The competitor release effect applied to carnivore species: how red foxes can increase in numbers when persecuted

J. Lozano, J. G. Casanovas, E. Virgós & J. M. Zorrilla

Abstract

The competitor release effect applied to carnivore species: how red foxes can increase in numbers when persecuted.— The objective of our study was to numerically simulate the population dynamics of a hypothetical community of three species of small to medium–sized carnivores subjected to non–selective control within the context of the competitor release effect (CRE). We applied the CRE to three carnivore species, linking interspecific competition with predator control efforts. We predicted the population response of European badger, the red fox and the pine marten to this wildlife management tool by means of numerical simulations. The theoretical responses differed depending on the intrinsic rate of growth (r), although modulated by the competition coefficients. The red fox, showing the highest r value, can increase its populations despite predator control efforts if control intensity is moderate. Populations of the other two species, however, decreased with control efforts, even reaching extinction. Three additional theoretical predictions were obtained. The conclusions from the simulations were: 1) predator control can play a role in altering the carnivore communities; 2) red fox numbers can increase due to control; and 3) predator control programs should evaluate the potential of unintended effects on ecosystems.

Key words: Predator control, Wildlife management, Competition, Generalist predator, Population dynamics, Population growth.

Resumen

El efecto liberador de competidores aplicado a las especies de carnívoros: cómo puede aumentar el número de zorros cuando son perseguidos.— El objetivo de nuestro estudio consistió en simular numéricamente la diná- mica de poblaciones de una comunidad hipotética de tres especies de carnívoros de talla pequeña y mediana sometidas a un control no selectivo en el contexto del efecto liberador de competidores. Aplicamos el modelo del efecto liberador de competidores, que relaciona la competencia interespecífica con el control de predadores, a tres especies de carnívoro. Así, pudimos predecir la respuesta de las poblaciones de tejón, zorro y marta frente a este mecanismo de gestión de la fauna silvestre por medio de simulaciones numéricas. Las respuestas teóricas fueron distintas en función de la tasa intrínseca de crecimiento (r), si bien estuvieron reguladas por los coeficientes de competencia. El zorro, con el valor de r más elevado, puede aumentar sus poblaciones a pesar del control de predadores si este es moderado. Por el contrario, las poblaciones de las otras dos especies dismi- nuyeron con el control hasta extinguirse. Obtuvimos también tres predicciones teóricas. Las conclusiones de las simulaciones fueron: 1) el control de predadores puede alterar las comunidades de carnívoros; 2) la población de zorros puede aumentar debido al control y 3) los programas de control de predadores deberían evaluar los efectos indeseados que podrían producirse en los ecosistemas.

Palabras clave: Control de predadores, Gestión ambiental, Competencia, Predadores generalistas, Dinámica de poblaciones, Crecimiento poblacional.

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Introduction

Populations of various taxonomic groups are declining sharply due to human activities in the environment (Groombridge, 1992). In particular, predator control has produced a negative and strong impact on populations of many species of large carnivores (*e.g.* Schaller, 1996; Breteinmoser, 1998; Rodríguez & Delibes, 2002). A lot of smaller carnivore species, such as the marten species (*Martes* spp.), the European wildcat (*Felis silvestris* Schreber, 1775) or the European badger (*Meles meles* L.), are also affected (Langley & Yalden, 1977; Lankester et al., 1991; Ruggiero et al., 1994; Caro & Stoner, 2003; Lozano et al., 2007). In contrast, adaptable species of carnivores, such as the red fox (*Vulpes vulpes* L.), can become more abundant in some places as the result of such activities (Baker & Harris, 2006; Beja et al., 2009).

