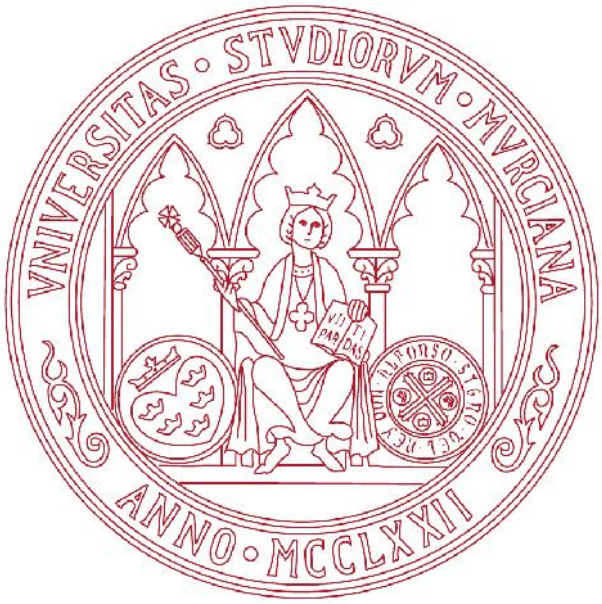

UNIVERSIDAD DE MURCIA

FACULTAD DE BIOLOGÍA

Territorial occupancy models in forest raptor populations

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Modelos de ocupación territorial en poblaciones de rapaces forestales

Dña. María Victoria Jiménez Franco

2014

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TESIS DOCTORAL

María Victoria Jiménez Franco

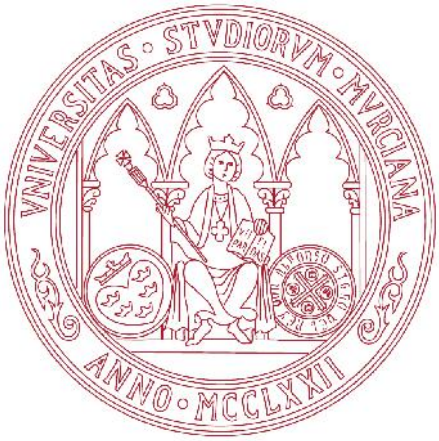
2014

Cover photographs: Carlos González Revelles.

Cover: Landscape of the study area, "Sierra de Burete, Lavia y Cambrón" (SE Spain). Species: Booted eagle *Aquila pennata* (left), Northern goshawk *Accipiter gentilis* (centre), Common buzzard *Buteo buteo* (right). Back cover: Landscape of the study area and Booted eagle *Aquila pennata*.

Cover design: Isa and Bea Hernández.

Chapters drawings: Javier Coll, Magdalena I. Romero, Francisco Robledano.



UNIVERSITY OF MURCIA

Faculty of Biology

Department of Ecology and Hydrology

Program of Doctorate Biodiversity and Environmental Management

PhD Thesis

Territorial occupancy models in forest raptor populations

Dissertation submitted by

Ms. María Victoria Jiménez Franco to obtain the

PhD degree in Biology with the International Mention

by the University of Murcia

Directors:

Dr. José Francisco Calvo Sendín

Dr. José Enrique Martínez Torrecillas

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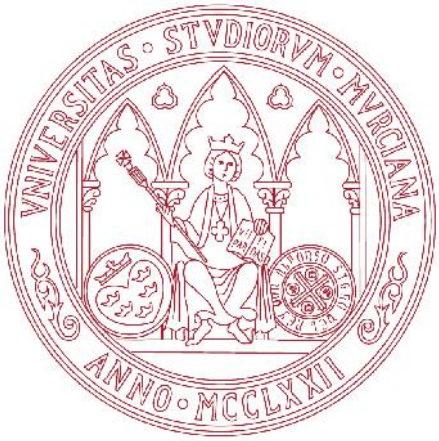

UNIVERSIDAD DE MURCIA

Facultad de Biología

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Tesis Doctoral

Modelos de ocupación territorial en poblaciones de rapaces forestales

Memoria de la Tesis Doctoral presentada por

Dña. María Victoria Jiménez Franco para optar al

Grado de Doctor en Biología con Mención Internacional

por la Universidad de Murcia

Directores:

Dr. José Francisco Calvo Sendín

Dr. José Enrique Martínez Torrecillas

Murcia 2014

A mis padres Pepe y Salud

A mis hermanos José y Fulgen

A mis abuelas Maruja y Conchita

INDEX

1. GENERAL INTRODUCTION

Booted eagle (*Aquila pennata*) in the nest

Javier Coll

1.1. Thesis structure

The present doctoral thesis entitled “Territorial occupancy models in forest raptor populations” is presented as a compendium of published articles to obtain the degree of Doctor with the "International Mention" in accordance with Royal Decrete 99/2011 (28 January, 2011), which regulates the official Doctorates, and the rules of the University of Murcia concerning PhD candidates (R-296/2014, of 12 April, articles 20 and 31). Accordingly, the thesis includes: 1) a general introduction, in which the publications are described and which justifies the scientific unity of the thesis; 2) the works themselves published in indexed international journals of repute; and 3) an general summary of the objectives of the research carried out and the final conclusions, which bring together the partial results presented in the individual articles. The report also includes a general discussion and mentions possible future lines of investigation.

1.2. Scientific context

The preservation of ecological systems and the organisms that comprise them is the subject of Conservation Biology, a multidisciplinary science that encompasses the application of basic science and management (Primack 1995). Hence, a new research model appears, where the results are intended to be immediately and directly applicable through the management of species and their habitat (Soulé & Wilcox 1980, Tellería 1999). Among the different disciplines applicable (Taxonomy, Genetics, Biogeography, etc), is Ecology, which studies biological systems and their interaction with the environment (Begon et al. 1996). Organisms are organised into different scales: individuals, populations and communities. Population ecology is a branch of ecology that studies the structure and dynamic of populations, as well as the environmental factors that influence on any changes of these populations (Newton 1979). It includes such aspects as abundance, social behaviour, movements, reproduction and mortality, which should be studied for the curricula of conservation practitioners (Oro 2013). One of the most studied stages of the life cycle of individuals is the reproductive period, since it provides direct information on reproductive descendance and the evolution of the population size. For this reason, within Conservation Biology, the measures taken in managing this stage (e.g., avoiding

human disturbances), and basic scientific studies that influence on this period are emphasised (Douglas & Pearce-Higgins 2014).

Within the reproductive period, nesting site establishment is an important process in reproductive success and the demographic equilibrium of bird populations (Citta & Lindberg 2007). According to Danchin et al. (2004), individuals acquire the information necessary to select a reproductive site in two, sometimes complementary, ways. For example, “personal information” is acquired from the physical characteristics of the habitat, which point to the quality of the same (Sergio & Newton 2003) and from the experience acquired by individuals (individual quality; Espie et al. 2004). The second way of acquiring information is known as “Inadvertent Social Information”, which is obtained from: 1) the previous reproductive success of conspecifics (Public information; Doligez et al. 2004); 2) cues based on information from reproductive individuals (Location cues), which may be social, such as the presence of conspecifics and heterospecifics (Sergio et al. 2004, Václav et al. 2011), or non-social, such as the presence of nests (Erckmannn et al. 1990).

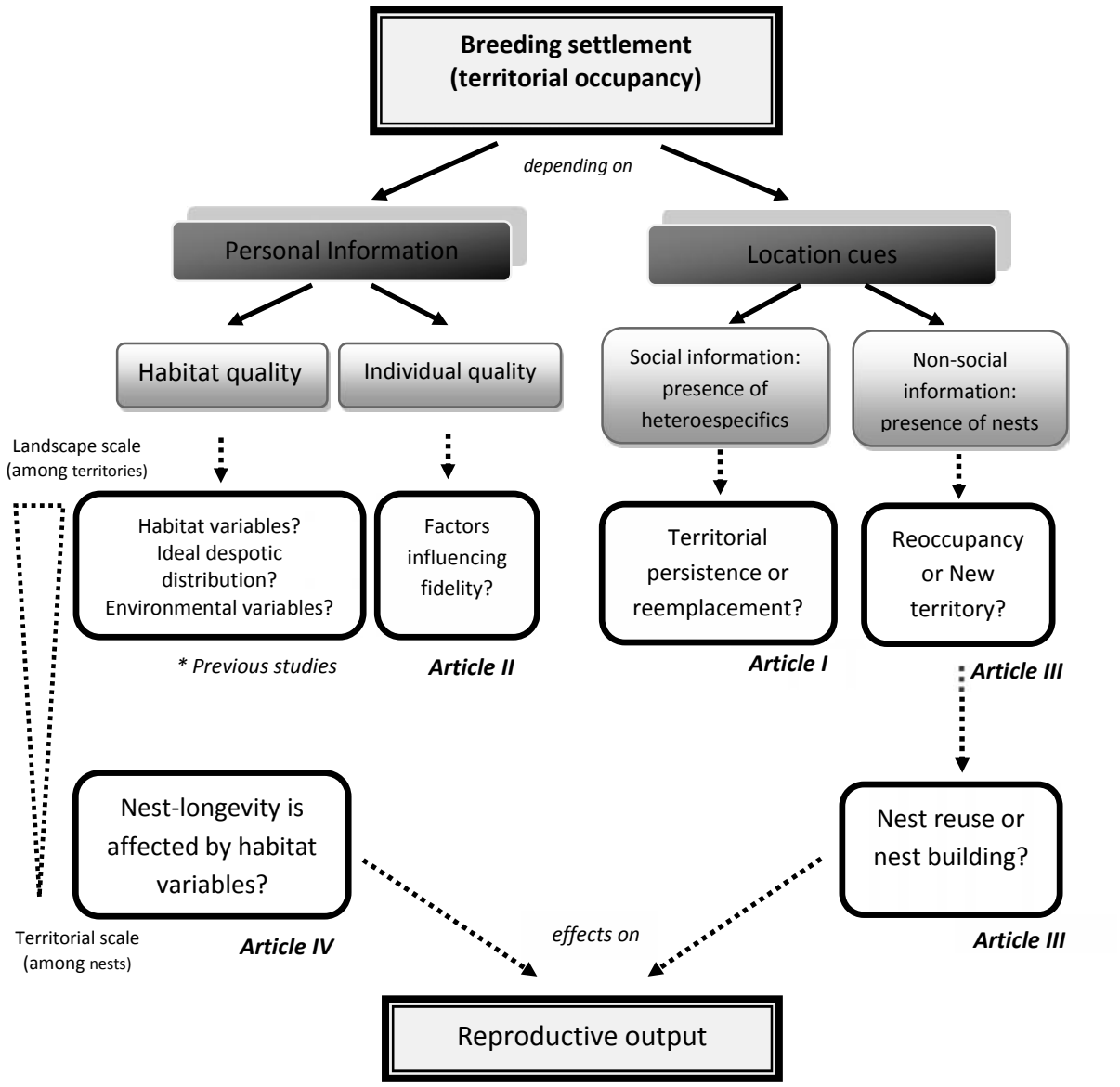
The selection of a breeding site is widely regarded as a hierarchical process, whereby individuals make choices at varying spatial scales, ranging from the regional, down to habitat type, and finally nest site (Citta & Lindberg 2007). In territorial species, the breeding site selection is important for defending the reproductive area, which is known as the territory (a habitat exclusively used by an individual or reproductive pair; Formica et al. 2004) during reproduction. According to Lande (1987), territorial establishment is defined with behaviour ranging from "the mere occupation of space to the active defence of the territorial space". The following spatial scale is the nesting site, a specific structure that may be artificial or created by individuals, and susceptible to be reused by breeding pairs in different reproductive periods (Ontiveros et al. 2008, Zhou et al. 2009, Václav et al. 2011). These nests are key breeding structures in areas of scant resources (Edworthy et al. 2012), when the habitat is susceptible to disturbance (Martínez et al. 2013) and when it is difficult to increase their availability artificially by means of nesting boxes or platforms (Björklund et al. 2013), as is the case with cavities (Edworthy et al. 2012). Although nest persistence along years may avoid energy costs to breeding pairs when nests are reused (Cavitt et al. 1999), such nests may also be harbour ectoparasites (Ontiveros et al. 2008) and act as ecological traps (Björklund et al. 2013). For this reason, an analysis of the lifespan of nests in the context of population conservation will help determine whether a given pool of nests is sufficient for species that depend on these resources. In territorial birds, the factors that

