Predicting the implications of conservation management: a territorial occupancy model of Bonelli's eagle in Murcia, Spain

4 AUTHORS:

Martina Carrete
Universidad Pablo de Olavide
103 PUBLICATIONS **1,693** CITATIONS

José A Sánchez-Zapata
Universidad Miguel Hernández de Elche
125 PUBLICATIONS **1,313** CITATIONS

José Enrique Martínez
University of Murcia
77 PUBLICATIONS **683** CITATIONS

José Francisco Calvo
University of Murcia
65 PUBLICATIONS **803** CITATIONS

Predicting the implications of conservation management: a territorial occupancy model of Bonelli's eagle in Murcia, Spain

Martina Carrete, José A. Sánchez-Zapata, José E. Martínez and José F. Calvo

Abstract Bonelli's eagle *Hieraaetus fasciatus* is a threatened cliff-nesting raptor mainly distributed in the coastal regions of the Mediterranean. The European population has declined and the species is considered Vulnerable in Spain. Before effective conservation programmes can be proposed the causes of this decline need to be considered. In a monitoring programme of the population of Bonelli's eagle in Murcia carried out since 1983 we observed a marked decline, followed by a period of stability that began in 1990. Using demographic data (territorial bird survival, non-territorial bird survival, and fecundity) for 1990–1998 we applied a territorial occupancy model to evaluate management alternatives

for the species. The model, which assumes demographic stability, estimates an equilibrium proportion of habitat occupancy as a function of life history parameters, dispersal behaviour and habitat suitability. In spite of some limitations the model identified the most important conservation measures required for an increase in the proportion of territories occupied: the improvement of the survival of both territorial and non-territorial birds, and an increase in the proportion of suitable habitat.

Keywords Bonelli's eagle, demography, *Hieraaetus fasciatus*, management, Mediterranean, Spain, survival, territorial occupancy model.

Introduction

With species facing demographic and habitat pressure it has become increasingly important to quantify the extinction risk faced by particular populations (Sutherland, 1998), thus providing objective criteria for determining whether or not management intervention is required to ensure long-term persistence. It is known that smaller populations are more susceptible to extinction (Simberloff 1988), although in general a greater understanding of the relationship between population size and the likelihood of extinction is needed in conservation biology. In this context the usefulness of modelling for the management of exploited or rare populations has been recognized (Shaffer, 1981; Silvert, 1989), and there are several

Martina Carrete[1] (Corresponding author) Departamento de Ecología e Hidrología, Universidad de Murcia, Campus de Espinardo, 30100, Murcia, Spain.

José A. Sánchez-Zapata Departamento de Biología Aplicada, Área de Ecología, Universidad Miguel Hernández, Ctra Beniel km 3.2, Orihuela, Alicante, Spain.

José E. Martínez Departamento de Ecología e Hidrología, Universidad de Murcia, Campus de Espinardo, 30100, Murcia, Spain.

José F. Calvo Departamento de Ecología e Hidrología, Universidad de Murcia, Campus de Espinardo, 30100, Murcia, Spain.

[1]Present address: Departamento de Biología Aplicada, Área de Ecología, Universidad Miguel Hernández, Ctra Beniel km 3.2, Orihuela, Alicante, Spain. E-mail: eco3@um.es

theoretical models available for predicting the probability that a small population will become extinct and the time that it will take to do so (e.g. Hanski *et al.,* 1996; Hanski, 1999). Lande (1987) adapted the metapopulation model of Levins (1969) to territorial populations in a random landscape to evaluate habitat occupancy and extinction thresholds under different management actions. Lande's model describes changes in occupancy rate, as determined by the rates of local extinction and colonization, at a scale of individual territories. This territorial occupancy model becomes particularly useful when the overall population viability is more dependent on within-population dynamics (birth rates and death rates) than on between-population dynamics (patch extinction and colonization rates) (Noon & McKelvey, 1996). With regards to management planning, the model could be used to predict the consequences of habitat destruction or improvement on the population size of rare or endangered territorial species. Lande's model has been used, for example, to illustrate how habitat fragmentation would affect the northern spotted owl *Strix occidentalis caurina* (Lande, 1988; Noon & McKelvey, 1996).

A number of raptors are included in the IUCN Red List (Birdlife International, 2000; Hilton-Taylor, 2000) and by far the greatest threat to these species is habitat loss and degradation, followed by interaction with other native species, accidental mortality and the effect of invasive species (Criado & Stattersfield, 2001). Although Bonelli's eagle *Hieraaetus fasciatus* is not globally threatened, it has been included in the Spanish Vertebrate Red Data Book as Vulnerable (Blanco & González, 1992) and

