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Nest site selection and productivity of the Spanish Imperial Eagle Aquila adalberti population of Doñana National Park, Spain

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March 1996

A thesis submitted to the Faculty of Graduate Studies and Research of McGill University in partial fulfilment of the requirements of the degree of Master of Science.

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A ma chère famille...

Aux enfants et aux animaux qui donnent à cette terre une raison de vivre...

#### ABSTRACT

I examined the nest site selection of the Spanish Imperial Eagle Aquila adalberti population of the Doñana National Park (SW Spain) from 1984 to 1994, in relation to the microhabitat and macrohabitat representing vegetative composition, degree of human influence and land use. The study included 75 active nest sites and 75 random sites. Univariate analyses and Generalized Linear Models were used. Nest sites differed significantly from the random sites for 87% of habitat variables measured. The model correctly classified 85.3% of the nest sites and 86.7% of the random sites. The probability of occupation of a site by a Spanish Imperial Eagle increased with tree height, angle of aperture of the wood stand, distance to paved roads, distance to urban centre and distance to water body.

Four productivity parameters (laying date, number of eggs, number of nestlings and number of chicks fledged) were measured over the same 10-year period for 16 territories in the Doñana Park. Spearman correlation coefficient analyses  $(r_s)$  were used to test for relationships between territory habitat characteristics, representing microhabitat, vegetative composition, degree of human influence and land use, and productivity. Egg-laying was later in territories situated closer to urban centres  $(n = 16 \ r_s = -0,529, P < 0.05)$  and those with more kilometres of power lines  $(n = 16, r_s = 0.518, P < 0.05)$ . No other productivity parameter was found to be

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influenced significantly by any of the territory features measured.

#### RÉSUMÉ

La sélection du site de nidification par la population Impériaux (Aquila adalberti) du Parc National de d'Aigles Doñana (SW de l'Espagne) a été étudiée pendant une période de 10 ans (1984 - 1994). Des variables représentant le microhabitat, la structure vegétale, le degré d'interférence humaine et l'utilisation d'habitat ont été échantillonnées pour 75 nids et 75 sites choisis au hasard. Les données ont été analysées utilisant la métode d'analyse univariée et les Modèles Linéaires Généralisés (GLM). Il y avait une différence significative entre les sites de nidification et les sites choisis au hasard pour 87% des variables d'habitat mesurées. Le modèle classifiait correctement 85.3% des sites de nidification et 86.7% des sites choisis au hasard. La probabilité qu'un Aigle Imperial occupe un site augmentait avec la hauteur de l'arbre, l'angle d'ouverture du peuplement forestier, la distance au chemin pavé, la distance à un centre urbain, et la distance au cours d'eau le plus près.

Quatre paramètres expliquant le succès reproducteur (la date de ponte, nombres d'oeufs, nombres d'aiglons, nombres d'aiglons envolés) ont été mesurés durant la même période de 10 ans dans 16 territoires du Parc de Doñana. Le coefficient de corrélation de Spearman  $(r_s)$  a été utilisé pour analyser la relation entre les caractéristiques d'habitat de chaque territoire et le succès reproducteur. La date de ponte était plus tardive dans les territoires qui étaient près des centres

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urbains ( $n = 16 r_s = -0,529$ , P < 0.05) et qui possédaient une haute concentration de lignes électriques (n = 16,  $r_s = 0.518$ , P < 0.05). Aucun autre paramètre expliquant le succès reproducteur n'a été influencé significativement par les caractéristiques d'habitat mesurées dans chaque territoire.

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#### Preface

The Doñana National Park population of Spanish Imperial Eagles has been the focus of many investigations (Calderón et al. 1987, Ferrer & Calderón 1990, Ferrer et al. 1990, Ferrer & Hiraldo 1991,1992) because of the sound background on the information pertaining to various aspects of the bird's biology (Doñana Biological Station Archives). This population has suffered great declines mainly due to human persecution but also as a result of habitat loss due to changes in land use (Meyburg 1989). The nesting habitat has been assessed quantitatively in only one other study (González et al. 1992) which focused on the macrohabitat of the entire population of Spanish Imperial Eagles. Because the Doñana population has failed to colonize the area around the park and because the Mediterranean marshland of Doñana is an unusual and rapidly changing habitat for this species (Ferrer & Calderón 1990, González et al. 1992), it is of crucial importance to study the habitat requirements of this population in a quantitative fashion.

This thesis examines the nest site selection both at the microhabitat and the macrohabitat levels, and the influence of territory structure on the productivity of the Doñana National Park population of Spanish Imperial Eagles over a 10-year period (1984-1994). It is part of a larger ongoing study conducted by members of the Doñana Biological Station and the

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Spanish National Institute for Nature Conservation (ICONA) on the factors influencing the productivity of the Spanish Imperial Eagle population of Doñana National Park. The thesis is divided into two papers to be published separately. The first paper pertains to the eagle's nest site selection comparing nest sites to randomly selected sites using both univariate analyses and Generalized Linear Models. Nest site selection by this particular population has not been studied previously.

The second paper examines the relationship between the habitat features in 16 territories in the Doñana Park and the productivity of the Spanish Imperial Eagle. Although nest tree species had previously been related to the hatching success (Calderón *et al.* 1987), no other habitat feature has been related to the reproductive success of this species.

The following is included in accordance with the regulations of the McGill Faculty of Graduate Studies:

"Candidates have the option of including, as part of the thesis, the text of one or more papers submitted or to be submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must be bound as an integral part of the thesis.

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The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". The thesis must include: A Table of Contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a comprehensive review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis.

In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of co-authored papers."

Section I will be submitted to "Ibis" under the title "Factors influencing nest site selection by the Spanish Imperial Eagle population of Doñana National Park, Spain". Section II will be submitted to the "Journal of Wildlife Management" under the title "Influence of territory structure on the productivity of the Spanish Imperial Eagle population of Doñana National Park, Spain".

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Primary authorship will be attributed to Isabelle Bisson with co-authorships to Miguel Ferrer and David M. Bird, supervisors of the thesis. Dr. Miguel Ferrer provided financial support, materials and literature as well as assisting in the initial elaboration of the methodology. Dr. David M. Bird provided some travel funds, offered guidance when requested and, contributed to the revision of all drafts. The candidate contributed to most of the tasks mentioned above, but especially to the final elaboration of the methodology, the collection of the data, their analysis and interpretation, and the writing of all drafts.

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#### LITERATURE REVIEW

Studies of habitat selection in avian species, as well as other vertebrates, are numerous as we strive to understand the habitat requirements of species urgently needing protection from the threats of habitat loss. Despite this, many of these studies have failed to answer the questions required to fulfil such a task (Gavin 1989, Keppie 1990). Nonetheless, quantitative descriptions of habitat are essential for the initial understanding of a species' ecology, and to lead us to a better understanding of possible management techniques that could be implemented in order to safeguard a species' survival.

This review is divided into four parts beginning with a brief overview at the theories of habitat selection in avian species in general followed by a review more specifically related to birds of prey. The third and fourth parts pertain to aspects of the ecology of the Spanish Imperial Eagle and more specifically, for the population of the Doñana National Park in southwestern Spain.

# Habitat selection in birds

It is widely recognized that many factors relevant to the survival of birds, such as availability of food, nest site requirements, and mode of locomotion effectively restrict the distribution of species. Early theories hypothesized that

these factors alone can trigger the habitat selection mechanism in bird species (see Hildén 1965 for review). More recent theories by Svärdson (1949) and Hildén (1965), proposed that habitat selection was instead controlled by external stimuli present in the environment. A classic example is seen in the Wood-warbler (Phylloscopus sibilatrix), whose settlement in an area is stimulated by an innate reaction of the species responding to the external stimuli provided by the topography or the vegetation (Svärdson 1949). Furthermore it was hypothesized that the settling reaction is controlled by a combination of different external stimuli together with an internal motivation, probably of a hormonal nature. When the summation of external stimuli attains a certain threshold, the reaction is released. Moreover, if external stimuli are absent or almost absent, the internal motivation may increase and in exceptional cases, reach the threshold of This often occurs when optimal habitats become response. crowded and consequently suboptimal habitats become occupied, the internal motivation overriding the absence of external factors. For example, the presence of a suitable nest site is enough to stimulate the settling reaction in the Western Kingbird (Tyrannus verticalis) in otherwise atypical habitats (MacKenzie & Sealy 1981). However, some factors in the environment may sometimes have a repellent effect on a bird like the presence of human structures for species that are sensitive to human disturbance. The absence of such factors

alone may be enough to trigger the settling reaction in otherwise less acceptable habitats (Hildén 1965). This is the case for many raptor species who will settle in atypical areas in exchange for the absence of human-related activities (Newton 1976, 1979).

Hildén (1965) defined two stages of habitat selection: (1) settling down and exploring the area and this is generally stimulated by features of the landscape and general characteristics of the terrain; (2) the acceptance of the area as a breeding territory or the rejection of it, depending on how close certain details conform to the other sign stimuli constituting the proximate factors in a given species' habitat selection mechanism. In order to understand this mechanism, one must first understand the distinction between ultimate and proximate factors, first defined by Baker (1938) and later developed by Lack (1949). Ultimate factors are essential for the survival of the species, and constitute the underlying reasons determining why each species breeds in its specific environment (Hildén 1965). These include food, the imposed by structural and functional requirements characteristics of the species, and shelter from enemies and Proximate factors serve to release the adverse weather. settling reaction and need not necessarily have any biological significance to the species as such. Hildén (1965) suggested the following factors as being proximate: landscape, terrain, nest-, song-, look-out and drinking sites, other animals. In

certain species, food also directly influence the choice of a territory.

