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Complete List of Authors:	Fernández-Olalla, Mariana; ETSI Montes. Universidad Politecnica de Madrid, Silvopascicultura Martínez-Abraín, Alejandro; IMEDEA (CSIC-UIB), Population Ecology Group Canut, Jordi; Parc Nacional d'Aigüestortes i Estany de Sant Maurici. Departament de Medi Ambient i Habitatge García-Ferré, Diego; Servei de Protecció de la Fauna, Flora i Animals de Companyia. Departament de Medi Ambient i Habitatge Afonso, Ivan; Asociación para la Conservación del Urogallo González, Luis Mariano; Ministerio de Medio Ambiente y Medio Rural y Marino, Subdirección General de Biodiversidad. Dirección General del Medio Natural y Política Forestal
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Assessing different management scenarios to reverse the declining trend of a relict capercaillie population: a modeling approach

Fernández-Olalla, Mariana^{1*}; Martínez-Abraín, Alejandro²; Canut, Jordi³; García-Ferré, Diego⁴; Afonso I⁵; González, Luis Mariano⁶

1. Dep. Silvopascicultura, ETSI de Montes, UPM, C/Ciudad Universitaria, s/n, 28040 Madrid, Spain. E-mail: mariana.fernandez@upm.es; telephone number: +34-915336414; fax number: +34-915439557.

* Corresponding author

2. IMEDEA (CSIC-UIB). Population Ecology Group. C/Miquel Marquès 21, 07190 Esporles, Mallorca, Spain. E-mail: amartinez@imedea.uib-csic.es

3. Parc Nacional d'Aigüestortes i Estany de Sant Maurici. Departament de Medi Ambient i Habitatge. C/ Prat del Guarda 4, 25597 Espot (Lleida). Tfno: 650952197. E-mail: jcanut@gencat.cat

4. Servei de Protecció de la Fauna, Flora i Animals de Companyia. Departament de Medi Ambient i Habitatge. C/ Dr Roux 80, 08017 Barcelona. E-mail: adgarfe@gencat.cat

5. Asociación para la Conservación del Urogallo (ACU) y MUSIA SCP. C/ Gramenet 3, 25510 La Plana (Lleida). E-mail: ivan@musia.cat

6. Subdirección General de Biodiversidad. Dirección General del Medio Natural y Política Forestal. Ministerio de Medio Ambiente y Medio Rural y Marino. C/ Ríos Rosas 24, 28003 Madrid. E-mail: lmgonzalez@mma.es

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Summary

1. Capercaillie populations are declining in most of its distribution area. In almost none of its populations the regressive trend can be explained by only one main cause but there are several interacting ones, whose effects are not easy to disentangle. Thus, often wildlife conservationists have to make decisions based on poor evidence.

2. This study analyzes the trend of the relict capercaillie population in the Spanish Pyrenees on the basis of bird densities estimated throughout the period 1989-2010, and constitutes the first attempt to modelling the dynamics of a capercaillie population in southern Europe.

3. We also explored two management actions commonly used to enhance endangered prey species, thought to be affected by hyperpredation: the release of captive-bred females, in varying numbers, the removal of terrestrial meso-carnivores and the combination of both actions, using available information from a past experience of captive breeding and from an ongoing experience of terrestrial meso-predator removal.

4. The population was declining at an annual rate of 4% for the last 20 years. Sensitivity analysis showed that recruitment (productivity+fledgling survival), rather than adult survival, was the demographic parameter which most likely could be increased by management.

5. The removal of terrestrial meso-carnivores may lead to the stabilization of the capercaillie population (λ 0.99 $\pm$ 0.06), although this result should be considered as preliminary. To be conservative, the only effective strategy was the combination of meso-predator removal in combination with the release of either 15, 30 or 45 adult females per year.

5. Synthesis and applications. We recommend to implement these urgency measures together with other complementary actions, as a more efficient long-term conservation

strategy. The control of wild ungulate numbers, in the absence of top predators, and the removal of carcasses generated by hunting activity may lead to the self-regulation of the meso-predator guild. Decreased densities of ungulates may also prevent damages in bilberry cover, a basic resource for the species. Additionally, habitat management practices, such as the thinning of the currently encroaching tree stands, after massive depopulation of rural areas, should also be considered, for its possible role on predation rates and bilberry persistence.

Key-words: capercaillie, captive-breeding, evidence-based conservation, habitat management, population viability analysis, predation management, predator removal, *Tetrao urogallus*.