has been listed as an Endangered European raptor (Rocamora, 1994). It is a cliff-nesting raptor found mainly in Mediterranean countries (Cramp & Simmons, 1980; del Hoyo *et al.*, 1994), and its main European population, in Spain, has declined by 25% over the last two decades (Sánchez-Zapata, 1997). The numerous studies of this species have been concerned with diet (Cheylan, 1981; Real, 1991; Martínez *et al.*, 1994; Gil-Sánchez *et al.*, 1994; Ontiveros & Pleguezuelos, 1999), habitat requirements (Gil-Sánchez *et al.*, 1996; Ontiveros, 1999; Sánchez-Zapata, 1999) and competition with other cliff-nesting raptors (Jordano, 1981; Donázar *et al.*, 1989; Fernández & Insausti, 1990; Gil-Sánchez, 1999). Causes that may lead to territorial desertion have been analyzed, and conservation strategies have been proposed (Real, 1991; Ontiveros, 1999). However, little is known about the life history parameters of Bonelli's eagle and the relative influence of these parameters on population trends and the threat of extinction. Such information is vital for designing and evaluating conservation plans.

We have used the territorial occupancy model (Lande, 1987) to identify the most appropriate management strategies for Bonelli's eagle. The aims of this paper are to model the proportion of suitable habitat occupied by the species as a function of the available habitat and the life history parameters of individuals, and to predict and discuss the value of different conservation strategies for the species.

Study area

The study area is the province of Murcia in south-east Spain, an area of 11,317 km² with a semi-arid Mediterranean climate, crossed by mountains that reach 2,000 m. The vegetation is typically composed of shrubs, grasslands and mixed forest, interspersed with cultivated lands (Carrete *et al.*, 2000). Bonelli's eagle uses cliffs for nesting, although in other regions its nests have been observed in trees (L. Palma, pers. comm.). Its home range includes open landscapes, where it obtains its food (Carrete, 2002). Although Murcia held one of the highest densities of Bonelli's eagle in the 1980s, the species has since declined considerably because of direct persecution, electrocution by and collision with power lines, and the pressure of recreational activities such as cycling and climbing (Sánchez-Zapata, 1997; Real *et al.*, 2001).

Methods

We studied the long-term changes in this population of Bonelli's eagle from 1983 to 1998. Known territories and potential breeding habitat for the species were visited during the breeding season. Breeding territories were located by observing territorial activity, courtship, brood-rearing activity, the presence of young, and any other conspicuous field signs (Fuller & Mosher, 1981).

The population was considered to be organized into three stage classes: fledging birds, non-territorial birds (juvenile, subadult, and adult birds that did not have a territory) and territorial birds (individuals occupying a breeding site, mainly adults). The annual survival rate s_t of territorial birds was calculated as the proportion of birds present in the population at the start of the breeding season that was still present in the population at the start of the following breeding season. A bird was considered to be dead if it had disappeared from its breeding site from one year to the next or if it had been replaced by another bird. Differential plumage colour during the first 4 years of life allows assessment of the rate of replacement of adults by birds younger than 4 years (Parellada, 1984), which provided us with the maximum territorial survival rate (Real & Mañosa, 1997). The absence of observations of a bird and of arranged nests and droppings on perches was taken as evidence of the disappearance of a pair. When only one bird was observed in a breeding territory, the loss of half a pair was recorded. When a pair was not recorded in its traditional site, we searched within a radius of several km for suitable breeding habitats, to exclude the possibility that the pair had moved to a new breeding site.

We assume that the region is made up of a number of territories H, a proportion h of which are suitable for Bonelli's eagle. The territorial occupancy model (for a detailed description see Appendix) uses the proportion p of suitable territories occupied by females at demographic equilibrium (i.e. when the population size and age structure are constant) and h to estimate the 'demographic potential' k of the population. The demographic potential gives the equilibrium proportion of territories that would be occupied by females in a completely suitable region, and it is determined by the life history parameters and dispersal behaviour of the species (Lande, 1987). The model allows us to predict the effects of environmental and demographic fluctuations (changes in h and k, respectively) on the proportion of suitable territories occupied by females.

We obtained k from estimates of p and h, and using this value and demographic data we calculated the search ability m (equation 4, Appendix), which is the mean number of searches that non-territorial birds are able to make for a suitable unoccupied territory before perishing of starvation or predation. The proportion h of the region that is suitable for Bonelli's eagle was determined from the number of territories occupied by the species during the period when the population was relatively stable, i.e. 1990–1998, and the total number of
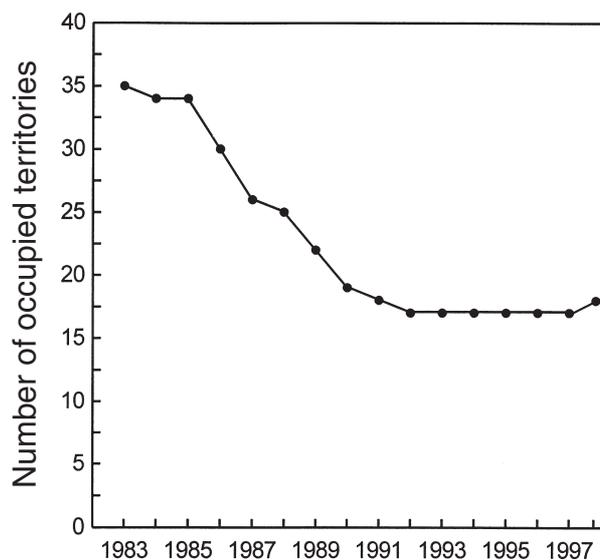
territories H known for cliff-nesting eagles (Bonelli's eagle and golden eagle *Aquila chrysaetos*, combined) in Murcia (120 territories, Sánchez-Zapata *et al.* 2000). The number of territories suitable for the species that were occupied during the year 1998 as a proportion of the total number of territories in the region available during the period 1990–1998 was used as a measure of p, the proportion of suitable territories occupied by females at demographic equilibrium.