Intraspecific and interspecific competition may modify habitat selection to a considerable degree. Dominant interspecific competition may cause a species to retreat to the most optimal habitats, that is to the adaptive peak of the species, while dominant intraspecific population pressure may cause a much greater variety in the habitats, forcing certain individuals to occupy suboptimal habitats decreasing the fitness of the overall species (Svärdson 1949). Intraspecific competition on habitat selection, more recently known as density-dependent habitat selection, has been reviewed in recent studies as having a major impact in the fitness of territorial individuals where fitness decreases with increasing density (Charnov 1976, Morris 1989). Population density therefore reflects the qualitative and quantitative differences between habitats.

# Nest site selection ---

Reynolds *et al.* (1982) defined a nest site as being "the area surrounding the nest tree, including the vegetation and topographic features, used by a nesting pair during an entire breeding season, exclusive of foraging areas".

Selection of a nesting site that meets the reproductive requirements of an animal is critical to its evolutionary fitness (Partridge 1978). Recently, studies of avian habitat

have recognized this and have turned to more specific investigations of the selection of a nest site, rather than the habitat as a whole (Rich 1986, González *et al.* 1992, Boe 1994, Blomqvist & Johansson 1995). These studies have become crucial in order to safeguard declining populations because for many species, the shortage of habitat is most pronounced in the lack of suitable nest sites (Svärdson 1949, Andrew & Mosher 1982).

#### Habitat loss ---

Habitat availability is the second major ecological variable that seems to influence population size in birds, the first being food (Gill 1990). In the managed forests of Britain, where dead trees and branches are routinely removed, the shortage of nest sites clearly limits the population densities of such species as the Pied Flycatcher (*Ficedula hypoleuca*) (Haartman 1951, Sternberg 1972). Other birds such as the Eurasian Kestrel (*Falco tinnunculus*, Cavé 1968) have also faced shortages of nest sites. In recent years, the loss or alteration of habitat has been recognized as one of the leading causes of the decline of avian species (Greenway 1967, Temple 1978, King 1981).

## Habitat selection in raptors

Raptors and the habitats they occupy have been the subject of many studies (Bechard 1982, Titus & Mosher 1982, Speiser &

Bosakowski 1987, Toland 1987, Donázar et al. 1993, Shiraki 1994). Many of these investigations however, have attempted to understand raptor habitat selection through studies of the habitat preferences of their prey. One reason for this approach is perhaps the tendency to view raptor populations more as part of a predator-prey system. Nonetheless, there are many aspects of the environment that can influence raptors more directly. These include factors that influence the foraging behaviour, the detection of prey, the location of nest sites, and the presence or absence of predators or competitors, as well as factors that relate to physiology via the thermal environment (Janes 1985).

Furthermore, as suggested by Svärdson (1949) and Hildén (1965), habitat use is influenced by the morphological, physiological and behavioural adaptations of the species, such as hunting techniques (Andrew & Mosher 1982, Janes 1985). Perch hunters, like the Red-tailed Hawk (*Buteo jamaicensis*), will select sparse habitat which provides an abundance of potential perching sites (Janes 1985). In larger species like eagles, open discontinuous forest stands and accessible nest sites for easier maneuverability are two features which usually limit the choice of habitat (Snow 1973, Gerrard *et al*. 1975). The importance of an accessible nest site has been documented in several species of raptors, e.g. the Bald Eagle (*Haliaeetus leucocephalus*, Brown & Amadon 1968), the Whitetailed Sea Eagle (*H. albicilla*; Mori 1980, Shiraki 1994), and

the Red-tailed Hawk (Titus & Mosher 1981, Bednarz & Dinsmore 1981). These two features may be critical external stimuli which trigger the settling reaction in an area for large raptors.

#### Nest site selection ---

The selection of nest sites may involve a host of rather specific concerns, ranging from local factors such as the thermal environment in the nest to broader factors including but not limited to the proximity of foraging areas (Janes 1985).

Local factors also include the substrate on which raptors build their nests. Species differ in the amount of nest building and in the range of sites they use for nesting. The falcons and cathartids do not build nests, but instead typically scrape out a hollow and arrange debris around the edges (Newton 1976). However, it is also common to see some large raptors building large stick nests on cliffs (e.g. Bald Eagle) or trees (e.g. White-tailed Sea Eagle). Local factors may play an important role in nest site selection at an even finer level. For example, Goshawks (*Accipiter gentilis*) and Cooper's Hawks (*A. cooperii*) select trees on north-facing slopes for nesting, possibly for thermal considerations (Reynolds et al. 1982).

One of the most crucial factors limiting nest site selection in raptors is perhaps the remoteness and safety of

a site. For example, Peregrine Falcons (F. peregrinus) usually nest on high cliffs or on islets surrounded by water or bog (Newton 1976). The security of a nest site against humans and other mammal predators is so important that at times birds may nest in otherwise unacceptable areas in exchange for the safety factor. Human disturbance may be termed as a negative characteristic having a repelling effect on the choice of a nest site (Hildén 1965). Again the example is seen in tundra-nesting Peregrine Falcons which will nest on earth slopes or even on flat ground in exchange for the extreme remoteness of these areas (Newton 1976). In other cases, human structures, e.g. buildings, bridges etc., have been used as substitutes for natural nest sites (Cade *et al.* 1996).

Nonetheless, the avoidance of humans and their activities by raptors is a well documented phenomenon (Newton 1976, 1979, Andrew & Mosher 1982, Levenson & Koplin 1984, Speiser & Bosakowski 1987, González *et al.* 1990, 1992, Holmes *et al.* 1993). On occasion the source of disturbance can originate from the investigators themselves (Fyfe & Olendorff 1976), leading to desertion of the nest site.

#### The territory and breeding success ---

The focal point of the home range in raptors is the nesting territory itself (Newton 1976). Birds often nest year after year at the same site, or alternate between different sites in

the same restricted territory (Hildén 1965, Newton 1976, 1979). Many theories have been developed in hopes of explaining the continued use of a particular site. Hickey (1942) proposed that it depended on the superiority of these sites in relation to local alternatives. Ferguson-Lees (1951) suggested that it was in direct relation to the young returning to their birth place. Whatever the reason, the stability of a population can only be acquired with the stability of its environment. Thus, a well-established territory likely reflects its quality which in turn will reflect the fitness of its inhabitants (Ferrer & Donázar 1996).

Territory quality influencing reproductive success is apparent in several species (Newton 1979, Högstedt 1980, Ferrer & Donázar 1996). Although a bird may be able to breed on a particularly good territory, it may be unable to breed on a poor one (Newton & Marquiss 1976, Ferrer and Donázar 1996). The quality may be assessed in terms of food availability but this seems only to be true in the absence of human intervention (Newton 1979). Again human-related factors play a crucial role in determining the quality of a habitat. For example, Hagar (*in* Hickey 1969) graded cliffs used by Peregrine Falcons according to height, human disturbance and suitability of ledges. Breeding success was better on cliffs he graded as higher quality than on lower-quality cliffs. More recent studies also found differences in breeding success

relative to the remoteness and inaccessibility from humans (Wiley 1975, Donázar et al. 1993).

Habitat loss ---

Snyder and Snyder (1975) drew attention in the United States to a progressive loss of suitable habitat, especially for many species of birds of prey, and suggested that habitat preservation was of prime importance in maintaining raptor populations at acceptable levels. This view coincides with that of various authors in different regions of the world (Newton 1979, Steyn 1983). Since then, numerous studies on the conservation and management of birds of prey threatened by local or global extinction have quantified data on nest sites (Grubb 1976, Morris 1980, Bednarz & Dinsmore 1981, Newton *et al.* 1981, Andrew & Mosher 1982, Reynolds *et al.* 1982, Gilmer & Stewart 1984, Rich 1986, Kostrzewa 1987).

## The Spanish Imperial Eagle

#### Taxonomy ---

This species was first described taxonomically at a conference of the German Ornithological Society in 1860 by Pastor Dr. Ludwig Brehm (1861). He described the species from three specimens (later identified as immature birds) that were brought to him by his son, Dr. Reinhold Brehm. It was given the scientific name of Aquila adalberti in honour of the Prince Adalbert of Bavaria. Only 10 years later was an adult clearly identified to be distinct from what had been used earlier to identify the species. It had a dark plumage and bright white shoulders, and was thus named the Whiteshouldered Eagle until the beginning of the 20th century (Verner 1909).

The identity of Aquila adalberti as a distinct species from its eastern congener, the Eastern Imperial Eagle (A. heliaca) has been subject for debate until only a few years ago (Meyburg 1989). Hiraldo et al. (1976) clearly distinguished the two as separate species by conducting a critical comparison of 220 skins taken from various European museums. More recent studies confirmed consideration of Aquila adalberti as a separate species from A. heliaca (Collar & Andrews 1988, González et al. 1989).

# Status and distribution ---

The Spanish Imperial Eagle is one of the rarest birds of prey at a worldwide level and is considered 'endangered' in the IUCN Red Data Book (King 1981, Wilcox 1988). The current world population is estimated at fewer than 150 pairs.

Its range has been greatly reduced over the last century. Data collected by González *et al.* (1989) from eggs and specimens preserved in natural history museums showed that at the beginning of the century, the range of this species extended over most of the Iberian Peninsula and northern

Morocco but was drastically reduced over the last 80 years. The species has since been lost from Morocco, Portugal, and the borders of its present range in Spain. The losses have resulted from intense human persecution and habitat loss due to changes in land use (Valverde 1960, Meyburg 1989, González *et al.* 1990). During the past 10 years, the eagle's distribution has remained relatively unchanged.

Today, the range of this species is restricted to southwestern Spain in seven principal areas: Extremadura, Guadarrama, Madrid Province, Sierra Morena, Montes de Toledo, Tajo River Valley and the Doñana National Park (Negro & Hiraldo 1994).

