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SHORT REPORT

First cases of polygyny for the Bearded Vulture *Gypaetus barbatus* in the central Pyrenees

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ABSTRACT
We report the first cases of polygyny for the Bearded Vulture *Gypaetus barbatus* in the central Pyrenees, Spain. Although polyandry is frequent in the study area (31.8% of all reproductive units in 2016), we only observed the occurrence of three cases of polygyny over the period 1994–2017. Polygyny in Bearded Vultures is possibly a consequence of habitat saturation.

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Cooperative breeding is widespread within diurnal raptors, occurring in 22 of 76 genera (29%) and 42 of 304 species (14%, Kimball *et al.* 2003). There is a phylogenetic component to cooperative breeding, such that the majority of cooperative breeders are restricted to a few avian lineages (Russell 1989, Edwards & Naeem 1993, Arnold & Owens 1998). The majority of cases consist of groups in which extra birds are primarily adult males (i.e. polyandry; Faaborg & Patterson 1981). On the other hand, polygyny, occurs regularly in a very small proportion of species in which multiple females lay into one nest or lay in separate, widely distributed nests (Korpimäki 1998, Kimball *et al.* 2003). According to Newton (1979), three types of polygyny have been described: (i) when the females use the same nest (cooperative polygyny); (ii) when females use separate nests that are close to each other and within a territory that would normally be occupied by a single reproductive unit (RU); and (iii) when females use nests that are far apart, in areas that would normally be occupied by distinct RUs. Importantly, more than one type has been found in the same species (Newton 1979).

According to Rivas-Fuenzalida (2015), polygyny in bird species can be explained in different ways: (1) some females may choose to form polygynous alliances in high quality territories, where their biological performance could be equal or higher than that which they would obtain by forming a monogamous pair in a low quality territory (Verner & Wilson 1966, Orians 1969); (2) females may prefer to breed in a polygynous relationship when breeding territories are limited and are monopolized by only a few males (Orians 1969); (3) two or more females might accept a polygynous relationship based on the reproductive quality of the male rather than the territory (Weatherhead & Robertson 1979); and (4) some males might establish a polygynous relationship with two females in separate breeding territories in order to increase their chances of producing offspring (Alatalo *et al.* 1981).

Bearded Vultures *Gypaetus barbatus* are generally monogamous, although RUs containing three or even four individuals have been previously reported (Margalida *et al.* 1997, Gil *et al.* 2011). Up until now only polyandrous trios (i.e. two males with one female) have been described in the Pyrenees (Elosegui 1989, Heredia & Donázar 1990, Bertran & Margalida 2005). Polyandrous trios have also been observed in other populations such as Corsica (Fasce *et al.* 1989), the Alps (Biollaz *et al.* 2011), Crete (Margalida *et al.* 2012), South Africa (Krüger 2007, Krüger *et al.* 2014), and the Himalayas (Gil *et al.* 2009), supporting the idea that polyandry in not related to particular geographic conditions. It was not until 2011 that a polygynous trio was first observed in the Italian Alps (Fasce & Fasce 2011). In the latter case, two females from the same RU laid eggs in nests that were 8 km apart, failing at the end of the incubation period and the beginning of chick-rearing, respectively. Here we report the occurrence of first cases of polygyny for the Bearded Vulture in the Pyrenees, Spain. We describe in detail the reproductive history of these RUs, and we discuss the likely causes behind this atypical mating behaviour.