The main goal of predator control, in both natural reserves interested in protecting sensitive species and hunting lands with an interest in harvest management, is to reduce the incidence of predation (Tapper et al., 1991; Harris & Saunders, 1993; Reynolds & Tapper, 1996; Côte & Sutherland, 1997). Predator control techniques vary greatly both in their degree of selectivity and effectiveness with regard to the persecuted species (*e.g.* Calver et al., 1989; Windberg & Knowlton, 1990; Tapper et al., 1991; Hein & Andelt, 1994; Reynolds & Tapper, 1996; Harding et al., 2001; Rushton et al., 2006; Beja et al., 2009). Unfortunately, many of these methods are non–selective (*e.g.* snares, traps, poisoned baits), and negatively affect both the species considered a pest and others of conservation concern (Herranz, 2000; Duarte & Vargas, 2001; Whitfield et al., 2003; Rodríguez & Delibes, 2004; Virgós & Travaini, 2005; Beja et al., 2009; Cabezas–Díaz et al., 2009; Estes & Terborgh, 2010; Lozano et al., 2010).

Many studies have been carried out around the world dealing with the effects of predator control on prey populations (Reynolds & Tapper, 1996; Côte & Sutherland, 1997; Valkama et al., 2005; Oro & Martínez–Abraín, 2007). Nevertheless, the effects of such control on the population parameters of the targeted predators, or on the structure of their natural communities, have received much less attention (*e.g.* Yoneda & Maekawa, 1982; Harris & Saunders, 1993; Reynolds et al., 1993; Estes & Terborgh, 2010).

It is well established that predation, competition and their interaction are important factors shaping natural communities (Chase et al., 2002; Caro & Stoner, 2003). Interspecific interactions within the communities of carnivores can cause the extinction or exhaustion of specialist species or larger predators (*e.g.* lynxes, wolves, coyotes). For example, such interactions may be interguild predation or competition through exploitation (Erlinge & Sandell, 1988; Polis & Holt, 1992; Palomares & Caro, 1999; Müller & Brodeur, 2002). After the disappearance of these top predators, numbers of smaller species could increase, a pattern also observed in more generalist species such as the Iberian mongoose (*Herpestes ichneumon* L.) or the red fox (see Palomares et al., 1995; Creel & Creel, 1996; Palomares & Caro, 1999).

These data imply that different predator management systems could have different effects on the communities of predators and indirectly affect the levels of predation on the prey species (Estes & Terborgh, 2010; Levi et al., 2012). This could even produce paradoxical effects, such as a reduction in the diversity and/or abundance of game species or those of conservation interest, as a result of the increase in the abundance of generalist carnivores (Soulé et al., 1988; Courchamp et al., 1999a; Crooks & Soulé, 2000; Caut et al., 2007).

However, given the lack of field data in relation to this issue, and the difficulty involved in obtaining such information, an alternative to study the possible effects of the applied control techniques on the predator populations consists of developing simple mathematical models. With a minimum number of assumptions, it is possible analyse the population dynamics of these species, and the interspecific interactions on community composition (see the application of this type of procedure in the works by Shorrocks & Begon, 1975; Courchamp et al., 1999a, 1999b; Caut et al., 2007; Fenton & Brockhurst, 2007).

Caut et al. (2007) used this theoretical approach to describe a new ecological mechanism named the Competitor Release Effect (hereafter CRE). According to this mechanism, an inferior competitor can increase in numbers if the superior competitor is controlled, due to the competitive interactions between them. This occurs even though the inferior competitor is also being killed. Moreover, at the same time, theoretical results show negative effects on the population of a shared prey. Shared prey can decline because while numbers of a superior competitor are decreasing, there may be an unwanted and unexpected increase in numbers of the inferior competitor. Caut et al used empirical data from an eradication program of rodents living on islands to test and support their competitor release hypothesis. They also suggested that the same effect could be found in communities of carnivore mammals, where the population of a competitor such as the red fox could increase if the community of predators is being managed using predator control.

The objective of our study was to numerically simulate the population dynamics of a hypothetical community of three species of small to medium–sized carnivores subjected to non–selective control (*i.e.* where all the individuals are being eliminating with similar probability), within the context of the proposed CRE (Caut et al., 2007). The selected species for the simulations were the European badger, the red fox and the pine marten (*Martes martes* L.). Reasons for this choice were: (i) these species are sympatric in a wide range of Europe (Mitchell–Jones et al., 1999); (ii) there is evidence of competition among them (Lindström et al., 1995; Palomares & Caro, 1999; Trewby et al., 2008); (iii) all three species are often controlled (*e.g.* Côté & Sutherland, 1997; Virgós & Travaini, 2005; Trewby et al., 2008) and; (iv) information about their populational parameters can be found in the scientific literature (Bright, 1993).

