Cooperative breeding in the Spanish Imperial Eagle *Aquila adalberti*: a case of polyandry with male reversed sexual behaviour?

Luis Mariano González,1 Antoni Margalida,3* Roberto Sánchez3 & Javier Oria4

1 Dirección General para la Biodiversidad, Ministerio de Medio Ambiente, Gran Vía San Francisco 4, E-28005 Madrid, Spain
2 Bearded Vulture Study and Protection Group. Apdo. 43, E-25520 El Pont de Suert (Lleida), Spain
3 Fundación CBD-Habitat, C/Nieremberg 8, bajo A, E-28002 Madrid, Spain
4 Bascaje. C/San Agustín 22, E-40001 Segovia, Spain

In cooperative breeding, three or more individuals raise the young in a nest. Their contribution generally consists of feeding nestlings or fledglings from a single nest, but may also include incubation and defence of the nest or territory. Co-breeders are often related to the focal breeding pair (Brown 1987). Cooperative breeding has been documented extensively in diurnal raptors (Kimball et al. 2003). In several species of raptors regarded as monogamous but occasionally breeding cooperatively, non-breeding helpers assist the breeding birds in caring for young birds (Brown 1987, Ligon 1999). The helpers are often the breeding pair’s offspring that have delayed dispersal (see Kimball et al. 2003). Cooperative polyandry with male reversed sexual behaviour? has been recorded in several species of raptors regarded as monogamous but occasionally breeding cooperatively, non-breeding helpers assist the breeding birds in caring for young birds (Brown 1987, Ligon 1999). The helpers are often the breeding pair’s offspring that have delayed dispersal (see Kimball et al. 2003).

Despite there being many documented cases of cooperative breeding in birds of prey, few quantify in detail the behaviour and parental contribution of each bird during reproduction (e.g. De Lay et al. 1996, Bertran & Margalida 2002), aspects that may help to understand the reasons for this kind of breeding behaviour.

The Spanish Imperial Eagle *Aquila adalberti* is one of the scarcest and most threatened birds of prey in the world (BirdLife 2004). Its distribution range covers 117,000 km² in the centre and south of the Iberian Peninsula (González & Oria 2003). The estimated breeding population in 2004 was 193 pairs (GTAI–MMA 2004). Systematic monitoring of breeding biology has been conducted over most of its distribution range since 1970 (Garzón 1972, Meyburg 1987, González 1991) and, since 1993, in a marginal subpopulation (Doñana) (Valverde 1960, Calderón et al. 1987). All pairs recorded in that regular population monitoring were monogamous. The general literature on this species has therefore regarded the Spanish Imperial Eagle as a monogamous species (Cramp & Simmons 1980, del Hoyo et al. 1994).

We document the incorporation of two subadults (a male and a female) into a territory held by a single male following the disappearance of the female, representing the first case of cooperative breeding described for the Spanish Imperial Eagle. We quantified the parental contribution of each bird and compared them with those of the monogamous pair. Finally, we discuss the factors that may have determined the formation of the trio.

**METHODS**

**Study area**

The study was carried out in a nesting territory in central Spain (Madrid province), considered ‘high quality’ on the basis of the large numbers of wild Rabbits *Oryctolagus cuniculus*, the Spanish Imperial Eagle’s staple prey in the study area (González 1991). The topography of the area consisted of extensive gently undulating plains where stands of Holm Oak *Quercus ilex* predominated (for detailed descriptions, see González et al. 1990, González 1991).

The study area has been monitored annually since 1981 and the pair’s specific territory was located for the first time in 1993. Since then sporadic monitoring has been carried out to determine their identity and breeding results.

The pair had four nests and the minimum distance from the nests to the nearest pair varied from 6 to 9 km over 4 years.

**Data collection**

The territory was occupied by the pair until 2000, and has been occupied by the trio since the breeding season of 2001. In 2000, 2001 and 2002, their behaviour was monitored intensively as follows: 1049 h of the pair (270 h during incubation and 779 h during chick-rearing), and 294 h of the trio (12 h during prelaying, 136 h during incubation in 2001 and 146 h during chick-rearing in 2002).
covered the entire incubation period (c. 42–45 days) and the first 5 weeks of the nestlings’ lives.

Observations were conducted from prominent locations within the territory using 20–60× telescopes approximately 600 m from the nest, a distance at which no alert reactions or alterations to their behaviour were noted (González et al. in press).

