

available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/biocon](http://www.elsevier.com/locate/biocon)

# Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*)

Luis Mariano González <sup>a</sup>, Antoni Margalida <sup>b,\*</sup>, Roberto Sánchez <sup>c</sup>, Javier Oria <sup>d</sup>

<sup>a</sup>Dirección General para la Biodiversidad, Ministerio de Medio Ambiente, Gran Vía San Francisco 4, E-28005 Madrid, Spain

<sup>b</sup>Bearded Vulture Study and Protection Group, Apdo. 43, E-25520 El Pont de Suert (Lleida), Spain

<sup>c</sup>Fundación CBD-Habitat, c/Nieremberg 8, bajo A. E-28002 Madrid, Spain

<sup>d</sup>c/San Agustín 22, E-40001, Segovia, Spain

## ARTICLE INFO

### Article history:

Received 30 May 2005

Received in revised form

6 November 2005

Accepted 20 November 2005

Available online 3 January 2006

### Keywords:

*Aquila adalberti*

Breeding success

Brood reduction

Spanish imperial eagle

Supplementary feeding

## ABSTRACT

We studied the factors that led to brood reduction in 1192 nest/years of 143 territories of the Spanish imperial eagle during the period 1988–2003 and we carried out an innovative supplementary feeding programme in perches near nests in order to mitigate nestling mortality and improve fledging rate. Chick mortality affected 9.3% of hatchlings and 13.9% of the nests monitored. Sibling aggression was the most important factor in brood reduction (54.8% mortality of chicks in the nest), and supplementary feeding limited the process of sibling aggression. In addition, we compared the fledging rate in nests with supplementary food to that of non-supplemented control nests. Supplementary food increased the number of fledglings per brood (1.56 vs 0.72 in the control nests). This increase was repeated in subadult pairs (1.57 vs 0.53 in the control nests) and occurred both in high-quality territories (2.32 vs 1.36) and in low-quality territories (1.35 vs 0.54). Our results also suggest that supplementary feeding does not appear to have any effect on the provisioning rate of either males or females or on the wild prey. Food supplementation led to the recovery of breeding success after a period of loss due to a reduction of prey as a consequence of viral haemorrhagic disease. We conclude that the Spanish imperial eagle's breeding output is food-limited during the nestling period and that food taken to the nest regulates sibling aggression. Supplemental feeding when food is scarce, or under emergency conditions, can be considered a good management tool for the conservation of this endangered species.

© 2005 Elsevier Ltd. All rights reserved.

## 1. Introduction

In raptors brood reduction may be caused by physical aggression or the intimidation by nest mates, which is known as siblicide or cainism (Simmons, 1988). Hatching

asynchrony and the smaller size of last-laid eggs facilitates a size hierarchy, which in turn enhances the early death of last-hatched chicks. Brood reduction is influenced by both size differences between chicks and by food availability (e.g., Edwards and Collopy, 1983; Bortolotti, 1986a,b; Sim-

\* Corresponding author: Tel./fax: +34 973 690 386.

E-mail address: [margalida@gauss.entorno.es](mailto:margalida@gauss.entorno.es) (A. Margalida).

0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.11.014

mons, 1988; Viñuela, 1999). In species where facultative siblicide occurs, it is not clear whether sibling aggression is related to food abundance or not (Mock et al., 1990; Forbes, 1991; Forbes and Mock, 1994) and it could be related to the parent–offspring conflict over brood reduction (e.g., Parker and Mock, 1987; Anderson, 1990; Nilsson, 1995; Rodríguez-Gironés, 1996; Viñuela, 1999).

With a population estimate of around 200 breeding pairs in south-western quadrant of the Iberian Peninsula (González and Oria, 2003), the Spanish imperial eagle (*Aquila adalberti*) is one of the rarest and most threatened birds of prey in the world (BirdLife International, 2004). Early studies of its reproductive biology (Valverde, 1960; Garzón, 1972; Meyburg, 1974, 1987) have suggested that mortality of chicks in the nest, although not quantified, occurred frequently and that the main cause was probably siblicide, with brood reduction being the factor that has the greatest influence on this species' breeding success. Later studies (González, 1991) showed quantitatively that this mortality affected 55.7% ( $n = 70$ ) of the monitored nests, with sibling aggression being the main cause (26.2%,  $n = 138$ ) and that it occurred most frequently in territories where its main prey species, the wild rabbit (*Oryctolagus cuniculus*), was scarce. Two causes were suggested for this factor leading to sibling aggression: the frequency with which food is taken to the nest (Meyburg and Garzón, 1973; Meyburg, 1974, 1978) and the abundance of food (wild rabbits) in their home ranges (González, 1991). Both factors concur with the Lack (1954) hypothesis, which argued that when food availability is insufficient to raise the whole brood, the premature death of the chicks could be favourable, since it would reduce the waste of resources (Gibbons, 1987; Wiebe and Bortolotti, 1995). Therefore, in the Spanish imperial eagle we would expect to find a mechanism (in this case siblicide), which would facilitate the death of the smallest chicks when insufficient food was available to feed the whole brood.

However, other studies (Calderón et al., 1987; Ferrer, 1993) disagreed with the above, since in addition to detecting a lower mortality of chicks in the nest (16.8%,  $n = 138$ ), most due to falls from the nest, they did not record any cases of sibling aggression. This would indicate that the mortality of chicks in the Spanish imperial eagle due to this reason was non-existent.

In 1989, in the species' range in the Iberian Peninsula, the wild rabbit was affected by an epizootic disease known as viral haemorrhagic disease (RHD) (Argüello et al., 1988; Villafuerte et al., 1994). RHD had a major effect on rabbit populations, reducing them to between one-half and two-thirds of their original size in just five years (1988–1993) or even inducing local extinctions where rabbit populations had low densities (Blanco and Villafuerte, 1993; Villafuerte et al., 1994, 1995). Reductions in rabbit populations had a negative effect on breeding success in Spanish raptors that prey extensively on rabbits, i.e., the eagle owl (*Bubo bubo*) (Martínez and Calvo, 2001), the golden eagle *Aquila chrysaetos* (Fernández, 1993) and the Spanish imperial eagle (González, 1996a), where shortly after the arrival of RHD (1989) a 44% increase in chick mortality and a 22% decrease in the productive pairs were recorded in comparison with the pre-RHD period. This caused great concern for the fu-

ture of the species and made it clear that steps should be taken to mitigate this situation (González, 1996b). In this context, it was first thought that the smallest chicks in multiple clutches should be removed and placed in other nests, or released into the wild as juveniles through “hacking”, a tool used successfully in the past to mitigate the mortality of chicks in the nest in situations where food was scarce (Meyburg and Garzón, 1973; Meyburg, 1978, 1987; González et al., 1996c). However, the discrepancies over the occurrence of siblicide and its causes in this species, which were mentioned above, and the fact that this technique was considered inefficient because it had little effect on the population's breeding parameters (Ferrer and Hiraldo, 1991; Ferrer, 1993), meant that it was rejected as a handling technique.