# Breeding biology and success ---

The Spanish Imperial Eagle is a long-lived (maturation period of 4-5 years and longevity of 21-22 years), sedentary bird of prey (Ferrer & Calderón 1990). Its relatively long reproductive period lasts 8 months, from the first two weeks of February to the first two weeks of October, the time when the last young reach independence (Ferrer 1990). They lay 1 to 4 eggs (usually 2 or 3), as early as 15 February and as Incubation lasts 45 days and hatching late as 26 March. occurs between late April and early May (Calderón et al. 1987, Ferrer 1993). The time the young spend in the nest from hatching to first flight is on average 75 days. The young leave their natal population at the age of 137 days and the

average age at first settlement is 164 days (Ferrer 1990). During this post-fledging period, the juvenile eagles occupy temporary settlement areas and frequently come back to the natal population before settling permanently (Ferrer 1990). Overall, the Spanish Imperial Eagle has a low reproductive rate, producing on average 1 to 2 fledging young (1.17 chicks per pair per year) (Calderón *et al.* 1987).

#### Habitat ---

The habitat of this species has been qualitatively described by several authors (Valverde 1960, Garzón 1974, Meyburg 1975) and quantitatively described in only one recent study (González et al. 1992). Investigating the factors influencing the Spanish Imperial Eagle's distribution, González et al. (1990) observed that it is associated with areas having a typical Mediterranean climate, i.e. relatively warm dry summers and temperate rainy winters. Furthermore, they generally remain in forested areas with lower levels of human land use and with a higher density of Rabbits (*Oryctolagus cuniculus*), the staple prey for the eagles (Delibes 1978).

The degree of human disturbance is probably the most important factor influencing the selection of its nest site. Nests are usually located in inaccessible areas with lower densities of roads (González *et al.* 1990, 1992). Eagles still possessing juvenile plumage have been observed nesting in areas with a higher intensity of human influence, due to the

high turnover rate in the pairs occupying these areas (González et al. 1992).

Spanish Imperial Eagles are tree nesters, although on a few occasions they have been observed to nest on electric pylons (González et al. 1990). Tree species determined to be used most frequently by nesting Spanish Imperial Eagles include: Stone Pines (*Pinus pinea*), the most frequently used tree; followed by Cork Oaks (*Quercus suber*), and Eucalyptus trees (*Eucaliptus* spp.) (Ferrer 1993). Paired birds show territorial behaviour and territories are exclusive and vigorously defended throughout the year. They build anywhere from 1 to 9 nests in a territory and occupy them alternate throughout the years. Sometimes the same nest is used in successive years within a territory (Valverde 1960).

# The Doñana National Park population

# History and status ---

According to Valverde (1960) and G. Mountford and J. Ferguson-Lees (unpublished data), the Spanish Imperial Eagle population in Doñana drastically declined to 2-4 pairs between the years 1865-1910 due to persecution by shooting and to the activities of egg-collectors. In 1959, 6 nests were found in the study zone (Lévêque 1960) and 8 in 1960 (González-Diez 1960). Twelve pairs were believed to exist in 1967 (Valverde 1967) and by 1976, 2 years after Doñana was declared a national

park, the population was estimated at 15-16 pairs (Ferrer 1993), thereafter remaining stable to this day. Today, it is the densest existing population (15-16 pairs in 20,000 ha), constituting more than 17% of the world population of this species and it is also the population which has been protected for the longest period of time, i.e. since 1973 (Ferrer & Hiraldo 1991).

This population of Spanish Imperial Eagles is considered geographically isolated from other breeding populations of the same species, the nearest of which is 300 km away (Ferrer & Calderón 1990).

# Breeding success ---

The reproductive success of this population has been consistently lower than that of other populations. From 77 nesting attempts measured in the Doñana population, the mean number of fledged chicks per nest was 0.891 (Calderón *et al.* 1987) compared to 1.36 chicks fledged per nest for other populations (González 1989).

In one previous study (Calderón *et al.* 1987), only one habitat feature, i.e. the nest tree species, was related to the hatching success of these eagles. Hatching success was significantly lower in nests built in Eucalyptus trees. Due to the high flexibility of the branches, nests are frequently blown by winds out of the tree and the eggs broken.

Habitat ---

The wetlands of Doñana National Park are an unusual habitat for this species (Ferrer & Calderón 1990). Other populations of the Spanish Imperial Eagle generally occupy areas of more rugged terrain such as the mountainous Extremadura region in southwestern Spain (González *et al.* 1992).

Two additional tree species, apart from the three mentioned previously, are occasionally used i.e.: the Lombardy Poplar (*Populus nigra*) and the White Poplar (*P. alba*). The frequency of utilization of the Eucalyptus tree as a nesting site increased from 1973 to 1985 (Calderón et al. 1987). Consequently, the use of the Cork Oak has decreased over this same period, from a 40-50% rate of utilization in the earlier years to a 10-20% rate in the recent years. This may prove detrimental to the population since the security of the nests in Eucalyptus trees is questionable under windy conditions.

Nests are usually positioned at the top of the tree where heights fluctuate between 5 and 30 m, the higher mean corresponding to those nests placed in Eucalyptus trees and the lower to those placed in Cork Oaks (Calderón *et al.* 1987).

Density plays an important role in the selection of habitat and particularly for this high density population of Spanish Imperial Eagles. The productivity of these eagles correspond to the "habitat heterogeneity" hypothesis which supports that, as density increases, a greater proportion of

individuals are forced to occupy lower quality habitats. The productivity was found to be lower in more recently occupied territories within the Doñana park as opposed to wellestablished ones (Ferrer & Donázar 1996).

A quantitative study on nest site selection for this population has not yet been investigated. Since the eagles of Doñana have failed to colonize the seemingly suitable surrounding park area, it is deemed crucial to provide quantitative data on the habitat requirements of the population inhabiting this rather unusual region.
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Section I: Factors influencing nest site selection by the Spanish Imperial Eagle population of Doñana National Park, Spain.

### ABSTRACT

We examined the nest site selection of the Spanish Imperial Eagle Aquila adalberti population of the Doñana National Park (SW Spain) from 1984 to 1994, in relation to the microhabitat and macrohabitat representing vegetative composition, degree of human influence and land use. The study included 75 active nest sites and 75 random sites. Univariate analyses and Generalized Linear Models were used. Nest sites differed significantly from the random sites for 87% of habitat variables measured. The model correctly classified 85.3% of the nest sites and 86.7% of the random sites. The probability of occupation of a site by a Spanish Imperial Eagle increased with tree height, angle of aperture of the wood stand, distance to paved roads, distance to urban centre and distance to water body.

## INTRODUCTION

The Spanish Imperial Eagle (Aquila adalberti), recently considered a separate species from the Eastern Imperial Eagle (A. heliaca) (Hiraldo et al. 1976, Collar & Andrews 1988, González et al. 1989), is the most endangered Aquila in Europe (Bijleveld 1974) and is in fact included in the list of the most endangered species of the world (King 1981). From 1865 to 1910, the Spanish Imperial Eagle population in the Doñana National Park had declined to 2 to 4 pairs, mainly due to human persecution. The urgent protection needed by the species at that time is now regarded as one of direct causes for the establishment of the Doñana Biological Reserve in 1965 which was funded by the World Wildlife Fund (WWF) (Meyburg Shortly after the present day National Park was 1989). created in 1974, the population increased to a stable 15 to 16 pairs, making it the densest recorded population (15 to 16 pairs in 20,000 ha) and one which has been protected for the longest period. Despite this, this population of Spanish Imperial Eagles has not colonized the surrounding area and their productivity has been consistently low.

Habitat loss has been documented as the most important cause of decline in many species (Greenway 1967, Newton 1979, González *et al.* 1992). Meyburg (1989) suggested that habitat protection was the most urgent requirement in safeguarding the

survival of Spanish Imperial Eagles. As with other raptor species (Andrew & Mosher 1982), the nesting habitat represents an important part of the annual environment for this territorial, long-lived sedentary bird of prey. If we are to apply management practices for habitat protection, it is crucial to identify the structural characteristics of the nesting habitat that elicit selection of a site (Hildén 1965) by these eagles. Habitat selection for the Spanish Imperial Eagle has been extensively described in a qualitative fashion (Valverde 1960a, Garzón 1974, Meyburg 1975). Only one other study (González *et al.* 1992) gives a quantitative description of the habitat at a macro level for the entire Spanish Imperial Eagle population in Spain.

The objective of this study is to quantitatively assess factors which influence nest-site selection by the Spanish Imperial Eagle population of the Doñana National Park on both a macrohabitat and microhabitat level in order to better understand the failure of the species to colonize the surrounding areas. We also provide suggestions for conservation measures.

### METHODS

## Study area

The study was conducted in the Doñana National Park, southwestern Spain (37°N, 6°30'W) from 1984 to 1994. Three main habitats can be distinguished in the area: Mediterranean scrubland, marsh, and coastal sand dunes. Mediterranean scrubland is characterized by Halimium spp., Cistus libanotis, Erica spp. with scattered Cork Oaks (Quercus suber), small (Pinus pinea) woods and Pine Eucaliptus Stone spp. plantations. The marsh, which is flooded during the winter and dry during the summer, is mainly covered by Scirpus spp., while the coastal sand dunes are characterized by Ammophilia arenaria, Corema album, and Juniperus phoenicea. The climate is of Mediterranean type with Atlantic influence, i.e. relatively warm dry summers and temperate rainy winters. Α more detailed description of this area can be found in Valverde (1960b), Allier et al. (1974), and Rogers and Myers (1980).

Only productive pairs or active nests (n = 6 to 12)involving the park population of 15-16 pairs were studied. A nest site was considered to be active when at least one egg was laid within a season.

