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3 **TITLE**

4 **Parental investment in two large raptors breeding in a high prey density area**

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18 Key words: Alps; *Aquila chrysaetos*; carrion abundance; *Gypaetus barbatus*; sexual investment.

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20   **SUMMARY**

21   We investigated breeding behaviour of *Gypaetus barbatus* and *Aquila chrysaetos* between 2008 and 2011 in the Stelvio

22   National Park (Alps, Italy), which harbours one of highest densities of wild ungulates in the Alps. Parental care

23   behaviours (incubation and chick brooding, nest attendance, changeover, food provisioning and nestling feeding) were

24   recorded at nests of both species (four vulture and 14 eagle pairs). Differences in investment between sexes and periods

25   were found in both species: the time spent in incubation and nest attendance was higher in females and decreased with

26   the progress of the breeding season (from incubation to post hatching and to pre-fledging). A significant effect of the

27   interaction between sex and period was also found. Compared to literature, our results suggested a lower contribution

28   by vulture males, whereas eagle males spent more time in incubation and nestling brooding than reported. The higher

29   investment shown by eagle males in our study area could potentially be due to the high availability of live preys and

30   ungulate carrions, which could allow males to spend less time in hunting, resulting in more time at the nest. Most

31   changeovers for both species took place in the central hours of the day. No difference in food provisioning was observed

32   between the sexes of the two species, consistent with information available for vultures, but not for eagles.

33   The patterns we found revealed a female-biased investment (unexpected for the vulture), although males significantly

34   contributed to nest behaviour, especially during the incubation period (unexpected for eagles). The large amount of

35   natural preys and carrion in the study area may contribute to shape the nest behaviour of these large raptors.

36 The involvement of breeding adult birds in parental investment is largely affected by the social mating system:

37 monogamy, polygyny and polyandry may imply different tasks for breeding males and females (Clutton-Brock 1991).

38 For instance, most monogamous birds perform biparental cares, even if the degree of involvement may vary between

39 sexes in different species and also in different pairs (Clutton-Brock 1991).

40 Species with long-lasting parental cares and breeding in sites characterized by harsh climatic conditions and low

41 accessibility because of topographical constraints are rarely investigated, and thus relatively few studies have focused

42 on breeding behaviour and parental investment in large raptors in mountain habitats (Brown 1990; Margalida andand

43 Bertran 2000; Väli and Lõhmus 2002; Margalida et al. 2007; Xirouchakkis and Mylonas 2007; Fasce and Fasce 2012).

44 Our study focuses on Bearded Vulture *Gypaetus barbatus* and Golden Eagle *Aquila chrysaetos*, two large raptors with

45 potentially different parental roles.

46 In Bearded Vulture, as well as in other vultures, parental loads are rather equally distributed between the sexes (Newton

47 1979; Margalida and Bertran 2000), even if Cramp and Simmons (1980) reported that wild Bearded Vulture females

48 likely spend more time in incubation than males, although quantitative data lack.

49 On the other side, in several monogamous species such as Golden Eagle, parental roles definitely differ, with males

50 being more active in territorial defence and prey hunting, while females invest more time in parental activities at the

51 nest (Newton 1979; Clutton-Brock 1991; Margalida et al. 2007).

52 The Bearded Vulture is an osteophagous vulture with a wide but disjunct distribution across the Palearctic, Afrotropical

53 and Indomalayan regions, but it is often very rare and probably declining (Ferguson-Lees and Christie 2001). Two

54 subspecies have been described (Hiraldo et al. 1984): *Gypaetus barbatus barbatus* in Eurasia and Northern Africa, and

55 *G. b. meridionalis* in Eastern and Southern Africa. The species became extinct in the Alps because of human

56 persecution across the end of the 19th Century and the beginning of the 20th (Mingozzi and Esteve 1997). It was

57 reintroduced in the Alps by means of a long-running release programme, started in 1986 in France and afterwards in

58 Austria, Switzerland and Italy (Frey 1992; Hirzel et al. 2004; Schaub et al. 2009; Bassi et al. 2013). A total of 197

59 young Bearded Vultures originating from captive breeding stocks were reintroduced between 1986 and 2013. The first

60 successful breeding attempts occurred in 1997 in Haute-Savoie, France (Lucker 1997), and in 1998 in the Stelvio

61 National Park (hereafter SNP), central Alps, Italy (Jenny 1999). The pairs settled in the central Alps significantly

62 contributed to the development of the re-established Alpine population of Bearded Vultures (Schaub et al. 2009), which

63 included 33 pairs in 2015 (Waldvogel 2015).

64 Current knowledge on Bearded Vulture parental cares come from studies carried out in other areas. Margalida and

65 Bertran (2000) provided a detailed picture based on a 5-year study (2180 hours) focused on 8 reproductive pairs, but

66   information about the parental roles in polyandrous (Bertran and Margalida 2002) and polygynous trios (Fasce and

67   Fasce 2012) is still scarce.

68   After population declines due to heavy human persecution over the past two centuries (Bechard and McGrady 2002),

69   many Golden Eagle populations in Europe are now stable or increasing (Ferguson-Lees and Christie 2001; BirdLife

70   International 2014). This species is the most widespread of the genus *Aquila*, ranging across the Nearctic and Palearctic

71   (70° N to 20° S), and fringing Indomalaya and the Afrotropics (Del Hoyo et al. 1994). Despite its widespread

72   occurrence, studies on parental cares and nest activities are very rare (Collopy 1984; Aoyama et al. 1988) and limited

73   for Alps (Jenny 1992; Haller 1996). These studies quantified the time spent by adults in different activities such as nest

74   attendance, changeovers, prey items delivered to the nest, time of presence within the territories and surveillance and

75   territorial activity.