are considered to influence on breeding settlement, more specifically territory occupancy, are depicted in Figure 1, eliminating “public information", which is typical of colonial or gregarious birds (Sergio & Penteriani 2005).

Raptors, the last link in the trophic chain, are one of the most threatened avifaunal groups (Kóvacs & Burfield 2011), since their population size and productivity are limited by, among other natural and anthropic factors, by the availability of home ranges (where they obtain food), and of reproductive areas (e.g. woods and rocky places). Although raptors use a wide variety of habitats, those that select woods as their reproductive sites (nesting on forest platforms), as their home ranges, or both, are known as forest raptors (Newton 1979). The present PhD thesis develops territorial occupancy models for forest raptor populations to ascertain which aspects play a role in such territorial establishment, considering the above mentioned spatial scales.

1.3. Study ecosystem and antecedents: territorial occupancy of a raptor community in a Mediterranean forest

Mediterranean ecosystems play an important role in biodiversity conservation, where the processes of global change and human activity throughout history have led to the diversification and adaptation of individuals, giving, for example, to numerous endemic and Ibero-African species since these individuals were in a biogeographically important area (Blondel & Aronson 1999). The Mediterranean forests of the south-eastern Iberian Peninsula are key ecosystems for raptors for a variety of reasons. Firstly, they are part of the reproductive areas and home ranges of species such as the golden eagle (*Aquila chrysaetos*), the Bonelli’s eagle (*Aquila fasciata*) or the Eurasian eagle-owl (*Bubo bubo*), providing them with an abundance of preys (mammals such as rabbit, reptiles and medium-sized birds). Secondly, these forests provide nesting sites to both migrating (e.g. booted eagle *Aquila pennata*, short-toed eagle *Circaetus gallicus*, etc.) and sedentary (common buzzard *Buteo buteo*, northern goshawk *Accipiter gentilis*) species, providing the forest mass the materials for nest construction (Martínez & Calvo 2006; Martínez et al. 2011). These ecosystems also represent a refuge for wintering species like the merlin (*Falco columbarius*) and migratory corridors towards the north of Europe for species like the black kite (*Milvus migrans*) and honey buzzard (*Pernis apivorus*; Martínez & Calvo 2006).



* Previous studies: Martínez et al. 2006, Pagán et al. 2009, Jiménez-Franco 2010, Martínez et al. 2013, Bosch et al. *under review*.

Figure 1. Factors that influence on the breeding settlement (theoretical concept, shaded boxes) and ecological processes analysed in the four articles that conform this PhD thesis, classified in two spatial scales (non-shaded boxes): landscape (among territories) and territorial (among nests). Source: personal elaboration, based on Danchin et al. (2004).

The forest ecosystem studied, the "Sierras de Burete, Lavia y Cambrón" is situated in the central part of the province of Murcia (38º00´ N, 1º45´ W, SE Spain), with an area of 10,000 ha and declared as a Special Protection Area for birds (SPA; "ZEPA ES0000267"; Figure 2a). The climate is dry Mediterranean with an annual precipitation of less 400 mm and mean temperature of 17 ºC. The mountainous landscape (between 550 and 1234 m above sea level) contains large forest patches dominated by Aleppo pine *Pinus halepensis* on hillsides, small groves of *Quercus rotundifolia* on the highest peaks, and extensive areas in the valleys dedicated to agriculture, mostly dry-land crops including vine, olives, almonds and cereals (Martínez et al. 2011). The area is designated as a SPA under Annex I of the EU directive 2009/147/EC relating to the conservation of wild birds, by including the short-toed eagle (*Circaetus gallicus*), the booted eagle (*Aquila pennata*), the European eagle-owl (*Bubo bubo*) and the red-billed chough (*Pyrrhocorax pyrrhocorax*). Moreover, a part of the studied area, "Sierra de Lavia", has been included in the list of sites likely to be included in the list of Special Areas of Conservation (SAC; "LIC ES6200021"). The territory proposed for inclusion as SAC occupies 10% of the total SPA. There is no intense commercial exploitation of the woodlands in the study area, only forest management and regeneration projects, both public and private lands. Quarrying and hunting are also activities, all of which means that the area can be considered ideal for studying ecological aspects applied to the management and conservation of raptors. The results obtained for the studied area can be extrapolated to other Mediterranean areas and European forest systems harbouring birds of prey (Petty 1998, Björklund et al. 2013).

The bird community studied comprises three species of forest raptors with similar reproduction habits: the booted eagle, the common buzzard and the northern goshawk (Figure 3a-c). The booted eagle is a trans-Saharan migrant, while the other two are both sedentary species in the studied area, which represents the southernmost limit of their distribution range (del Hoyo et al. 1994). The abundance of species in the study zone differs (booted eagle being the most common, followed by common buzzard and northern goshawk; Martínez et al. 2013). Their conservation status also differs, northern goshawk being listed as in critical danger at regional level and booted eagle vulnerable; Robledano et al. 2006). All three species show a strongly territorial behaviour (Newton 1979, Krüger 2002a,b, Martínez et al. 2011), interchanging territories and reusing nests in different reproductive years (Martínez et al. 2013).

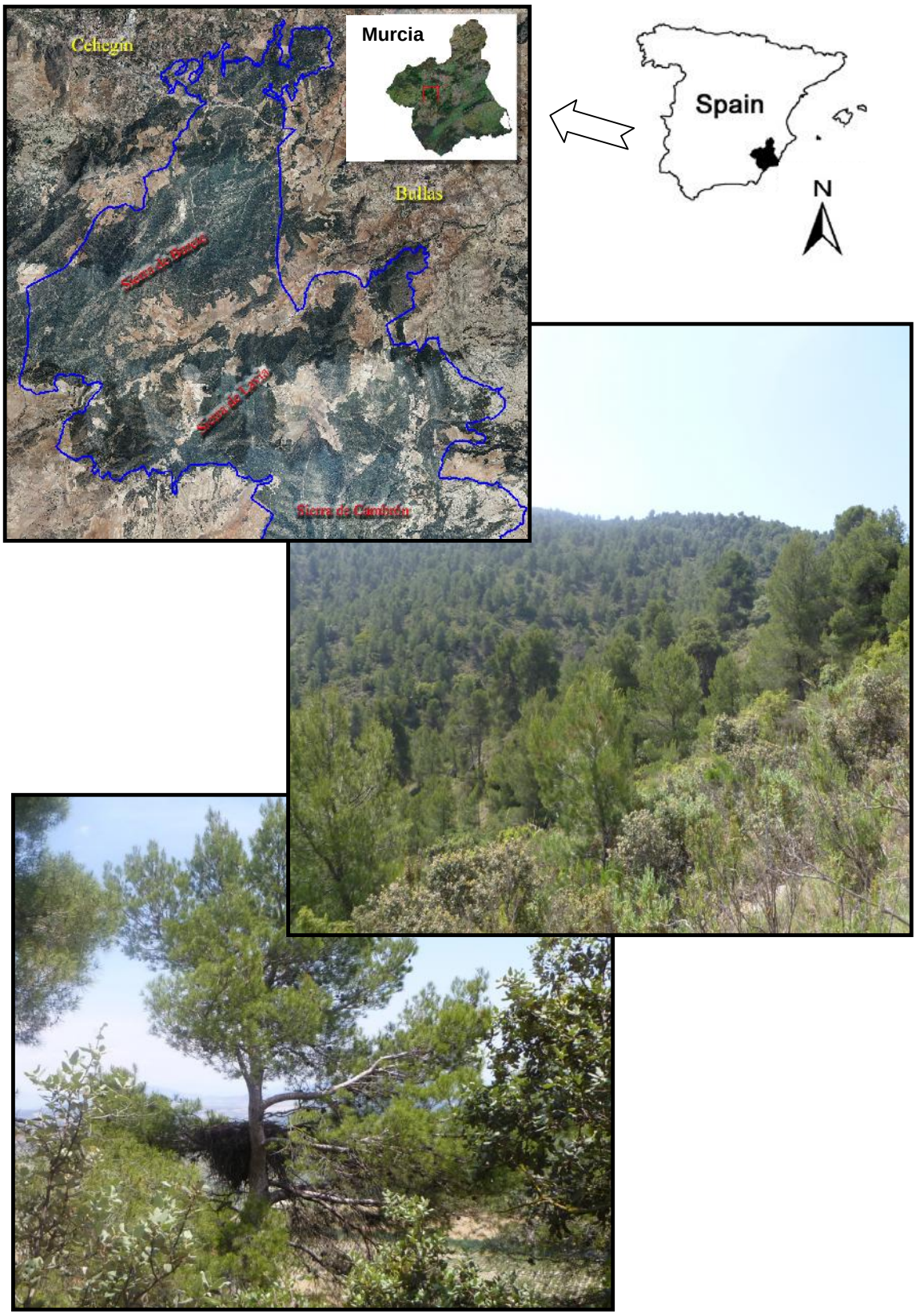


Figure 2.Study area and spatial scales studied in the territorial occupancy. a) Special Protection Area (SPA) "Sierras de Burete, Lavia y Cambrón" (SE Spain), b) landscape scale, appearance of a territory, c) territorial scale, nesting stand.