Another tool that was also considered, and which we used with this species before 1989, although only occasionally (authors unpubl. report), was the provisioning of supplementary food to the nest. Supplementary feeding is a conservation tool that has been used with numerous vertebrate species (e.g., Boutin, 1990). Existing studies show that in vertebrates, the breeding period, the age at first breeding and growth rates are limited by the availability of food (Boutin, 1990; Schmidt and Hoi, 2002; Tarr and Pekins, 2002); and that in raptors, supplementary feeding tends to advance laying (Aparicio and Bonal, 2002), increase clutch size (Newton and Marquiss, 1981; Aparicio, 1994; Korpimäki and Wiehn, 1998) and improve breeding success (Hansen, 1987; Gehlback and Roberts, 1997; Wiehn and Korpimäki, 1997; but see Gende and Willson, 1997). Although it has been criticised because it interferes with the normal behaviour of the individuals it is trying to help (Boutin, 1990), this technique was recommended by handbooks on how to manage threatened raptors, but only in cases when food resources are inadequate or contaminated (Newton, 1979; Olendorff et al., 1980; Millsap et al., 1987; Cade and Temple, 1995). This led to the national strategy for the species and the regional (autonomous communities) recovery plans recommending the study and use of this technique (González, 1996b; MMA, 2001), which ideally: (a) could be applied selectively to nesting pairs with food shortage problems, (b) does not require access to the nests or the chicks to be handled and (c) would be tested to check how effective it was in improving the population's breeding parameters.

From a global perspective, the following factors are thought to limit the species' breeding success: (1) an increase in the number of inexperienced pairs as a result of high adult mortality (Ferrer et al., 2003); (2) a lack of wild rabbits (especially after 1989), as a result of a decrease in their population because of RHD and (3) the mortality of chicks in the nest and young fledglings as a result of poor parental quality (González, 1991). Therefore, we predict that by increasing food availability with supplementation the breeding success should increase.

The aims of this paper were to study: (1) the causes and occurrence of nestling mortality, (2) the factors that lead to sibling aggression and how they are related to the availability of food; (3) the effect of supplementary feeding on this species' breeding success and (4) to describe a supplementary feeding system that can be carried out properly during

chick-rearing and to discuss its implications in the management and conservation of this threatened species.

## 2. Materials and methods

### 2.1. Study species

The Spanish imperial eagle is a sedentary, territorial and monogamous species. The highest densities of its population are found on plains and mountain ranges with scattered Mediterranean forest and open savannah (*dehesas*), where wild rabbits are abundant (González, 1991). Their clutch size can range from 1 to 4 eggs and the birds may raise up to four chicks. The eggs hatch asynchronously with a difference of up to 7 days between the chicks, and sibling aggression mainly occurs in the first two weeks of the chicks' lives (García, 1973; Meyburg, 1987; González, 1991). Incubation, brooding, the feeding of the chicks and nest-building tasks are mainly taken care of by the females, except for the food provisioning to the female, which is generally carried out by the males. Food transfers from males to females are mainly carried out near the perches where they generally eat the prey (Margarida et al., in press).

### 2.2. General methods

The study was carried out within the framework of the Species Recovery Plans of the Autonomous Communities of Castilla y León, Castilla-La Mancha, Madrid and Extremadura (west central Spain), which constitute most of the Spanish imperial eagle's range.

The nests were monitored around hatching and during the first days of the chicks' lives, every 2–4 days, in order to check the number of chicks that had hatched. After the chicks were approximately two weeks old, observations were carried out every 5–7 days until the chicks fledged. Observations were conducted from prominent spots using 20–60× spotting scopes located approximately 600–800 m from the nest, a distance at which no alert reactions or alterations to adult behaviour were noted (González et al., 2006). Observers only approached the nest or its surrounding area if a chick or the whole clutch had disappeared, in order to determine the possible causes and to collect any remains or carcasses. When we found that there were no remains of the chicks that had disappeared – either in the nest or under it – we assumed that partial brood disappearance was due to siblicide, based on the fact that we have observed cannibalism by aggressive siblings (see also Meyburg, 1975, 1987). In the cases of the other known causes (e.g., illness, collapse of the nest, predation, theft, or poison), we observed that they usually lead to the loss of the whole brood, since all chicks are affected equally.

The food used in the supplementary feeding programme (SFP) was the domestic European rabbit, with a similar colour to the wild species and obtained from farms free of infectious/contagious or parasitic diseases. The rabbits were placed on high and visible branches of trees (perches) situated within the pair's nesting territory and in places that did not disturb the birds in the nest. Moreover, the perches were inaccessible to carnivores and carrion-eating mammals such as red foxes

and dogs. The age of the rabbits ranged between 8 and 12 weeks and each weighed about 1 kg. The rabbits were eviscerated (except for the liver) immediately after they were killed, and those that were stored (frozen until used) were not kept for more than five days. After the rabbit was placed on the branch, the nest and the roost were watched from the vantage point until the rabbit was taken and we recorded whether the rabbit was taken by the pair or not. Food was only provided to nests with more than one chick, and this supplementary feeding (SF) started after the hatching of the second chick. The feeding began approximately a few days after the chicks hatched and it stopped when they were fledging from the nest. Food consisted of one rabbit each time and was provided every 2 days in broods of three chicks, and every 4 days in broods of two.

### 2.3. Sample sizes and statistical analyses

We used non-parametric statistics throughout (Sokal and Rohlf, 1995). The statistical significance was set at  $P < 0.05$ . Values are presented as means  $\pm$  SD.

In order to study the occurrence of nestling mortality and its causes, 1192 nesting events (hereafter called "nests") (in which there was at least one chick) belonging to 143 territories, were monitored during the period 1988–2003.

To study the possible factors that could lead to sibling aggression, we carried out detailed observations of aggressive chick behaviour in 59 nests in 42 territories where sibling aggression was detected. Of these, 22 nests in 17 territories were provided with SF, while 37 nests in 25 territories were not provided with SF.