Our study differs from that of Caut et al. (2007) in that we evaluated a third species in the mathematical

model. Moreover, known (*i.e.* real) values for the population growth rates were used, so the model should be more realistic. We specifically wanted to know whether the CRE could increase the population of red fox when the three species are being controlled, and if so, under what conditions such an increase occurs. Furthermore, we used the results of numerical simulations from the theoretical model to obtain a set of predictions which could be tested with empirical data when available.

Material and methods

We modified the CRE model from Caut et al. (2007) by adding an equation to simulate the populational dynamics of a third competitor. This model was based on the classical Lotka–Volterra equations (Powell & Zielinski, 1983; Begon et al., 1996), which were modified to incorporate an additional factor of linear mortality (in a similar way that in Shorrocks & Begon, 1975; Fenton & Brockhurst, 2007). The slope of this new factor is independent from the density and represents the mortality caused by the predator control involved (degree of non–selectivity). Thus, this modification of the classical model, which only includes density–dependent mortality implicitly in the population growth rate, is analogous to those previously proposed by Gause (1934, 1935). In these studies, the author considered mortality independent from density, possibly caused by factors such as parasites, non–specific diseases, or other mortality factors (*e.g.* Caut et al., 2007; Fenton & Brockhurst, 2007).

Our model is defined by three equations that govern the coupled dynamics of three species of competing carnivores:

$$A_{t+1} = A_t + r_A A_t \left(1 - \frac{A_t + \alpha_{AB} B_t + \alpha_{AC} C_t}{K_A}\right) - \omega A_t$$

$$B_{t+1} = B_t + r_B B_t \left(1 - \frac{B_t + \alpha_{BA} A_t + \alpha_{BC} C_t}{K_B}\right) - \omega B_t$$

$$C_{t+1} = C_t + r_C C_t \left(1 - \frac{C_t + \alpha_{CA} A_t + \alpha_{CB} B_t}{K_C}\right) - \omega C_t$$

where *A, B* and *C* represent the number of individuals of each particular species at time t. The intrinsic growth rates of each population are r_A, r_B and r_C. The effect of the interspecific competition of one species against another is represented by α (which is the competition coefficient), and the carrying capacity of the environment for each population is *K*. Finally, included in each equation is the parameter ω (control coefficient) which represents the extraction rate of each species as a result of the non–selective control applied. This can be interpreted as the proportion of the population of a given species which dies during a period *t* as a consequence of the control. Because the model attempts to determine the effect of non–selective control, this ω parameter was fixed with the same value for all the species of the community, although more complex scenarios could be developed within the premise of non–selective control.

In this scenario, the set of values of the parameters was chosen to take into consideration that each species of the model represented one for which the intrinsic growth rate (*r*) was available (Bright, 1993). These values are from British populations of each species, but we assumed that the growth rates were similar for other regions of Europe (Turchin, 2003). The three carnivore species were the European badger (species A), the pine marten (species B), and the red fox (species C). The carrying capacities (*K*) were set as constant and identical to facilitate the interpretation of results from the numerical analysis. The selected value is theoretical but also realistic in function of the considered spatial scale (*K* = 30, approximately equivalent to 25–30 km^2 considering mean density values of the species in Europe; Wilson & Mittermeier, 2009), and it allows a sufficient range of variation to compare the populational dynamics among species. Likewise, the competitive interactions among the species were considered symmetrical (*i.e.* AB = AC = BA = BC = CA = CB). Although asymmetries can be expected in the wild (*e.g.* Palomares & Caro, 1999), unfortunately no quantitative data are available to create more realistic scenarios. Table 1 shows the demographic values used for the parameters in the model.