Introduction

The southern European peninsulas housed many boreal species which were isolated there after the retreat of the ice sheet originated during the last glacial period of the Pleistocene (Hewitt 1999). These marginal populations are known to be more prone to extinction and genetically impoverished, as they tend to occur in less favourable habitats and at lower and more variable densities (Vucetich & Waite 2003). Predation may compromise the persistence of such isolated populations, in the case of prey species (Macdonald, Mace & Barretto. 1999).

Although many studies have demonstrated that predators may affect considerably only those prey populations which are under unfavorable conditions (Genovart *et al.* 2010) (i.e. predation as a compensatory factor), many authors have stated that predators can, at least, limit prey populations under a wide range of situations (Connolly 1978; Sinclair *et al.* 1998) (i.e. predation as an additive factor). Hyperpredation refers to situations with an enhanced predation impact on an alternative prey due to an increase in predator numbers caused by either a rapid increase or a sudden drop in the abundance of its main prey (Moleón, Almaraz & Sanchez-Zapata 2008). Unintended supplementary feeding or subsidization of predators by human activities (i.e. landfills, hunting and fishing remains) may play the same role of an increase in the abundance of their alternative preys, leading to a numerical response by predators that can drastically impact prey populations, especially when those are in low numbers (Gompper & Vanak 2008).

To alleviate the effect of predation on vulnerable prey many possible management strategies may be proposed, but all of them should consider both the whole assemblages of predators and alternative prey. The restoration of the original top predator community (Gompper & Vanak 2008), the elimination of subsidization sources for predators (Bino *et*

al. 2010; Tablado *et al.* 2010) or the improvement of shelter availability within prey habitat (Evans 2004; Lombardi, Fernández & Moreno 2007), have been widely invoked in conservation programs. Although these strategies are more advisable because they aim the long-term continued increase or recovery of the target species, often other shorter-term strategies are carried out, sometimes because it is necessary to gain years before addressing the roots of the problem (Igual *et al.* 2009), but often also because they are more visible to the donating public (Ludwig, Mangel & Haddad 2001). Two of the most widespread examples of these “hard” strategies are predator control and the translocation or release of captive-bred individuals. However, both strategies may be controversial, due to ethical and practical problems (e.g. Beck 1995; Reynolds & Tapper 1996; Smith *et al.* 2010).

The positive effects of predator control tend not to be maintained over time, because density-dependent buffering processes tend to counter-balance the effect of removals (see e.g. Bosch *et al.* 2000; Smith *et al.* 2010). In addition, most studies have evaluated the effect of predator removal in terms of improved breeding success, although, it has seldom been assessed whether the associated increase in productivity actually represents a relevant effect on the growth rate of the prey population (Fletcher *et al.* 2010; Lavers, Wilcox & Donlan 2010). In relation to reintroduction of captive-reared wildlife, this technique has experienced increased popularity recently (Seddon, Armstrong & Maloney 2007). However, the success of these programs may be low when the causes of the original decline have not been reversed at the moment of the release or because captive-reared animals have not had previous exposure to local predators or food sources in the wild (Snyder *et al.* 1996; Wolf, Garland & Griffith 1998, Fischer & Lindenmayer 2000).

In this paper, we analyse the trend of a relict population of a ground-nesting prey species, the capercaillie (*Tetrao urogallus*) in the Pyrenees Mountains, classified as

“vulnerable” under the Spanish law. We examine different management scenarios to enhance population trend, using a population modeling approach, in an attempt to deal with the uncertainty that involves its management. We use an integrative procedure, which combines field monitoring data for more than 20 years and simulations, which accounts for environmental stochasticity. Specifically, we explore the effects of the release of captive-bred birds and of the removal of terrestrial meso-predators on capercaillie population, as it is suspected that predation may be aggravating the situation of this isolated population, due to multiple and complex anthropogenic changes in a high-mountain environment. We have worked within an adaptive management framework, using available information from a past experience of captive breeding and from an ongoing experience of terrestrial meso-predator removal, to ensure that models reflect realistic management options and applying the precautionary principle.