To measure the effect of SF on the breeding success, we used the fledging rate, defined as the number of chicks that fledged in relation to the number of nests in which there was at least one chick (Cheylan, 1981). Since data coming from the same territory are not necessarily independent, and to avoid any pseudoreplication problems, we used each territory as a sample unit (instead of each breeding event). Using Wilcoxon-signed rank tests, we compared the average fledging rate for each territory for the years before receiving supplementary food, with the average fledging rate for the years when supplementary food was provided. In order to do this, and so as to make averages biologically meaningful, of the global sample of territories we selected those in which: (a) the breeding parameters had been studied for a minimum of nine years, (b) the incubation process in those nine years had proceeded without incident and at least one chick had hatched in each nest, and (c) the SFP had been carried out for a minimum of three years. Thus, of the 69 territories where the SFP (Table 1) was applied, a control sample of 37 territories was selected, which met all three of the above criteria. In this control sample, we compared the fledging rate of the 240 nesting events with SF with that of 236 nests without SF. Later we also studied whether the possible differences in the fledging rates between territories with and without SF were due to:

- (1) the pair's age class. Here we used data from 19 territories chosen at random from the sample, in which at least one member of the pair had subadult plumage (aged under 6 years, authors unpubl. data), hereafter named subadults territories. Within those territories, 52 nests

**Table 1 – Number of Spanish imperial eagle nests involved in the annual supplementary feeding programme and the total number of young that fledged each year**

Year	Nests (n)	Number of young fledged (n)
1990	2	2
1991	6	5
1992	8	12
1993	6	10
1994	8	13
1995	10	22
1996	15	21
1997	16	31
1998	26	46
1999	37	76
2000	49	71
2001	49	67
2002	46	67
2003	41	49
Total	319	492

received SF and 46 nests did not. Wilcoxon-signed rank tests were used to compare fledging rates for each territory before and after SF for this subsample.

- (2) *habitat quality*, in terms of the abundance of rabbits in the Spanish imperial eagle's home ranges. The abundance of rabbits was established in accordance with the classification established in rabbit studies carried out in our study area after the arrival of RHD (Blanco and Villafuerte, 1993; Villafuerte et al., 1995), which indicated that the rabbit could be considered abundant when it was found in relative average densities over 1 rabbit/ha (range found 1–7.8). These values were associated with at least one hunting preserve devoted to rabbit hunting, whilst below this figure the rabbit was considered scarce or very scarce (range 0.9–0), values associated with areas that contained no hunting preserves devoted to rabbit hunting. Bearing in mind the close relation between the range and the abundance of rabbits and that of the Spanish imperial eagle (see González et al., 1992), we considered the territories where the rabbit was classified as abundant as being of *high quality* and those where it was classified as scarce or very scarce as being of *low quality*. The home range was defined as an area measuring 5000 ha (the average home range size of five radio-tagged breeding individuals was 5553 ha, authors unpubl. data). We thus performed two extra Wilcoxon-signed tests comparing the fledging rate before (62 nests) and after (42 nests) SF in high quality territories ( $n=8$ ), and before (174 nests) and after (189 nests) SF in low quality territories ( $n=29$ ). Comparison of the average fledging rate between territories of high or low quality were performed with Mann–Whitney *U*-tests, using the average value for each territory in each category as a data unit.
- (3) *the influence of RHD*. We compared the breeding success obtained in the period before RHD, from 1971 to 88 (González, 1991), with success in the same area after the arrival of the disease (1989–2003) without supplementary feeding. For

this we compared the fledging rate of the 37 control sample territories (post-VDH), with a sample of 42 territories (243 nests) during the period 1971–1987, in other words before the arrival of RHD (see González, 1991), which met the abovementioned criteria (a) and (b) of the selection of territories in the control sample and which we called the pre-RHD sample. Moreover, and to see if in the age class influenced the possible differences between the fledging rates in these samples, we compared the fledging rates of 20 subadults pre-RHD territories (26 nests) with those of 19 subadults post-RHD territories (46 nests). And, in order to check the effect of the abundance of rabbits in the territory, we compared the fledging rates of 20 high-quality pre-RHD territories (110 nests) with those of 8 high-quality post-RHD territories (62 nests) and 20 pre-RHD low-quality territories (133 nests), with the sample of 29 post-RHD low-quality territories (174 nests) that did not receive SF. As before, breeding success was compared using Wilcoxon-signed ranked tests.

- (4) *the frequency of the years of SF*; using Kruskal–Wallis tests, we compared the average fledging rates of the territories according to whether they had received SF for 1–2 years (20 territories), 3–4 years (17 territories), 5–6 (17 territories) or more than 7 years (15 territories).

To assess whether the feeding programme succeeded in avoiding brood reduction, we used data from 37 territories, comparing between nests with (21 nests) and without (62 nests) brood reduction, comparing (with Mann–Whitney *U*-tests) between both groups the average of chicks that fledged, their approximate age (in accordance with the age-classification in González, 1991) at the start and the end of the feeding, the number of days the feeding lasted for, the number of days and the interval between successive rabbit deliveries.

To assess whether the provisioning of natural prey and behaviour at the nests was modified by the SF, we used data from 51 nests of 18 territories where the rabbits in the feeding programme had white or black-and-white fur that could be easily differentiated at a distance from the brown fur of a wild rabbit. In these cases, the natural prey taken to the nest was recorded. In addition, the frequency with which adults, by sex, took prey to the nest was recorded at three control nests, which did not receive supplements. These observations were carried out in nest surveys involving a total of 5499 hours over 503 field days (average  $721.6 \pm 276.54$  h observation per pair, range 207–1011). A Mann–Whitney *U*-test was used to monitor differences in the provisioning rate between males and females in nests with SF vs those without SF.

### 3. Results

#### 3.1. Mortality of chicks in the nest

We recorded the death or disappearance of 209 chicks in 166 nesting events in our study period (Table 2). This mortality constitutes 9.3% ( $n=2252$ ) of the chicks hatched and 13.9% ( $n=1192$ ) of the nests monitored. Of 41.1% of the chicks that died or disappeared, no bodies or remains were found in the nests or the surrounding area. Of these cases in 28 nests (41 chicks), the entire clutch disappeared, whilst in 41 nests (45

**Table 2 – Frequency and causes of mortality of Spanish imperial eagle chicks in the nests**

Cause	Chicks	Nests (n)
Siblicide	47	45
Disease-malnutrition	18	14
Predation	1	1
Collapse of the nest	22	12
Theft	11	7
Poisoning	13	7
Storm	1	1
Accidental falling from nest	10	10
Disappearance	86	69
Total	209	166

chicks), one or two chicks disappeared, with at least one chick remaining.

