, C. & Delibes-Mateos, M. (2010). Wild rabbit management in the Iberian Peninsula: state of the art and future perspectives for Iberian lynx conservation. *Wildl. Biol. Pract.* **6**, 48–66. https://doi.org/10.2461/wbp.lynx.4

Fischer, J. & Lindenmayer, D.B. (2000). An assessment of the published results of animal relocations. *Biol. Conserv.* **96**, 1–11. https://doi.org/10.1016/S0006-3207(00)00048-3

Fiske, I.J. & Chandler, R.B. (2011). Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* **43**, 1–23. https://doi.org/10.18637/jss.v043.i10.

Garcia, J., Hankins, W.G. & Rusiniak, K. (1974). Behavioral regulation of the milieu interne in man and rat. *Science* **185**, 824–831. https://doi.org/10.1126/science.185.4154.824

Gaston, K.J. (2010). Valuing common species. *Science* **327**, 154. https://doi.org/10.1126/science.1182818

Gustavson, C.R., Garcia, J., Hankins, W.G. & Rusiniak, K.W. (1974). Coyote predation control by aversive conditioning. *Science* **184**, 581–583. https://doi.org/10.1126/science.184.4136.581

Holt, A.R., Davies, Z.G., Tyler, C. & Staddon, S. (2008). Meta-analysis of the effects of predation on animal prey abundance: evidence from UK vertebrates. *PLoS One* **3**, e2400. https://doi.org/10.1371/journal.pone.0002400

IUCN/SSC. (2013). *Guidelines for reintroductions and other conservation translocations. Version 1.0*. Gland, Switzerland: IUCN Species Survival Commission, viiii + 57 pp.

Lennox, R.J., Gallagher, A.J., Ritchie, E.G. & Cooke, S.J. (2018). Evaluating the efficacy of predator removal in a conflict-prone world. *Biol. Conserv.* **224**, 277–289. https://doi.org/10.1016/j.biocon.2018.05.003

Letty, J., Aubineau, J., Marchandeau, S. & Clobert, J. (2003). Effect of translocation on survival in wild rabbit (*Oryctolagus cuniculus*). *Mamm. Biol.* **68**, 250–255. https://doi.org/10.1078/1616-5047-00092

Letty, J., Marchadeau, S., Reitz, F., Clobert, J. & Sarrazin, F. (2002). Survival and movements of translocated wild rabbits (*Oryctolagus cuniculus*). *Game Wildl. Sci.* **19**, 1–23.

Mangiafico, S. S. (2016). *Summary and analysis of extension program evaluation in R, version 1.15.0*. New Brunswick, NJ: Rutgers Cooperative Extension.

Martins, H., Barbosa, H., Hodgson, M., Borralho, R. & Rego, F. (2003). Effect of vegetation type and environmental factors on European wild rabbit *Oryctolagus cuniculus* counts in a southern Portuguese Montado. *Acta Theriol.* **48**, 385–398. https://doi.org/10.1007/bf03194177

Massei, G., Lyon, A.J. & Cowan, D.P. (2003). Levamisol can induce conditioned taste aversion in foxes. *Wildl. Res.* **30**, 633–637. https://doi.org/10.1071/wr03003

Mateo-Tomás, P., Olea, P.P., Sánchez-Barbudo, I.S. & Mateo, R. (2012). Alleviating human-wildlife conflicts: identifying the causes and mapping the risk of illegal poisoning of wild fauna. *J. Appl. Ecol.* **49**, 376–385. https://doi.org/10.1111/j.1365-2664.2012.02119.x

McDonald, T.L., Erickson, W.P. & McDonald, L.L. (2000). Analysis of count data from before-after control-impact studies. *J. Agr. Biol. Envir. Stat.* **5**, 262–279. https://doi.org/10.2307/1400453

McNamara, J.A. & Houston, A.I. (1987). Starvation and predation as factors limiting population size. *Ecology* **68**, 1515–1519. https://doi.org/10.2307/1939235

Monclús, R., Saavedra, I. & de Miguel, J. (2014). Context-dependent responses to neighbours and strangers in wild European rabbits (*Oryctolagus cuniculus*). *Behav. Proc.* **106**, 17–21. https://doi.org/10.1016/j.beproc.2014.04.004

Moreno, S. & Villafuerte, R. (1995). Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park. *Spain. Biol. Conserv.* **73**, 81–85. https://doi.org/10.1016/0006-3207(95)90069-1

Moreno, S., Villafuerte, R., Cabezas, S. & Lombardi, L. (2004). Wild rabbit restocking for predator conservation in Spain. *Biol. Conserv.* **118**, 183–193. https://doi.org/10.1016/j.biocon.2003.07.020

Moseby, K., Carthey, A. & Schroeder, T. (2015). The influence of predators and prey naivety on reintroduction success: current and future directions. In *Advances in reintroduction biology of Australian and New Zealand fauna*: 29–42. Armstrong, D., Hayward, M., Moro, D. & Seddon, P. (Eds.). Melbourne: Csiro Publishing. https://doi.org/10.1071/9781486303021