Materials and methods

Study population and monitoring data

Capercaillie (*Tetrao urogallus*) is the greater grouse species in Europe and has been proposed as an ‘umbrella’ species (Suter, Graf & Hess 2002). Two of the twelve subspecies described for the species (*T. u. cantabricus* and *T. u. aquitanus*) are present in the Iberian Peninsula. Both populations are located in the southernmost edge of their world distribution, and are geographically isolated both among them and with respect to the other European populations. More than the 80% of the known leks of Pyrenean capercaillie are located in Catalonia, north-eastern Iberian Peninsula (Robles, Ballesteros & Canut 2006). The estimated number of males at leks has decreased by 31% in Catalonia since the early

90s (op. cit.). The study population is located in the Pallars Sobirà region, which accounts for 35% of the known leks in Catalonia. Most of the study area is included in the Alt Pirineu Natural Park. The species mainly inhabits subalpine forests, located between 1500 and 2000 m a.s.l. They are dominated by mountain pine (*Pinus uncinata*), usually with a bilberry and rhododendron (*Rhododendron ferrugineum*) shrub cover.

Empirical data consisted on “route censuses” (Leclercq 1987) from the summer monitoring program carried out by the Catalanian environmental agency since 1988. Censuses consists on a line transect of 4-14 people arranged at 10 m intervals walking simultaneously through forest patches. By the time of the census, chicks are well grown and most of them are able to fly, so hereafter we will call them “fledglings”. The number of flushed males, females and fledglings is recorded, as well as the surface covered by each census. Undetermined birds are omitted from demographic parameters calculations. The number of people who has participated in each field day exceeds 100 people per year, since 1988.

Empirical estimation of population trend

Density of adult birds (birds/100 has) was estimated by dividing the number of adult males and females by the surface covered by each census. Annual density was calculated as the mean value of all the densities of the censuses carried out each year. This is the first occasion in which the available time series of summer counts has been compiled to estimate the trend of the Spanish Pyrenean population. Nevertheless, the use of this type of density data to estimate population trends is common in other countries (see Lecqlerq 1987). The total surface covered every year may affect the validity of the density estimates obtained, leading to non-representative estimates in those years in which the sampling effort was low

due to logistic limitations. Preliminary linear regressions of density estimates with the surface covered each year, determined that the minimum surface sampled to obtain density estimates independent of surveying effort was 450 hectares.

We used population densities from 1989 to 2010, duly filtered ($n=17$ years), to estimate the population growth rate. The finite annual population growth rate or deterministic growth rate (λ) was calculated considering that N_t (the population size at time t) asymptotically is proportional to $N_0 \lambda^t$, and hence estimated λ is $\lambda=(N_t/N_0)^{1/t}$. Finally, to analyse the population trend, we performed a linear regression of population density and time to obtain the 95% confidence interval for the slope of the regression line. We tested the null hypothesis of population stability by checking whether the 95% confidence interval of the slope bracketed the value zero or not.

Simulated trend: modelling approach

Our modelling approach used a stage-structured matrix population model to simulate the retrospective growth of the population between 1989 and 2010. We considered only one sex (females) and two age classes: fledglings (for birds less than one year old) and adults (thereafter) due to the lack of more structured information (Figure 1). We assumed, as in previous modelling approaches for the species (Sachot, Perrin & Neet 2006), that males are not the limiting sex in lekking species. Hence, to parameterize the model we needed three vital rates: number of daughters per adult female in the population (hereafter, productivity *Prod*), survival of fledgling females (S_{Fl}) and survival of adult females (S_{Ad}). We ran 1000 replications of what we defined as our baseline model (see below) for a 22 years period with an annual time step, using RAMAS Metapop (Akçakaya, Burgman & Ginzburg 1997).

Productivity or fecundity was calculated, each year, as the number of fledglings divided by the total number of females, including both females with brood and broodless females observed during summer counts (post-breeding census). In the simulation process we included the number of daughters per female (i.e. maternity or fertility) duly corrected by the sex ratio for fledglings (0.69 male fledglings per adult female) estimated by Moss *et al.* (2000). The standard deviation of this parameter was calculated using the Delta method to combine the standard deviations of productivity and sex ratio (Seber 1982). To avoid possible biases due to small sample size we only considered those annual productivity estimates based on a minimum of 10 flushed females (Moss *et al.* 2000; Summers *et al.* 2004).

There are no annual survival probability estimates for our study population. Regarding adult female annual survival, literature provides a range of possible values from 0.63 in Scotland (Moss *et al.* 2000) to 0.82 in the Jura Mountains in France (Leclercq 1987). Intermediate values were obtained for Finland (0.71 in Lindén 1981) or Germany (0.65 in Storch 1993). With respect to immature survival, the availability of estimates was lower and variable depending on whether immatures were considered to be chicks, juveniles or fledglings in each study. For fledglings, values ranged from 0.50 in Scotland (Moss *et al.* 2000) to 0.16 in the Jura Mountains in France (Leclercq 1987).