## Nest site selection

A total of 75 active nest sites was sampled over the 10-year period (1984-1994). Data on nest locations for the years 1984 to 1993 were taken from the Doñana field diaries (Doñana Biological Station archives). However, in 1994, nest locations were found through repeated searches for nest sites conducted from the beginning of the breeding season (February to April). Searches were made within each of the 16 known breeding areas within the park, first by verifying the nest sites used in 1993.

In addition, 75 random sites were sampled to evaluate habitat available to the species. They were located on a 1:50,000 land use map of the Doñana National Park and its surrounding area (Ministry of Agriculture) using randomly generated coordinates. They were at least 3.5 km from any known nest site (average distance between neighbouring nests for the Doñana population). Since the eagles only nest in trees (Stone Pines, Cork Oaks, Eucalyptus trees *Eucaliptus* spp. and Poplar trees *Populus* spp.), random sites which did not fall near these species of trees were rejected. In the field, only trees at least 10 m in height were used since the Spanish Imperial Eagles have never been known to nest in trees shorter than that (Calderón *et al.* 1987).

A total of 39 habitat variables (Table 1) was measured for each randomly selected and active nest site. Three

variables were measured exclusively for nest sites: height of the nest above the ground, orientation (azimuth) of the nest in the crown measured with a compass relative to the tree trunk and the direction of the closest open area from the nest tree (marshland, Mediterranean scrubland, sand dunes or cultivated land). From April to October 1994, each of the 75 active nest sites and 75 random sites was visited once to conduct measurements at the tree. Visits were carried out by 2 to 3 people, one of whom climbed to the nest. Variables representing vegetative composition, degree of human influence and land use were sampled within a 1.75 km radius of the nest or random tree using 1:10 000 and 1:20 000 aerial photographs from 1984, 1991, 1992 and 1993 (Junta de Andalucia) and land use maps (1985, 1991 Ministry of Agriculture).

# Statistical analysis

Due to small sample sizes (6 to 12 active nests per year), we pooled the data from the 10 years and treated each nest tree as an independent observation. Eagles generally express nest fidelity (Newton 1976, 1979) and it is therefore assumed that the nest trees that were reused in successive years involved the same pairs. This problem of pseudoreplication of samples is not uncommon in studies on raptor habitat selection (Hurlbert 1984, Schooley 1994). However, adult Spanish Imperial Eagles were not tagged and therefore data on which

pair occupied which nest in a given year were not available. Thus, sound conclusion of the assumption of a pseudoreplication can not be made. Furthermore, repeated measure analysis could not be conducted for the same reason. In short, the methodology followed in this study has been the conventional one used in most raptor habitat selection studies conducted over a substantial period of time and where sample sizes are too small to be analyzed for individual years (Newton et al. 1981, González et al. 1992, Donázar et al. 1993).

A univariate analysis of the data using 1-way ANOVA (analysis of variance), Kruskal-Wallis, and Chi-square (for 2 categorical variables: tree species and type of wood stand) were first conducted with the Statgraphics statistical package (Manugistics, Inc. 1992).

Generalized Linear Models, or GLM (Nelder and Wedderburn 1972, Dobson 1983, and McCullagh & Nelder 1983) were then used to make a mathematical description of the nest site selection for the Doñana National Park population of the Spanish Imperial Eagle following the methodology of Nicholls (1989) and Donázar *et al.* (1993). The following descriptive equation was derived:

 $LP = a + bx_1 + cx_2 + \dots,$ eqn 1

where LP is the linear predictor (sum of effects of the predictor variables) and a, b, c, ... are the parameters to be estimated from the observed data and  $x_1, x_2, \ldots$  the explanatory variables. These parameters define the effect of the variables on the LP. We assumed a binomial distribution of errors in which the response variable had the value 1 (site selected as nest site) or 0 (site not selected as nest site). One appropriate link function for a binomial distribution is the logistic function, which can be expressed as:

$$p = (e^{L^{p}}) / (1 + e^{L^{p}}),$$
 eqn 2

where p is the probability of obtaining a positive response and e is the base of the natural logarithm. This last expression can be transformed into a linear function:

$$\ln[p/(1-p)] = LP \qquad \text{eqn } 3$$

where ln is the natural logarithm. From the LP, we can therefore obtain the probability (p) of a site being occupied by a Spanish Imperial Eagle.

## Analytical Procedure for GLM

3

We first fitted the full model by including all of the explanatory variables, using the program GLIM (Baker & Nelder 1978). We proceeded by removing each variable in turn following the traditional backward stepwise regression. Once each variable was removed, all variables which did not improve the model significantly were eliminated. Because of the large number of variables analyzed, we chose a 1% level of significance to keep a variable in a model. A quadratic function was also fitted for every variable to ensure that a higher order polynomial was not necessary to improve the model. Because some variables had missing observations, 146 observations were used for this analysis (n = 71 for nest sites and n = 75 for random sites).

Once a model had been found, three diagnostic measures were used to evaluate the fit of the model to the data: a measure of the residual lack of fit, the potential influence, and the coefficient of sensitivity of each observation (Pregibon 1981, Nicholls 1989, Donázar *et al.* 1993). The jack-knife procedure was also used to test the robustness of the model (Donázar *et al.* 1993).

We tested for correlations between nest orientation in the crown with direction to the nearest open area and, with the angle of aperture of the wood stand using circular

statistics (Batchelet 1981) for nest sites exclusively. Isolated nest trees were excluded from this analysis (n = 13).

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RESULTS

Nest site selection

The nest sites were found to differ significantly from the random sites for 32 of the 39 habitat variables measured (Table 2). Tree species and type of wood stand used at nesting sites were also found to differ significantly from the random sites ( $x^2$ , = 18.71, P < 0.01 and  $x^2$ , = 32.85, P < 0.001, respectively; n = 150, Chi-square test). Nests sites were found more frequently in Eucalyptus trees (33.3%), Cork Oaks (13.3%) and Poplar trees (5.3%) and in smaller wood stands (BLUFF1 (18.67%), BLUFF2 (10.67%), and BLUFF4 (20.0%)).

The best GLM model obtained using a binomial distribution of errors and logistic link included 5 variables (Table 3): tree height, angle of aperture of the wood stand, distance to the nearest paved road, distance to the nearest body of water, and distance to the nearest urban centre. The predicted probability of a site being occupied by an eagle was calculated by inserting the parameters given in Table 3 into the following equation:

LP = -12.39 + 0.2813 TREEHT + 0.0136 OPENNESS + 0.001033 DISTPV + 0.001321 DISTWATER + 4.812 x 10-4 DISTUC

The estimate LP is the linear predictor and was transformed into an estimated probability (p) of a site being occupied by an eagle relative to each of the 5 explanatory variables in our GLM model using eqn 3 (see Methods) (Fig. 1). The model shows that there is an increasing probability of a site being occupied by a Spanish Imperial Eagle with increasing tree height, angle of aperture of the wood stand, distance to paved roads, distance to water body, and distance to urban centre.

Observations with P > 0.5 were considered to be classified as nesting sites and those with P < 0.5 as random sites. The model correctly classified 85.3% of the nest sites and 86.7% of the random sites. Thus the jack-knife classification, which demonstrated the robustness of the model, correctly classified 84% of the nesting sites and 86.7% of the random sites. The jack-knife test misclassified ally 1.3% more observations on nest sites than the complete model.

Three outliers were found with the sensitivity analysis, but removal of the corresponding observations only caused an average of 6% change in parameter estimates. Observations with a high potential influence were removed from the model and the parameters were refitted. Changes in parameter estimates were less than 15%.

The orientation of the nest in the crown was found to be significantly correlated with the angle of aperture of the wood stand  $(r_{36}^2 = 1.277, P < 0.001, Circular-linear$ 

correlation). Nests were mainly located in the northeastern section of the crown (mean azimuth =  $78.6^{\circ}$ , n = 37, Circular statistics) positioned at the opening of the wood stand at a mean height of 14.3 m (n = 37). No significant correlation was found between the orientation of the nest in the crown and the direction of the closest open area from the tree ( $r_{36}^2 = 0.087$ , n.s., Circular correlation).

## DISCUSSION

# Nest site selection

The nest sites differed significantly from the random sites at both the microhabitat and macrohabitat levels for 87% of the variables measured, suggesting an unsuitability of the latter sites for nesting Spanish Imperial Eagles. This may in part explain why they have not colonized the surrounding area despite their high density in the park.

Our univariate analysis showed that the habitat of the nest sites differed from the sites selected at random in terms of vegetation structure and land use. The percentage of Eucalyptus and Stone Pine trees was higher at nest sites than at random sites and eagles nested more often in Eucalyptus trees, Cork Oaks and Poplar trees with a larger diameter (DBH) than at the random sites.

The percentage of pastureland was significantly higher at nest sites, while the percentage of cultivated land was considerably lower. However, the GLM model showed that neither vegetation structure nor land use were main factors conditioning the selection of a site for nesting. Eagles likely select a nesting tree in terms of its height and large diameter to support the large nest, regardless of the species. Other populations of Spanish Imperial Eagles have shown similar trends in habitat selection (González *et al.* 1992). The low percentage of cultivated land at nest sites was likely

the result of the absence of cultivated land inside the park boundaries. Sections of the park are still privately owned and mainly used for grazing cattle.

The nest sites differed mainly in variables representing the accessibility of the nest and the degree of human influence. Tree height and angle of aperture of the nest stand were the main factors in our GLM model pertaining to the accessibility of the nest. Eagles chose tall trees that were isolated or in small wood stands with a large opening. Nests were placed near the top of the tree and were positioned in the direction of the opening of the stand, allowing better visibility of the territory and a higher accessibility to and from the nest. Golden Eagles (A. chrysaetos) also have been found to place their nests on cliff faces in a non-random fashion, i.e. to minimize the exposure of the young to temperature extremes. This presumably reduces thermal stress and subsequent mortality of nestlings during the first 6 weeks after hatching (Mosher & White 1976).