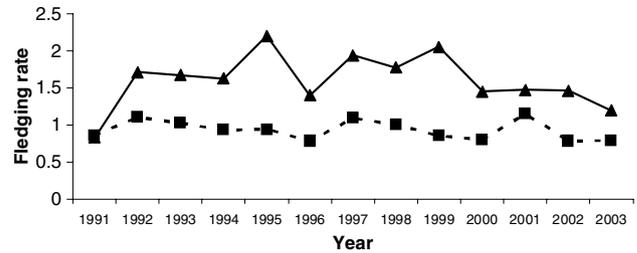
Necropsies determined that 38.2% of the deaths had been caused by traumatic lesions and wounds attributable to sibling aggression (possible siblicide), 17.9% caused by the nest collapsing, 14.6% due to disease/starvation, 10.6% caused by poisoning, 8.9% due to theft, 8.1% due to the chick falling from the nest and the remaining 1.6% due to adverse weather conditions and predation.

In the sample of nests in which we observed sibling aggression and no SF was provided (see Section 2), we directly recorded the death of 39 chicks due to siblicide (45.3%,  $n = 86$  chicks born). Moreover, in the sample of 22 nests in which SF was carried out and where siblicide behaviour was detected, only three chicks died (6%,  $n = 50$  chicks born) of which one was due to disease not siblicide; the proportion of hatched chicks dying due to siblicide was significantly different between nests with SF and with no SF ( $\chi^2 = 22.935$ ,  $df = 1$ ,  $P < 0.0001$ ). In the sample of nests with SF where sibling aggression was monitored, sibling aggression ceased a few days (2–4 days) after the SF started. In this context and adding the 45 chicks assumed to have died due to siblicide that disappeared from clutches with more than one chick mentioned above (see Section 2), then this implies that in 54.8% of the chicks that died ( $n = 168$ ) and in 69.6% of the nests with mortality ( $n = 138$  nests), sibling aggression was the cause involved.

**3.2. Fledging rate before and after the feeding programme**

The average fledging rate of the territories before receiving SF was  $0.72 \pm 0.56$  young/pair while their rate after receiving SF was  $1.56 \pm 0.64$  young/pair (Wilcoxon-signed ranks test  $z = 5.03$ ,  $df = 36$ ,  $P = 0.0001$ ) (Table 2). In 33 (89.2%) of the pairs it was possible to increase the number of chicks fledged, in one (2.7%) it remained constant and in 3 (8.1%) it was lower.

During the years of the study period, the annual fledging rate of the territories with SF was higher than in those without the SF (Mann-Whitney U-test,  $z = 3.87$ ,  $P < 0.0001$ , Fig. 1), and, despite the slight decrease observed in the last few years, the tendency over time is not significant (with SF: Spearman rank correlation index  $r_s = -0.14$ ,  $P > 0.25$ ,  $n = 13$ ; without SF:  $r_s = -0.36$ ,  $P > 0.10$ ,  $n = 13$ ).



**Fig. 1 – Annual variation in the fledging rate of Spanish imperial eagle territories with supplementary feeding (continuous line) and without supplementary feeding (broken line).**

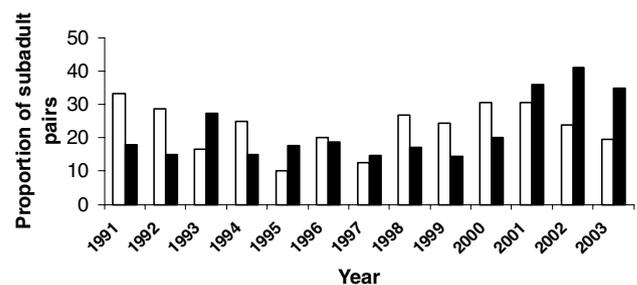
**3.3. Fledging rate in subadults territories**

The fledging rate in the subadults territories before receiving SF was  $0.53 \pm 0.69$  young/pair, while their rate after receiving SF was  $1.57 \pm 0.66$  young/pair (Wilcoxon-signed ranks test  $z = 3.29$ ,  $df = 18$ ,  $P = 0.001$ ).

In territories with SF there was a negative, significant correlation between the fledging rate and the proportion of nests with subadults pairs ( $r_s = -0.49$ ,  $P < 0.05$ ,  $n = 13$ ). This was not the case in the pairs that did not receive SF ( $r_s = -0.29$ ,  $P > 0.05$ ,  $n = 13$ ) where the fledging rate remained constant over time despite the observed increase in the number of subadults territories in the last 3 years (Fig. 2).

**3.4. Fledging rate differences linked to the habitat quality**

In high quality territories, fledging rate was significantly greater when SF was carried out than when it was not (Table 3, Wilcoxon-signed rank test  $z = -2.52$ ,  $df = 7$ ,  $P = 0.0117$ ). In low-quality territories, these differences were noticeably higher, with supplemented nests producing 2.5 times more fledglings (Table 3, Wilcoxon-signed rank test  $z = -2.52$ ,  $df = 28$ ,  $P = 0.0001$ ). Overall, there were also significant differences in the fledging rate between high- and low-quality habitats with SF (Mann-Whitney U-test,  $z = 3.54$ ,  $P = 0.0004$ ) and without SF (Mann-Whitney U-test,  $z = 4.04$ ,  $P = 0.0001$ ).



**Fig. 2 – Annual variation in the proportion of subadults territories of Spanish imperial eagle with (white columns) and without (black columns) supplementary feeding during the period 1991–2003.**

**Table 3 – Differences in fledging rate in territories with high- and low-quality habitats, with and without supplementary feeding**

	High-quality habitat (n = 8)		Low-quality habitat (n = 29)	
	SF	No. SF	SF	No. SF
Fledging rate	2.32 ± 0.5	1.36 ± 0.65	1.35 ± 0.5	0.54 ± 0.38
Nests (n)	42	62	189	174

### 3.5. Fledging rate in pre- and post-RHD periods

#### 3.5.1. Territories without supplementary feeding

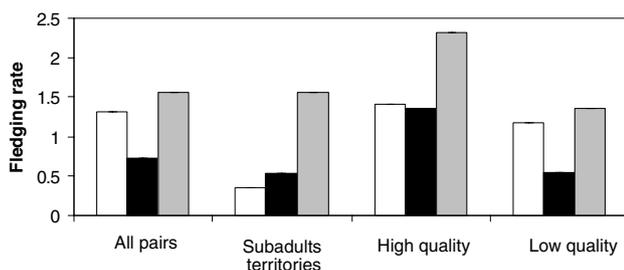
The fledging rate recorded in the post-RHD period in territories that did not receive SF (Fig. 3) was significantly lower than the fledging rate in the pre-RHD period (pre-RHD:  $1.31 \pm 0.62$ ,  $n = 243$  vs post-RHD:  $0.72 \pm 0.56$ ,  $n = 236$ , Wilcoxon-signed rank test  $z = -3.66$ ,  $P = 0.0003$ ); although this tendency does not occur if we consider only the subadults territories (pre-RHD:  $0.35 \pm 0.57$ ,  $n = 26$  vs post-RHD:  $0.53 \pm 0.69$ ,  $n = 46$ , Wilcoxon-signed rank test  $z = 1.019$ ,  $P = 0.308$ ) or the high-quality territories (pre-RHD:  $1.42 \pm 0.74$ ,  $n = 110$  vs post-RHD:  $1.36 \pm 0.65$ ,  $n = 62$ , Wilcoxon-signed rank test  $z = -1.01$ ,  $P = 0.31$ ). In contrast, it was notable and significant in the low-quality territories (pre-RHD:  $1.18 \pm 0.42$ ,  $n = 133$  vs post-RHD:  $0.54 \pm 0.38$ ,  $n = 174$ , Wilcoxon-signed rank test  $z = -3.36$ ,  $P = 0.0008$ ).