Parameter combinations to set the baseline matrix

To deal with parameter choice uncertainty, we established a protocol to determine which combination of parameters ($Prod$, S_{Fl} , S_{Ad}) would provide the same λ than that calculated from our empirical adult densities. This combination was used to parameterize what we called the baseline matrix, used for subsequent modelling. On the basis of our fixed

empirical average population productivity value, we searched for the possible values that both survival rates (S_{Fl} and S_{Ad}) could take to achieve the observed empirical λ value. For adult survival we considered all values ranging from 0.62 to 0.82. These values together with productivity, allowed us to calculate what might be the survival of fledglings in each case. Fledgling survivals lower than 0.16 or higher than 0.50 (limits from the literature) were discarded as biologically meaningless. Thus, we obtained two biologically sensible combinations of parameters (Table 1) which accounted for the observed population trend since 1989. To choose the final combination to be used in our modelling, elasticities were calculated for the three vital rates included in each combination. We employed these elasticities to ensure that the choice of a baseline matrix or another, from among the two candidates, would not result in subsequent biases in modelling. This was done by means of the software and environment R (<http://www.r-project.org/>).

Initial population abundances, stochasticity and density dependence

Our observed population trend was based on densities, thus we had to back-transform them into absolute abundances to allow modelling. We did so by multiplying each annual density by approximately the core surface area currently occupied by the capercaillie in the study zone (5,360 has). The initial number of adult females was obtained using the average adult sex ratio observed in the route censuses. The average observed proportion of fledglings per adult was used to obtain the initial number of fledglings. To calculate the number of female fledglings we used the ratio provided by Moss *et al.* (2000).

After an initial simulation including demographic stochasticity, we finally excluded it from our simulations as its effect was found to be negligible. We incorporated environmental stochasticity only in productivity since this was the only vital rate for which we knew its standard deviation from field data for the study population. In addition,

capercaillie productivity is known to be highly variable from year to year, mainly due to variable temperature and rain conditions during the incubation and hatching periods (Moss, Oswald & Baines 2001). In our simulations of environmental stochasticity, productivity was sampled randomly from a lognormal distribution, with the mean and standard deviation estimated from procedures explained above. Density-dependent effects were not modelled because no evidence of them acting on any vital rate has been detected in the study population so far, and these are poorly known for the species (Grimm & Storch 2000).

Modelling management scenarios

We explored two management actions included in the capercaillie conservation strategies in Spain

(http://www.mma.es/portal/secciones/biodiversidad/especies_amenazadas/estrategias_planes/index.htm), and their combination: a) the reinforcement of the current population by means of the captive-breeding and release of individuals, b) the removal of terrestrial meso-predators and c) the combination of reinforcement and removal. Management scenarios were modelled for an 8 year period, starting in 2010. This is the duration of two consecutive hypothetical LIFE+EU projects (<http://ec.europa.eu/environment/life>). The initial population size for the prospective simulations was the value predicted by the retrospective baseline model for the year 2010. Prospective simulations were carried modifying the matrix parameters of the baseline model required to simulate each scenario. We maintained the same stochasticities as in the retrospective analysis. In addition, we were interested in the amount in which vital rates needed to be improved to achieve, at least, population stability ($\lambda=1$).

a) Release scenarios. From 1983 to 1992 the regional environmental authorities carried out a program of release of captive-bred capercaillies (García-Ferré, unpublished report). The

approximate number of birds released each year was 15. Released capercaillies were 3 months old at release (fledglings), and the sex ratio of releases depended on bird availability. Releases were done in September. The available information was mainly descriptive and showed that approximately 65% of the birds died during the first two months after release and less than 16% managed to survive one year in the wild. Newly released birds were predated in ca. 50% of the cases. These numbers illustrated that the mortality of newly released birds was very high, so we had to penalize somehow the survival rates of immediately released birds (“cost of release” hereon) in our simulations. The information from the former program did not include annual survival estimates corrected by the probability of recapture for released birds, so it could only be used as a raw orientation. Since there is no further information about the magnitude of the cost of release of captive-bred capercaillies, or other closely related species, in the literature, we decided to use the cost of release estimated for another herbivore ground-nesting prey bird species, the crested coot (*Fulica cristata*) (Tavecchia *et al.* 2009). Coot survival during the first year after release experimented a 79 % decrease. We initially considered the release of both fledglings and adults. We applied proportionally the cost of release to both capercaillie fledgling and adult survival rates. Survival rates affected by the cost of release were 0.10 and 0.17 for the releases of fledglings and adults, respectively. We modelled this scenario by adding a third stage to the baseline matrix, the released birds (Figure 1). We also changed bird abundances in each time step of the simulation process to account for the incorporation of the newly released birds to population numbers. Preliminary results showed that the release of juvenile birds resulted in a negligible effect on the population, due to their low intrinsic survival rate together with the high cost of release. Therefore, we only modelled the release of adult females and in variable number: 15, 30 and 45 annually,