The importance of an accessible nest site has been documented for other species of raptors, e.g. the Bald Eagle (*Haliaeetus leucocephalus*, Brown & Amadon 1968), the Whitetailed Sea Eagle (*H. albicilla*; Mori 1980, Shiraki 1994), and the Red-tailed Hawk (*Buteo jamaicensis*; Titus & Mosher 1981, Bednarz & Dinsmore 1981). The tendency to use open discontinuous forest stands has been particularly noted in eagle species (Snow 1973, Gerrard *et al.* 1975). As suggested

by Svärdson (1949) and Hildén (1965), habitat use is influenced by the morphological, physiological and behavioral adaptations of a given species, such as hunting techniques in the case of raptors (Andrew & Mosher 1982, Janes 1985). Likely, Spanish Imperial Eagles, being large aerial hunters, will avoid densely wooded areas for easy maneuverability in order to optimize foraging activities.

The avoidance of humans and their activities by raptors is a well documented phenomenon (Newton 1976, 1979, Andrew & Mosher 1982, Levenson & Koplin 1984, Speiser & Bosakowski 1988, González et al. 1990 and 1992, Holmes et al. 1993). Our GLM model showed that paved roads and urban centres were the two main factors influencing nest site selection in the Spanish Imperial Eagle population of Doñana in terms of degree of human influence. These eagles are still being persecuted and thus a low level or absence of human disturbance is a crucial attribute for a suitable nest site. In our analysis, distance to paved roads and distance to urban centres correctly classified 69.3% and 68.0% of the nest sites, respectively. These human structures may represent a higher intensity of human activity than the other human-related variables measured. Urban centres contain a high density of human inhabitants; paved roads permit access to a higher number of vehicles than unpaved roads and slower traffic than highways, allowing time to spot nearby eagles.

The fifth parameter in our model was the distance to the

nearest body of water (lagoon, river or salt mine). Most raptor species nest near water, an adaptive behaviour for optimizing foraging activities since prey populations are generally more abundant around water (Snow 1973, Gerrard et al. 1975, Andrew & Mosher 1982, Reynolds et al. 1982, Anderson 1985, Fraser et al. 1985). In Doñana, nesting near water should be advantageous for the eagles because an important part of their diet during the reproductive period consists of both Rabbit (Oryctolagus cuniculus) and aquatic birds, mainly the Common Coot (Fulica atra) (Ferrer 1993). However, we found that the Spanish Imperial Eagles in Doñana seem to avoid nesting near water. This can be interpreted in two ways. First, there is a tendency for a higher intensity of human activities (fishing, recreational, industrial) to be concentrated around waterways. Andrew & Mosher (1982) observed that Bald Eagle nests which were closer to water had significantly lower reproductive success, presumably because of the higher levels of human disturbance. This phenomenon has been observed in several raptor studies (Brown & Watson 1964, Titus & Mosher 1981, Fraser et al. 1985, Watson et al. 1992). Therefore, despite the important food source found in and around water bodies, human presence (or another nonidentified correlated parameter), may be the overriding factor influencing nest site selection by the Spanish Imperial Eagle. Alternatively, the main concentrations of animals (particularly Rabbits) in Doñana occurs in the area where the

sand dunes or the Mediterranean scrubland meet the marsh (Rogers & Myers 1980). Thus, this ecotone may represent a more important food source for eagles than the water bodies measured in this study. Nests within the park were more or less situated along this border (marsh/scrubland-sand dunes).

The Doñana National Park is an unusual nesting habitat for the Spanish Imperial Eagle (Ferrer & Calderón 1990). The marsh, constituting 75% of the park area, and the absence of rugged terrain (González *et al.* 1992) are what differentiate Doñana from the habitat used by other populations of this species. We hypothesize that Spanish Imperial Eagles choose nest sites on the basis of overall structural characteristics, and then focus on the selection of a particular nest tree. Open sites with a low level of human activity likely trigger the settling reaction (Hildén 1965). The preserved area of Doñana with its tall trees bordering the marsh make it an attractive nesting area.

# Management implications

Strict management policies concerning the protection of the Spanish Imperial Eagle population of the Doñana National Park have been enforced since 1973. However, Doñana is under constant threat of development from the expanding surrounding area. Urgent management policies must be created for the park's surrounding area in order to provide a suitable nesting habitat into which eagles could expand.

Reforestation programs eliminating Stone Pines and Cork Oaks to make way for plantations of Eucalyptus trees must be kept to a minimum in order to let the existing short Stone Pine and Cork Oak stands grow in height. Furthermore the expansion of paved roads should be reduced to keep human disturbance at a low level. Eucalyptus trees have been found to decrease hatching success in Spanish Imperial Eagles because nests frequently fall out due to the flexibility of the branches (Calderón et al. 1987).

It is also important to provide adequate nesting structures and open woodland sites for these eagles. Currently, outside the park cultivated lands are the only available open spaces which represent a high risk of persecution for the Spanish Imperial Eagles by land owners. Management techniques must be implemented in order to provide safe open woodland sites which would benefit both the land owners and the eagles.

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Table 1. Habitat characteristics measured in the Doñana National Park and the surrounding area for 75 Spanish Imperial Eagle nest sites and 75 randomly chosen sites for the years 1984-1994

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Mnemonic	code	Meaning	Mnemonic code	Meaning
TREEHT		Height of tree above ground (m)	AREAPA	Percentage of surface occupied by pasture land within the circular sampling area
DBH		Width of tree measured as diameter at breast height (cm)	AREAM	Percentage of surface covered by Mediterranean scrubland within the circular sampling area
DISTBLUFF		Distance from tree to nearest edge of the wood stand (m)	AREAD	Percentage of surface covered by sand dunes in the circular sampling area
OPENNESS		Angle of the opening of the wood stand at the tree (0° for closed wood stands to 360° for isolated trees), measured using a protractor with tree as center point	DISTWATER	Distance from tree to nearest body of water (lagoon, river, stream or salt mine) (m)
DISTMA		Distance from tree to marsh	DISTNEST	Distance from tree to the nearest active Spanish Imperial Eagle nest of the same year (m)
AREAMA		Percentage of surface occupied by marshland within the circular sampling area	KMCF	Kilometers of non-paved road passable by vehicle obstructed by vegetation in the circular sampling area

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Mnemonic	code Meaning	Mnemonic code	Meaning
КМСС	Kilometers of non-paved road passable by vehicle not obstructed by vegetation in the circular sampling area	AREAAG3	Percentage of surface occupied by irrigated cultivated land in the circular sampling area
КМСО	Kilometers of firebreak (strips cut out of vegetation for fire control) in the circular sampling area	DISTAG2	Distance from tree to nearest non- irrigated cultivated land (m)
KMPV	Kilometers of paved road in the circular sampling area	DISTAG3	Distance from tree to nearest irrigated cultivated land (m)
KMCR	Kilometers of highway in the circular sampling area	DISTCF	Distance from tree to nearest non paved road passable by vehicle obstructed by vegetation (m)
KMROC	Kilometers of non-paved road used for pilgrimage by local people	I DISTCG	Distance from tree to nearest non paved road passable by vehicle no obstructed by vegetation (m)
KMCOO	Kilometers of non-paved road used by ICONA park staff	I DISTCO	Distance from tree to nearest firehreak (m)
AREAAG2	Percentage of surface occupied by non-irrigated cultivated land in the circular sampling area	DISTPV	Distance from tree to nearest paved road (m)

Mnemonic code	Meaning		
DISTCR	Distance from tree to nearest highway (m)		
DISTROC	Distance from tree to nearest road used for pilgrimage with off-road vehicles or horses to the village hordering the park (m)		
DISTCOO	Distance from tree to nearest road used by ICONA workers (m)		
DISTUC	Distance from tree to nearest urban centre (m)		
DISTBLDG	Distance from tree to nearest building (m)		
KMPOLINE	Kilometers of electric power line in the circular sampling area		
DISTPOLINE	Distance to the nearest electric powerline (m)		

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Table I. (continued)

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Table 2. Comparisons of 37 habitat variables measured in the Doñana National Park and surrounding area (means and standard deviations) between 75 Spanish Imperial Eagle nest sites and 75 randomly chosen sites

Variables	Nest sites		Random sites	
	Mean	± SD	Mean	±SD
aTREEHT***	17.23	5.68	13.88	3.22
aDBH***	55.92	26.67	38.72	14.37
DISTBLUFF***	93.10	277.46	313.03	469.46
bOPENNESS <sup>+++</sup>	160.84	136.69	38.48	93.30
DISTMA+++	1732.66	2013.31	8949.72	3735.75
AREAMA+++	27.70	31.87	1.57	7.83
AREAPA <sup>+++</sup>	7.80	7.88	3.50	5.27
AREAM <sup>+</sup>	24.54	32.0	4.97	6.89
AREAD+++	9.76	15.23	0.84	4.01
AREAI+++	6.56	14.99	18.81	21.63
AREA2+++	21.61	22.29	43.30	27.31
AREA3 <sup>ns</sup>	0.65	2.89	1.23	2.45
AREA4 <sup>ns</sup>	0.03	0.08	0.08	0.31

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# Table 2. (continued)