Figure 3. Forest raptor community studied. a) Booted eagle (*Aquila pennata*), b) Common buzzard (*Buteo buteo*), c) Northern goshawk (*Accipiter gentilis*). Photographs: Carlos González Revelles.

The spatial scales studied in this thesis include the above mentioned key structures for reproduction, covering a total of 70 territories and 157 nests (Figure 2b-c). Territory is defined as "any stretch of forest containing one (usually) or several nests (up to seven) within less than 300 m from each other, which is defended by breeding pairs", which is not to be confused with the home range for obtaining food, which may reach up to 17 km from the reproductive zone (Martínez et al. 2007). A nest is defined as "a large platform constructed of twigs and leaves, and placed either between the trunk and the branches or on the branches of the trees" (Petty 1998, Martínez et al. 2006). Although nest size may vary in different years (tending to increase when birds repair nests with new material in their reuse and diminish when nests are deteriorated or affected by adverse weather conditions; Martínez et al. 2013), they have a mean surface area of between 0.08 and 1.07 m^2 and vary in thickness from 13 to 88 cm (Martínez 2002).

Although research into booted eagle has increased in recent years (García-Dios 2005), its biology is little known. However, studies focused on the occupation habits and interactions between the common buzzard and northern goshawk have been more frequent in northern Europe (Krüger 2002a,b, Hakkarainen et al. 2004). In an attempt to partially remedy this situation, the Mediterranean Ecosystem Research Group of the Ecology and Hydrology Department of the University of Murcia began a long term monitoring programme, the aims of which were to look at general aspects of the ecology of the most abundant populations of booted eagle in the Iberian Peninsula. The results of this research have been the subject of two PhD theses (Martínez 2002, Pagán 2008) and are synthesised in Martínez et al. (2011).

The aspects already studied in relation with the present thesis have focused on regional scale (among different forested areas, including the sierras under the study area) and landscape scale (among territories), mainly considering the influence of habitat characteristics. At regional scale, the booted eagle population shows an aggregated distribution pattern, i.e., the individuals select the study zone (SPA "Sierras de Burete, Lavia y Cambrón") from among the different potential forested areas of the province of Murcia (Pagán 2008). The reasons for this pattern are not due to the characteristics of the habitat since forested areas both with and without nests in the region are similar. The main reason, it has been suggested, is the conspecific attraction, a common pattern of colonial species (Sergio & Penteriani 2005). In this sense, the presence of other individuals of the same species is interpreted as an indirect signal for selecting a reproductive area (Cornulier & Bretagnolle 2006), while

the habitat conditions do not determine the nesting sites. At landscape scale (considering the study area of this thesis), the best occupation model revealed that the probabilities of occupancy were also conditioned by a competition variable (intraspecific nearest-neighbour distance) and two habitat variables (the location of the nest on the valley slope and the distance to the nearest forest track; Martínez et al. 2006). However, the booted eagles select territories randomly, without following an ideal despotic distribution model, which points to the existence of territories of greater or lesser habitat quality (Pagán et al. 2009). Booted eagle reproductive success increases with the previous reproductive success in the territory (Jiménez-Franco 2010), with a NNE orientation of the nest and with the height of the first branch of the tree trunk (Martínez et al. 2006). However, meteorological effects (for example, the heavy rainfall and strong winds and snow) suffered in the area in 2007 had no influence on productivity (Martínez et al. 2013, Bosch *under review*).

1.4. General methodology: observational study and models

The study of the ecology of forest raptors, the subject of this thesis, is based on an observational study of the environment, of non-manipulative nature (sampling). The raptor community was monitored during the reproductive period (March-September) from 1998 to 2013. It was considered that all the territories and nests were known during the study period, since an intensive search was carried out to locate them in 1996 and 1997, and subsequent searches were performed to find new nests each breeding period. The data compiled included the territorial occupation or presence of reproductive individuals in territories (articles I, II, III) and nests (articles III, IV), where the detection of occupation is perfect, p=1, (see methodological description in the above articles). This type of data made it possible to detect processes such as colonization, abandonment, persistence and species alternation in territories (article I), and processes of territory creation, new establishments, nest creation or destruction (article III) and alternation of species in the same nests (article IV). In addition, when the territories were occupied, productivity was monitored (number of fledglings over 45 days; Steenhof 1987) and reproductive success (territory with productivity above 0; see description of methods in articles II, III and IV). Microhabitat variables were also measured in 10 m diameter plots around nest trees (see variables in article IV). Finally, 86 booted eagle individuals were marked by visual identification, using photographs and drawings of the plumage, and variables such as experience or sex were recorded (see article II for details).

Conservation Biology and natural sciences in particular, require simplified abstractions or models of the real world in order to make inferences concerning the implications of environmental change. We used a first order Markovian model (deterministic projection matrix; Caswell 2001) to analyse the dynamic of the different states of territorial occupation as time progressed (article I). To test territorial fidelity and patterns of nest reuse by the species, we used logistic and discrete regressions in mixed generalised linear models (articles II and III, respectively; McCulloch & Searle 2000). Finally, two analyses were made of nest longevity (article IV), one using a Kaplan-Meier survival model (Kaplan & Meier 1958) and the other a demographic model of populations applied to the nests after making a transition matrix among the different nest occupation states with time and considering nest destruction as an "absorbing state" (Caswell 2001).

1.5. Presentation of the different studies and justification

The present PhD thesis is composed of four scientific works, all original studies and published in international journals ranked in the ISI (*Institute for Scientific Information*) and included in the Thomson Reuters *Journal Citation Report* (JCR). All the studies have been carried out by the same research group of the Department of Ecology and Hydrology of the University of Murcia. Each study represents an independent article of the thesis, and each follows the standard scientific format of Introduction, Methods, Results and Discussion. The four articles are:

I. Jiménez-Franco, M.V.; Martínez, J.E. & Calvo, J.F. 2011. Territorial occupancy dynamics in a forest raptor community. *Oecologia*, 166: 507-516. doi:10.1007/s00442-010-1857-0.

II. Jiménez-Franco, M.V.; Martínez, J.E.; Pagán, I. & Calvo, J.F. 2013. Factors determining territory fidelity in a migratory forest raptor, the Booted Eagle *Hieraaetus pennatus*. *Journal of Ornithology*, 154: 311-318. doi:10.1007/s10336-012-0895-2.

III. Jiménez-Franco, M.V.; Martínez, J.E. & Calvo, J.F. 2014. Patterns of nest reuse in forest raptors and their effects on reproductive output. *Journal of Zoology*, 292: 64-70. doi:10.1111/jzo.12085.

IV. Jiménez-Franco, M.V.; Martínez, J.E. & Calvo, J.F. 2014. Lifespan analyses of forest raptor nests: patterns of creation, persistence and reuse. *Plos One*, 9(4): e93628. doi:10.1371/journal.pone.0093628.

The mentioned articles are interrelated and form a scientific unit – the PhD thesis in question – since they deal with the process of nesting site selection as influenced by different aspects or factors (Figure 1), using the same study ecosystem, from territorial to nest scale (Figure 2) and the same community of forest raptors (Figure 3). Besides representing a continuation of previous studies on booted eagle (Figure 1; Section 1.3), the thesis widens the study of the patterns observed to include common buzzard and northern goshawk. In choosing a nesting site, individuals must select an area or territory, so that the following questions are posed (ordered as in Figure 1): Which is greater – territorial persistence or replacement between species? Which factors influence territorial fidelity in booted eagle? Do individuals prefer to reoccupy or construct territories? Once a territory has been chosen, the individuals must establish in a nest and the following questions arise (Figure 1): Do individuals prefer to reuse or construct nests? What effect do nest reuse and construction have on reproductive success? Do habitat variables affect the longevity of forest platforms?

Below, the four articles that make up this PhD thesis are described:

The article I analyses the territorial occupancy dynamic of the forest raptor community and their heterospecific and conspecific interactions, all of them described by means of the processes of territorial colonization, abandonment, reemplacement and persistence of the species. To do this, a Markovian chain model was developed by using a transition matrix for all the study period, which is defined by a finite set of territorial occupancy states (booted eagle, common buzzard, northern goshawk and vacant). Moreover, a perturbation analysis simulates the effects of potential management strategies by changing the transition probabilities along the years, aimed at increasing the number of the territories by the less common species.

After observing high probabilities of territorial reoccupancy in the studies species, mainly in booted eagle, the factors determining territory fidelity of booted eagle are analysed in the article II. Territory fidelity was analysed in relation to different variables of the individual (previous breeding success, sex, mate switching and experience) and territory (average productivity in the territory). The data used refer to 86 eagles individually identified in the study area. The previous hypothesis was that booted eagles follow the ‘‘win-stay: lose-switch’’ rule, which suggests that the probability of site fidelity of individuals significantly increases with prior breeding success.