The eagles were sexed and identified individually on the basis of the following criteria.

Individual differences in plumage
Spanish Imperial Eagle adult plumage includes lesser wing-coverts, lesser scapulars and bright white shoulders (Hiraldo et al. 1976), which differ between individuals and are present throughout life after successive mouls without significant variation in extent or form (pers. obs.). The original adult male (hereafter MA) had adult plumage and continuous white on the lesser wing-coverts and lesser scapulars; in the original female (hereafter FA) the white was discontinuous.

Age differences in plumage
The two new birds joining in 2001 (MB and FB) had non-adult plumage, so-called ‘advanced chessboard’, and in 2002 they had ‘imperfect adult’ plumage consistent with the plumage characteristics described by González (1991) and Forsman (1999), and attributable to 4- and 5-year-old birds, respectively. Furthermore, the birds differed in the amounts and in the distribution of white on the wing-coverts, scapulars and shoulders.

Reversed sexual size dimorphism
The females were slightly larger than the males, clearly evident when both were observed together. Records indicate that females are heavier and 10% larger than males in terms of body, wing and tail length (Valverde 1967, Hiraldo et al. 1976, Cramp & Simmons 1980).

The variables in behaviour and parental care studied were: (1) copulation attempts and positions during copulations, (2) nest building (number of visits providing branches and twigs), (3) territorial defence (number of attacks against conspecifics and heterospecifics), (4) incubation (daily percentage of time at the nest covering the eggs in relation to total observation time), (5) attendance to chicks (daily percentage of adult time at nest in relation to total observation time), (6) prey delivered (number of prey items provided to the nest) and (7) chick feedings (number of feeding bouts).

RESULTS

Pair (MA and FA)
The female (FA) incubated most, including brooding/shading and nestling feeds (88 vs. 12%), whereas the male (MA) brought more prey items to the nest (90 vs. 10%, n = 135, Table 1). Investment in nest reconstruction was unequal (χ² = 18.89, P < 0.001) and whereas the contribution of MA to nest reconstruction was greater during the incubation period (70 vs. 30%, n = 30), the contribution of FA was greater during rearing (78 vs. 22%, n = 72).

During 1993–2000, average productivity of the territory occupied by FA and MA was 2.87 chicks/yr (n = 8).

Trio (original MA, MB and FB)
In January 2001, FA ceased to be observed in the area. On 14 February two new birds MB and FB were seen at the nest with MA. No agonistic interactions were recorded. They reared two chicks successfully in 2001. During the 4 years of monitoring these birds as a trio unit (2001–04), productivity was 1.5 chicks/yr (n = 4).

The characteristics of each bird’s parental contribution (see Table 2) are given below.

Sexual activity
Of the trio’s four observed mountings, one was heterosexual (MA with FB on 31 March 2002) and the rest homosexual (two by MB with MA on 5 and 12 April 2002 and one by MA with MB on 22 April 2002).

Nest building
Material was observed being brought to the nest on 16 occasions: five during prelaying, seven during incubation and four during rearing (Table 2). MA provided material

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<th>Table 1. Parental contribution in a Spanish Imperial Eagle pair in 2000 (MA: male; FA: female).</th>
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<td><strong>Incubation</strong></td>
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<td>Nest building</td>
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<td>MA</td>
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<td>FA</td>
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<td>Total</td>
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on two occasions (12.5%), MB on five (31.25%) and FB on nine (56.25%).

**Territorial defence**

During pre-laying and incubation periods, four in-flight attacks were recorded and interpreted as territorial defence. Two were against Cinereous Vultures *Aegypius monachus* and two against conspecifics. Two were made by each male.

**Incubation**

All three Eagles incubated, although MA incubated significantly less than MB and FB (Kruskal–Wallis $H_2 = 26.72, P < 0.001$, Table 2). Notably, on three occasions, MB incubated together with FB for 25–90 min, although only FB covered the clutch.

**Parental contribution during chick-rearing**

MA accounted for 61% of prey provisioning, MB for 28% and FB for 11% ($n = 18$ items). Figures for observed chick feedings were MB 41.6% and FB 58%. By contrast, MA was not involved in any feeding ($X^2 = 19.17, P < 0.001$). Attention at the nest was also unequal, FB and MB devoting significantly more time to the chicks than did MA (Kruskal–Wallis $H_2 = 32.45, P < 0.001$, Table 2).