For fledging survival rate s_o we used 0.78 (Real & Mañosa, 1997). Productivity P was calculated as the number of young fledged per territorial pair. Demographic analyses are usually formulated exclusively in terms of females and therefore, assuming a 1 : 1 sex ratio (Real & Mañosa, 1997), the number of female offspring of a female per year b was calculated as $P/2$. The survival rate s_n of non-territorial birds was obtained by equating it with the probability of successful juvenile dispersal (equation 2, Appendix) (Noon & McKelvey, 1996).

We used the model to examine the relationship between p and h, and the effect of changes in demographic parameters on p and on the relationship between p and h.

Results

We surveyed a total of 112 known territories of cliff-nesting eagles in Murcia, i.e. areas with cliffs that hold nests constructed by golden or Bonelli's eagles. The Bonelli's eagle population of Murcia declined from 35 breeding pairs in 1983 to 18 in 1990, since when they appear to have stabilised (Fig. 1). During the 1970s the study area held 42 breeding pairs (Sánchez-Zapata, 1997) but during the 1980s many territories were abandoned, mainly because of direct persecution, and today only 26 of these areas could be considered suitable for the species. Golden eagles have colonized eight of the abandoned territories, and in the other eight territories direct persecution could still be taking place. Table 1 summarizes demographic and other parameters for the period 1990–1998.

The relationship between p and h is shown in Fig. 2. When h increases, p increases until a value, k, that represents the equilibrium proportion of territories that would be occupied in a completely suitable habitat ($h = 1$). A decrease in the proportion of suitable territories lowers the equilibrium occupancy rate, with a steep decline as the proportion of suitable habitat declines. The demographic potential estimated for the species in Murcia is $k = 0.93$ and the minimum proportion of suitable habitat at which the population would become extinct (the extraction threshold, $p = 0$) is $1 - k = 0.07$ (8 territories). We estimated the minimum search ability, m, to be 3.7.

The equilibrium occupancy of suitable habitat by females p responds in different ways to changes in fecundity b, fledgling survivorship s_o, search ability m, and annual survival rate of territorial birds s_t (Fig. 3). Considering only the most likely ranges of these parameters for Bonelli's eagle (Real & Mañosa, 1997) we found that s_t had the strongest influence on p (Fig. 3a), followed by m and b (Fig. 3b and c, respectively). Fledgling survivorship s_o, did not seem to influence p to any great extent (Fig. 3d).

Using the highest values recorded in the literature (Arroyo & Garza, 1995; Real & Mañosa, 1997) for the

Fig. 1 The number of territories occupied by Bonelli's eagle *Hieraaetus fasciatus* from 1983 to 1998 in Murcia, south-east Spain.

Table 1 Estimates of demographic statistics, habitat variables, and the 'demographic potential' and extinction threshold (in terms of number of territories) of Bonelli's eagle in Murcia over 1990–1998 (see text and Appendix for details).

Parameter	Value
Probability of survival of fledglings s_o	0.78
Probability of survival of non-territorial birds s_n	0.24
Probability of annual survival of territorial birds s_t	0.89
No. female offspring per year b	0.59
Mean lifetime production of female offspring by a female R'_0	4.18
Potential habitat H, i.e. number of territories	112
Proportion of habitat suitable h (number of territories)	0.23 (26)
Proportion of habitat occupied p (number of territories)	0.69 (18)
Demographic potential $k \pm \sigma^2$	0.93 ± 0.02
Extinction threshold $1 - k$ (number of territories)	0.07 (8)
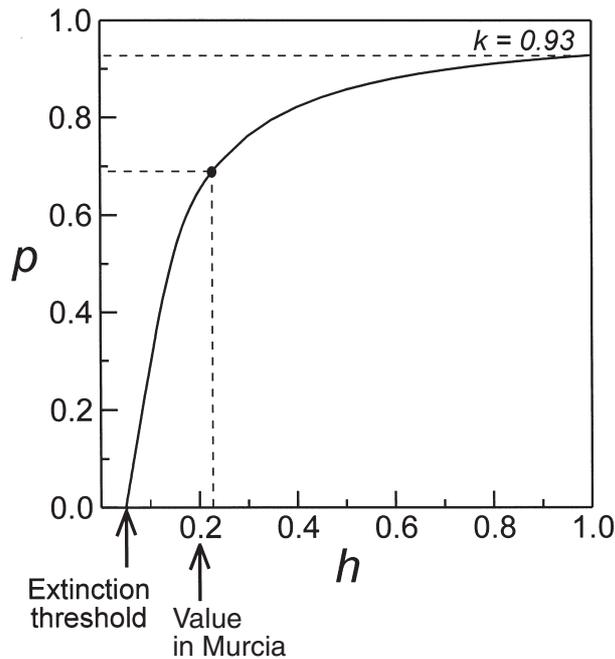
Fig. 2 Changes in the proportion of territories p occupied by females at demographic equilibrium as a function of the proportion of territories h that are suitable. The extinction threshold at $p = 0$, the 'demographic potential' k at $h = 1$, and the values of h and p in Murcia are indicated (see text and Table 1 for details).