The article III analysed the influence of old nests in territorial settlement patterns of booted eagle and common buzzard (new territories, new establishments in old territories and reoccupancies). Furthermore, the patterns of nest reuse versus nest building are described for both species and this article also describes whether the effect of nest building is costly in terms of current reproductive output. The previous hypothesis is that nests act as location cues and that booted eagle and common buzzard would have different reuse patterns as a result of different distribution strategies during the annual cycle (migrant and sedentary, respectively).

After observing that nests are highly reused, the article IV determined the longevity of the forest nesting-platforms and analysed the factors affecting nest persistence. These studied factors included nest characteristics (nesting-platform height), nest-tree dimensions (nest-tree height, nest-tree diameter, crown cover of the nest-tree), the nest builder species and the frequency of platform use. Finally, this article tests whether the frequency of nest use increase the breeding success.

2. PUBLISHED STUDIES

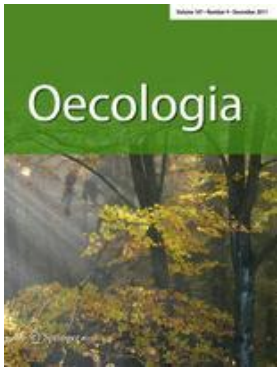
Booted eagle (*Aquila pennata*) and nestling in the nest

Javier Coll

2.1. ARTICLE I. Territorial occupancy dynamics in a forest raptor community

Jiménez-Franco, M.V.; Martínez, J.E. & Calvo, J.F.

Oecologia, 2011, 166: 507-516.



Abstract: A Markovian modeling approach was used to explore territorial interactions among three forest raptors coexisting in a forested natural area in southeast Spain: the booted eagle (*Hieraaetus pennatus*), the common buzzard (*Buteo buteo*) and the northern goshawk (*Accipiter gentilis*). Using field data collected over a period of 12 years, 11 annual transition matrices were built, considering four occupancy states for each territory. The model describes transitional processes (colonization, abandonment, replacement and persistence), permits temporal variations in the transition matrix to be tested, and simulates territorial occupation for a few subsequent years. Parameters for the species and community dynamics were described in terms of turnover times and damping ratio. A perturbation analysis was performed to simulate the effects of changes in the transition probabilities on the stable state distribution. Our results indicate the existence of a stable community, largely dominated by the booted eagles, and described by a time-invariant transition matrix. Despite the stability observed, the territorial system is highly dynamic, with frequent abandonment and colonization events, although interspecific territorial interactions (the replacement of one species by another) are uncommon. Consequently, the three species appear to follow relatively independent occupancy dynamics. Simulation of potential management actions showed that substantial increases in the number of territories occupied by the less common species (goshawk and buzzard) can only be attained if relatively large increases in their reoccupation and colonization rates are considered.

Keywords: Interspecific interaction; Markov chain; Population management; Perturbation analysis; Transition probability.

How to cite this article: Jiménez-Franco MV, Martínez JE & Calvo JF. 2011. Territorial occupancy dynamics in a forest raptor community. *Oecologia* 166: 507-516. doi:10.1007/s00442-010-1857-0.

URL: http://dx.doi.org/10.1007/s00442-010-1857-0

2.2. ARTICLE II. Factors determining territory fidelity in a migratory forest raptor, the Booted Eagle *Hieraaetus pennatus*

Jiménez-Franco, M.V.; Martínez, J.E.; Pagán, I. & Calvo, J.F.

Journal of Ornithology, 2013, 154: 311-318.

Abstract: Territory fidelity defines a process in which individuals reoccupy a territory during different reproductive periods. In this study, we used generalized linear mixed models to analyse the territory fidelity of the Booted Eagle *Hieraaetus pennatus* in relation to different variables of the individual (previous breeding success, sex, mate switching and experience) and territory (average productivity in the territory). The data used refer to 86 eagles (48 females and 38 males) individually identified between 1996 and 2009 in a Special Protection Area of ''Sierras de Burete, Lavia y Cambrón'' (Murcia, southeastern Spain). The results indicated that the breeding success in the previous year had significant effects on territory fidelity. The probability of reoccupation in cases of reproductive success in the previous year was 0.73, whereas in cases of reproductive failure, the probability of reoccupation in the following year was 0.41. Models which relate territory fidelity to biological variables of the individual (sex, mate switching and experience) and habitat quality were not significant. In conclusion, Booted Eagles show territory fidelity following the ''win-stay:lose-switch'' rule, which suggests that individuals are able to assess their previous reproductive experience to decide whether or not to return to the same territory the following year.

Keywords: Breeding success; Individual quality; Reproductive experience; Territory quality; Win-stay:lose-switch rule.

How to cite this article: Jiménez-Franco MV, Martínez JE, Pagán I & Calvo JF. 2013. Factors determining territory fidelity in a migratory forest raptor, the Booted Eagle *Hieraaetus pennatus*. *Journal of Ornithology* 154: 311-318. doi:10.1007/s10336-012-0895-2.

URL: http://dx.doi.org//10.1007/s10336-012-0895-2

2.3. ARTICLE III. Patterns of nest reuse in forest raptors and their effects on reproductive output

Jiménez-Franco, M.V.; Martínez, J.E. & Calvo, J.F.

Journal of Zoology, 2014. 292: 64-70.

Abstract: The presence of old nest structures can be an influential resource in reuse patterns and reproductive output for some birds. We used 15-year territorial occupancy data referring to the booted eagle *Aquila pennata* (a trans-Saharan migrant) and the common buzzard *Buteo buteo* (a sedentary species in southeastern Spain) to analyse old nest effects in territorial settlement patterns (new territories, new establishments in old territories and reoccupancies), to describe the patterns of nest building versus nest reuse and to test whether nest building is costly in terms of current reproductive output. The results indicated that the rates of reoccupancy and new establishments in old territories were higher than the rates of creating new territories for both booted eagles (74.13, 23.35 and 2.52%, respectively) and common buzzards (58.25, 38.84 and 2.91%, respectively). When breeding pairs settled in old territories, we observed a noticeably lower pattern of nest building than nest reuse both in booted eagles (10.03 vs. 89.97%) and common buzzards (8.00 vs. 92.00%). The nest-building rate by booted eagles was significantly lower in reoccupancies than in new establishments in old territories. Reproductive output for each species was not increased by nest reuse, although breeding success and productivity were significantly higher when newly established booted eagles constructed new nests than when reusing old nests. Our findings provides an interesting view on how forest raptors use old nests as important resources, probably taking them as location cues for nesting site selection and suggesting that unused nest sites should be left undisturbed since they could attract breeding raptor pairs in future years.

How to cite this article: Jiménez-Franco MV, Martínez JE & Calvo JF. 2014. Patterns of nest reuse in forest raptors and their effects on reproductive output. *Journal of Zoology*, 292: 64-70. doi:10.1111/jzo.12085.

Keywords: *Aquila pennata*; *Buteo buteo*; booted eagle; common buzzard; location cue; reoccupancy; territorial establishment.

URL: http://dx.doi.org/10.1111/jzo.12085

2.4. ARTICLE IV: Lifespan analyses of forest raptor nests: patterns of creation, persistence and reuse

Jiménez-Franco, M.V.; Martínez, J.E. & Calvo, J.F.

Plos One, 2014, 9(4): e93628.

Structural elements for breeding such as nests are key resources for the conservation of bird populations. This is especially true when structural elements require a specific and restricted habitat, or if the construction of nests is costly in time and energy. The availability of nesting-platforms is influenced by nest creation and persistence. In a Mediterranean forest in southeastern Spain, nesting-platforms are the only structural element for three forest-dwelling raptor species: booted eagle, common buzzard and northern goshawk. From 1998 to 2013, we tracked the fate of 157 nesting-platforms built and reused by these species with the aim of determining the rates of creation and destruction of nesting-platforms, estimating nest persistence by applying two survival analyses, describing the pattern of nest reuse and testing the effects of nest use on breeding success. Nest creation and destruction rates were low (0.14 and 0.05, respectively). Using Kaplan Meier survival estimates and Cox proportional-hazards regression models we found that median nest longevity was 12 years and that this was not significantly affected by nest characteristics, nest-tree dimensions, nest-builder species, or frequency of use of the platform. We also estimated a transition matrix, considering the different stages of nest occupation (vacant or occupied by one of the focal species), to obtain the fundamental matrix and the average life expectancies of nests, which varied from 17.9 to 19.7 years. Eighty six percent of nests were used in at least one breeding attempt, 67.5% were reused and 17.8% were successively occupied by at least two of the study species. The frequency of nest use had no significant effects on the breeding success of any species. We conclude that nesting-platforms constitute an important resource for forest raptors and that their longevity is sufficiently high to allow their reuse in multiple breeding attempts.

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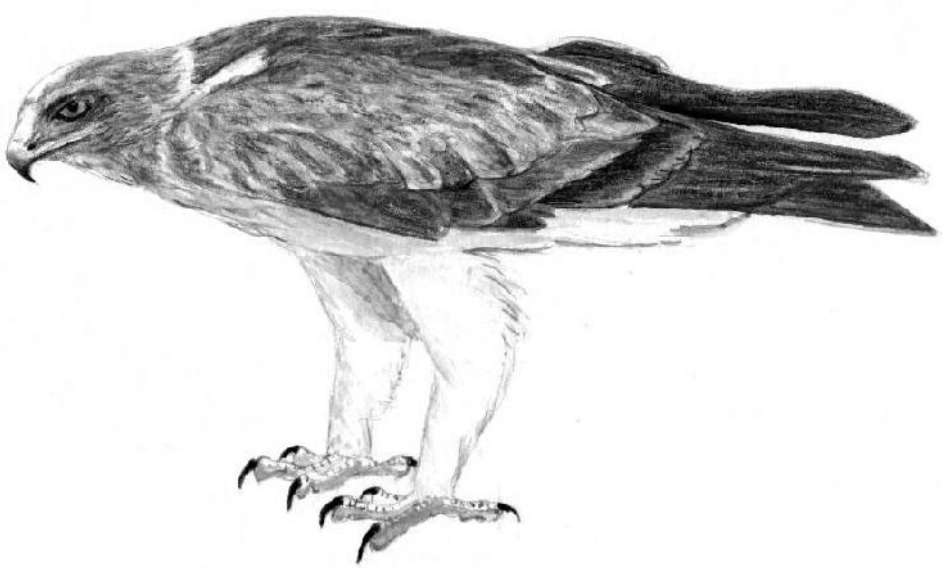
3. DISCUSSION



Booted eagle (*Aquila pennata*)

Magdalena I. Romero

3.1. Discussion

This thesis demonstrates that the forest raptor community studied selects breeding sites based on different factors or information, which range from personal information to location cues (Danchin et al. 2004). This process has been studied on two scales: landscape scale (among territories) and territory scale (among nesting stands). A previous study looked at this process at a regional scale (Pagán 2008), finding that the booted eagle population selects the area studied in this thesis (SPA "Sierras de Burete, Lavia y Cambrón") from among different and potential forested areas of the Murcia region, and shows an aggregated distribution pattern (Pagán 2008). The habitat characteristics analyzed in previous studies, which were not relevant for territorial establishment by booted eagles (Martínez et al. 2006), which select territories at random due to the lack of strong environmental heterogeneity (Pagán et al. 2009).