Variables	Nest sites		Random sit	Random sites	
	Mean	± SD	Mean	± SD	
DISTWATER <sup>ns</sup>	1107.45	949.69	923.99	833.55	
DISTNEST***	4395.12	2953.59	7809.53	3687.48	
KMCF**	12.98	6.48	17.52	10.07	
KMCG***	6.26	4.13	10.20	7.06	
KMCO <sup>ns</sup>	6.40	6.23	7.09	6.10	
KMPV***	0.75	2.10	4.08	4.20	
KMCR+++	0.13	0.67	1.49	1.72	
KMROC++	2.0	1.72	1.24	1.58	
КМСОО***	1.08	1.65	0.03	0.23	
AREAAG2+++	0.60	2.45	6.72	11.92	
AREAAG3+++	1.0	3.88	14.46	19.76	
DISTAG2+++	9280.47	4078.48	3864.08	5217.54	
DISTAG3+++	7354.87	3587.13	1538.35	1897.53	
DISTCF <sup>ns</sup>	244.58	274.83	249.85	302.36	
DISTCG**	652.40	559.18	396.51	486.02	
DISTCOns	1484.03	2552.31	964.0	1631.57	
DISTPV***	3246.33	2017.29	1116.87	1300.62	

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Variables	Nest sites		Random sites	
	Mean	± SD	Mean	± SD
DISTCR***	6346.15	2884.13	1710.57	1434.52
DISTROC <sup>ns</sup>	2114.40	2687.72	2489.73	1877.82
DISTCOO***	5837.73	5601.83	14646.87	8485.43
DISTUC***	8381.53	2947.34	5839.13	2772.87
DISTBLDG***	1717.93	960.14	1102.25	763.40
KMPOLINE+++	0.39	1.38	2.89	3.74
DISTPOLINE***	6081.27	3067.76	1702.13	1354.33

Table 2. (continued)

For variables marked a, n=71 for nest sites. Those marked b, n=74 for nest sites. For all other variables n=75. Significance of 1-way ANOVA for difference between means: \*\* = p<0.01, \*\*\* = p<0.001; and of Kruskal-Wallis test for difference between average ranks: \* = p<0.05, \*\* = p<0.01, \*\*\* = p<0.001; ns = not statistically significant

	Parameter estimate	Standard error
Constant	-12.39	2.276
TREEHT	0.2813	0.07323
OPENNESS	0.01360	0.003048
DISTPV	0.001033	2.489 x 10 <sup>-4</sup>
DISTWATER	0.001321	3.573 x 10 <sup>-4</sup>
DISTUC	4.812 x 10 <sup>-4</sup>	$1.236 \times 10^{-4}$
Residual deviance	82.34	
df	140	
Residual deviance df	82.34 140	

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Table 3.Variables in the GLM nest site selection model using binomial error andlogistic link for Spanish Imperial Eagle population of Doñana National Park

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Figure 1. The predicted probability of finding Spanish Imperial Eagles occupying a site as a function of the five variables in the nest site selection GLM model.



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# Connecting Statement

In the first section nest site selection by the Spanish Imperial Eagle population of Doñana National Park was studied by comparing nest sites with randomly chosen sites. In the following section, selected habitat features of Spanish Imperial Eagle territories are tested for their possible influence on the productivity of the eagles.

# Section II : Influence of territory structure on the productivity of the Spanish Imperial Eagle population of Doñana National Park

#### ABSTRACT

We report a 10-year study (1984-1994) on the influence of the micro- and macrohabitat, representing vegetative composition, degree of human influence and land use on 4 productivity parameters (laying date, clutch size, number of nestlings, and number of chicks fledged) among 16 Spanish Imperial Eagle territories of the Doñana National Park (SW Spain). According to the Spearman correlation coefficient ( $r_s$ ) analyses, egg-laying was later on territories situated closer to urban centres ( $r_s = -0.529$ , P < 0.05) and those with more kilometres of power line ( $r_s = 0.518$ , P < 0.05). No territory features were found to significantly influence clutch size, number of nestlings or the number of chicks fledged.

#### INTRODUCTION

Significant variation in reproductive success among territories is a common phenomenon in avian species (Newton 1979, Högstedt 1980, Ferrer & Donázar 1996). The differences in productivity can be directly related to the quality of the territory (Newton 1976a, Janes 1984, Dhondt *et al.* 1992, Ferrer & Donázar 1996) which in turn varies with food availability and for birds of prey in particular, the security of the nest site (Lack 1949, Brown 1969, Wiley 1975, Newton 1976b, Alatalo *et al.* 1986, Donázar *et al.* 1993). The vegetative composition and land use within breeding areas of raptors have also been hypothesized as having a possible influence on reproductive success (Howell *et al.* 1978, Newton *et al.* 1981a, Gawlik & Bildstein 1990).

Brown (1976) recognized that one of the critical times in the breeding cycle of raptors is the pre-laying/laying period. Differences in egg-laying date between individuals may therefore be the product of individuals reacting to differences in resource availability on a local scale (Daan *et al.* 1990, Perdeck & Cavé 1992).

The Spanish Imperial Eagle (Aquila adalberti) is the most endangered member of the genus Aquila in Europe, and one of the rarest raptors in the world (Collar & Andrew 1988). It is a large (2500-3500 g) bird of prey which occupies the same territory year round. The Spanish Imperial Eagle has a low

reproductive rate (Ferrer & Calderón 1990) and its total population is currently estimated at fewer than 150 pairs. The densest recorded population (15-16 pairs in 20,000 ha) and that which has been protected the longest, i.e. since 1973, occurs in the Doñana National Park in southwestern Spain. Despite its density, the eagles in Doñana have not colonized the surrounding area and their productivity has been consistently lower than that of other existing populations (Ferrer 1993).

The influence of habitat structure on the reproductive performance of birds has been assessed in several studies (Howell et al. 1978, Scott & Birkhead 1983, Birkhead et al. 1983, Janes 1984, Donázar et al. 1993, Donázar et al. 1994, Siikamäki 1995). For the Spanish Imperial Eagle, habitat has been quantitatively and qualitatively described (Valverde 1960a, Garzón 1974, Meyburg 1975, González et al. 1992), but to date only one habitat feature, i.e. nest tree species, has been related to the reproductive performance of these eagles (Calderón et al. 1987). In this study, we examine the relationship of various territory features to the reproductive success in the breeding Spanish Imperial Eagle population of Doñana National Park in southwestern Spain. We hypothesize that the territory structure will influence the overall reproductive performance of the Spanish Imperial Eagle.

#### METHODS

#### Study area

The study was conducted in the Doñana National Park, southwestern Spain (37°N, 6°30'W) from 1984 to 1994. Three main habitats can be distinguished in the area: Mediterranean scrubland, marsh, and coastal sand dunes. Mediterranean scrubland is characterized by Halimium spp., Cistus libanotis, Erica spp. with scattered Cork Oaks (Quercus suber), small (Pinus pinea) woods Stone Pine and Eucaliptus spp. The marsh, which remains flooded during the plantations. winter and dry during the summer, is mainly covered by Scirpus spp., while the coastal sand dunes are characterized by Ammophilia arenaria, Corema album, and Juniperus phoenicea. The climate is of Mediterranean type with Atlantic influence, i.e. relatively warm dry summers and temperate rainy winters. A more detailed description of this area can be found in Valverde (1960b), Allier et al. (1974), and Rogers & Myers (1980).

# Territory structure

In total, 107 nests were sampled over the 10-year period (1984-1994). Data on nest locations for the years 1984 to 1993 were taken from the Doñana field diaries (Doñana

Biological Station archives). However in 1994, nest locations were found through repeated searches conducted during the beginning of the breeding season (February to April), within each of the 16 known territories in the park beginning with the verification of the nest sites used in 1993. These 16 territories were delimited from a 1:50,000 map of the Doñana National Park (Ministry of Agriculture) where all nest locations have been marked over a period of 32 years (Fig. 1). These territory boundaries have been established on a longterm basis and are considered to be stable. A territory has been defined as an area with a high concentration of marked nest locations over a succession of years (Ferrer & Donázar Successive locations of different nests were 1996). considered to be in the same territory if the distance between their locations was smaller than the average distance between neighbouring pairs for the Doñana population, i.e. 3.5 km.

Thirty-five variables (Table 1) representing microhabitat, degree of human influence, vegetative composition, and land use were sampled for each nest. From April to October of 1994, each of the 107 nests was visited by 2 to 3 people in order to conduct microhabitat measurements. All other variables were sampled within 1.75 km radius of the nest using aerial photographs (Junta de Andalucia 1984, 1992) and land use maps (Ministry of Agriculture).

# Productivity

We measured laying date (date the first egg was laid), as well as various measures of productivity including clutch size, number of nestlings and number of chicks fledged. Data were taken from the Doñana Biological Station archives. Over the 10-year study period, nests were visited by 2 to 3 people on average 3 times during each breeding season (February to September): once at the egg-laying stage, nestling stage, and fledgling stage (when the nestling reached at least 50 days of age). One person climbed to the nest in order to record the number of eggs or young. Observations were conducted from a distance of 500 m or more from the nest to determine whether eggs had been laid. A quick visit ( $\leq 5 \text{ min.}$ ) would then be conducted, in the fashion described above, to count the eggs. Egg-laying date was most often estimated by subtracting 45 days from the date when the eggs had hatched. The 45 days correspond to the average length of the incubation period in the Spanish Imperial Eagle (Ferrer 1993). Strict precautions were taken during all visits at the nests in order to minimize disturbance caused by the researchers (Fyfe & Olendorff 1976). The time spent at the nest was as brief as could be possible. At the nestling stage, while one person climbed to the nest, other researchers were placed at various observation points in case a nestling prematurely fled the nest. Furthermore, observations at approximately 500 m from

the nest sites were conducted after each visit to ensure that the adults returned to the nest.

# Statistical analysis

For each of the 16 territories, means for each habitat variable were calculated from the 107 nests sampled.

Laying date was given a numerical value by considering the earliest laying date of each year as day number one. The mean numerical value representing laying date was then computed again for each territory from the nests sampled. For productivity, we used the total numbers of eggs laid, nestlings and young fledged over the 10 years within each territory (Table 2) in order to consider the true output of each territory. Each territory was in turn treated as an independent datum (n = 16).