fecundity and survival rate for territorial birds ($b = 0.62$ and $s_t = 0.96$, respectively) and the optimum values obtained with the model for search ability and survival rate of fledglings ($m = 7$ and $s_o = 0.83$, respectively) we can see how the equilibrium occupancy of suitable habitat changes with the proportion of the region that is suitable (Fig. 4) under different management options. Increasing the proportion of suitable habitat, h, increases the number of breeding pairs. However, for the same quantity of suitable habitat h, the proportion of occupancy p expected is higher when the survival rate of territorial birds s_t increases. Management actions focused on improving m would also increase p, although not to the same extent as increases in s_t. Increases in b and s_o have a lesser effect on p.

Discussion

Lande's (1987) model is a useful tool to predict how numbers of a breeding population of a territorial species may change as a function of the proportion of suitable habitat in a region, h, and life history parameters (adult survivorship s_t, fledging survivorship s_o, non-territorial survivorship s_n, and rate of production of female offspring b). The model is able to predict, qualitatively, the

likely outcomes of management strategies that focus on improvement of habitat availability and 'improvement' of these demographic parameters.

If the proportion of suitable habitat is increased, the proportion of territories occupied increases up to a maximum known as the 'demographic potential'. Because the model considers proportions, increments in suitable habitat are always matched by a greater number of breeding pairs. To increase the amount of suitable habitat, factors related to territorial desertion should be taken into account. Mortality is the most important cause of abandonment of territories by Bonelli's eagle in Murcia, but the situation is complex because direct persecution, habitat quality and competition with golden eagles may all be involved. Habitat quality plays a role because when prey (mainly rabbits *Oryctolagus cunniculus*) availability is low Bonelli's eagle may feed on pigeons, and breeding pairs may be persecuted by pigeon fanciers. The absence of a pair of Bonelli's eagles from a territory is then exploited by golden eagles, and whilst this species may not be responsible for displacement, it may be preventing recolonization. In this way, controls and actions to prevent conflicts between eagles and people may increase habitat availability if applied in areas where direct persecution is still active (Carrete *et al.*, 2002). Although Bonelli's eagle seems to be tolerant of habitat transformation such as increases in irrigated and urban lands, it is important that there are no increases in such landscape components around breeding areas because in other regions habitat degradation is known to be a major problem for the species (Arroyo & Garza, 1995). Even if the improvement in adult and non-territorial bird survivorship is the most important demographic conservation action for the species, providing breeding area for birds that are searching for territories would increase the breeding population size. This is particularly important if we consider that the species has a high value of the demographic potential k, i.e. it tends to occupy a high proportion of the available habitat.