#### 3.5.2. Territories with supplementary feeding

The fledging rate recorded in the pre-RHD period in territories with SF was greater than in territories post-RHD (Fig. 3) in all cases, although the differences were only statistically significant in the case of the subadults territories (pre-RHD:  $0.35 \pm 0.57$ ,  $n = 26$  vs post-RHD:  $1.57 \pm 0.66$ ,  $n = 52$ , Wilcoxon-signed rank test  $z = 3.68$ ,  $P = 0.0002$ ).

### 3.6. Fledging rate related with the frequency of feeding years, chick age and the duration and frequency of the supplementary feeding

No significant differences were found in the fledging rate in relation to the number of years over which the SFP was carried out (Kruskal–Wallis  $H = 2.51$ ,  $df = 3$ ,  $P = 0.47$ , Table 4);



**Fig. 3 – Fledging rate recorded in territories in the pre-RHD period (white columns) and in the post-RHD period without (black columns) and with supplementary feeding (grey columns).**

However, the fledging rate in territories where the SFP was carried out for >7 years was greater than in territories where it was carried out for a shorter period.

The only significant difference found between the different variables that explain the success or failure of SF in altering brood reduction (Table 5) was in the days the feeds were carried out (with brood reduction:  $41.25 \pm 16.62$  vs without brood reduction:  $57.43 \pm 16.39$  days Mann–Whitney  $U$ -test  $z = 2.82$ ,  $P = 0.0048$ ). We could not detect a difference in the age at the start of feeding (with brood reduction:  $4.65 \pm 6.21$  vs without brood reduction:  $2.59 \pm 4.84$  Mann–Whitney  $U$ -test  $z = -1.66$ ,  $P = 0.097$ ) and the interval between feeds (with brood reduction:  $2.74 \pm 0.55$  vs without brood reduction:  $2.60 \pm 0.99$  days Mann–Whitney  $U$ -test  $z = -1.80$ ,  $P = 0.072$ ). Nevertheless, the results suggest a tendency for territories in which SF of the chicks began at an earlier age, and in those with more frequent feeds and smaller intervals between feeds, to be those in which brood reduction was avoided.

### 3.7. Effects of the supplementary feeding programme on the provisioning of natural prey and on the provisioning of food to the nest

The proportion of domestic rabbits (food supply) in the birds' diet of 51 nests from 18 territories that received SF ( $87.76 \pm 11.78\%$ ; range 31.7–100%,  $n = 6251$  prey items) was similar to the proportion of wild rabbit in three nests that did not receive SF ( $86.05 \pm 13.68\%$ ; range 66.7–95.87,  $n = 394$  prey items).

The prey provisioning rate of males and females (Table 6) was not different in nests with SF compared with those that did not receive SF in males (Mann–Whitney  $U$ -test  $z = -0.91$ ,  $P = 0.361$ ) or in females (Mann–Whitney  $U$ -test  $z = 0.36$ ,  $P = 0.715$ ).

## 4. Discussion

The causes of chick mortality in the Spanish imperial eagle nests recorded in our study continue to be the same as those found in the same study area during the period 1971–1987 (Garzón, 1973; González, 1991). However, the frequency of mortality detected (9.3%) was a third lower than in the comparison period (26.2%,  $n = 138$ ) (González, 1991). During our study period, there was a great increase in activities aimed at conserving Spanish imperial eagle nests, e.g.: mainly nest monitoring and surveillance, securing nest structures and supplementary feeding (González and Oria, 2003). There is no doubt that these activities can be associated with the decrease in the frequency of the mortality of chicks in the nest during our study period.

**Table 4 – Variation in the fledging rate in the Spanish imperial eagle according to the number of years the supplementary feeding programme was carried out**

	1–2 years	3–4 years	5–6 years	>7 years
Fledging rate	1.45 ± 0.84	1.46 ± 0.72	1.41 ± 0.63	1.74 ± 0.61
Nests (n)	28	62	93	136
Territories (n)	20	17	17	15

**Table 5 – Average and ranges of the chicks (in days), of the frequencies and interval in days between feeds and of the number of rabbits taken to the nest in nests that received supplementary feeding with or without brood reduction**

Chicks hatched	Chicks fledged	Age of chick when SF started	Age of chick when SF ended	Days of SF	Interval between days of SF	Number of domestic rabbits in the SF (n)	Nests (n)
<i>With brood reduction</i>							
4	3	6	96	35	3.5	102	1
3	2	8 (3–20)	103 (50–137)	48.7 (41–63)	3 (2–4)	79.4 (18–138)	6
3	1	0	118	70	2	129	1
2	1	8.6 (0–17)	98.7 (28–136)	34.4 (16–66)	2.6 (2–4)	60 (16–130)	13
<i>Without brood reduction</i>							
3	3	1.7 (0–8)	130 (105–153)	59.7 (35–78)	2.4 (2–4)	170.1 (101–208)	16
2	2	2.9 (0–19)	127 (76–155)	56.7 (13–84)	2.7 (2–6)	120.2 (24–155)	46

**Table 6 – Prey items delivered per hour by males and females in nests with and without supplemental feeding**

	Male	Female	Male–female	Prey items (n)	Nests (n)
With SF	0.093 ± 0.039	0.043 ± 0.032	0.136 ± 0.057	490	6
Without SF	0.090 ± 0.084	0.041 ± 0.020	0.131 ± 0.086	412	5

Unlike other studies (in other study areas) of the Spanish imperial eagle in which this was not even detected (Calderón et al., 1987; Ferrer, 1993), in our study sibling aggression continues to be the main cause of mortality, accounting for 54.8% of all cases. The reason why mortality due to sibling aggression was not detected in previous studies possibly lies in the methodology used, which, unlike ours, did not include the regular observation of chicks in the nest, especially when they were very young (see Calderón et al., 1987; Ferrer, 1993). Our results also showed that sibling aggression, as recorded in other studies of large eagles (Meyburg, 1978), stopped when supplementary food was brought to the nest in 100% of the cases (n = 59) in which this was carried out. This implies that supplementary feeding in nests with a risk of, or the beginnings of, sibling aggression, is an effective alternative for mitigating the mortality of chicks in the nest. This makes the removal of chicks (which may die because of this) from the nests unnecessary and unjustified.