Correlation analysis was conducted with the non-parametric Spearman correlation coefficient  $(r_s)$  using the Statgraphics statistical package (Manugistics, Inc. 1992).

# Laying date

Egg-laying was initiated from 14 February to 3 May. The overall mean laying date was in the second week of April (numerical value = 30.28). Mean laying date varied greatly among territories ranging from  $13.12 \pm 7.38$  to  $47.50 \pm 30.40$  (Table 2).

The laying date was found to be positively correlated with the kilometres of electric power line presen: in a given territory ( $r_s = 0.518$ , P < 0.05) and negatively correlated with the distance to the nearest urban centre ( $r_s = -0.529$ , P < 0.05). The correlations between mean laying date with both the distance to the nearest firebreak and the kilometres of firebreak within a territory approached significance ( $r_s =$ -0.488, P = 0.059 and  $r_s = 0.483$ , P = 0.062, respectively). Egg-laying tended to be later in territories close to, and containing more kilometres of firebreaks (Table 1).

No territory features representing microhabitat, vegetative composition and land use were found to be significantly correlated with laying date (Table 1).

# Clutch size

Clutches contained 1 (n = 8), 2 (n = 36), 3 (n = 37), 4 (n = 37)

10) or 5 (n = 2) eggs for an average of 2.6 eggs overall (n = 93). The laying of 5 eggs was the result of the loss of 1 or 2 eggs through undetermined sources. The lost eggs were not included in the analyses.

The total number of eggs laid within a territory over the 10 years varied greatly among the 16 territories, ranging from 2 (territory 6) to 29 eggs (territory 12) (Table 2). However, the total number of eggs was not found to be significantly related to any of the territory features measured (Table 1).

#### Number of nestlings

Nests contained 0 (n = 38), 1 (n = 19), 2 (n = 32), 3 (n = 16)or 4 (n = 2) nestlings (mean = 1.1, n = 107). Among the territories, the variation in total number of nestlings was great, ranging from 1 (territory 6) to 19 nestlings (territory 15) in the 10 years (Table 2). However, the total number of nestlings was not found to be significantly related to any of the territory features measured (Table 1).

# Number of chicks fledged

The number of fledged chicks per successful nest, i.e. where at least one chick had fledged, was 1 (n = 22), 2 (n = 28), or 3 (n = 12) chicks. Overall, a total of 45 nests did not fledge chicks. The mean number of young fledged over the 10 years for all territories was 1.0 chick (n = 107). The total number of chicks fledged varied among the territories from none in 10 years (territory 12) to 17 (territories 9 and 15) (Table 2). The number of chicks fledged was not found to be significantly related to any of the territory features measured (Table 1).

#### DISCUSSION

# Territory structure and productivity

Territory structure appears to influence the timing of breeding in the Spanish Imperial Eagle population of the Doñana National Park. The laying date was found to be later on those territories closer to urban centres and containing more kilometres of electric power line. Furthermore, the laying date tended to be later, but not significantly so, in territories closer to, and containing more kilometres of firebreaks (strips cut out of the vegetation in order to control fires and frequently used by off-road vehicles to circulate within and outside the park). Subsequent measures of reproductive success (clutch size, number of nestlings and number of chicks fledged) were not significantly influenced by any of the territory features measured. Thus, territory structure representing microhabitat, vegetative composition and land use did not significantly influence the productivity of the Spanish Imperial Eagle in Doñana National Park. Vegetative composition was also not found to influence nest site selection in these birds, however land use was one of the limiting factors affecting selection (González et al. 1992).

The degree of human influence therefore appears to be the overriding factor influencing the productivity of these eagles (particularly at the timing of breeding). However, the  $r_s$ 

values for both the kilometres of power line within the circular sampling area and distance to the nearest urban centre are not especially high and their probabilities barely reach significance at the 95% level (Table 1). It is also possible that the significant findings could have occurred by chance alone (Rice 1989). Furthermore, despite our extreme precautions taken during visits to the nests, the observers conducting the visits could have caused some disturbances (Major 1990) and, consequently, induced biases in the results (Parsons & Burger 1982).

Nevertheless, humans and their activities have been found to decrease the reproductive success in many raptors and other avian species (Watson 1957, Newton 1979). Significant differences in breeding success between territories were found to be dependent on remoteness and inaccessibility to humans in the Golden Eagle (A. chrysaetos, Brown 1969), the Red-tailed Hawk (Buteo Jamaicensis), the Red-shouldered Hawk (B. lineatus, Wiley 1975) and in the Bearded Vulture (Gypaetus barbatus, Donázar et al. 1993).

Electrocution by power lines is the main known cause of non-natural death for the Doñana population of Spanish Imperial Eagles (Ferrer *et al.* 1991). The second most important known cause of death is persecution by shooting (Ferrer & Hiraldo 1992) which likely occurs more frequently near urban centres due to the higher density of human activity. Therefore, the delay in timing of breeding in

territories near urban centres and with high densities of power lines, may be interpreted in two ways: (1) it may be associated with replacement of a missing member of a pair (Newton 1976b) due to the high turnover rates among the pairs occupying these territories; (2) the higher frequency by occupation by immature birds in territories with a higher degree of human disturbance, i.e. lower-quality territories (Steenhof et al. 1983, Reese & Kadlec 1985, González et al. 1992) age-related difference causing an in breeding However, these two hypotheses may not be performance. mutually exclusive since replacement of a missing adult member by a subadult has frequently been observed in Spanish Imperial Eagles (Valverde 1960a, Calderón et al. 1988, Ferrer & Calderón 1990, Ferrer 1993). Furthermore, in raptors, subadults may breed when human persecution artificially depletes adult members, as has been observed not only in this species (Valverde 1960a) but also in Peregrine Falcons (Falco peregrinus, Ratcliffe 1980) and in Golden Eagles (Steenhof et al. 1983). In this population, territories with higher exposure to human activities, (closer to urban centres and highways, and containing more kilometres of power lines) are those located at the park borders (Fig. 1). For example, territory 16 had the latest laying date, territory 12 did not produce a single fledged young in all 10 years, and territories 1 and 14 had only 3 active nests. All of these territories are frequently occupied by juveniles (Luis García,

unpublished data).

Age has been found to influence breeding success in birds where older birds are more successful than younger ones (Newton 1979, Reese & Kadlec 1985, Nol & Smith 1987, Desrochers & Magrath 1993). In raptors, the differences in breeding performance is particularly marked in the early stages of the breeding cycle such as in the initiation of egglaying and in the clutch size but not in subsequent stages (Newton 1976a, Perdeck & Cavé 1992).

The timing of breeding has been identified as a sensitive stage of the breeding cycle in avian species, as it seems to control the overall success of the subsequent breeding stages (van Balen 1973, Brown 1976, Tinbergen & Daan 1990, Daan et al. 1990). This might explain the fact that human disturbance appeared to have an effect only on the egg-laying date of the Spanish Imperial Eagle. This behaviour might be adaptive in that it might be more profitable to postpone or abandon the breeding attempt, following a human-related disturbance, than to expend further effort on a probable failure (Newton 1979). This is particularly true for long-lived large species which can afford to delay breeding. For example, forestry activities affected egg-laying of Red Kites (Milvus milvus). Laying date was later in areas with higher intensities of forestry activities, but subsequent stages in the breeding cycle were not affected (Newton et al. 1981b).

# Management implications

In recent years, efforts have been made to decrease mortality by electrocution in the Doñana population of Spanish Imperial Eagles. Between 1987 and 1988, 9 km of power lines inside the park were buried (Ferrer & Hiraldo 1991) and 33 km of live line were substituted with wires that are linked and covered with a plastic case (Cadenas & Mañez 1988). This management technique has proven to be successful in reducing mortality of the eagles (Ferrer & Hiraldo 1991). The buried power lines were not within Spanish Imperial Eagle territory boundaries but, some of the covered ones were. Nonetheless, the presence of these power lines within eagle territories still appears to affect the breeding success of these eagles. Further investigation needs to be conducted on the pairs occupying the territories with high densities of power lines in order to determine how the management techniques have failed to protect these birds.

The risk of persecution is unfortunately still high for this population, more particularly for those nesting near urban centres. Intensifying the protection at those territories and increasing the awareness of the bird's endangered status and fragile existence to nearby villagers and land owners are strongly recommended.