Changes in life-history parameters influence the persistence of a population by means of the demographic potential. Increases in the survival rates of territorial and non-territorial birds, s_t and s_n, had the greatest effect on the demographic potential, while fecundity b and fledgling survivorship s_o had lesser effects. Adult survival is one of the most important factors influencing the population growth rate of other long-lived birds (Mertz, 1971; Newton, 1979; Real & Mañosa, 1997). Because reproductive performance of birds, in general, improves with age (Forslund & Pärt, 1995; Pärt & Forslund, 1996; Sánchez-Zapata *et al.*, 2000), increasing adult survival will have an additional benefit on the long-term productivity of the population (Newton, 1989). The territorial
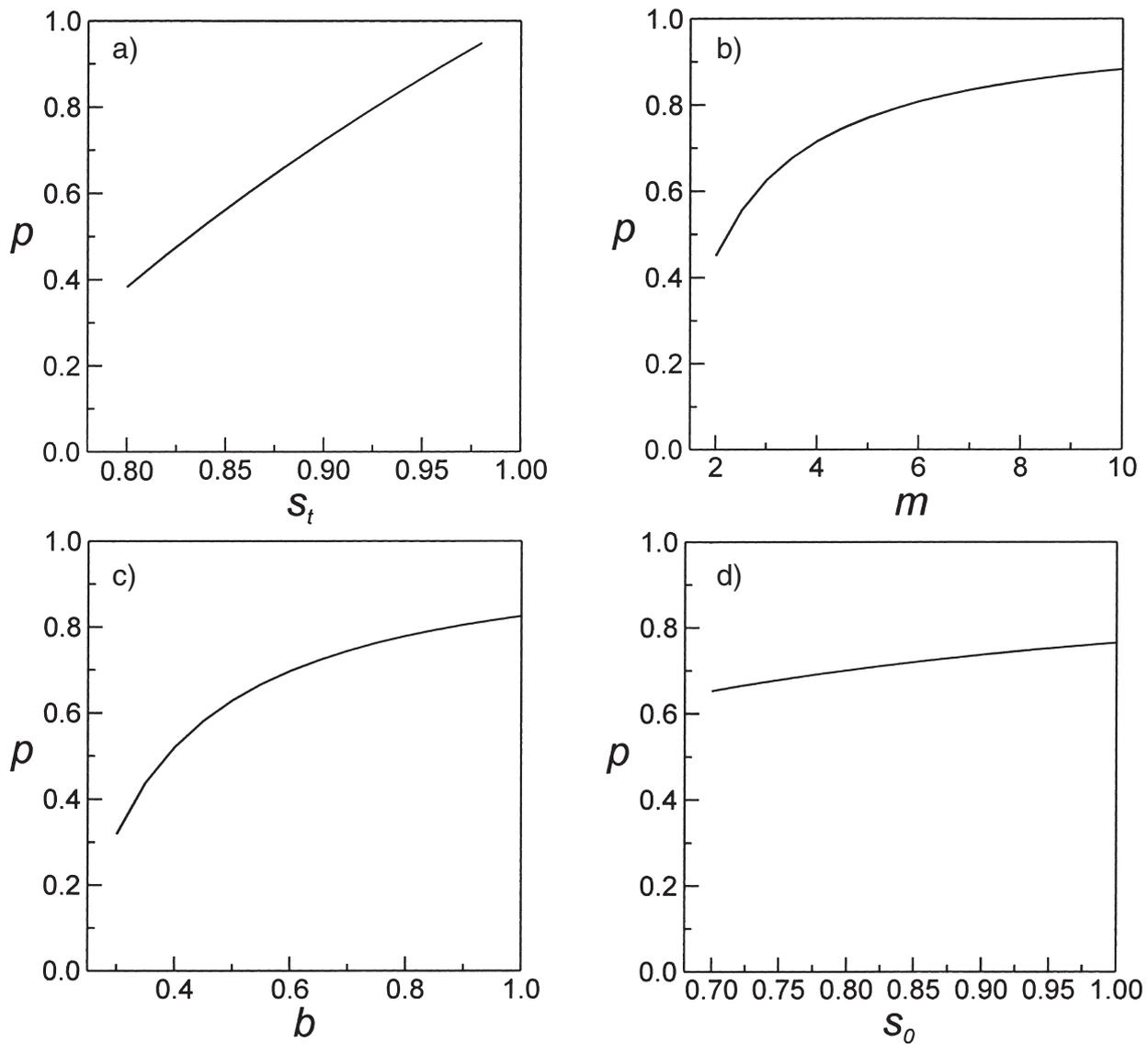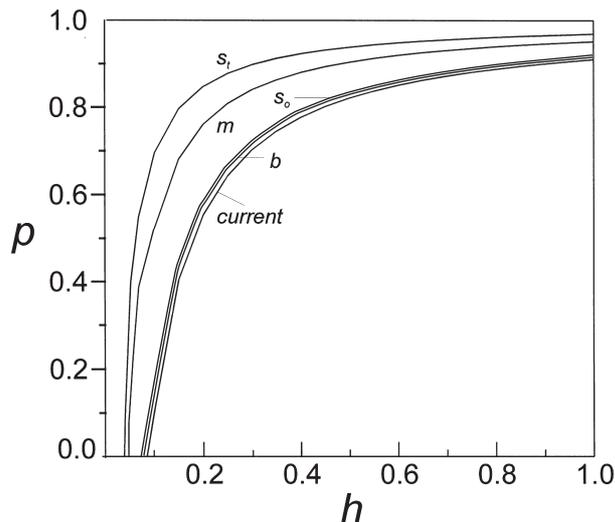
Fig. 3 Relationship between the proportion of suitable territories p occupied by females at demographic equilibrium, i.e. when the population size and age structure are constant, and (a) territorial bird survivorship s_t, (b) search ability m, (c) fecundity b, and (d) fledgling survivorship s_o.

bird survivorship used in the model, which was a maximum estimation, was lower than that found in other areas (Real & Mañosa; 1997), and so efforts could be made to improve it. Because direct persecution has been found to be responsible for territorial abandonment in the study area (Carrete *et al.*, 2002), increases in vigilance by forest guards, combined with reintroduction of prey such as rabbits, and installation of pigeon cotes to reduce the predation pressure of eagles on racing pigeons in areas where conflicts with pigeon fanciers occur (Sánchez-Zapata, 1997), could help to reduce the capture and killing of eagles. Such management actions would have effects at two levels: increasing the proportion of

available habitat occupied p and increasing the proportion of suitable habitat h by making abandoned territories more suitable.