A total of 72 deterministic numerical analyses were performed per species: one for each combination of parameters, varying in equal intervals α from 0.1 to 0.9, and ω from 0 to 0.7. The value reached by the population in the equilibrium for each combination of parameters was graphically represented. Furthermore, to test whether the predictions arising from the theoretical model were sufficiently robust to stand up against small variations in the values for the intrinsic growth rate (*r*), a sensitivity analysis was conducted. This consisted of creating simulations varying by a single parameter and leaving the other parameters constant. Thus, α = 0.5, ω = 0.3, r_A = 0.46 and r_C = 1.1 were fixed, whereas r_B (the intermediate intrinsic growth rate regarding original values) varied in five intervals from 0.4 to 1.1. This also could be equivalent to simulating the population dynamics of a competing species other than the pine marten (species B), showing different values of intrinsic growth rate. All these analyses were performed using the computer program STELLA v.9.1.4 for Windows (ISEE, 2010).

The basic model used here and the Lotka–Volterra equations have been analytically studied elsewhere using the same assumptions (for more details see Gilpin, 1975; Shorrocks & Begon, 1975; Caut et al., 2007). Therefore, our work is an extension of these basic models, incorporating a level of predator community complexity more commonly found in natural systems.

Results

Simulation results

From our numerical simulations, we found a qualitatively different behaviour among the carnivore popu-

Table 1. Demographic values for parameters of the model: *r* is the intrinsic growth rate for each species, and *K* is the carrying capacity of the environment.

Tabla 1. Valores demográficos utilizados para los parámetros del modelo: r *es la tasa intrínseca de crecimiento para cada especie y* K *es la capacidad de carga del medio.*

Letter in equation	A	B	C
Species	*M. meles* (badger)	*M. martes* (pine marten)	*V. vulpes* (red fox)
r	0.46	0.57	1.1
K	30	30	30

lations, considering the competitive interactions that can occur in the community as a result of a predator control program. The sensitivity analysis of the system with regard to the value of species B ($r = 0.57$, the pine marten) indicates that when there is intermediate competition (0.5) and moderate control (0.3), the variation in the intrinsic growth rate affects the equilibrium value of species C ($r = 1.1$, the red fox) but does not appear to affect the species A ($r = 0.46$, the European badger). There is a critical value for r_B, at 0.9, above which the red fox population does not rise above K* (the maximum population value in the presence of the other two species, in this scenario K* = 15 individuals). At intermediate levels of competition, the model predicts a 'paradoxical effect' produced by the non–selective control. In other words, when species B shows an $r > 0.9$ (this being a threshold value), the population increases rather than decreases, despite the applied control.

The simulations of the general scenario, where the intrinsic growth rates were fixed (0.46, 0.57 and 1.1), produced a system dynamic showing very clear patterns of population change depending on competition and predator control intensity. Thus, if the intrinsic growth rate (r) of one species was below the threshold value $r' = 0.9$, then the population would change in time, always showing a decrease in its numbers (see figs. 1, 2). The simulated population with the lowest intrinsic growth rate, corresponding to the European badger ($r = 0.46$, fig. 1), showed a linear decrease in its numbers when predator control was applied. This population became completely extinct with an intermediate degree of control intensity (0.5), in conditions of minimum competition (0.1). The increase in competition implies that the population could be destroyed under conditions of even less intense non–selective control.

Likewise, the general pattern observed in the change of the population with a slightly higher growth rate ($r = 0.57$), belonging in this case to the pine marten, was practically the same (see fig. 2). The difference was that the higher growth rate implied that the population of this species needed a slightly higher level of control intensity than the badger to disappear: a value of 0.6, under conditions of minimum competition (0.1).

In strong contrast, the population of the red fox behaved in a very different manner under conditions of non–selective control, and depending on competition (see fig. 3). The pattern presented a very marked non–linearity which could be attributed to their high intrinsic growth rate ($r = 1.1$). Without competition, or with very low levels of competition (up to 0.2), control efforts reduced the population in a linear sense, such as in the previous species, but maintained a large number of individuals even under conditions of very intense control (0.7). The red fox population could reach extinction only with a very high degree of control intensity, the value of control coefficient being near the maximum. At a medium level of control intensity, the population maintained approximately half the individuals of the population maximum (K), regardless of competition.