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Variables	Laying date		Clutch size		Number of nestlings		Number of fledglings			
	rs	Р	r s	P	rs	Р	<u>r s</u>	Р		
1. Height of nest tree above ground (m)	0.288	0.264	-0.184	0.476	-0.326	0.206	-0.425	0.100		
2. Width of nest tree measured as diameter at	0.085	0.741	-0.009	0.973	-0.038	0.882	-0.007	0.977		
J breast height (cm) 3. Distance from nest tree to nearest edge of the wood	0.060	0.817	-0.065	0.802	0.084	0.745	0.067	0.794		
stand (m) 4. Angle of aperture of the wood stand at the nest tree (0° for closed wood stands and 360° for isolated trees),	-0.268	0.299	0.149	0.563	-0.104	0.688	-0.055	0.832		
measured using a protractor with tree us center point										

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Table 1. Correlations between 4 productivity parameters and variables characterizing territory structure of the Spanish Imperial Eagle population of Doñana National Park (df = 15)

Table 1. (continued)

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Variables	Laying date		Clut	Clutch size		Number of nestlings		Number of fledglings	
	r 5	Р	r <u>s</u>	P	rs	Р	r	Р	
5. Distance from nest tree to marsh (m)	0.359	0.165	-0.012	0.963	0.171	0.507	0.037	0.886	
6. Percentage of surface occupied by marshland within the circular sampling	-0.421	0.103	0.072	0.780	-0.250	0.332	-0.118	0.647	
area 7. Percentage of surface area occupied by pasture land within the circular sampling	0.235	0.362	0.070	0.787	-0.067	0.797	-0.015	0.954	
area 8. Percentage of surface covered by Mediterranean scrubland within the	-0.034	0.895	0.333	0.200	0.376	0.146	0.294	0.254	
circular sampling area 9. Percentage of surface covered by sand dunes in the circular sampling area	0.198	0.444	-0.325	0.208	-0.081	0.753	-0.005	0.985	

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Variables	Layi	Laying date		Clutch size		Number of nestlings		Number of fledglings	
	۲ ۶	P	۲ ۶	P	r s	P	rs	Р	
10. Distance from nest tree to nearest body of water (lagoon, river, stream or salt mine) (m)	0.268	0.300	-0.129	0.617	0.301	0.243	0.210	0.417	
11. Distance from tree to nearest active Spanish Imperial Eagle nest of the	-0.047	0.855	-0.123	0.633	-0.044	0.864	-0.100	0.702	
same year (m) 12. Kilometers of non-paved road passable hy vehicle obstructed by vegetation in the circular sampling area	-0.194	0.452	0.237	0.358	0.316	0.221	0.186	0.471	
<ul> <li>13. Kilometers of non-paved</li> <li>road passable by vehicle not</li> <li>obstructed by vegetation in</li> <li>the circular sampling area</li> </ul>	0.124	0.632	0.186	0.473	0.449	0.082	0.475	0.066	

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Table 1. (continued)

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Variables	Laying date		Clutch size		Number of nestlings		Number of fledglings	
	rs	Р	rs	P	r s .	Р	r s	Р
14. Kilometers of firebreak (strips cut out of vegetation for fire control) in the	0.483	0.062	-0.072	0.780	0.002	0.993	-0.128	0.621
15. Kilometers of paved road in the circular sampling area	-0.075	0.771	0.171	0.507	0.381	0.140	0.318	0.219
16. Kilometers of highway in the circular sampling area	0.308	0.233	-0.311	0.229	-0.084	0.744	-0.112	0.663
17. Kilometers of non-paved road used for pilgrimage by local people	0.251	0.332	0.009	0.972	0.077	0.765	0.145	0.574
18. Kilometers of non-paved road used by ICONA park staff	0.137	0.596	-0.201	0.436	0.031	0.906	0.080	0.758

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Table 1. (continued)

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Variables	Layi	Laying date		Clutch size		Number of nestlings		Number of fledglings	
	rs	P	r s	P	r	<u>P</u>	r <u>ş</u>	F	
19. Percentage of surface occupied by non-irrigated cultivated land in the circular sampling area	-0.196	0.448	0.000	1.000	0.422	0.102	0.394	0.128	
20. Percentage of surface occupied by irrigated cultivated land in the circular sampling area	-0.196	0.448	0.000	1.000	0.422	0.102	0.394	0.128	
21. Distance from nest tree to nearest non-irrigated cultivated land (m)	o 0.100	0.699	-0.009	0.973	-0.025	0.923	0.069	0.788	
22. Distance from nest tree to nearest irrigated cultivated land (m)	-0.385	0.136	-0.037	0.886	-0.033	1.000	0.064	0.806	

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Variables	Layi	Laying date		Clutch size		aber of stlings	Number of fledglings	
	r <u>s</u>	Р	r s	Р	r <u>s</u>	Р	r s	P
23. Distance from nest tree to nearest non-paved road passable by vehicle	0.371	0.151	-0.083	0.748	-0.160	0.537	-0.084	0.745
obstructed by vegetation (m) 24. Distance from nest tree to nearest non-paved road passable by vehicle not	-0.309	0.232	-0.356	0.168	-0.219	0.397	-0.170	0.511
obstructed by vegetation (m) 25. Distance from nest tree to	-0.488	0.059	0.273	0.290	0.092	0.723	0.195	0.45 i
nearest firebreak (m) 26. Distance from nest tree to	-0.021	0.936	-0.105	0.683	-0.394	0.127	-0.295	0.253
nearest paved road (m) 27. Distance from nest tree to nearest highway (m)	-0.147	0.596	0.013	0.959	-0.108	0.676	0.004	0.986

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Table 1. (continued)

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	Variables	Laying date		Clutch size		Number of nestlings		Number of fledglings	
	······································	r <u>s</u>	Р	<u>r</u> s	Р	rs	P	r	P
	28. Distance from nest tree to nearest non-paved road used for pilgrimage by local people (m)	-0.062	0.811	-0.215	0.405	-0.114	0.660	-0.161	0.533
81	29. Distance from nest tree to nearest non-paved road used by ICONA park staff (m)	-0.153	0.554	0.209	0.418	0.024	0.927	-0.021	0.936
	30. Distance from nest tree to nearest urban centre (m)	-0.529	0.040	-0.082	0.752	0.126	0.627	0.238	0.357
	31. Distance from nest tree to nearest building (m)	-0.212	0.412	-0.288	0.265	-0.210	0.417	-0.162	0.530
	32. Kilometers of electric power line in the circular sampling area	0.518	0.045	-0.144	0.578	-0.412	0.111	-0.444	0.086
	<ul><li>33. Distance from tree to</li><li>nearest electric power line</li><li>(m)</li></ul>	-0.397	0.124	0.010	0.968	0.137	0.595	0.220	0.394

Table 2. Maximum number of active nest sites, mean laying date (February 14 = 1), total and mean number of eggs, nestlings, and young fledged for each of the 16 Spanish Imperial Eagle territories in 10 years (1984-1994). For each mean, the  $\pm$  SD and sample size (in brackets) are given.

Т.	erritory	No. of nests	Laying date	Total no. of eggs	Mean no. of eggs	Total no. of nestlings	Mean no. of nestlings	Total no. of young fledged	Mean no. of young fledged
	1	3	36 ± 7 (7)	4	20 ± 00 (2)	3	10 + 10 (3)	2	07 + 12 (3)
	2	10	$47 \pm 23(9)$	19	2.0 = 0.0 (2) $2.1 \pm 0.6 (9)$	11	$1.0 \pm 0.9 (10)$	10	$10 \pm 08 (10)$
	3	9	$22 \pm 6 (7)$	15	$2.1 \pm 0.0$ (2)	8	$09 \pm 09$ (9)	7	$0.8 \pm 10$ (9)
	4	9	$24 \pm 20(7)$	20	$2.5 \pm 0.8$ (8)	11	$1.2 \pm 1.3 (9)$	9	$1.0 \pm 1.2 (9)$
	5	11	21 ± 6 (9)	20	2.2 ± 0.7 (9)	12	1.1 ± 1.0 (11)	11	1.0 ± 1.0 (11)
	6	I	37 (l)	2	2.0 (1)	1	1.0 (1)	1	I.O (I)
ŝ	7	6	36 ± 9 (6)	15	2.5 ± 0.8 (6)	9	1.5 ± 1.4 (6)	7	1.2 ± 1.2 (6)
-	8	3	18 ± 0 (2)	7	2.3 ± 1.5 (3)	3	1.0 ± 1.7 (3)	3	1.0 ± 1.7 (3)
	9	10	13 ± 7 (8)	23	2.9 ± 1.2 (8)	18	1.8 ± 1.0 (10)	17	1.7 ± 1.1 (10)
	01	9.	28 ± 7 (7)	19	2.7 ± 0.8 (7)	15	1.7 ± 1.1 (9)	11	1.2 ± 0.8 (9)
	11	8	26 ± 8 (7)	20	2.5 ± 0.9 (8)	5	0.6 ± 1.4 (8)	4	0.5 ± 1.1 (8)
	12	9	36 ± 8 (7)	29	3.2 ± 0.7 (9)	2	$0.2 \pm 0.4 (9)$	0	0.0 ± 0.0 (9)
	13	6	26 ± 11 (6)	26	3.5 ± 1.0 (6)	12	2.0 ± 1.1 (6)	8	1.3 ± 0.8 (6)
	14	3	$42 \pm 9$ (3)	5	2.5 ± 0.7 (2)	<b>7</b> ·	$2.3 \pm 0.6$ (3)	4	1.3 ± 1.5 (3)
	15	8	23 ± 13 (7)	16	2.7 ± 0.5 (6)	19	2.4 ± 0.7 (8)	17	2.1 ± 0.8 (8)
	16	2	48 ± 30 (2)	6	3.0 ± 0.0 (2)	3	1.5 ± 2.1 (2)	3	1.5 ± 2.1 (2)

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Figure 1. The study area (Doñana National Park) showing the 16 Spanish Imperial Eagle territories, nearest urban centres, and marsh and park borders.



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#### GENERAL CONCLUSIONS

In the nest site selection study (section I), nest sites were found to significantly differ from the randomly chosen sites for 87% of the habitat variables measured, representing both micro and macrohabitat. From our GLM model, the probability of occupation of a site by a Spanish Imperial Eagle was calculated and it was found to increase with tree height, angle of aperture of the wood stand, distance to paved roads, distance to urban centre and distance to water body.

In the study pertaining to the influence of territory structure on the productivity of Spanish Imperial Eagles (section II), egg-laying was later on territories situated closer to urban centres and in those containing more kilometres of power line. However, no territory features were found to significantly influence clutch size, number of nestlings or the number of chicks fledged.

Human-related variables, particularly the proximity to urban centres, thus appear to be crucial factors influencing both the selection of a nest site and the productivity of the eagle population of Doñana National Park. Urban centres probably represent the highest densities of human activities and thus a higher risk of persecution for the eagles.

The choice of a nest site and the reproductive success of these eagles is not influenced by habitat features representing vegetative composition. The microhabitat

probably plays a minor role in both the selection of a nest site and the productivity of the Spanish Imperial Eagle, as human-related factors seem to be the overriding factors.