The study area is located on the southern slope of the central Pyrenees (Aragón region, Spain), a mountainous

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area belonging to the Eurosiberian biogeographic region, which encompasses the three geomorphological units of the Pyrenees: the 'Axial Pyrenees', 'Internal Sierras', and 'External Sierras'. Since 1994, field technicians from the Foundation for the Conservation of the Bearded Vulture (FCQ) have carried out annual population surveys, following the method used for other large cliff-nesting raptors. This consists of a series of consecutive visits to nesting areas of the RUs, during the pre-laying and nest construction, incubation and nestling periods, which allow the recording of reproductive parameters (e.g. Margalida *et al.* 2003). In order to record the sexes present in each RU reported in this study, a total of 182 hours of observations were carried out during 2010–17, in which copulations were recorded. Copulations typically occur in the vicinity of the nest, usually on the perches most frequently used by RUs. The first copulations begin in October (Gil 2013), with maximum peaks of sexual activity between days 70–61 and 30–21 prior to egg laying (Bertran & Margalida 2005). Although some morphometric measures such as wing chord, wing width, bill length, bill depth, tail length, and body mass are significantly greater in females than in males (López-López *et al.* 2011), it is not possible to determine the sex of an individual based on distant field observation of dimorphic features. Therefore, high-resolution optical equipment (20–60× magnification Leica and Zeiss field spotting scopes) were used to observe the positions adopted by the birds during copulation. In addition, four Bearded Vultures included in this study were individually identifiable by wing tags, plastic colour leg rings, and sexed by DNA analysis (García *et al.* 2008) (Table 1). It must be taken into account that according to Margalida *et al.* (1997), homosexual pairings might also occur.

Here, we report two cases of polygynous trios and one case of a polygynandrous quartet (Table 1). The first reproductive unit (hereafter RU#1) was located in a new territory in a high-density area for Bearded Vultures located in the 'Internal Sierras' in 2006. It was composed of a couple from 2006 to 2012. A marked female (Gb12036) first laid eggs in 2007, at the age of six years. Between 2007 and 2012, RU#1 laid six clutches and only two chicks were hatched, but neither fledged. In 2013, a second female, verified by her position during the observation of copulations, was incorporated into RU#1. During this first year, the trio was consolidated but they did not manage to lay eggs. In 2014, the marked female left the territory and in 2015 RU#1 was composed of the remaining couple, which raised its first chick successfully. In 2016 and 2017, the marked female was still alive and without a stable territory.

Table 1. Polygamous RUs of Bearded Vultures recorded in central Pyrenees (Aragón, Spain) from 1994 to 2017.

RU#	Composition	Marked individuals
1	1 male and 2 females	'Lucía' Gb12036 (female)* marked on 19-11-2002 and aged 1 year and 8 months at capture
2	2 males and 2 females	'Chistau' Gb12101 (male)* marked on 25-5-1998 when aged 3 months and 'Carrodilla' Gb12098 (female)* marked on 20-12-2006 aged >6 years
3	1 male and 2 females	'Eva' Gb12012 (female)* marked on 13-1-1999 when aged 4 years and 10 months

Note: Status of individual: * alive in September 2017.

Reproductive unit 2 (RU#2) was located in a new territory in a low density area in the 'External Sierras' in 2007. It was composed of a couple from 2007 to 2009. The female (Gb12098) and the male (Gb12101), both marked, laid their first clutch in 2008 but failed to produce young. In 2009, they moved the nesting area 15 km to the east and the nest failed again. In 2010, a trio was formed and copulations of the marked male (Gb12101) with an unmarked female were observed. As in 2011, a fourth individual (probably a male) was integrated into the RU and copulations of the two unmarked birds were observed. In 2012, both the marked and unmarked males copulated with the unmarked female and eggs were laid but subsequently failed. In 2012, 2013, and 2015 (no data were available for 2014), the two males made attempts at copulation with the marked female (Gb12098) but she refused their advances. In 2016 and 2017, all four individuals were still alive and occupying the territory, copulation was observed between the marked male and the marked female but no breeding attempt was recorded.

Reproductive unit 3 (RU#3) was also located in a high-density area located in the 'Internal Sierras'. One of its members, a marked female (Gb 12012) occupied the territory in 1999 at the age of five, and remained alone until 2004 (Table 1). In 2004, a pair was formed, and they built their first nest in 2007, with the first copulations being observed in 2008. In 2011, a third individual was incorporated into RU#3 and in 2014 observations of the copulations indicated that this was a female. In 2016, RU#3 laid its first clutch, which subsequently failed. In 2017, the unit was still made up of the same three individuals, one of them, the marked female, then aged 22 years.