being the latter amount a possible upper limit for the availability of captive-bred capercaillie to be released at any time (Marshall & Edwards-Jones 1998).

b) Predator removal scenarios.

We took advantage of an ongoing experimental program of removal of terrestrial meso-predators carried out by the environmental authorities, to quantify the effect of predation by terrestrial carnivores on capercaillie vital rates. Two controls (C) and one treatment (T) areas were set. Individuals were trapped and translocated (except for red foxes which were legally euthanized) during the spring and early summer, to try to induce a positive effect on capercaillie laying, hatching and fledging success. This program is providing the first initial results after three years of continued implementation starting in 2008 (own unpublished data). Within an adaptive management framework we explored whether observed changes in productivity (between treatment and control areas during the three years of the experiment), if any, could affect the population growth rate or not. The overall effect size was calculated as the standardized mean difference in productivity between pairs of treatment and control (duly weighted by sample size), using a random effects meta-analysis approach by means of the software Comprehensive Meta-Analysis v12 (Englewood 2000). The survival rates in the matrix were kept the same as in the baseline model since, in the absence of information, we were not able to assign any possible relationship between the removal of carnivores and improvements in the survival rates of the species.

c) Combination of predator removal and captive-bred releases.

We simulated the combined effect of the two previous management scenarios because many previous attempts to reinforce wild capercaillie populations using captive-bred individuals have failed because of high predation rates acting on the inexperienced birds

(Klaus 1997, 1998; Storch 2007). However, in the absence of data on the possible increase in survival in the newly released birds due to meso-predator removal, the combination of both management strategies was done in an additive way. These scenarios were modelled by including in the matrix structure the possible changes in productivity obtained from removal field experiments and the reduced survival rates of released birds. Again, initial abundances were modified in each step to simulate the contribution of introduced birds.

Results

Population growth rate and trend

Empirically-obtained density data from 1988 to 2010 are showed in Figure 2, where the values discarded for further calculations due to previous filtering (years 1988, 1990, 1991, 1992 and 1997) suggest the same trend than the rest of the time series, except for 1995 which is considered to be an outlier. The observed population growth rate between 1989 and 2010 was 0.96 (4% annual decrease). The population moved from a density of 0.11 adults per hectare to 0.04 in that period. A general linear model showed that the slope of the regression of density with time was negative and its departure from zero was statistically significant (slope estimate= -0.0025; 95% confidence interval of the slope: (-0.0035, -0.0016).

Baseline model and retrospective simulation

None of the combinations that included an adult survival lower than 0.79 were considered to be possible, from a biological perspective, given that they implied survival rates for fledglings much higher than those mentioned in the literature. The combinations that led to a deterministic lambda of 0.96 are presented in Table 1. Provided that the proportion

between the relative contributions of each parameter to the population growth rate remained constant (approximate proportion 5:1:1 for S_{Ad} , S_{Fl} and $Prod$), we were confident that model choice would not affect the main results. We arbitrarily chose combination defined by $S_{Ad}=0.82$ and $S_{Fl}=0.48$ to parameterize the baseline matrix.

Figure 3 shows the fit of the baseline model (baseline matrix+environmental stochasticity) to the overall trend observed in the population, with almost all the observed points being included within the simulated mean trajectory 95% confidence bounds, except for the unusually low data recorded in 1994. The stochastic lambda calculated from this model was 0.96 (SE = 0.06).

From the baseline matrix, we estimated what should the improvement in any of the vital rates be to lead to population stability (that is, to a deterministic lambda=1) (Table 2). Our sensitivity analysis, indicated that the only vital rate susceptible of improvement to at least reaching population stability in our study is productivity, considering that values of survival in our modelling are already in the upper limits of the values in the literature. However, any combined increase in recruitment parameters (productivity+fledgling survival), that summed up to 33% may also lead to stabilization.