Furthermore, with a low level of competition (0.3) this population was not affected by the number of individuals when low intensities of non–selective control were applied (< 0.4). Surprisingly, when starting from this low level of competition (0.3), the low control intensities (< 0.4) led to a sharper population increase (the paradoxical effect mentioned above) if there was a higher degree of competition with the other two species. The increase in red fox occurred precisely when there was a decrease in the number of their competing species, whose populations showed lower intrinsic growth rates. The final result of the application of predator control under these conditions could therefore be a red fox population with double the initial number of individuals. When the degree of competition was higher, the intensity of control needed to be lower to reach the maximum level of increase. The absolute population maximum was then also reached when competition was maximal.

Predictions of the theoretical model

Based on the results of the numerical analysis and due to the CRE, we made the following set of three predictions: i) populations of red fox showing maximal abundances (or those of other generalist predators showing a high intrinsic growth rate) will be present in areas subjected to predator control (usually areas devoted to small game hunting); ii) statistically signi-
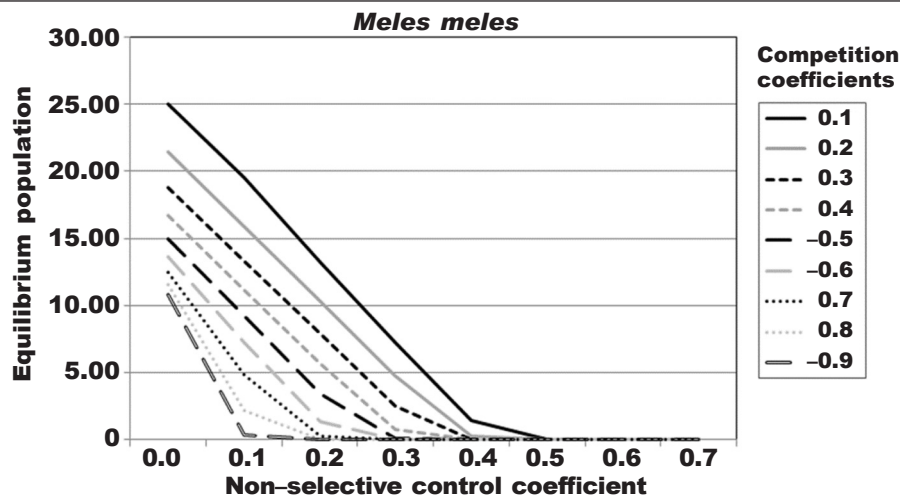
Fig. 1. Functions for European badger (*Meles meles*) populations considering the competition coefficients (α) that relate the value for the population in dynamic equilibrium according to the intensity degree of non–selective control (ω). All populations become extinct at intermediate degrees of control intensity, following a linear pattern.

*Fig. 1. Funciones de las poblaciones de tejón (*Meles meles*) teniendo en cuenta los coeficientes de competencia (α) que relacionan el valor de la población en equilibrio dinámico con el grado de intensidad de control no selectivo (ω). Todas las poblaciones se extinguen con una intensidad de control intermedia siguiendo un patrón lineal.*

ficant differences between controlled and uncontrolled areas will not be found in the abundance of red fox (or those of other generalist predators showing a high intrinsic growth rate). But according to prediction 1), if differences appear, the red fox will be more abundant in controlled areas; and iii) the most abundant populations of competing species showing low intrinsic growth rates will be found in areas where predator control programs are not implemented. Thus, statistically significant differences will be found in the abundance of predator populations with low intrinsic growth rate between controlled and uncontrolled areas, with the more abundant populations inhabiting the uncontrolled areas.

Discussion

Many managers of natural areas, gamekeepers and the hunting community in general have the perception that generalist predators (including several species of rodents, corvids, gulls, and carnivores) increase continuously and are so abundant that their populations should be controlled (*e.g.* Herranz, 2000; Garrido, 2008). One of the most persecuted species is the red fox, blamed for reducing populations of game species (Herranz, 2000; Virgós & Travaini, 2005; Rushton et al., 2006; Beja et al., 2009). Although the belief that red fox populations are increasing everywhere and continuously is probably an exaggeration (see the case of a large Spanish region in Sobrino et al., 2009), it seems true that under certain conditions this species

can increase above normal values (*e.g.* Beja et al., 2009; Trewby et al., 2008). Surprisingly, the paradox is that these real increases in abundance, as in the case of other generalist predators, occur even though their populations are subjected to permanent control campaigns (Herranz, 2000; Virgós & Travaini, 2005; Beja et al., 2009).