Our results show that the production of fledglings was limited by food, as has been suggested by previous studies on avian reproduction (e.g., Simons and Martin, 1990; Richner, 1992; Wiehn and Korpimäki, 1997). In accordance with other studies (Wiehn and Korpimäki, 1997), this happened not only in low-quality but also in high-quality territories. Likewise, our results show that in the Spanish imperial eagle, as it was suggested in the past (Meyburg, 1974, 1978) and as in other species (Wiebe and Bortolotti, 1995; Estes et al., 1999), food-limited reproductive output, either directly through starvation or indirectly through sibling competition and siblicide varies in accordance with the food-amount hypothesis (Mock and Parker, 1987; Dewey and Kennedy, 2001). In the Spanish imperial eagle, a species with facultative siblicide, asynchronous hatching facilitates the appearance of size and dominance hierarchies and thus brood size reduction to match the available levels of resources provided by parents, thus creating a regulatory mechanism that facilitates the death

of the chicks in situations when food is scarce, in accordance with Lack's (1954) hypothesis. Our experimental food supplementation provides support for this hypothesis, unlike the findings of another study of the Spanish imperial eagle (Ferrer, 1993) and coinciding with what has been observed in other species such as the Black Kite (*Milvus migrans*) (Viñuela, 2000).

Like the findings of other studies, (e.g., Hansen, 1987; Wiebe and Bortolotti, 1994; Gehlback and Roberts, 1997; Wiehn and Korpimäki, 1997; Redpath et al., 2001) our results show that supplementary feeding is effective in increasing breeding success, both in subadults and non-subadults territories and high- and low-quality territories. The results show that territories with additional food produced twice the number of young as those in the control territories without extra food. Moreover, in the case of subadults territories or low-quality territories, the number of young almost tripled. The fact that most of the subadults territories were located in marginal, low-quality habitats (González et al., 1992), could explain why the effect of supplementary feeding on their fledging rate was greater than in non-subadults territories. For this reason, it appears reasonable to recommend that such subadult territories be given priority for supplemental feeding. On the other hand, the fact that supplementary feeding also increased the fledging rate of territories of high-quality habitats suggests that the supplementary food, as we mentioned earlier, may be more important than the abundance of rabbits in the wild. However, it could be interpreted that in high-quality territories (based on the abundance of rabbits), the availability of food could be lower than the species' potential productive capacity.

We have shown that supplementary feeding helped mitigate the effects of the decrease in the rabbit populations due to RHD on the breeding success of the eagles. Territories subjected to supplementary feeding after the arrival

of the RHD recovered and even exceeded pre-RHD levels. This effect was more notable in the case of subadults territories. In this context, the effect of supplementary feeding programme in maintaining the fledging rate in the post-RHD period on a large number of territories and during a considerable number of years (15) (see Table 1) may have had a great impact on the annual growth rate of the population of this species (almost 4% in the last decade (González and Oria, 2003).

The methodology of the supplementary feeding programme carried out in our study avoids intraspecific conflicts because the food is located in places (perches) that are inaccessible to terrestrial carnivores and are situated inside of the limits of the territory defended by the eagles. The Spanish imperial eagle is a territorial species; the defence of the resources within its territory will avoid intrusions by conspecifics that may have a negative effect on its breeding success. Also the extra food is provided regularly (every 2–3 days) and in small quantities (1–3 rabbits), which covers the birds' feeding requirements without producing any accumulation.

In this respect, it should be pointed out that although artificial feeding stations could be used as an alternative method to our method, since the Spanish imperial eagle frequently feeds on carrion (Hiraldo et al., 1991; González, 1991), feeding stations do not meet the requirement of being selective, which is necessary in order to be effective. This is because the feeding stations do not guarantee that the adults in a specific territory will exploit the food. Another possibility would be to place the feeding station near a target nest, but it could provoke an increase of disturbance and interactions with the carrion-eating birds (vultures, eagles and crows), which would no doubt be attracted to the area. Similarly, taking prey items directly to the nest is not advisable because it entails the risk of disturbing the birds' parental care, which may have negative effects, as has been studied in raptors (Newton, 1979; Grier and Fyfe, 1987). Instead we took advantage of the fact that the individuals in the territory generally have regular perches, far away from the nests, where the male takes prey and where the female goes to take collect it before taking it to the nest. By placing domestic rabbits on these perches at distances greater than 600 m, which do not disturb the birds (González et al., 2006), and at times when the male was absent, we avoided interrupting the parental care and could substitute the role of the male in a manner than minimised disturbance.

In conclusion, the Spanish imperial eagle's supplementary feeding programme, as we have described it, can be considered an effective, safe tool, which can help reduce the mortality of chicks in the nest due to sibling aggression. It can also help maintain, and even improve, the fledging rate of the population in situations when food is scarce or under emergency conditions.

### Acknowledgements

We thank to the field team formed by Javier Sánchez, María Fernández, Julio Caballero, Salvador Pacheco, Michel Cedennilla, Isabel López, Fernando Aparicio, José Antonio Blanco, David Martín y Fernando de Antonio. Thanks also to Carlos

Soria, Maximiliano Panadero, Rosa Jiménez, Samuel Pla, Javier Sánchez-Guijaldo, Rubén Ramos, Raúl Tomas, Cristina Giner-Abati, Agustín Mogena, José María Tercero, Francisco, Manuel Martín, Ángel Arredondo, José Guzmán, Eutimio Morales, Juan Panadero, José Duque, José Mirón y Luis Bolonio. We are particularly grateful to Victor G. Matarranz, who, with his usual skill and know-how, tagged all the nestlings. Thanks also go to Antonio Aranda, Juan Pablo Castaño, Juan Manuel Blanco, Luis Prada, Agustín Madero, Francisco Sánchez, Nicolás González, Félix de la Orden, Francisco Jiménez, Jose Ignacio Mosqueda, Angel Sánchez, Javier Caldera, María José Palacios, Jose Ignacio Molina, Soledad Centenera, Borja Heredia, Carlos Rodríguez-Vigal and the official wardens of the Autonomous Communities for the information on sightings they kindly provided. We also thank Gary R. Bortolotti, Beatriz E. Arroyo and two anonymous reviewers for their comments aimed at improving the manuscript and Sheila Hardie for translating the text into English. This study was jointly funded by the framework of the National Strategy and Recovery Plans for the species by the Dirección General para la Biodiversidad del Ministerio de Medio Ambiente and the Consejerías de Medio Ambiente of the Autonomous Communities of Madrid, Castilla y León, Castilla-La Mancha and Extremadura; and by the European Commission throughout LIFE-projects 99/NAT/E/006336 and 03/NAT/E/000050. The basic information was provided by the five Autonomous Communities represented in the National Spanish Imperial Eagle Working Group, for which we are grateful.