Prospective simulations: Management scenarios

The results of the terrestrial meso-predator removal experiment are presented in Table 3. The overall effect size was 0.14. This meant that this strategy increased by 36% and 32% the mean productivity in the treatment area with respect to controls 1 and 2, respectively. The fact that the 95% confidence interval of this estimate included the value zero (-0.18, 0.46) was most likely due to the low number of treatment-control pairs available for meta-analysis. However, we used the overall effect size for our modelling as

the best estimate available so far of the effect of the removal experiment on capercaillie productivity within an adaptive management approach to inform future conservation actions. Keeping this in mind, and applying the precautionary principle, we decided to model only the less optimistic of the situations (the 32% of increase on total productivity). We converted this increase into the female portion of the fledglings, which implied a change in the number of female fledglings per female from 0.30 to 0.40, for the subsequent modelling. For our simulations we assumed that the effect in 2010 was maintained during the 8 years of simulated management. The results from the simulation of the eight possible management scenarios established (i.e. no action, meso-predator removal, three scenarios of release (15/30/45 annual release of adults) and the three combined scenarios) are shown in Table 4 and Figures 4 and 5. The stochastic population growth rate for scenarios 2 to 4, involving bird releases, did not change but released birds contributed to population numbers. Therefore, and in order to show the magnitude of the effect of releases on population size at the end of the management period we examined the simulated number of adult females at that time (Table 4). If we take into account not only the average number of adult females at the end of the management period but its 95% confidence intervals (Figure 5), the only strategies whose 95% CIs do not overlap with the 95% CI of the non-action scenario were the combinations of meso-predator removal together with the release of either 15, 30 or 45 adults annually. Hence only these strategies can be considered to be effective.

With respect to the expected population trend, in Figure 4 we show that scenarios 2 and 3 do not succeed in reversing the declining trend of the population, while predator removal does (scenario 1, stochastic $\lambda = 0.99$, $SD = 0.06$). The rest of simulated

scenarios (from 4 to 7) indicate that the population could increase, at least, until the end of the management period.

Discussion

The low observed rate of decline (4% annual decline) coincides with the annual decrease estimated for capercaillies recently in Finland (Sirkiä *et al.* 2010), and it can be framed within the general decline of capercaillie populations throughout Europe (Storch 2007). The reduction is more intense in western and central Europe, where several local extinctions have occurred recently (Storch 2007). We caution that the transformation of our density estimates into number of capercaillie females must not be interpreted as real absolute population size estimates, as they depend on the estimate of surface area we have used as the species current range in the study area. It is important to make clear that we were interested in modelling the population trend (i.e. comparable estimates of relative abundance from year to year) not the absolute numbers, which are not confidently known. We succeeded in this respect since the 95% confidence intervals of our simulations bracketed most empirically-derived data.

Not all the simulated management scenarios were able to reverse the declining trend of the population, although all of them caused relative ratios of increase ranging from 1.15 to 2.35 in the simulated number of adult females. Only the release of 45 adult females per year could compensate for current population losses. Certainly we have imposed a strong cost of release (around 80%) to all scenarios involving the release of captive-bred birds, but this is probably not very unlikely because data from the past experience of release of captive-bred individuals in the area showed that only 16% of birds released survived more

than one year in the wild. In fact the IUCN Grouse Specialist Group strongly discourages reintroduction and reinforcement attempts for capercaillie because chances of success are remote for this species (Storch 2007).

Also, according to our simulations the removal of terrestrial meso-carnivores may lead to the stabilization of the capercaillie population, contrary to the review by Lavers, Wilcox & Donlan (2010) who found that in ca. 30-67% of the bird species studied the predicted increase in productivity due to predator removal alone was insufficient to reverse the predicted population declines. The duration of other removal experiments in the literature has been longer than 3 years (e.g. 6 years in Kauhala, Helle & Helle 2000 and Baines, Moss & Dugan 2004 and 8 years in Marcström, Kenward & Engren 1988), what may help to explain why the 95% confidence interval of the overall effect size of the removal experiment included the value zero, in addition to the scarcity of replications. We analyzed the data after 3 years of experiment to inform managers on the viability (or lack of it) of continuing implementing such an experiment for a longer time.