The main findings of this thesis (at landscape scale) show a high degree of territorial persistence in the three species and a very slight role for interspecific competition in the community studied, in contrast to the results of other studies on forest raptors where goshawks were the main predators (e.g., Kostrzewa 1991, Hakkarainen et al. 2004, Krüger 2002a,b). The competitive ability of the goshawk may be constrained in the study area because of the low population size of this species in relation to buzzards and booted eagles and its location at the periphery of the species' breeding range, a circumstance that has been shown to influence the demographic rates of some raptor species (García & Arroyo 2001, Ontiveros & Pleguezuelos 2003). In all the simulations carried out to increase the community diversity, a high number of vacant territories exists, especially when rates affecting the booted eagle were changed, which means that, even by decreasing the number of territories occupied by this species, the number of territories occupied by other species would not substantially increase. This result also demonstrates that no strong competition occurs among the three species to occupy territories, and that intraspecific factors might outweigh interspecific ones (Katzner et al. 2003; Carrete et al. 2005). In our case, more appropriate management measures should be aimed at increasing the persistence and colonization probabilities of the buzzard and the goshawk, as these would not modify the occupation rate of the booted eagle. Reoccupation rates can be promoted through executing management strategies directed at: (1) reducing unnatural mortality (e.g., by shooting or electrocution) during dispersal movements outside the breeding season

(Robledano et al. 2006), and (2) favoring territory fidelity through increasing reproductive success (Sergio & Newton 2003). In contrast, increasing colonization rates is a complicated task because there are many mechanisms involved in the selection of a breeding territory (Sergio & Newton 2003).

The territory fidelity of booted eagles considering different individual factors (sex, experience, mate change and previous breeding success) shows that individuals are able to use their previous breeding experience to decide whether or not to return to the same territory, following the ‘‘win-stay:lose-switch’’ rule. Habitat quality measured as the average productivity of a territory was not relevant in territory fidelity. These results corroborate the findings of previous works with this population in which territorial occupancy was seen to be significantly related to previous breeding success (Martínez et al. 2006) but not with habitat quality (Pagán et al. 2009). A similar pattern of territory fidelity was found in a black kite *Milvus migrans* population, where approximately 87% of the successful breeders returned to the same nest the following year, but only 58% did so if they had failed (Forero et al. 1999). Another study in individually identified peregrine falcon *Falco peregrinus* also supports our hypothesis that variation in breeding success is explained by individual identity, rather than territory (Zabala & Zuberogoitia 2014).

As regards other location cues, such as the influence of the presence of breeding structures or nests on territorial and nest reuse, our results suggest that old nests may represent location cues which could be used by birds to settle in breeding sites (old nest hypothesis; Erckmann et al. 1990). However, our study does not include experimental methods to explicitly test the old nest hypothesis (Yahner 1993). Both in new establishments and reoccupancy events the reuse rate was higher than the building rate. This pattern explains that nests are important breeding resources to be reused. In reoccupancy events, this pattern may be attributed to more experienced individuals that tend to reoccupy territories, preferring to reuse nests rather than building new ones following the ‘win-stay:lose-switch’ rule, which has already been tested in our booted eagle population (article II).

The findings of the third article did not support the hypothesis that building a nest has a cost in reproductive output, nor that booted eagle and common buzzard pairs benefit from nest reuse with a high probability of breeding success, or more fledglings. In agreement with these results, nest building does not influence reproductive output by tree swallows *Tachycineta bicolour* (Rendell & Verbeek 1996). In most papers reviewed by Mazgajski (2007), the presence of old nest holes did not

influence breeding parameters. Newly established booted eagle pairs had a probability of breeding success and productivity significantly higher when they built new nests than when they reused nests. These pairs tend to build nests, especially in new territories, and they are likely to be experienced individuals which do not follow territory fidelity after breeding success the previous year (30% of booted eagles; article II). The breeding success and productivity of both studied species in reoccupied territories was higher in reused nests than built ones. These results suggest that experienced individuals tend to reuse old nests, returning to the same territory due to previous breeding success, following the win-stay: lose-switch rule (70% of booted eagles; article II). Since alternations among nests were not relevant in our reoccupancy events and the number of nests was not as high as reported for some other species (e.g. Ontiveros et al. 2008), we reject the idea that any negative influence on breeding was due to ectoparasites (Mazgajski 2007, Ontiveros et al. 2008, Kochert & Steenhof 2012).

Since article III considered that breeding structures are important resources for the conservation of forest raptors, the longevity and patterns of nest building and destruction were analyzed in the following article (IV). Our results show that the survival estimates for the nesting-platforms, in general, were high and in accordance with the occupancy patterns of the breeding populations, as nests in the study area were occupied for a mean of 3.31 breeding attempts. These results for nest longevity agree with previous studies in the raptor community: high fidelity to the breeding sites, consecutive occupancies by booted eagle in the same territory ranging from 1 to 6 years (article II), and reoccupations by pairs of booted eagle and common buzzard, with around 85% reuse of the same nests (article III). Nest persistence in the present study was higher than that of nests built by European magpies and used by forest raptors, which persist for around 3 years (Zhou et al. 2009) and lower than that of nests created on cliffs, which may remain for hundreds of years (Burnham et al. 2009).

Persistence of nesting-platforms was not related to nesting-platform height, nest-tree height, nest-tree diameter, crown cover of the nest-tree, the nest builder species or the frequency of platform use. These results suggest that the habitat and nest-trees are sufficiently homogeneous for nests to be persistent, as the Aleppo pine is the only tree species that supports the nesting-platforms of raptors and has a good protective crown cover (Lõhmus 2006). Moreover, these results agree with those of Pagán et al. (2009), who indicated that territorial occupancy of the study area does not follow any occupancy pattern related to nest-trees and other habitat characteristics.

Our results show that the frequency of nest use did not have a significant effect on the breeding success of any of the studied species. These results are in agreement with those of a previous study, in which the reproductive success of pairs of booted eagle and common buzzard did not differ significantly between pairs reusing an old nest and pairs that built a new one (Article III).

3. 2. Future research directions

This thesis and the previous studies performed from 1996 onwards explain different aspects of the ecology and population dynamic of the booted eagle, common buzzard and northern goshawk in a Mediterranean ecosystem. However, there are some aspects that still need to be clarified:

The factors of individual quality that determine a higher reproductive output should be studied, perhaps by marking all individuals, or using satellite telemetry or non-invasive techniques, such as genetic analyses of the feathers. These techniques would provide more information about the age structure of the population, the survival of individuals and the movements both of floaters and adults breeders. Another factor that could influence the individual fitness and productivity is the kind of prey, hatching date and meteorological conditions, predation, as well as the behaviour of breeding pairs (García-Dios 2006, Krüger 2004, Martínez & Calvo 2005, Leikonen et al. 2013, Bosch et al. *under review*), which could be studied by installing cameras in the nesting-platforms to obtain more information about these aspects. Plumage polymorphism in the booted eagle (light and dark plumage) could be another relevant factor in reproduction and behaviour which should be explored (Galván et al. 2010). Finally, some aspects such us parasites in blood or ectoparasites could be a cause of nest failure, which is another topic that should be studied in detail.

Considering nesting-platforms, which are the only breeding stands for the occupant raptors in the study area, experimental designs to study the old nest hypothesis could be performed. For example, by removing all nests in some territories to analyze whether the breeding pairs select the same places again by building new nests, or whether individuals prefer to move to other hillsides where old nests may act as location cues. Another experiment could be to install artificial nesting-platforms to analyze the patterns of nest reuse and the effects of reproductive output between natural and artificial nests (Björklund et al. 2013). Moreover, the lifespan analysis used in article IV, which involved a transition matrix, could be useful for simulating the effects

of creating artificial nests (after incorporating the rate of artificial nest creation as a parameter of fertility in the model; Caswell 2001) in order to ascertain the temporal dynamic of the nests and its effect on the abundance of the forest raptor community.

Another phase of the life cycle that should be explored in booted eagles is their migration to Africa and wintering period. A few individuals have been tracked thanks to satellite telemetry (Chevallier et al. 2010, Mellone et al. 2013), so that information could be obtained about the migration routes and wintering places. In the same way, information about the dispersal of yearlings and floaters should be explored to describe the complete life cycle of this species. Nevertheless, the inconvenience of this study would be the cost of marking a great number of the forest raptor population.

After all the studies performed in the study area (SPA "Sierras de Burete, Lavia y Cambrón"), it is important that these local results be included in a more general context to understand more of the general and ecological patterns of forest raptor populations. Along the same lines, some studies describing the reproductive output of common buzzard and booted eagle have already been performed (Zuberogoitia et al. 2006, Bosch et al. *under review*). However, it is also relevant to compare the interspecific interactions of our study area with other forested areas (e.g. German forests; Krüger 2002a), or the different patterns of brood reduction (e.g. with the booted eagle population in Doñana National Park; Casado et al. 2008). Regarding the nesting-platforms used in our study, which were placed in only one tree species, Aleppo pine, future studies should be directed at estimating the longevity of raptor nesting-platforms in different types of forest tree species (Wesołowski 2012) or forest habitats (Edworthy et al. 2012). The next step would be to determine the relationship between the longevity of nesting-platforms and tree longevity. For example, other studies developed in cavities showed that cavity longevity is related to the stage of decay of the nest tree (Edworthy et al. 2012).