### REFERENCES

- Anderson, D.J., 1990. Evolution of obligate siblicide in boobies. 2. Food limitation and parent-offspring conflict. *Evolution* 44, 2069–2082.
- Aparicio, J.M., 1994. The seasonal decline in clutch size: an experiment with supplementary food in the kestrel, *Falco tinnunculus*. *Oikos* 71, 451–458.
- Aparicio, J.M., Bonal, R., 2002. Effects of food supplementation and habitat selection of timing of lesser kestrel breeding. *Ecology* 83, 873–877.
- Argüello, J.L., Llanos, A., Pérez-Ordoy, L.I., 1988. Enfermedad vírica hemorrágica del conejo en España. *Medicina Veterinaria* 5, 645–650.
- BirdLife International, 2004. *Threatened Birds of the World 2004*. BirdLife International, Cambridge (CD-ROM).
- Blanco, J.C., Villafuerte, R., 1993. Factores ecológicos que influyen sobre las poblaciones de conejos. *Incidencia de la Enfermedad Hemorrágica*. TRAGSA-Ministerio de Medio Ambiente, Madrid.
- Bortolotti, G., 1986a. Evolution of growth rates in eagles: sibling competition versus energy considerations. *Ecology* 67, 182–194.
- Bortolotti, G., 1986b. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *American Naturalist* 127, 495–507.
- Boutin, S., 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. *Canadian Journal of Zoology* 68, 203–220.
- Cade, T.J., Temple, S.A., 1995. Management of threatened bird species: evaluation of the hands-on approach. *Ibis* 137, 161–172.
- Calderón, J., Castroviejo, J., García, L., Ferrer, M., 1987. El Águila Imperial (*Aquila adalberti*) en Doñana: algunos aspectos de su reproducción. *Alytes* 5, 47–72.

- Cheyland, G., 1981. Description des principaux paramètres de la reproduction. *Rapaces Méditerranéens* 1, 3–5.
- Dewey, S.R., Kennedy, P.L., 2001. Effects of supplemental food on parental-care strategies and juvenile survival of Northern Goshawks. *The Auk* 118, 352–365.
- Edwards, T.C., Collopy, M.C., 1983. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. *The Auk* 100, 630–635.
- Estes, W.A., Dewey, S.R., Kennedy, P.L., 1999. Siblicide at Northern Goshawk: does food play a role? *Wilson Bulletin* 111, 432–436.
- Fernández, C., 1993. Effect of the viral haemorrhagic pneumonia of the wild rabbit on the diet and breeding success of the golden eagle (*Aquila chrysaetos* L.). *Revue d'Ecologie, Terre et Vie* 48, 323–329.
- Ferrer, M., 1993. El Águila Imperial Ibérica (*Aquila adalberti*). Editorial Quercus, Madrid.
- Ferrer, M., Hiraldo, F., 1991. Evaluation of management techniques for the Spanish imperial eagle. *Wildlife Society Bulletin* 19, 436–442.
- Ferrer, M., Penteriani, V., Balbontín, J., Pandolfi, M., 2003. The proportion of immature breeders as a reliable early warning signal of population decline: evidence from the Spanish imperial eagle in Doñana. *Biological Conservation* 114, 463–466.
- Forbes, L.S., 1991. Hunger and food allocation among nestlings of facultatively siblicidal ospreys. *Behavioral Ecology and Sociobiology* 29, 189–195.
- Forbes, L.S., Mock, D.W., 1994. Proximate and ultimate determinants of avian brood reduction. In: Parmigiani, S., vom Seal, F.S. (Eds.), *Infanticide and Parental Care*. Hardwood Academic Publ., Chur, Switzerland, pp. 237–256.
- Garzón, J., 1972. Especies en peligro: el Águila imperial. *Adena* 4, 8–12.
- Garzón, J., 1973. Contribución al estudio del status, alimentación y protección de las Falconiformes en España Central. *Ardeola* 19, 279–330.
- Gehlback, F.R., Roberts, J.C., 1997. Experimental feeding of suburban Eastern Screech-Owls *Otus asio* has few effects on reproduction apart from non-experimental factors. *Journal of Avian Biology* 28, 38–46.
- Gende, S.M., Willson, M.F., 1997. Supplemental feeding experiments of nesting Bald Eagles in Southeastern Alaska. *Journal of Field Ornithology* 68, 590–601.
- Gibbons, D.W., 1987. Hatching asynchrony reduces parental investment in the jackdaw. *Journal of Animal Ecology* 56, 403–414.
- González, L.M., 1991. Historial natural del Águila Imperial Ibérica (*Aquila adalberti* Brehm, 1861). Tesis Doctoral, Universidad Autónoma de Madrid, Colección Técnica, ICONA, Madrid.
- González, L.M., 1996a. Tendencias poblacionales y estatus de conservación del Águila imperial ibérica (*Aquila adalberti*) en España durante los últimos veinte años. In: Muntaner, J., Mayol, J. (Eds.), *Biología y Conservación de las Rapaces Mediterráneas*, 1994, Monografía, vol. 4. SEO, Madrid, pp. 61–65.
- González, L.M., 1996b. Action plan for the Spanish imperial eagle (*Aquila adalberti*). In: Heredia, B., Rose, L., Painter, M. (Eds.), *Globally Threatened Birds in Europe, Action Plans*, Strasbourg. Council of Europe Publ, France, pp. 175–189.
- González, L.M., Arroyo, B.E., Margalida, A., Oria, J., Sánchez, R., 2006. Effect of human activities on behaviour and success of breeding Spanish imperial eagles *Aquila adalberti*. *Animal Conservation*, in press.
- González, L.M., Bustamante, J., Hiraldo, F., 1992. Nesting habitat selection by the Spanish imperial eagles *Aquila adalberti*. *Biological Conservation* 59, 45–50.
- González, L.M., Cadenas, R., González, J.L., Heredia, B., García, L., 1996c. Manejo de la productividad del Águila imperial (*Aquila adalberti*): aumento de la tasa de supervivencia de los pollos. V International Conference on Mediterranean Raptors, Evora, Portugal.
- González, L.M., Oria, J., 2003. Águila imperial Ibérica, *Aquila adalberti*. In: Martí, R., del Moral, J.C., (Eds.), *Atlas de las aves reproductoras de España*. Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología, Madrid, pp. 186–187.
- Grier, J.W., Fyfe, R.W., 1987. Preventing research and management disturbance. In: Giron Pendleton, B.A., Millsap, B.A., Cline, K.W., Bird, D.M. (Eds.), *Raptor Management Techniques Manual*, National Wildlife Federation, Scientific and Technical Series No. 10, Washington, pp. 173–182.
- Hansen, A.J., 1987. Regulation of bald eagle reproductive rates in Southeast Alaska. *Ecology* 68, 1387–1392.
- Hiraldo, F., Blanco, J.C., Bustamante, J., 1991. Unspecialized exploitation of small carcasses by birds. *Bird Study* 38, 200–207.
- Korpimäki, E., Wiehn, J., 1998. Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos* 83, 259–272.
- Lack, D., 1954. *The Natural Regulation of Animal Numbers*. Oxford University Press, London.
- Margalida, A., González, L.M., Sánchez, R., Oria, J., in press. Parental behaviour of Spanish imperial eagles (*Aquila adalberti*): sexual differences in a moderately dimorphic raptor. *Bird Study*.
- Martínez, J.E., Calvo, J.F., 2001. Diet and breeding success of eagle owl (*Bubo bubo*) in southeastern Spain: effect of rabbit haemorrhagic disease. *Journal of Raptor Research* 35, 259–262.
- Meyburg, B.U., 1974. Sibling aggression and mortality among nestling eagles. *Ibis* 116, 224–228.
- Meyburg, B.U., 1975. On the biology of the Spanish Imperial Eagle (*Aquila heliaca adalberti*). *Ardeola* 21, 245–283.
- Meyburg, B.U., 1978. Sibling aggression and cross-fostering of eagles. In: Temple, S.A. (Ed.), *Endangered Birds Management Techniques for Threatened Species*. University of Wisconsin Press, Madison, pp. 195–200.
- Meyburg, B.U., 1987. Clutch size, nestling aggression and breeding success of the Spanish imperial eagle. *British Birds* 80, 308–320.
- Meyburg, B.U., Garzón, J., 1973. Sobre la protección del Águila imperial ibérica (*Aquila heliaca adalberti*) aminorando artificialmente la mortalidad juvenil. *Ardeola* 19, 107–128.
- Millsap, B., Cline, K.W., Giron Pendleton, B.A., 1987. Habitat management. In: Giron Pendleton, B.A., Millsap, B.A., Cline, K.W., Bird, D.M. (Eds.), *Raptor Management Techniques Manual*, National Wildlife Federation, Scientific and Technical Series No. 10, Washington, pp. 215–237.
- MMA, 2001. Estrategia nacional para la conservación del Águila imperial ibérica (*Aquila adalberti*). Dirección General para la Biodiversidad, Ministerio de Medio Ambiente, Madrid.
- Mock, D.W., Parker, G.A., 1987. *The Evolution of Sibling Rivalry*. Oxford University Press, Oxford.
- Mock, D.W., Drummond, H., Stinson, H., 1990. Avian siblicide. *American Science* 78, 438–449.
- Newton, I., 1979. *Population ecology of raptors*. Berkhamsted. Poyser, London.
- Newton, I., Marquiss, M., 1981. Effects of additional food on laying date and clutch size in sparrowhawks. *Ornis Scandinavica* 12, 225–229.
- Nilsson, J.A., 1995. Parent–offspring interaction over brood size: cooperation or conflict. *Journal of Avian Biology* 26, 255–259.
- Olendorff, R.R., Motroni, R.S., Call, M.W., 1980. *Raptor management: the state of the art in 1980*. US DOI, BLM, Denver, CO.
- Parker, G.A., Mock, D.W., 1987. Parent–offspring conflict over clutch-size. *Evolutionary Ecology* 1, 161–164.