However, if we were to focus only on the average number of females obtained by simulation after the period of management, our expectations could be too optimistic. Thus, we evaluated the efficacy of the different management scenarios by using the 95% confidence intervals of the abundance estimates. That way, the only strategies which can be said to be effective are the combined ones (i.e. removal+the three release scenarios). Environmental authorities should assess the economics of these combined strategies, because the cost of predator control must be added to the cost of captive breeding.

The positive effect of removals on the population could be much greater if there was an effect on adult survival rates, the vital rate with a higher elasticity. Similar previous

experiences (Marcström, Kenward & Engren 1988; Kauhala, Helle & Hello 2000; Baines, Moss & Dugan 2004) showed that predator control may have a positive effect on capercaillie breeding success, although none of them modelled its subsequent implications on population dynamics. The effect of predator removal on adult numbers was not so evident for Kauhala et al. (2000), despite it increased the counts of adults after two years of predator removal in islands of Sweden (Marcström, Kenward & Engren 1988). Of the 23 radio-marked capercaillies in an ongoing experience in our study area since 2007, six of them (26%) were killed by predators (four females and two males). Although it cannot be stated with certainty if they had died because of other reasons previously and they were subsequently predated, this shows that predation also affects adult capercaillie survival and not only offspring survival. As deduced from the value of the parameters in the literature, it does not seem likely to increase adult survival rates any further. Hence, adult mortality caused by predators is most likely compensatory, rather than additive in our population. All our results point towards the need of focussing on improving recruitment (productivity+fledgling survival) to enhance the capercaillie population in the Pyrenees.

Exploration of ultimate causes of predation

In all modelled scenarios the population came back to the original declining trend as soon as management ceased, as a consequence of our modelling procedure. However, this is likely to happen if the causes that are producing the current decline are not removed. Under the current circumstances, the releases may constitute only a temporal buffer to the loss of birds originated by the ultimate causes. According to the literature, the removal of predators seldom has had self-sustainable effects over time (Reynolds & Tapper 1996; Smith *et al.* 2010), although, short-term control of predators may allow prey species to achieve

permanently higher densities when predator-prey dynamics is subjected to a predator pit situation (Evans 2004).

Among the principal threats for the species mentioned by the IUCN Specialist Group (Storch 2007), pollution, collisions and exploitation, can be discarded as affecting our study population. The effect of other causes such as small population size, habitat degradation, human disturbance, predation and climate change is still to be studied. However, the study area, as most of the mountain areas in southern Europe, has experienced strong socio-economical changes over the last 60 years, characterized by a strong depopulation trend and abandonment of traditional land uses, such as the cease of the silvicultural practices (Lasanta-Martínez, Vicente-Serrano, & Cuadrat-Prats 2005). Synchronously, predator removing practices, traditionally, rewarded economically by the Spanish Government, were prohibited (Martínez-Abraín *et al.* 2008). Some studies have shown the negative effect of fragmentation-edge effects on capercaillie, increasing predation risk (Storch, Woitke & Krieger 2005), although little is known about the effect of forest densification. In this sense, a recent study by Ameztegui, Brotons & Coll (2010) shows that mountain pine forests, the main habitat for capercaillies, has almost doubled its density (trees/ha) in the Catalan Pyrenees between 1956 and 2006. This densification may influence two of the most commonly cited factors in relation to the general decline of capercaillie populations: a) predation rates, and b) bilberry cover.

In much of the study area the abundance of big game species (i.e. roe deer, fallow deer –an introduced species- and wild boar) has greatly increased in the last decades, as it has been the case in most of the Iberian Peninsula (Gortázar *et al.* 2002; Rosell 2001; Carranza 2002). It seems reasonable that the larger the population the higher the number of carcasses in the wild caused by heavy snowfalls in these mountains. Moreover, during

the hunting season (October-February), hunters usually collect only their hunting trophies and leave behind the main portion of the carcasses. All these remains most likely serve as food for meso-carnivore guild during the winter season, when food availability typically is lower. In the absence of top predators and with the possible subsidization of meso-predators by hunting discards, this guild may be impacting on scarce prey, such as capercaillie (Gompper & Vanak 2008). In addition, several studies have shown that overabundant ungulate populations may also have a substantial detrimental effect on capercaillie and other closely related species, such as black grouse, by damaging ground vegetation, mainly bilberry (Pollo *et al.* 2003; Baines 1996).