Finally, scientific studies which form part of Conservation Biology, as does this thesis, should publicize the results and recommendations obtained for them to be considered by wildlife managers (Oro 2013). Many management and conservation problems may be solved through by follow-up studies on the same topic. Although our study area does not suffer any relevant impact caused by human activities, management practices or weather conditions (Zuberogoitia et al. 2006, Martínez et al. 2013), some conservation measures could still be introduced to improve the breeding success of booted eagle (García-Dios & Viñuela 2000, Suárez et al. 2000, Martínez et al. 2007) or to increase the occupancy of common buzzard and goshawk.

4. GENERAL SUMMARY AND CONCLUSIONS

Booted eagles (*Aquila pennata*) in Torreguil

Francisco Robledano

4. 1. Overview

This thesis "Territorial occupancy models in a forest raptor population" represents an overview of aspects of Population Ecology that influence the reproductive settlement of bird populations, based on occupancy data and visual identification of some individuals. The study is focused on a forest raptor community (the booted eagle, the common buzzard and the northern goshawk) located in a Mediterranean forest ecosystem in southeastern Spain "Sierras de Burete, Lavia y Cambrón". This raptor community has been monitored for several years (1997-2013), and studies have focused mainly on general aspects of biology and ecology of the booted eagle, which has culminated in two previous doctoral theses (Martínez 2002, Pagán 2008).

The four research articles of this report provide new information about the factors that influence the territorial occupancy of forest raptor species, both at landscape scale considering territories (interspecific relationships, territory fidelity and reoccupancy) and at territorial scale considering nests (importance of reusing nests, nest longevity and the impact of nest reuse on productivity). This information will be useful for conservation and community management of raptors and their ecosystems during the reproductive period.

4.2. Objectives

The general aim of this thesis was to analyze the process of breeding settlement of three forest-dwelling raptors (booted eagle, common buzzard and northern goshawk) considering the different factors that influence this process, both related to individual quality and location cues (presence of heterospecifics and presence of nests). The specific objectives of this thesis were structured and developed in four scientific articles. The results of the first study were considered to establish the objectives of the second study and this process was repeated for the four studies consecutively.

Therefore, the specific aims of the first study were to construct a Markovian occupancy state model in order to examine the patterns of interspecific interactions among the three species (colonization, abandonment, replacement and persistence), assess the influence of temporal variations on the transition probabilities, and estimate representative parameters of the transient dynamics of the territorial system studied. This study also performs a perturbation analysis by means of an elasticity matrix of the

community structure to understand the transitions which produce the greatest changes in the structure of the stable state distribution, as measured by the Shannon-Wiener diversity index, and to simulate the effects of potential management strategies on the number of territories occupied by the two less common species, the common buzzard and northern goshawk by changing the transition rates with a high elasticity values.

In the second study we assessed territory fidelity in the booted eagle (using identified individuals over a 14-year period) in relation to the previous breeding success of the individuals, other individual-related factors (sex, years of consecutive experience in the same territory and mate change), and territory quality, measured as the average productivity of each territory during the study period.

The objectives of the third study were to describe and compare the territorial settlement pattern (territorial creations, new establishments in old territories and reoccupancy events) of booted eagles and common buzzards, to examine and compare the pattern of nest building and nest reuse in old territories by both species and to test whether nest building is costly to pairs in terms of current reproductive output.

Finally, the aims of the fourth study were to determine the rates of construction and loss of nesting-platforms during the study period, to estimate nest persistence by using two types of lifespan analysis and to test whether nest persistence is related to nest characteristics (nest height), nest-tree dimensions (nest-tree height, DBH and nest-tree crown cover), nest-builder species and frequency of use of the platform. This study also describes the pattern of nest reuse and alternation by different forest raptor species and assesses the effects of nest use on breeding success.

4.3. Results

The structured objectives described above were developed in their respective papers, obtaining results which were deciding factors in establishing the objectives of the subsequent works, giving to this thesis scientific unity and a lineal structure. From the first to the fourth paper, this thesis has provided information to explain the process of breeding site settlement from landscape scale to territorial scale (among nests), and considering information acquired in different ways, both personal information obtained from breeding pairs and location cues, obtained from the presence of heteroespecific and breeding structures such us nesting-platforms (Figure 1).

In the first study presented in this thesis, the Markovian modeling approach used to explore territorial interactions among three forest raptors indicated the existence of a stable community, largely dominated by the booted eagle. The loglinear analysis indicated that there were no significant differences among the annual transition matrices, describing a deterministic model and a time-invariant transition matrix for the raptor community with the processes of colonization, abandonment, replacement and persistence. The observed transition probabilities were higher for the diagonal elements of the transition matrix (persistence probabilities), while interspecific transitions were much less frequent. This result suggests a very slight role for interspecific competition in the community studied. Colonization frequencies were quite similar to disturbance frequencies, a characteristic suggesting a stabilized system of occupancy dynamics. Two dynamic parameters were obtained for the community: the turnover times and the damping ratio. The turnover times were low in all cases, indicating the existence of a highly dynamic territorial system with frequent abandonment and colonization events. The damping ratio was 1.73, indicating a high rate of convergence to the stable state distribution.

Regarding the perturbation analysis performed, the elasticity matrix showed the highest values for territorial persistence, colonization and abandonment probabilities for the booted eagle. In most cases, the elasticities of transitions affecting this species were negative, which indicates that a decrease in the corresponding probabilities results in an increase in the Shannon–Wiener diversity index of the stable state distribution. Probabilities involving interspecific transitions showed very low elasticities. Simulation of changes in the most elastic parameters of the probability matrix to increase the number of territories occupied by common buzzard and northern goshawk pointed to negligible effects on the stable state distribution, even after considering very large changes in the parameters (50–100%).

The second paper deals with the identification of factors affecting the territory fidelity of booted eagle. The results showed that the average occupancy period of booted eagle individuals was 1.89 ± 1.25 years, with no significant differences between sexes. The probability of reoccupation in cases of reproductive success in the previous year was 0.73, whereas in cases of reproductive failure, the probability of reoccupation in the following year was 0.41. This result corroborates the ‘‘win-stay:lose-switch’’ rule in which individuals remain faithful to sites in which past reproductive success was high, but leave sites where past reproductive success was low. Models which relate territory fidelity to biological variables of the individual (sex, mate switching and

experience) and habitat quality (average productivity of each territory during the study period) were not significant.

The third study analyses the importance of nests as breeding structures in the process of territorial settlement of booted eagle and common buzzard, by describing the patterns of territory reoccupancy and nest reuse. The rates of reoccupancy and new establishments in old territories were higher than the rates of creating new territories for both booted eagles (74.13, 23.35 and 2.52%, respectively) and common buzzards (58.25, 38.84 and 2.91%, respectively). When breeding pairs settled in old territories, we observed a noticeably lower pattern of nest building than nest reuse both in booted eagles (10.03 vs. 89.97%) and common buzzards (8.00 vs. 92.00%). The nest-building rate by booted eagles was significantly lower in reoccupancies than in new establishments in old territories, but there were no differences in common buzzards. Considering newly established pairs in old territories, the rate of nest building was higher in booted eagles (21.62%) than in common buzzards (10.00%), although for reoccupied territories, the rate of nest building was similar for booted eagles and common buzzards (6.38 vs. 6.67%). Anyway, there were no significant differences in any of the analyses.

Reproductive output for each species was not increased by nest reuse, although breeding success and productivity were significantly higher when newly established booted eagles constructed new nests than when reusing old nests (success: 58.33 vs. 25.86%; productivity: 0.87 vs. 0.41). This high reproductive output was due to breeding pairs establishing new territories, since the reproductive output of pairs that built new nests in old territories showed no significant differences with respect to nest reuse. In reoccupied territories, contrary to the reproductive pattern of new establishments, both the probabilities of breeding success and productivities of booted eagles and common buzzards were lower when breeding pairs built a nest than when they reused old nests, although without significant differences in any case.

The fourth study focused on nests as breeding structures that are created by breeding pairs, persist through different breeding attempts and are reused by different forest raptors. The rate of nest construction was 0.14 (±0.09) new nests per year, northern goshawks constructing significantly more nests than booted eagles and common buzzards. The 157 nesting-platforms monitored were distributed among a total of 70 territories and 51.4 % territories were constituted by one nesting-platform. The average rate of nest destruction was 0.05 (± 0.04) nests per year, being higher in 2007 (0.10) as a result of a severe storm. The nest longevity was high in the two

survival analyses used, although slightly different: whereas the Kaplan-Meier survival estimate provided a median nest longevity of 12 years, the population matrix model provided the average life expectancies of nests depending on the different occupancy states, which ranged from 17.9 to 19.7 years for vacant and occupied by booted eagle, respectively. Cox proportional-hazards regression models, used to know factor affecting to nest persistence, showed that nest longevity was not significantly affected by nest characteristics (nest height), nest-tree dimensions (nest-tree height, DBH and nest-tree crown cover), nest-builder species or frequency of use of the platform.

The description of the patterns of nest reuse and alternation among species showed that 86% of nesting-platforms were occupied in at least one breeding attempt during the study period and 60%, 28% and 16% of all nests were occupied by booted eagle, common buzzard and northern goshawk, respectively. Although no nest was shared by all three studied species, 18% nests were used alternately in different breeding periods during the study period. The average frequency of nest reuse, considering nests that were available for five or more years, was 0.39 (±0.31) and had no significant influence on the probability of breeding success of any of the studied species.

4.4. Conclusions

The general conclusions of this thesis are:

1. The Mediterranean forest studied represents a suitable area to analyse the patterns of territorial establishment, creation, destruction and persistence, as well as the patterns of reuse of natural nests by the forest raptors studied (booted eagle, common buzzard and northern goshawk). These patterns could be extrapolated to other forest ecosystems and birds of prey.
2. The territorial occupancy dynamic of the forest raptor community is stable across the years, the main characteristic being a high territorial persistence of the three studied species. The most abundant species in the community is booted eagle and the interspecific territorial interactions among species are uncommon.
3. The Markovian models of territorial occupancy and perturbation analyses are effective tools for simulating the effects of potential management strategies aimed at increasing the diversity of the forest raptor community.