Caut et al.´s competitor release effect (CRE) described an ecological mechanism that is applicable to mesocarnivore populations and could theoretically explain this paradox (2007). The CRE framework implies a scenario where the carnivores community is shaped by a number of species presenting **negative** interspecific interactions (–,–) and experiencing a non–selective predator control program. Under these conditions, our theoretical results predicted that certain changes will occur in the composition and structure of the community. Thus, predator control efforts might eliminate populations with a low intrinsic growth rate (*r*) and only the population with a high rate of increase might persist (in our case the red fox, whose populations showed a growth rate higher than 0.9), unless the control is extremely intense. Surprisingly, if the control level is moderate, then the populations of these species of generalist predators could increase in a paradoxical way, even surpassing the theoretical value for maximum population in equilibrium in the presence of the remaining species. This is due to both the disappearance of competitors and their higher reproductive capacity. Moreover, the ecological consequences of a mechanism such as the CRE might be similar to those produced by
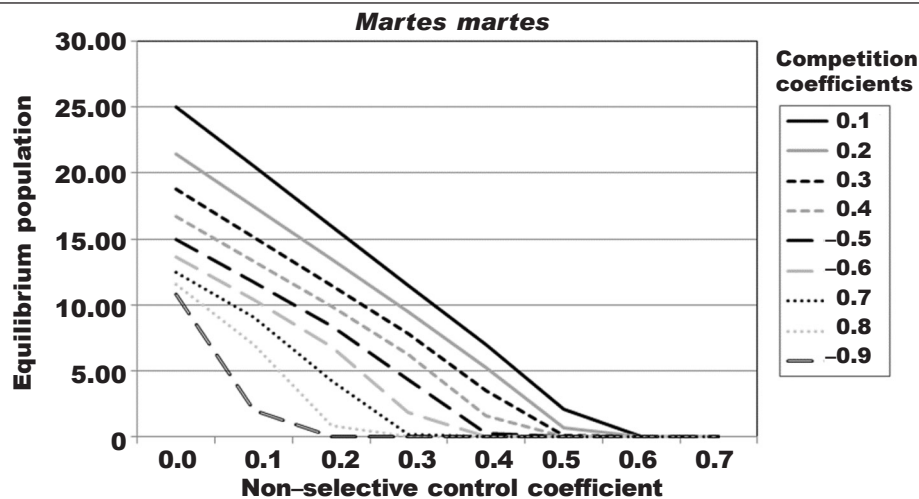
Fig. 2. Functions for pine marten populations (*Martes martes*) follow a similar pattern to those of European badger, although their higher growth rate requires more intense control to completely eliminate the populations.

*Fig. 2. Las funciones de las poblaciones de marta (*Martes martes*) siguen un patrón parecido a las de tejón, aunque su mayor tasa de crecimiento hace necesario intensificar el control para eliminar totalmente las poblaciones.*

the mesopredator release effect (see Soulé et al., 1988; Courchamp et al., 1999a), if net predation on certain prey species were to increase as a result of the population increase of control–resistant predators (Caut et al., 2007). Our modelling therefore supports both the CRE hypothesis and the MRE hypothesis.

We found three predictions from our model evaluation that should be specifically tested with empirical data obtained in the field. In general, these predictions are based on the fact that red fox populations (in our case scenario) will increase or maintain their numbers despite the implementation of predator control efforts (Predictions 1 and 2), while other species of carnivores will become less abundant (Prediction 3). It is expected that the most sensitive species disappear over time, so that species richness will decrease in controlled areas (see Estes & Terborgh, 2010). Interestingly, the few data available in the scientific literature seem to support our findings. For example, the results of a study carried out in Portugal showed that in hunting grounds where predator control was practised, the abundance of red fox was almost twice as high as in non–hunting areas (Beja et al., 2009), which appears to bear out Predictions 1 and 2. Moreover, other species of predators tended to be more abundant in uncontrolled areas, supporting Prediction 3 in our study.