### DISCUSSION

This is the first documented case of cooperative breeding in the Spanish Imperial Eagle and has three interesting features. First is the stability of the trio unit over time, which may be included among the cases of cooperative breeding involving helpers. The second is trio formation. Documented cases of cooperative breeding in raptors generally involve the incorporation of one or several subordinate birds of the same sex (males in the case of polyandry) in a territory held by a behaviourally dominant breeding pair (see reviews in Brown 1987, Stacey & Koenig 1990, Ligon 1999). Our case study involved birds of different sexes simultaneously settling in a territory with a vacancy through the disappearance of the original female. But the most interesting feature is the role of MB in the trio. MB’s parental investment, with intensive involvement in incubation, brooding and feeding, but little in prey provision at the nest, more closely resembled female behaviour. For example, parental investment by the original male in the territory (MA), both before and after trio formation, featured a significant involvement in prey provision to the nest, but little involvement in incubation, brooding/shading and feeds. This behaviour fits the division of parental care observed in males of seven monogamous pairs in the same study area (pers. obs.) and that described for other species such as the Golden Eagle (Collopy 1984). Finally, agonistic interactions were not observed between the three Eagles during the trio formation process. Such behaviour may be normal in other kinds of polyandrous formations until the group is consolidated (see Margalida et al. 1997). As the Spanish Imperial Eagle is a markedly territorial species, the absence of agonistic interactions between the males may be due to (1) attempts at homosexual mounting behaviour, the function of which may be interpreted in a context of specific aggression regulation that improves group cohesion (Heg & van Treuren 1998, Bertran & Margalida 2003), and/or (2) male reversed sexual behaviour. As stated above, MB’s observed contribution differed noticeably from the pattern seen in species with reversed sexual size dimorphism, in which parental tasks are highly differentiated (Andersson & Norberg 1981, Clutton-Brock 1991). The reverse behaviour of the new male involved a reduction in female parental investment and no food transfers during incubation relief, enabling the female to hunt for her own prey. In other species it has been suggested that, by means of copulation, females may exert social control and acceptance of the presence of other males (Bertran & Margalida 2004). In conclusion, we consider that MB’s breeding behaviour, which was closer to that of a female, may not only have helped to reduce the intrasexual tension typical of a territorial species, but may also explain acceptance, formation and stability of the trio.

Several hypotheses, independent of delayed dispersal, to explain cooperative breeding in raptors have been proposed (see Kimball et al. 2003): (1) the limited number of suitable territories in which territory acquisition and defence of a territory may favour cooperative breeding (e.g. Faaborg et al. 1980, Faaborg 1986); (2) the benefits

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**Table 2.** Parental contribution in a Spanish Imperial Eagle trio 2001–02 (MA: alpha male; MB: beta male; FB: beta female).

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<td>Nest building</td>
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<td>Total</td>
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of cooperative hunting and/or foraging (Bednarz 1988, Malan 1998); (3) patchy resources within or between years (e.g. Faaborg & Bednarz 1990, Heredia & Donázar 1990); (4) a skewed sex-ratio caused by a higher death rate of females (Newton 1979, Faaborg et al. 1980); and (5) to improve survivorship and long-term reproductive success (Faaborg et al. 1980, Faaborg 1986, Faaborg & Bednarz 1990).

Our results only fit with reference to the last hypothesis (5): the tolerance among all three Eagles may be explained by lifetime fitness in a high-quality territory that may increase their survival (see Ligon 1999) and probably their long-term breeding success. The benefits for the female would lie in a reduction in parental investment as a result of direct help from MB and increased chick survival. MA's presence may benefit the group by helping to defend quality territory (additional males might be required to defend it successfully) and so increase chick survival. There may be costs related to loss of paternity if MB copulated. MB would benefit from remaining in quality territory and would increase the chances of chick survival. Costs, in the latter’s case, would be associated with a loss of paternity as a consequence of MA’s copulations. Our study suggests support for hypothesis 5.

In short, our results suggest that this first case of cooperative breeding in the Spanish Imperial Eagle is probably a case of polyandry with male reversed sexual behaviour, possibly related to the improvement in survival and long-term reproductive success of the breeding unit. Nevertheless, genetic analyses are necessary to determine whether the second male is a helper (in which case this is cooperative breeding) or a parent (polyandry).

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REFERENCES


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