Moseby, K.E., Read, J.L., Paton, D.C., Copley, P., Hill, B.M. & Crisp, H.A. (2011). Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biol. Conserv.* **144**, 2863–2872. https://doi.org/10.1016/j.biocon.2011.08.003

Newsome, T.M., Crowther, M.S. & Dickman, C.R. (2014). Rapid recolonisation by the European red fox: how effective are uncoordinated and isolated control programs? *Eur. J. Wildl. Res.* **60**, 749–757. https://doi.org/10.1007/s10344-014-0844-x

Nicolaus, L.K. (1987). Conditioned aversions in a guild of egg predators: implications for aposematism and prey defense mimicry. *Am. Midl. Nat.* **117**, 405–419. https://doi.org/10.2307/2425983

Nielsen, S., Travaini, A., Vassallo, A.I., Procopio, D. & Zapata, S.C. (2015). Conditioned taste aversion in the grey fox (*Pseudalopex griseus*), in Southern Argentine Patagonia. *Appl. Anim. Behav. Sci.* **163**, 167–174. https://doi.org/10.1016/j.applanim.2014.12.006

Norbury, G. & Jones, C. (2015). Pests controlling pests: does predator control lead to greater European rabbit abundance in Australasia? *Mammal Rev.* **45**, 79–87. https://doi.org/10.1111/mam.12034

O'Brien, T.G., Kinnaird, M.F. & Wibisono, H.T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Anim. Conserv.* **6**, 131–139. https://doi.org/10.1017/s1367943003003172

O'Donnell, S., Webb, J.K. & Shine, R. (2010). Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. *J. Appl. Ecol.* **47**, 558–565. https://doi.org/10.1111/j.1365-2664.2010.01802.x

Palomares, F. (2001). Comparison of three methods to estimate rabbit abundance in a Mediterranean environment.

Wildl. Soc. Bull. **29**, 578–585. https://doi.org/10.2307/3784183

Parer, I. & Wood, D.H. (1986). Further observations of the use of warren entrances as an Index of the number of rabbits, *Oryctolagus cuniculus*. *Wildl. Res.* **13**, 331–332. https://doi.org/10.1071/wr9860331

Popescu, V.D., De Valpine, P., Tempel, D. & Peery, M.Z. (2012). Estimating population impacts via dynamic occupancy analysis of Before-After Control–Impact studies. *Ecol. Appl.* **22**, 1389–1404. https://doi.org/10.1890/11-1669.1

Porteus, T.A., Reynolds, J.C. & McAllister, M.K. (2019). Population dynamics of foxes during restricted-area culling in Britain: advancing understanding through state-space modelling of culling records. *PLoS One* **14**, e0225201. https://doi.org/10.1371/journal.pone.0225201

R Core Team. (2018). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Real, R., Barbosa, A.M., Rodríguez, A., García, F.J., Vargas, J.M., Palomo, L.J. & Delibes, M. (2009). Conservation biogeography of ecologically interacting species: the case of the Iberian lynx and the European rabbit. *Divers. Distrib.* **15**, 390–400. https://doi.org/10.1111/j.1472-4642.2008.00546.x

Reynolds, J.C. & Tapper, S.C. (1996). Control of mammalian predators in game management and conservation. *Mammal Rev.* **26**, 127–155. https://doi.org/10.1111/j.1365-2907.1996.tb00150.x

Rouco, C., Ferreras, P., Castro, F. & Villafuerte, R. (2008). The effect of exclusion of terrestrial predators on short-term survival of translocated European wild rabbits. *Wildl. Res.* **35**, 625–632. https://doi.org/10.1071/wr07151

Royle, J.A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics* **60**, 108–115. https://doi.org/10.1111/j.0006-341x.2004.00142.x

Ruiz-Aizpurua, L. & Tortosa, F.S. (2018). When more is less: the negative effect of European rabbit release upon local warren occupancy. *Acta. Ethol.* **21**, 101–107. https://doi.org/10.1007/s10211-018-0286-7

Rusiniak, K.W., Hankins, W.G., Garcia, J. & Brett, L.P. (1979). Flavor–illness aversions: potentiation of odor by taste in rats. *Behav. Neural Biol.* **25**, 1–17. https://doi.org/10.1016/s0163-1047(79)90688-5

Seddon, P.J.,Strauss, W.M. & Innes, J. (2012). Animal translocations: what are they and why do we do them? In *Reintroduction biology: integrating science and management*: 1–32. Ewen, J.G., Armstrong, D.P., Parker, K.A. & Seddon, P.J. (Eds). Oxford, UK: Blackwell Publishing Ltd.

Short, J., Bradshaw, S.D., Giles, J., Prince, R.I.T. & Wilson, G.R. (1992). Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia- a review. *Biol. Conserv.* **62**, 189–204.