4. Territory fidelity of booted eagles is not influenced by biological variables of the individual (sex, mate switching and experience), or habitat quality, measured as the average productivity of each territory.

5. The booted eagle population (70% individuals) shows territory fidelity following the ‘‘win-stay:lose-switch’’ rule, which suggests that individuals are able to assess their previous reproductive experience to decide whether or not to return to the same territory the following year. This pattern attributed to individual quality should be studied in order to apply effective management measures in increasing the territory reoccupancy.

6. Nesting-platforms are important breeding resources for the forest raptor community since: 1) old nests may represent location cues which could be used by birds to settle in breeding sites (old nest hypothesis); 2) booted eagles and common buzzards also prefer to reuse these structures instead of building new ones; 3) nest construction rates are low; 4) most of the nests constitute a territory with only one nest.

7. Nest longevity determined through two kinds of survival analyses (Kaplan Meier survival estimate and population matrix model) was sufficiently high (12 and 18.5 years, respectively) to permit the studied bird community to reuse and alternate nests in multiple breeding attempts. The nest persistence is not affected by microhabitat characteristics, the builder species or the frequency of nest use.

8. All the forest nesting-platforms should be kept as a management measure in order to preserve an adequate supply of breeding sites for the raptors in our study area.

9. The reproductive output is not increased when booted eagles and common buzzards reused old nests instead of building new ones or with the frequency of nest use in any of the studied species. Moreover, in the case of newly established booted eagle pairs, the productivity and breeding success are higher with nest reuse. These were likely to be experienced individuals which do not follow territory fidelity after breeding success the previous year (30% of booted eagles).

10. The breeding site establishment of the studied forest raptors is a complex process determined by different factors, such as the individual quality and the presence of old nests. More studies should be made to clarify these factors and their effects on reproductive output.

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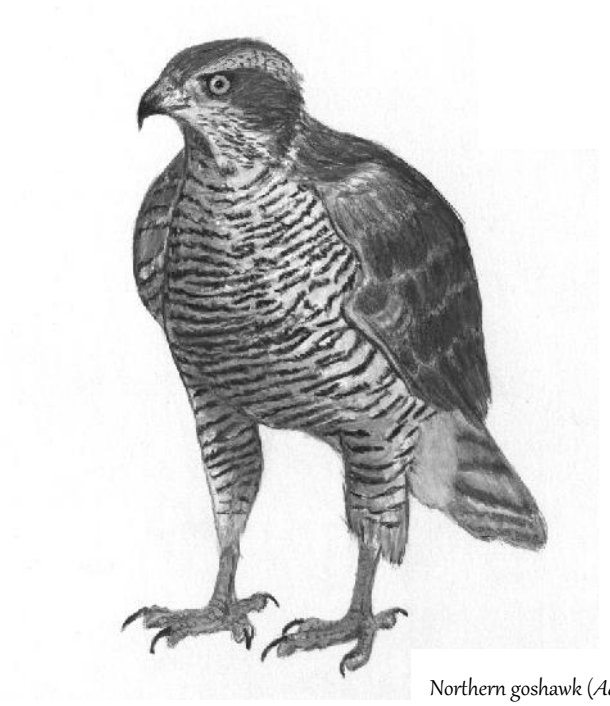

Northern goshawk (*Accipiter gentilis*)

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6. RESUMEN

Northern goshawk (*Accipiter gentilis*)

Francisco Robledano

6. 1. Resumen

La presente tesis "Modelos de ocupación territorial en poblaciones de rapaces forestales" aporta una visión general de aspectos de la Ecología de Poblaciones que influyen en el establecimiento reproductivo de poblaciones de aves, basada en datos de ocupación territorial y de identificación visual de algunos individuos. El estudio está enfocado en una comunidad de rapaces forestales (el Aguililla calzada, el Busardo ratonero y el Azor común) localizada en un ecosistema forestal Mediterráneo en el sureste de España, "Sierras de Burete, Lavia y Cambrón". Esta comunidad de rapaces ha sido monitoreada a lo largo de diferentes años (1997-2013), y sus estudios han sido enfocados principalmente sobre aspectos generales de la biología y ecología del Aguililla calzada, los cuales han culminado en dos tesis doctorales previas (Martínez 2002, Pagán 2008).

Los cuatro artículos de investigación de esta memoria aportan información novedosa sobre los factores que influyen en la ocupación territorial de especies de rapaces forestales, tanto a escala de paisaje considerando los territorios (relaciones interespecíficas, fidelidad territorial y reocupación), como a escala territorial considerando los nidos (importancia de la reutilización de los nidos, longevidad e influencia de la reutilización de nidos en la productividad de las especies). Esta información será útil para la conservación y gestión de la comunidad de rapaces y para los ecosistemas donde se encuentran durante el periodo reproductivo.

6.2. Objetivos

El objetivo general de esta tesis fue analizar el proceso de establecimiento reproductivo de tres rapaces forestales (Aguililla calzada, Busardo ratonero y Azor común) considerando diferentes factores que influyen en este proceso, tanto relacionados con la calidad del individuo y con las pistas de localización (presencia de heteroespecíficos y presencia de nidos). Los objetivos específicos de esta tesis fueron estructurados y desarrollados en cuatro artículos científicos. Los resultados del primer estudio fueron considerados para establecer los objetivos del segundo estudio y este proceso fue repetido para los cuatro estudios consecutivamente.

Por tanto, los objetivos específicos del primer artículo fueron construir un modelo Markoviano de estados de ocupación para examinar los patrones de interacciones interespecíficas entre las tres especies objeto de estudio (colonización, abandono, reemplazo y persistencia), evaluar la influencia de las variaciones temporales sobre las probabilidades de transición, y estimar parámetros representativos de las dinámicas de transición del sistema territorial del estudio. En este estudio también se realiza un análisis de perturbación por medio de una matriz de elasticidad de la estructura de la comunidad para conocer las transiciones cuyos cambios producen los mayores cambios en la estructura de la distribución estable de estados, como medida del índice de diversidad de Shannon-Wiener. El último objetivo es simular los efectos de estrategias de gestión potenciales mediante el cambio de las tasas de transición con valores de elasticidad elevados y que están encaminados a incrementar el número de territorios ocupados por las especies menos comunes, el Busardo ratonero y el Azor común.

El objetivo del segundo estudio fue evaluar la fidelidad territorial en el Aguililla calzada (usando individuos identificados sobre un periodo de 14 años) en relación al éxito reproductivo previo de los individuos, a otros factores relacionados con el individuo (sexo, años de experiencia consecutiva en el mismo territorio y el cambio de pareja) y en relación a la calidad del territorio, medida como la productividad media de cada territorio durante el periodo de estudio.

En el tercer artículo se tuvieron como objetivos describir y comparar el patrón de asentamiento territorial (creación de territorios, nuevos establecimientos en territorios ya creados y eventos de reocupación) de las aguililla calzadas y busardos ratoneros, examinar y comparar el patrón de construcción de nidos frente a la reutilización de los mismos en territorios ya creados por ambas especies y testar si la construcción de nidos es costosa para las parejas en términos de éxito reproductivo.

Finalmente, los objetivos de cuarto estudio fueron determinar las tasas de construcción y pérdida de las plataformas forestales a lo largo del periodo de estudio, estimar la longevidad de los nidos usando dos tipos de análisis de supervivencia y testar si la longevidad de los nidos está relacionada con las características de los mismos (altura del nido), las dimensiones del árbol que soporta el nido (altura, DBH y cobertura del árbol), la especie constructora del nido y la frecuencia de uso de la plataforma de nidificación. Otros objetivos de este estudio también son describir los patrones de reutilización y alternancia de los nidos por diferentes especies de rapaces

forestales y evaluar los efectos de la reutilización de los nidos sobre el éxito reproductivo.

6.3. Resultados

Los objetivos descritos y estructurados arriba fueron desarrollados en sus respectivos artículos de investigación obteniendo resultados, que fueron a su vez factores decisivos para establecer los objetivos de los siguientes trabajos, dando a este tesis una unidad científica y una estructura lineal. Desde el primer al cuarto artículo, esta tesis aporta información para explicar el proceso de establecimiento en un lugar de nidificación, desde la escala paisajística a la escala territorial, y considerando información adquirida por diferentes vías, tanto información personal obtenida de las parejas reproductivas, como pistas de localización obtenidas de la presencia de heteroespecíficos y estructuras reproductivas tales como plataformas forestales de nidificación (Figura 1).

En el primer estudio presentado en esta tesis, la aproximación de modelos Markovianos usados para explorar las interacciones territoriales entre rapaces forestales nos permiten conocer la existencia de una comunidad de rapaces estable, altamente dominada por las aguilillas calzadas. El análisis loglineal indica que no habían diferencias significativas entre las matrices de transición anual, describiendo un modelo determinista y una matriz de transición invariable con el tiempo para la comunidad de rapaces, describiendo los procesos de colonización, abandono, reemplazo y persistencia. Las probabilidades de transición de la matriz de transición fueron más elevadas para los elementos en diagonal (probabilidades de persistencia), mientras las transiciones interespecíficas fueron mucho menos frecuentes. Este resultado sugiere una baja competición interespecífica de la comunidad estudiada. Las frecuencias de colonización fueron bastante similares a las frecuencias de perturbación, una característica que sugiere un sistema estabilizado de las dinámicas de ocupación territorial. Se obtienen dos parámetros de dinámica de la comunidad: las tasas de retorno fueron bajas en todos los casos, indicando la existencia de un sistema territorial altamente dinámico con eventos frecuentes de abandono y colonización. El parámetro *damping ratio* o coeficiente de amortiguación fue 1,73, indicando una tasa alta de convergencia al estado de distribución estable.