In 2016, a third of the RUs in Spanish central Pyrenees (Aragón) were composed of more than two individuals, most of them forming polyandrous trios (31.8% of all RUs, authors' unpubl. data). This population was estimated at 129 pre-adult individuals in 2010, in addition to 227 adults (Gómez de Segura *et al.* 2012), whose sex ratio was balanced at birth (50:50, $N = 40$; López-López *et al.* 2011, and 45:55

male:female ratio for 110 birds sexed between 2006 and 2011; García *et al.* 2012). Pre-adult individuals do not reproduce since they have no available territories and they remain in the so-called floating population until they are recruited into the breeding population (López-Sepulcre & Kokko 2005). However, they may occasionally be able to integrate into RUs with high quality territories (i.e. those territories with a higher number of years of occupation; Sergio & Newton 2003) and develop a cooperative breeding unit, the point being that a good territory can be inherited when one of the dominant individuals dies (Carrete *et al.* 2006). In exchange, the individuals in the existing RU can benefit from the collaboration of the subordinates in reproductive tasks, reducing their reproductive cost (Bertran & Margalida 2002). Nevertheless, this is not the case in the RUs reported here. The lifetime reproductive success (LRS), expressed as the cumulative number of offspring throughout the lifetime of each RUs, was extremely low. In fact, only RU#1 successfully reached one chick whereas the other two failed. Moreover, RU#1 successfully bred only after the divorce of the first female. Until now, it was accepted that habitat saturation could hinder the settlement of breeding birds in optimal territories, hence they access those already occupied, avoiding marginal territories (Carrete *et al.* 2006). In this way, the RUs formed by trios or quartets are located in traditional breeding areas, with a high density of breeding birds, as well as a greater availability of trophic resources (Heredia & Donázar 1990). Remarkably, in two of the three cases reported here (RU#1 and RU#3), Bearded Vultures settled in high-density areas but establishing new territories that were not previously occupied.

Natal dispersal, understood as the distance between the place of birth and the nest where the first breeding attempt takes place, indicates that the Bearded Vulture exhibits phylopatric behaviour (Cramp & Simmons 1980, Hirzel *et al.* 2004, López-López *et al.* 2013). This behaviour could be reinforced by the low quality of territories in the marginal and adjacent areas of the mountain range, as well as by conspecific attraction (Serrano & Tella 2003). The latter could be causing individuals to settle in the vicinity of already occupied zones, producing concentric growth and progressive packing of the territories in the central core of the Pyrenean mountain range.

Korpimäki & Hakkarainen (2012) suggested that food abundance and nest site quality are probably the crucial factors determining the breeding status in cases of polygyny of Boreal Owls *Aegoleous funereous*, although it is also likely that male quality is at least a contributing factor. In this case, Korpimäki and Hakkarainen's results would support hypotheses 1, 3, and 4 as explanations for polygyny (introduction; Rivas-Fuenzalida 2015). However, the polygynous RUs described in this paper do not provide support for any of the hypotheses because: (i) polygynous RUs are not in high quality territories since otherwise at least annual hatches would be expected; (ii) access to males is not limited in the population, it is just the opposite according to the high rate of polyandrous trios observed in the Pyrenean population (e.g. Heredia & Donázar 1990, authors' unpubl. data); (iii) the LRS of the target males suggests that none of the males might be considered high quality breeders; and (iv) RUs focused only on one nest site per year, thus the male chances of producing more offspring did not vary. Therefore, we suggest an alternative hypothesis, in accordance with Carrete *et al.* (2006), in which habitat saturation could be increasingly forcing older floaters to be integrated into the breeding population, regardless of habitat quality in terms of reproductive history or time of occupation, probably as an extreme strategy to produce offspring at any cost before reaching senescence.

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