- Redpath, S.M., Thirgood, S.J., Leckie, F.M., 2001. Does supplementary feeding reduce predation on red grouse by hen harriers? *Journal of Applied Ecology* 38, 1157–1168.
- Richner, H., 1992. The effect of extra food on fitness in breeding Carrion Crows. *Ecology* 73, 330–335.
- Rodríguez-Gironés, M.A., 1996. Siblicide: the evolutionary black mail. *American Naturalist* 148, 101–122.
- Schmidt, K.T., Hoi, H., 2002. Supplemental feeding reduces natural selection in juvenile red deer. *Ecography* 25, 265–272.
- Simmons, R.E., 1988. Offspring quality and the evolution of cainism. *Ibis* 130, 339–357.
- Simons, L.S., Martin, T.E., 1990. Food limitation of avian reproduction an experiment with the cactus wren. *Ecology* 71, 869–876.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, second ed. Freeman, San Francisco.
- Tarr, M.D., Pekins, P.J., 2002. Influences of winter supplemental feeding on the energy balance of white-tailed deer fawns in New Hampshire, USA. *Canadian Journal of Zoology* 80, 6–15.
- Valverde, J.A., 1960. Vertebrados de la Marisma del Guadalquivir. *Archivos del Instituto de Aclimatación de Almería CSIC*, vol. IX, pp. 1–168.
- Villafuerte, R., Calvete, C., Gortázar, C., Moreno, S., 1994. First epizootic of rabbit haemorrhagic disease (RHD) in free living populations of *Oryctolagus cuniculus* at DNP, SW Spain. *Journal of Wildlife Diseases* 30, 176–179.
- Villafuerte, R., Calvete, C., Blanco, J.C., Lucientes, J., 1995. Incidence of viral haemorrhagic disease in wild rabbit populations in Spain. *Mammalia* 59, 651–659.
- Viñuela, J., 1999. Sibling aggression, hatching asynchrony, and nestling mortality in the black kite (*Milvus migrans*). *Behavioural Ecology and Sociobiology* 45, 33–45.
- Viñuela, J., 2000. Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. *Behavioural Ecology and Sociobiology* 48, 333–343.
- Wiebe, K.L., Bortolotti, G.R., 1994. Energetic efficiency of reproduction: the benefits of asynchronous hatching for American kestrels. *Journal of Animal Ecology* 63, 551–560.
- Wiebe, K.L., Bortolotti, G.R., 1995. Food-dependent benefits of hatching asynchrony in American Kestrels *Falco sparverius*. *Behavioral Ecology and Sociobiology* 36, 49–57.
- Wiehn, J., Korpimäki, E., 1997. Food limitation on brood size: experimental evidence in the Eurasian kestrel. *Ecology* 78, 2043–2050.