SIAR. (2019). *Servicio Integral de Asesoramiento al Regante de Castilla-la-Mancha*. http://crea.uclm.es/siar/datmeteo/. Consulted in March 14, 2019.

Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P. & Newsome, A.E. (1998). Predicting effects of predation on conservation of endangered prey. *Conserv. Biol.* **12**, 564–575. https://doi.org/10.1111/j.1523-1739.1998.97030.x

Swaisgood, R.R., Montagne, J.P., Lenihan, C.M., Wisinski, C.L., Nordstrom, L.A. & Shier, D.M. (2019). Capturing pests and releasing ecosystem engineers: translocation of common but diminished species to re-establish ecological roles. *Anim. Conserv.* **22**, 600–610. https://doi.org/10.1111/acv.12509

Taylor, G., Canessa, S., Clarke, R.H., Ingwersen, D., Armstrong, D.P., Seddon, P.J. & Ewen, J.G. (2017). Is reintroduction biology an effective applied science? *Trends Ecol. Evol.* **32**, 873. https://doi.org/10.1016/j.tree.2017.08.002

Tobajas, J., Descalzo, E., Mateo, R. & Ferreras, P. (2020). Reducing nest predation of ground-nesting birds through conditioned food aversion. *Biol. Conserv.* **242**, 108405. https://doi.org/10.1016/j.biocon.2020.108405

Tobajas, J., Gómez-Ramírez, P., Ferreras, P., García-Fernández, A.J. & Mateo, R. (2019*a*). Conditioned food aversion in domestic dogs induced by thiram. *Pest Manage. Sci.* **76**, 568–574. https://doi.org/10.1002/ps.5548

Tobajas, J., Gómez-Ramírez, P., María-Mojica, P.M., Navas, I., García-Fernández, A.J., Ferreras, P. & Mateo, R. (2019*b*). Conditioned taste aversion mediated by odour cue and microencapsulated levamisole to avoid predation by canids. *Eur. J. Wildl. Res.* **65**, 35. https://doi.org/10.1007/s10344-019-1271-9

Tobajas, J., Gómez-Ramírez, P., María-Mojica, P.M., Navas, I., García-Fernández, A.J., Ferreras, P. & Mateo, R. (2019*c*). Selection of new chemicals to be used in conditioned aversion for non-lethal predation control. *Behav. Proc.* **166**, 103905. https://doi.org/10.1016/j.beproc.2019.103905

Trout, R.C. & Tittensor, A.M. (1989). Can predators regulate wild rabbit *Oryctolagus cuniculus* population density in England and Wales? *Mammal Rev.* **19**, 153–173. https://doi.org/10.1111/j.1365-2907.1989.tb00409.x

Van Eeden, L.M., Newsome, T.M., Crowther, M.S., Dickman, C.R. & Bruskotter, J. (2019). Social identity shapes support for management of wildlife and pests. *Biol. Conserv.* **231**, 167–173. https://doi.org/10.1016/j.biocon.2019.01.012

Villafuerte, R., Castro, F., Ramírez, E., Cotilla, I., Parra, F., Delibes-Mateos, M., Recuerda, P. & Rouco, C. (2017). Large-scale assessment of myxomatosis prevalence in European wild rabbits (*Oryctolagus cuniculus*) 60 years after first outbreak in Spain. *Res. Vet. Sci.* **114**, 281–286. https://doi.org/10.1016/j.rvsc.2017.05.014

Villafuerte, R. & Delibes-Mateos, M. (2019). *Oryctolagus cuniculus*. The IUCN Red List of Threatened Species 2019: e.T41291A170619657

Virgós, E., Cabezas-Díaz, S., Malo, A., Lozano, J. & López-Huertas, D. (2003). Factors shaping European rabbit abundance in continuous and fragmented populations of central Spain. *Acta Theriol.* **48**, 113–122. https://doi.org/10.1007/bf03194271

Virgós, E. & Travaini, A. (2005). Relationship between small-game hunting and carnivore diversity in central Spain. *Biodivers. Conserv.* **14**, 3475–3486. https://doi.org/10.1007/s10531-004-0823-8

Williams, D., Acevedo, P., Gortazar, C., Escudero, M.A., Labarta, J.L. & Villafuerte, R. (2007). Hunting for answers: rabbit (*Oryctolagus cuniculus*) population trends in northeastern Spain. *Eur. J. Wildl. Res.* **53**, 19–28. https://doi.org/10.1007/s10344-006-0056-0

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Bait station.

Data S2. Rabbit translocation.

Data S3. Previous experimental study of vanilla essence effect on the rabbit behavior.

Data S4. Rabbit abundance estimation.

Data S5. Bait intake, as percentage from the total number of baits available, by species in the control and treatment areas during the experimental phases.

Data S6. Model selection results for initial abundance, detection probability and population dynamics.

Data S7. Averaged model parameter estimates for rabbits: detection probability (p), abundance (λ), recruitment (γ), and apparent survival (ω).

Data S8. Graphical assessment of model fit by parametric bootstrapping.