Respecto al análisis de perturbación llevado a cabo, la matriz de elasticidad muestra los valores más altos en las probabilidades de persistencia, colonización y

abandono del Aguililla calzada. En la mayoría de los casos, los valores de las elasticidades correspondientes a las transiciones de esta especie fueron negativos, lo que indica que una disminución en dichas probabilidades de transición resulta en un incremento en el índice de diversidad Shannon-Wiener para la distribución estable de los estados de ocupación. Las probabilidades relacionadas con las transiciones interespecíficas mostraron valores de elasticidad bajos. La simulación de los cambios realizados en las probabilidades de transición con mayor elasticidad para incrementar el número de territorios ocupados por Ratonero común y Azor común muestran efectos insignificantes sobre la distribución estable de los estados de ocupación, incluso después de considerar cambios elevados de los parámetros (sobre el 50-100%).

El segundo estudio trata de identificar los factores que afectan a la fidelidad territorial del Aguililla calzada. Los resultados muestran que el periodo de ocupación media de los individuos de Aguililla calzada fue de 1,89 ± 1,25 años, sin diferencias significativas entre sexos. La probabilidad de reocupación en los casos de éxito reproductivo en el año previo fue de 0,73, mientras que en los casos de fracaso reproductivo el año previo fue de 0,41. Este resultado corrobora la regla "win-stay:lose-switch" en la cual los individuos permaneces fieles a los sitios en los cuales el éxito reproductivo previo fue alto, pero abandonan los sitios donde el éxito reproductivo previo fue bajo. Los modelos que relacionan la fidelidad territorial con las variables biológicas del individuo (sexo, cambio de pareja y años de experiencia consecutiva en el mismo territorio) y con la calidad del hábitat (productividad media de cada territorio durante el periodo de estudio) no fueron significativos.

El tercer estudio analiza la importancia de los nidos como estructuras reproductivas en el proceso de establecimiento territorial del Aguililla calzada y el Busardo ratonero, mediante la descripción de los patrones de reocupación territorial y de reutilización de los nidos. Las tasas de reocupación y de nuevos establecimientos en territorios ya creados fueron mayores que las tasas de creación de nuevos territorios tanto para aguilillas calzadas (74,13, 23,35 y 2,52%, respectivamente) como para busardos ratoneros (58,25, 38,84 and 2,91%, respectivamente). Cuando las parejas reproductivas ocupan territorios ya creados, observamos un patrón notablemente más bajo de construcción de nidos que de reutilización de los mismos tanto en aguilillas calzadas (10,03 *vs*. 89,97%) como en busardos ratoneros (8,00 *vs*. 92.00%). La tasa de construcción de nidos por aguilillas calzadas fue significativamente más baja en las reocupaciones que en los nuevos establecimientos en territorios ya creados, aunque no hubieron diferencias significativas en los busardos

ratoneros. Considerando las parejas establecidas nuevamente en los territorios ya creados, la tasa de construcción de nidos fue mayor en las aguilillas calzadas (21,62%) que en los busardos ratoneros (10,00%), aunque para territorios reocupados, la tasa de construcción de nidos fue bastante similar para las aguilillas calzadas y busardos ratoneros (6,38 *vs*. 6,67%). En cualquier caso, no hubieron diferencias significativas en ninguno de los análisis.

La productividad de cada una de las especies no fue incrementada por la reutilización de los nidos, aunque el éxito reproductivo y la productividad fueron significativamente mayores cuando las aguilillas calzadas nuevamente establecidas construyeron nidos nuevos que cuando reusaron nidos antiguos (éxito: 58,33 *vs*. 25,86%; productividad: 0,87 *vs*. 0.41, respectivamente). Esta productividad alta fue debida a las parejas reproductivas que construyen territorios nuevos, ya que el éxito reproductivo de las parejas que construyeron nidos nuevos en territorios antiguos no mostraron diferencias significativas con respecto al reuso de los nidos. En territorios reocupados, contrario a los patrones reproductivos de nuevos establecimientos, tanto las probabilidades de éxito reproductivo y productividades de aguilillas calzadas y busardos ratoneros fueron más bajas cuando las parejas reproductivas construyeron un nido que cuando dichas parejas reutilizaron nidos antiguos, aunque sin diferencias reproductivas en ningún caso.

El cuarto estudio está enfocado sobre los nidos como estructuras reproductivas que son creadas por las aves reproductivas, persisten a lo largo de diferentes periodos reproductivos y son reusadas por diferentes rapaces forestales. La tasa de construcción de nidos fue 0,14 (±0,09) nidos nuevos por año y los azores construyen significativamente más nidos que las aguililllas calzadas y los busardos ratoneros. Las 157 plataformas forestales monitoreadas fueron distribuidas entre un total de 70 territorios y el 51,4% de los territorios fueron constituidos por una sola plataforma de nidificación. La tasa media de destrucción de nidos fue 0,05 (± 0,04) nidos por año, siendo mayor en 2007 (0,10) como resultado de una tormenta severa. La longevidad de los nidos fue alta en los dos análisis de supervivencia usados, aunque ligeramente diferente: mientras la estima de supervivencia de Kaplan-Meier aportó una mediana de la longevidad de los nidos de 12 años, el modelo de matriz de la población aportó una esperanza de vida media de los nidos dependiendo de los diferentes estados de ocupación, los cuales variaron desde 17,9 a 19,7 años para el estado vacío y ocupado por Aguililla calzada, respectivamente. Los modelos de regresión "Cox proportiona-hazards" usados para conocer los factores que afectan a la persistencia de un nido

mostraron que la longevidad del nido no fue significativamente afectada por las características del nido (altura del nido), las dimensiones del árbol del nido (altura del árbol, DBH y cobertura del árbol), la especie constructora o la frecuencia de uso de la plataforma forestal.

La descripción de los patrones de reutilización de un nido y alternancia entre especies mostraron que el 86% de las plataformas forestales fueron ocupadas en al menos un periodo reproductivo durante el periodo de estudio y el 60%, el 28% y el 16% de todos los nidos fueron ocupados por Aguililla calzada, Busardo ratonero y Azor común, respectivamente. Aunque ningún nido fue compartido por las tres especies estudiadas, el 18% de los nidos fueron usados alternativamente por las especies en diferentes periodos reproductivos a lo largo del periodo de estudio. La frecuencia media de reutilización de los nidos, considerando nidos que estuvieron disponibles durante cinco o más años, fue 0,39 (±0,31) y dicha frecuencia no tuvo una influencia significativa sobre la probabilidad de éxito reproductivo de ninguna de las especies estudiadas.

6.4. Conclusiones

Las conclusiones generales de esta tesis son:

1. El bosque mediterráneo objeto de estudio representa un área idónea para analizar los patrones de establecimiento, creación, destrucción y reocupación de territorios, así como los patrones de reutilización de nidos naturales por las rapaces forestales estudiadas (el Aguililla calzada, el Busardo ratonero y el Azor común). Dichos patrones podrían ser extrapolados a otros ecosistemas forestales y a otras aves de presa.
2. La dinámica de ocupación territorial de la comunidad de rapaces forestales es estable a lo largo de los años, teniendo como transición principal una alta reocupación territorial de las tres especies estudiadas. La especie más abundante en la comunidad es el Aguililla calzada y las interacciones territoriales entre especies son poco frecuentes.
3. Los modelos Markovianos de ocupación territorial y los análisis de perturbación son herramientas efectivas para simular los efectos de estrategias potenciales de gestión, encaminadas a incrementar la diversidad de la comunidad de rapaces forestales.

4. La fidelidad territorial de las aguilillas calzadas no está influenciada por variables biológicas del individuo (sexo, cambio de pareja y años de experiencia consecutiva en el mismo territorio), ni por la calidad del hábitat, medida como la productividad media de cada territorio.

5. La población de Aguililla calzada (70% de los individuos) muestra fidelidad territorial siguiendo el regla "win-stay:lose-switch'', lo cual sugiere que los individuos son capaces de evaluar su éxito reproductivo previo para decidir si vuelven o no al mismo territorio el año siguiente. Este patrón atribuido a la calidad del individuo debe de ser estudiado para aplicar medidas de gestión efectivas en incrementar la reocupación territorial.

6. Las plataformas forestales son recursos reproductivos importantes para la comunidad de rapaces ya que: 1) los nidos antiguos pueden representar pistas de localización las cuales podrían ser usadas por las aves para establecerse en los lugares reproductivos ("hipótesis de los nidos antiguos"); 2) las aguilillas calzadas y busardos ratoneros también prefieren reutilizar estas estructuras en lugar de construir nidos nuevos; 3) las tasas de construcción de nidos son bajas; 4) la mayoría de los nidos conforman un territorio con un solo nido.

7. La longevidad de los nidos, determinada a través de dos tipos de análisis de supervivencia (estimas de supervivencia Kaplan Meier y modelo de matriz de poblaciones), es suficientemente alta (12 y 18,5 años, respectivamente) para permitir a la comunidad de aves estudiadas reusar y alternar dichos nidos a lo largo de múltiples eventos reproductivos. La persistencia de un nido no es afectada por las características de microhábitat, ni por la especie constructora ni por la frecuencia de reuso del nido.

8. Todas las plataformas forestales deben ser mantenidas como una medida de conservación, preservando así un aporte adecuado de sitios reproductivos para las rapaces del área objeto de estudio.

9. La productividad no es incrementada cuando las aguilillas calzadas y los busardos ratoneros reutilizan nidos antiguos en lugar de construir nidos, ni cuando la frecuencia de uso del nido por las especies estudiadas es elevada. Además, en el caso de las parejas de Aguililla calzada establecidas nuevamente en un territorio, la productividad y el éxito reproductivo son mayores con la construcción de nidos nuevos que con el reuso. Estas parejas son probablemente individuos con experiencia que no mantienen la fidelidad

territorial después del éxito reproductivo en el año previo (30% de aguililas calzadas).

10. El establecimiento en un lugar reproductivo de las rapaces forestales estudiadas es un proceso complejo determinado por diferentes factores, como la calidad del individuo y la presencia de nidos antiguos. Futuros estudios deben ser realizados para esclarecer estos factores y sus efectos en el éxito reproductivo.

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Common buzzard (*Buteo buteo*) and nestlings in the nest

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