The model also predicts that Bonelli's eagle is relatively sensitive to the search ability of dispersers m, the mean number of territories that a disperser visits before it dies. High dispersal mortality, mainly caused by electrocution by and collisions with power lines and persecution in dispersal areas (Real *et al.*, 2001), results on average in few territories being searched. This means that, although some individuals visit a lot of breeding areas, a high proportion of disperser do not visit any. Despite the importance of a knowledge of movement

Fig. 4 Changes in the proportion of suitable territories *p* occupied by females at demographic equilibrium, i.e. when the population size and age structure are constant, as a function of the proportion of territories *h* that are suitable suitable, in response to changes in territorial bird survivorship s_t, search ability *m*, fledgling survivorship s_o, and fecundity *b* (see text for details).

patterns (Wiens, 1996), little is known about the dispersal of most species, and in the case of Bonelli's eagle, although young birds have been wing-tagged and ringed to estimate pre-adult mortality (Real *et al.*, 1996), no detailed data on dispersal behaviour exists. However, during dispersal juveniles do leave the breeding population in which they were born, and so non-local conservation measures could improve survival. Our estimation of the survival rate of non-territorial birds was higher than that obtained previously for the species in Levante and Cataluña in Spain and in southern France (Real & Mañosa, 1997). Although the model cannot discriminate which part of non-territorial survival rate corresponds with local dispersal mortality and which with movements among neighbouring populations, we considered that this value of survival rate is useful for modelling because, in practice, it is the actual contribution of dispersing birds to the local population. Productivity of the population in Murcia was similar to that of other populations (Real & Mañosa, 1997), and as prey availability does not seem to be limiting reproduction (Ontiveros and Pleguezuelos, 1999; Carrete *et al.*, 2002), actions to improve it for this reason do not appear to be necessary at the present time.

Competitive relationships with other raptor species such as the golden eagle may interact with dispersal, affecting patterns of patch occupancy and extinction. Whereas Bonelli's eagle appears to be decreasing in numbers overall, golden eagles seem to be recovering and occupying territories abandoned by other species (Fernández & Insausti, 1990; Sánchez-Zapata, 1997). In areas where the two species are sympatric, interactions between these species should be taken into account in conservation programmes.

Lande's model is too optimistic in several respects because of the simplifying assumptions made. Allée effects (the difficulty in finding a mate), edge effects (resulting from the finite extent of regions containing suitable habitat), competition with sympatric species, and the influence of stochastic fluctuations on life history parameters may increase the extinction threshold of a territorial population (Lande, 1987). Therefore, as with other conservation problems, the results should be applied only as general guidelines. Practical considerations and local constraints will govern the best decisions in any single instance.

The Bonelli's eagles that we studied are not a discrete population, but a segment of a much larger one (del Hoyo *et al.*, 1994), and birds appear to be move between Murcia and the surrounding areas. Thus, the regulation of local breeding densities may depend not only on local events but also on the dispersal of individuals over a wider area. The decline of Bonelli's eagle throughout its range requires conservation action and, to be effective, these actions need to take place at both local and regional scales. The stability observed in the population in Murcia since 1990 has allowed us to apply Lande's (1987) territorial occupancy model, which could be a useful planning tool for management of the species in this region. Integrating information from different populations to obtain a large-scale conservation programme for the species should be the next step in the conservation of the species.

Acknowledgements

References

Arroyo, B. & Garza, V. (1995) Factores de regresión del Águila perdicera *Hieraaetus fasciatus* en España. *I Congreso de Rapaces del Holártico. Resúmenes.* Mérida, Spain.

Birdlife International (2000) *Threatened Birds of the World.* Lynx Editions & Birdlife International, Barcelona, Spain and Cambridge, UK.

Blanco, J.C. & González, J.L. (1992) *Libro Rojo de los Vertebrados de España*. Ministerio de Agricultura, Pesca y Alimentación, ICONA, Madrid, Spain.

Carrete, M. (2002) *El Águila real y el Águila perdicera en ambientes mediterráneos semiáridos: distribución, ocupación territorial, éxito reproductor y conservación.* PhD thesis, Universidad de Murcia, Murcia, Spain.

Carrete, M., Sánchez-Zapata, J.A. & Calvo, J.F. (2000) Breeding densities and habitat attributes: golden eagle in southeastern Spain. *Journal of Raptor Research*, **34**, 48–52.

Carrete, M., Sánchez-Zapata, J.A., Martínez, J.E., Sánchez, M.A. & Calvo, J.F. (2002) Factors influencing the decline of a Bonelli's eagle *Hieraaetus fasciatus* population in southeastern Spain: demography, habitat or competition? *Biodiversity and Conservation*, **11**, 975–985.

Cheylan, G. (1981) Sur le role determinant de l'alimentation dans le succés de reproduction de l'Aigle de Bonelli *Hieraaetus fasciatus* en Provence. *Rapaces Méditerranées*, **1**, 95–99.