Similarly, predator control on badgers in the UK increased the red fox population, again appearing to meet Prediction 1 (Trewby et al., 2008). The results obtained by Virgós & Travaini (2005) in Spain also appear to generally support the CRE predictions. These authors detected the absence of some carnivores

in controlled areas, while the red fox frequency of occurrence in both controlled and uncontrolled areas was similar. However, field data collected following a carefully designed study protocol are needed to reliably test the CRE model predictions found in this study.

In our model, no explicit consideration was given to the effects that spatial heterogeneity, landscape pattern, and structure of a territory could have on the behaviour of population and community dynamics. There is evidence that landscape composition and quality affect interactions among species (Erlinge & Sandell, 1988; Hanski, 1995), the efficacy of predator control programs (Schneider, 2001; Rushton et al., 2006), and therefore the persistence at a regional level of a given pool of species. Given that the model predicts the probabilities of differential extinction of the species in fragmented landscapes and complex environments, the long–term configuration of the communities will also depend on the different probabilities of recolonisation (Hanski, 1994; Schneider, 2001; Rushton et al., 2006). It is possible to speculate about the existence of deterministic processes within a community of carnivores subjected to non–selective control. These processes would occur at the local level, but predictable consequences would result at the landscape scale. These aspects should also be tested independently through further research with empirical data.

The fundamental objective of predator control is an effective increase in the populations of prey species of interest to hunting or conservation (Trout & Tittensor, 1989; Reynolds & Tapper, 1995, 1996; Côte & Sutherland, 1997; Virgós & Travaini, 2005;
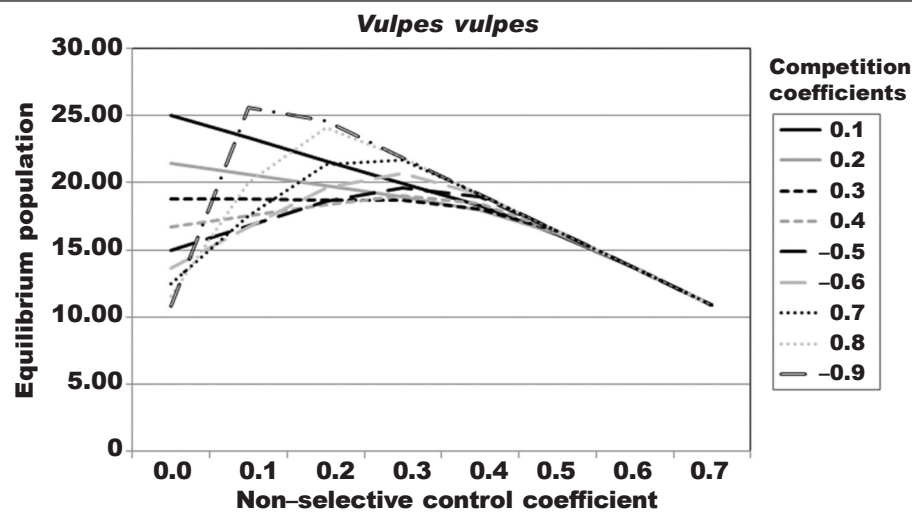
Fig.3. Functions for red fox populations (*Vulpes vulpes*) are qualitatively different from those of the previous species due to an intrinsic growth rate higher than 0.9. Red fox populations thus show a non–linear response when persecuted depending on the level of competition: populations increase when competition coefficients are greater than 0.3 and control intensity is moderate. Furthermore, red fox populations do not become extinct despite intense predator control.

*Fig. 3. Las funciones de las poblaciones de zorro (*Vulpes vulpes*) son cualitativamente diferentes de las de las especies anteriores debido a una tasa intrínseca de crecimiento mayor que 0,9. Así, las poblaciones de zorro muestran una respuesta no lineal cuando son perseguidas dependiendo del grado de competencia: las poblaciones aumentan cuando los coeficientes de competencia son mayores que 0,3 y la intensidad del control es moderada. Además, las poblaciones de zorro no se extinguen aunque se aplique un control de predadores intenso.*

Reynolds et al., 2010). This is based on studies that found direct effects of control or natural reduction of predators on the abundance and dynamics of prey populations (*e.g.* Marcström et al., 1988, 1989; Small & Keith, 1992; Lindström et al., 1994). However, the success of predator control campaigns is variable and, in general, very expensive (Reynolds & Tapper, 1996; Côte & Sutherland, 1997).