As applied implications, since the management target is to prevent or correct a possible hyperpredation, the removal of predators or the release of captive-bred birds would only address proximate causes. We believe that these strategies should be implemented as urgency measures while longer term strategies, for the management of predation rather than predators, are implemented. In this sense, the reduction of wild ungulate numbers may have a double effect, reducing meso-predator numbers and preventing bilberry overgrazing. Similarly, the removal of hunting remains and of any other source of subsidization, could also have similar long-lasting effects. Also, the recovery of former pine densities could reduce the impact of predation (i.e. increasing chances to escape from terrestrial predators) and benefit the growth of bilberry, which is prevented within too dense forests.

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Table 1. Parameter combinations that led to the observed population growth rate ($\lambda=0.96$). Productivity (*Prod*) value 0.30 is the empirical population mean obtained in the field for 1989-2010. S_{Ad} , S_{Fl} adult and fledgling survival rates. Combinations 1 and 2 are included to illustrate the parameterization process, although they were discarded because they slightly exceed the highest survival probabilities cited in the literature for fledgling females.

<i>Combination</i>	<i>Prod</i>	S_{Ad}	S_{Fl}	<i>Elasticities</i> [*]
1	0.30	0.79	0.54	0.15-0.70-0.15
2	0.30	0.80	0.51	0.14-0.71-0.14
3	0.30	0.81	0.48	0.13-0.73-0.13
4	0.30	0.82	0.45	0.13-0.74-0.13

^{*} Elasticity for *Prod*, S_{Ad} and S_{Fl} respectively

Table 2. Vital rates increases to reach population stability. All the values are referred to the female part of the population.

<i>Vital rate</i>	<i>Baseline matrix</i>	<i>Value for stability</i>	<i>Range of values from literature</i>
Productivity	0.30	0.40 (↑33%)	0.42-2.12*
S _{Fl}	0.45	0.60 (↑33%)	0.19-0.50
S _{Ad}	0.82	0.86 (↑4.9%)	0.63-0.82

* The lowest value derived from Summer et al. 2000, for Scotland, and the highest derived from Kurki et al. 1997, for Finland.

Table 3. Preliminary results of the three-year predator removal experiment (2008-2010). Data refer to capercaillie productivity (fledglings/female) in the treatment area and in two control areas (1 and 2). The overall effect size was calculated as the standardized mean difference using a meta-analysis approach. N: number of detected adult females in that period; Mean and SD: average productivity for that period and its standard deviation.

<i>Zone</i>	<i>N</i>	<i>Mean</i>	<i>SD</i>
Treatment	42	0.57	1.33
Control 1	26	0.38	0.90
Control 2	46	0.43	0.81
Overall effect size		Mean=0.14	
		95% CI=(-0.18,0.46)	

Table 4. Average number of females after the implementation of each management scenario (calculated as the arithmetic mean for all the estimates in 1000 replications) and its 95% confidence interval (CI). Ratio is the quotient between the number of adult females from each management scenario in relation to the no-management scenario.

<i>Scenario</i>	<i>Description</i>	<i>Adult females</i>	<i>CI</i>	<i>Ratio</i>
0	No-management	100	68-132	1.00
1	Predator removal	134	92-176	1.34
2	Release_15 adults	115	81-150	1.15
3	Release_30 adults	128	93-164	1.28
4	Release_45 adults	148	111-186	1.48
5	Removal +Release 15adults	171	134-208	1.71
6	Removal +Release 30adults	203	161-244	2.03
7	Removal +Release 45adults	235	192-278	2.35

Figure 1. Life cycle used to build the Lefkovitch stage-based matrix models for capercaillie dynamics. FI=Fledglings; Ad=Adults; Release=Released adults; Prod=Productivity estimate; S_{FI} , S_{Ad} and S_{Rel} =Annual survival rates for fledglings, adults and released adults, respectively. The “Release” stage is only used in the management scenarios which include the release of captive-bred birds.

Figure 2. Density of adult capercaillie (males+females), from route census (birds/100 has). Crosses represent the discarded annual estimates, as they were obtained on the base of a field effort lower than 450 has. Triangles represent the values considered to estimate the population trend.

Figure 3. Observed number of adult females (broken line) and average number of adult females simulated by population modelling (continuous line). Vertical bars are 95% confidence intervals.

Figure 4. Mean trajectory of simulated management scenarios. Scenarios numeration is: 0_No management action; 1_Predator removal; 2_Release 15 adults; 3_Release 30 adults; 4_Release 45 adults; 5_Removal+release 15; 6_Removal+release 30; 7_Removal+release 45.

Figure 5. Estimated number of females in each management scenario after management period, and its 95% confidence intervals.