Cramp, S. & Simmons, K.E.L. (1980) *The Birds of the Western Paleartic. Vol II.* Oxford University Press, Oxford, UK.

Criado, J. & Stattersfield, A. (2001) *Threatened Raptors of the World*. Fourth Eurasian Conference on Raptors: Abstracts. EBD-RRF, Sevilla, Spain.

del Hoyo, J., Elliot, A. & Sargatal, J. (1994) *Handbook of the Birds of the World. Vol II. New World Vultures to Guineafowl*. Lynx Edicions, Barcelona, Spain.

Donázar, J.A., Ceballos, O. & Fernández, C. (1989) Factors influencing the distribution and abundance of seven cliff-nesting raptors: a multivariate study. In *Raptors in the Modern World* (eds B.U. Meiburg & R.D. Chancellor), pp. 545–552. W.W.G.B.P., Berlin, London, Paris.

Fernández, C. & Insausti, J.A. (1990) Golden eagles take up territories abandoned by Bonelli's eagles. *Journal of Raptor Research*, **24**, 124–125.

Forslund, P. & Pärt, T. (1995) Age and reproduction in birds: hypothesis and tests. *Trends in Ecology and Evolution*, **10**, 374–378.

Fuller, M.R. & Mosher, J.A. (1981) Methods of detecting and counting raptors. *Studies in Avian Biology*, **6**, 235–246.

Gil-Sánchez, J.M. (1999) Solapamiento de hábitat de nidificación y coexistencia entre el Águila-Azor perdicera *Hieraaetus fasciatus* y el Halcón peregrino *Falco peregrinus* en un área de simpatría. *Ardeola*, **46**, 31–38.

Gil-Sánchez, J.M., Molino, F. & Valenzuela, G. (1994) Parámetros reproductivos y alimentación del Águila real *Aquila chrysaetos* y del Águila perdicera *Hieraaetus fasciatus* en la provincia de Granada. *Aegypius*, **12**, 47–51.

Gil-Sánchez, J.M., Molino, F. & Valenzuela, G. (1996) Selección de hábitat de nidificación por el Águila perdicera *Hieraaetus fasciatus* en Granada. *Ardeola*, **43**, 189–197.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford, UK.

Hanski, I., Moilanen, A. & Gyllenberg, M. (1996) Minimum viable population size. *The American Naturalist*, **147**, 527–541.

Hilton-Taylor, C. (compiler) *2000 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland, and Cambridge, UK.

Jordano, P. (1981) Relaciones interespecíficas y coexistencia entre el Águila real *Aquila chrysaetos* y el Águila perdicera *Hieraaetus fasciatus* en Sierra Morena Central. *Ardeola*, **28**, 67–88.

Lande, R. (1987) Extinction threshold in demographic models of territorial populations. *The American Naturalist*, **130**, 624–635.

Lande, R. (1988) Demographic model of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia*, **75**, 601–607.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.

Mañosa, S., Real, J. & Codina, J. (1998) Selection of settlement areas by juvenile Bonelli's eagle in Catalonia. *Journal of Raptor Research*, **32**, 208–214.

Martínez, J.E., Sánchez, M.A., Sánchez-Zapata, J.A. & Carmona, D. (1994) Donnés sur l'alimentation de l'aigle de Bonelli *Hieraaetus fasciatus* pendant le period d'elevage dans Murcia (SE Espagne). *Alauda*, **62**, 51–56.

Mertz, D.B. (1971) The mathematical demography of the California condor population. *The American Naturalist*, **105**, 437–453.

Newton, I. (1979) *Population Ecology of Raptors*. T. & A.D. Poyser. Berkhamsted, UK.

Newton, I. (1989) *Lifetime Reproduction in Birds.* Academic Press, London, UK.

Noon, B.R. & McKelvey, K.S. (1996) A common framework for conservation planning: linking individual and metapopulation models. In *Metapopulations and Wildlife Conservation* (ed. D.R. McCullough), pp. 139–165. Island Press, Washington, D.C., USA.

Ontiveros, D. (1999) Selection of nest cliff by Bonelli's eagle *Hieraaetus fasciatus* in southeastern Spain. *Journal of Raptor Research*, **33**, 110–116.

Ontiveros, D. & Pleguezuelos, J.M. (1999) Influence of prey densities in the distribution and breeding success of Bonelli's eagle *Hieraaetus fasciatus*: management implications. *Biological Conservation*, **93**, 1–7.

Parellada, X. (1984) Variació dels plomatges i identificació de l'àliga cuabarrada *Hieraaetus fasciatus*. *Rapinyaires Mediterranis*, **2**, 70–79.

Pärt, T. & Forslund, P. (1996) Age and breeding performance in monogamous birds: the importance of mate experience. *Trends in Ecology and Evolution*, **11**, 220.