Some studies have thus suggested that these practices are effective (regarding the above indicated objective) when applied at the local level, in conditions of very intense control, but only in the short–term (*e.g.* Reynolds et al., 1993; Harding et al., 2001; Keedwell et al., 2002). Other studies have shown that the predator control was ineffective in meeting management goals (Reynolds & Tapper, 1996; Côte & Sutherland, 1997; Banks, 1999; Herranz, 2000; Kauhala et al., 2000; Keedwell et al., 2002; Martínez–Abraín et al., 2004; Baker & Harris, 2006; King et al., 2009). Moreover, there are many predator species that do not affect game or threatened species. Thus, it has been argued that predator control can not be effective when focused on them (see for the cases of lizards, snakes and large gulls Herranz, 2000; Oro & Martínez–Abraín, 2007). Overall, it has been considered that the unique nature of predator–prey relationships within communities makes it difficult to make generalizations, and that evaluation of the effectiveness of conducting a predator control

program thus requires individual consideration (Sih et al., 1998; Abrams & Ginzburg, 2000; Turchin, 2003; Holt et al., 2008; Valkama et al., 2005).

On the other hand, predator management could have ecological costs that depend on the relative importance of the different uses and intrinsic values of the territory. For example, the ecological consequences of controlling one or various species of predators might be appraised positively or negatively depending on the environmental perception, and on the type of local use of the natural resources (Langley & Yalden, 1977; Banks et al., 1998). Thus, perception might be different if predator control is used to enhance an endangered species rather than a game species (*e.g.* Côte & Sutherland, 1997; Keedwell et al., 2002). Furthermore, predator control also appears to affect different demographic parameters of the target predator species, including density, age structure, and inmigration patterns (see Yoneda & Maekawa, 1982; Rushton et al., 2006).

However, the more notable and more harmful effects of non–selective predator control are related to the conservation of threatened species of predators and the unwanted consequences on ecosystems due to the alteration of natural communities, such as the increase of generalist predators (including target species of the control) and pest species (including rodents), the decline of shared prey species (including

those of game interest), and unforeseen effects on vegetation, ecosystem function, and similar owing to chain reactions (*e.g.* Herranz, 2000; Martínez–Abraín et al., 2004; Rodríguez & Delibes, 2004; Virgós & Travaini, 2005; Caut et al., 2007; Cabezas–Díaz et al., 2009; Estes & Terborgh, 2010).

The theoretical results obtained in this study highlight the importance of competitive ecological interactions among predators in the design of an optimum management strategy for their communities (Courchamp et al., 1999a, 1999b; Trewby et al., 2008). Caut et al´s CRE has shown how the complex network of interactions (see also Polis & Holt, 1992; Chase et al., 2002; Caro & Stoner, 2003) among carnivore mammals can also lead to undesired effects, such as a population increase in the target species (the red fox or any predator with high reproductive capacity in our study, or the American mink *Neovison vison* Schreber 1777; see Bright, 1993; King et al., 2009), and the elimination of more sensitive species that might be of conservation interest. The obtained results support the idea that the design of programs to manage predator populations should consider potential consequences to communities and the ecosystem as a whole (Schneider, 2001; Zavaleta et al., 2001; Courchamp & Caut, 2005; Caut et al., 2007), as well as the biological traits of the involved species. To validate our model findings, empirical data should evaluate these responses and not just the individual species' responses of the targeted predator and prey. The development of management strategies for species such as the red fox populations should take the ecological framework into account, and predator control programs should be thoroughly evaluated to determine the potential impact on the community and ecosystem. This is particularly important for predator control programs using non–selective methods (*e.g.* Herranz, 2000; Virgós & Travaini, 2005; Beja et al., 2009), where numbers of red foxes and other generalist predators can increase despite the efforts of managers.

Acknowledgements

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