Real, J. (1991) *L'Aliga perdiguera* Hieraaetus fasciatus *a Catalunya: status, ecología trófica, biología reproductora i demografia*. PhD thesis, Universitat de Barcelona, Barcelona, Spain.

Real, J., Grande, J.M., Mañosa, S. & Sánchez-Zapata, J.A. (2001) Geographical variation of causes of death of Bonelli's eagle *Hieraaetus fasciatus* in Spain. *Bird Study*, **48**, 221–228.

Real, J. & Mañosa, S. (1997) Demography and conservation of western European Bonelli's eagle populations. *Biological Conservation*, **79**, 59–66.

Real, J., Mañosa, S., Cheylan, G., Bayle, P., Cugnasse, J.M., Sánchez-Zapata, J.A., Sánchez, M.A., Carmona, D., Martínez, J.E., Rico, L., Codina, J., del Amo, R. & Eguía, S. (1996). A preliminary demographic approach to the Bonelli's eagle *Hieraaetus fasciatus* population decline in Spain and France. In *Eagle Studies* (eds B.U. Meyburg & R.D. Chancellor), pp. 523–528. W.W.G.B.P., Berlin, London and Paris.

Rocamora, G. (1994) Bonelli's eagle *Hieraaetus fasciatus*. In *Birds in Europe, their Conservation Status* (eds G.M. Tucker & M.F. Heath). Birdlife International, Cambridge, UK.

Sánchez-Zapata, J.A. (1997) *Plan de Recuperación del Aguila perdicera en la Región de Murcia*. Ambiental S.L., Consejería de Agricultura, Agua y Medio Ambiente, Murcia, Spain.

Sánchez-Zapata, J.A. (1999) *Las aves rapaces y su relación con la estructura del paisaje en ambientes mediterráneos semiáridos.* PhD thesis, Universidad de Murcia, Murcia, Spain.

Sánchez-Zapata, J.A., Calvo, J.F., Carrete, M. & Martínez, J.E. (2000) Age and breeding success of a golden eagle (*Aquila chrysaetos*) population in SE Spain. *Bird Study*, **47,** 235–237.

Shaffer, M.L. (1981) Minimum population sizes for species conservation. *BioScience*, **31,** 131–134.

Silvert, W. (1989) Modelling for managers. *Ecological Modelling*, **47,** 53–64.

Simberloff, D. (1988) The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics*, **19,** 473–511.

Sutherland, W.J. (ed.) (1998) *Conservation Science and Action.* Blackwell Science, Oxford, UK.

Wiens, J.A. (1996) Wildlife in patchy environments: metapopulations, mosaics and management. In *Metapopulations and Wildlife Conservation* (ed. D.R. McCullough), pp. 53–84. Island Press, Washington, D.C., USA.

Biographical sketches

The authors are studying various aspects of avian biology, particularly of raptors. Their interests include the factors limiting reproduction and survival, competition, habitat selection processes and dispersal patterns, and the elaboration of management actions that may ensure the conservation of the species being studied.

Appendix – The territorial occupancy model

In this model (Lande 1987) we assume that the region is made up of territories H, a proportion h of which are suitable; p is the proportion of suitable territories occupied by females at demographic equilibrium. If we assume that the expected rate of production b of female offspring by a female and adult survivorship s_t are independent of age of first reproduction α, then the mean lifetime production of female offspring by a female, R_o, is

$$R_o = s_o s_n \sum b s_t^{x-\alpha} = s_o s_n b / (1 - s_t) \tag{1}$$

where s_o and s_n are fledging and non-territorial survivorship.

If the probability that an obligately dispersing juvenile, as with Bonelli's eagle (Sánchez-Zapata, 1997; Mañosa *et al.*, 1998), succeeds in finding a suitable unoccupied territory in m searches is $1 - (ph + 1 - h)^m$ (Noon and McKelvey, 1996) when the population is at demographic equilibrium, i.e. with constant population size and age structure, $R_o = 1$ or

$$[1 - (ph + 1 - h)^m]R_o' = 1 \tag{2}$$

where $R_o' = s_o b / (1 - s_t)$ is the mean lifetime production of female offspring by a female. Solving equation 2 for p gives

$$p = \begin{cases} 1 - (1-k)/h, & h > 1 - k \\ 0, & h \leqslant 1 - k \end{cases} \tag{3}$$

where

$$k = [1 - 1/R_o]^{1/m} = [1 - ((1 - s_t)/(s_o b))]^{1/m} \tag{4}$$

is a measure of the 'demographic potential' of the population (Lande, 1987), the equilibrium proportion of territories that would be occupied by females in a completely suitable region. When detailed information on life history parameters is not available k can be calculated directly from p and h as $k = 1 - (1 - p)h$ (Lande, 1988). The sampling variance of k can be estimated as $\sigma_k^2 = h^2 \sigma_p^2$, where $\sigma_p^2 = p(1-p)N_p$ and N_p is the number of suitable territories sampled for occupancy. The extinction threshold, $h_{min} = 1 - k$, is the minimum proportion of suitable habitat necessary for population persistence.