76   This study investigated parental investment and time budgets of a small population of Golden Eagles (14 pairs) and

77   Bearded Vultures (4 pairs) breeding in sympatry within the SNP, where both species nest on rocky cliffs and live in

78   similar mountain environments. Our study thus represents the first investigation of parental activities in Bearded Vulture

79   in a re-introduced population.

80   With this work providing novel information on the breeding behaviour of these two species in the Alps we aimed to: (*i*)

81   assess the contribution of partners in terms of investment in different parental activities, (*ii*) describe the sex-specific

82   pattern of variation in parental cares in relation to the breeding period and to offspring growth, (*iii*) compare results

83   from this reintroduced vulture population in the central Alps with a previous study carried out on the native population

84   in the Catalan Pyrenees (Margalida and Bertran 2000), and *(iv)* obtain new information on Golden Eagle parental tasks

85   and compare the results with the few papers available in the literature.

86

87   **Methods**

88   **Study area**

89   The study was conducted from 2008 to 2011 in an area covering 600 km^2 and included within the SNP (central Alps,

90   northern Italy). Elevation ranges from 1000 m to 3905 m asl. Wild ungulates are very abundant in the study area, with

91   high densities of Alpine Chamois *Rupicapra rupicapra* (6.7/km^2), Alpine Ibex *Capra ibex* (15/km^2) and Red Deer

92   *Cervus elaphus* (5-25/km^2; Carro and Pedrotti 2010). No supplementary feeding sites were active.

93   To provide a description of the climate of the study area, we analysed data from four weather stations located at an

94   elevation similar to the average one at which Golden Eagle and Bearded Vulture nests occurred (weather stations: mean

95   elevation 2045 m asl; nests: mean elevation 2130 m), considering data from 2008 to 2011. The average temperature of

96   the coldest and warmest months were respectively -6.5°C (January) and 11.7°C (August). In SNP, the average minimum

97   temperature in January was -9.7 °C (for comparison, -5 °C in the Pyrenean study area studied by Margalida and Bertran

98   2000), while the average maximum temperature in August was 16.1°C (for comparison: ≤ 30 °C in July within the

99   above cited Pyrenean study area). Absolute minimum temperatures recorded in SNP were on average -18.8°C (range -

100 21.6 / -15.4 °C).

101 The average elevation of Bearded Vulture and Golden Eagle nests in the SNP was respectively 2225 m asl (all known

102 nests in the study area/period; $n = 14$; sd 102.5 m; range 2028 - 2440 m) and 2035 (all known nests in the study

103 area/period; $n = 124$; range 1317 - 2496 m; sd 230.5 m; Bassi et al. 2013). The average elevation of Bearded Vulture

104 and Golden Eagle nests monitored during this study was respectively 2212 m asl ($n = 5$ nests of the four studied pairs;

105 sd = 33.6 m; range 2171 - 2240 m) and 2048 m asl ($n = 16$; sd = 124.4 m; range 1700 - 2189 m). The average distance

106 between neighbouring nests (NND) of Bearded Vulture was 7096 m ($n = 4$; sd = 1396 m; range: 5890 - 8302 m),

107 whereas NND for nests of Golden Eagle was 5342 m ($n = 16$; sd = 2373 m; range: 1956 - 9537 m).

108 **Field methods**

109 An intensive monitoring programme of breeding pairs started in 2004 and included 14 Bearded Vulture nests and 124

110 Golden Eagle nests, respectively belonging to 4 vulture and 14 eagle territorial pairs (Bassi et al. 2013).

111 We investigated by means of the focal sampling method (Sutherland et al. 2004) 10 breeding attempts of Bearded

112 Vulture (period 2009-2011) and 16 of Golden Eagle (period 2008-2010). We carried out a total of 1133 h for monitoring

113 bearded vulture breeding behaviour, and 1132 h for the breeding behaviour of Golden Eagle, over 289 days (144 for

114 Bearded Vulture and 145 for Golden Eagle). We related our observations to two different breeding phases, the 'total

115 dependence phase', and the 'partial dependence phase'; during the latter, nestlings are less strictly dependent on the

116 continuous presence of an adult. The total dependence phase included two periods: 1a) incubation (52-55 days for

117 Bearded Vulture according to Margalida et al. (2004) and 42 days for Golden Eagle) and 1b) the first part of post-

118 hatching, when nestlings are strictly dependent on the presence of an adult (28 days after hatching for Bearded Vulture

119 and 21 for Golden Eagle). In the incubation period, we carried out 6-h observation slots, leading to 260 hours of

120 observation spread over 44 days for Bearded Vulture and 197 hours spread over 35 days for Golden Eagle. During the

121 post-hatching period, 22 days of observations were made for Bearded Vulture (130 h) and 37 days for Golden Eagle

122 (216). Observations began in the morning (8:30-11:30 am). Within the Alps, egg-laying in Bearded Vulture usually

123 starts in January, and 6 hours of observation therefore accounted for c. 50% of the daylight hours (average day-light 12

124 h 04'). For alpine Golden Eagle pairs (egg-laying between March and April), the time spent for the observations

125 accounted for 41% of the daylight hours (average 14 h 53'). The partial dependence phase coincided with the second

126 part of the post-hatching period and with the pre-fledging period, from the fifth week of life until chick fledging for

127 Bearded Vulture and from the fourth week of life for Golden Eagle. During this phase, we carried out observations of 10

128 hours each one, starting at 7:00 am or at 8:00 am (Bearded Vulture: 743 hours of observation spread over 78 days;

129 Golden Eagle: 719 hours spread over 73 days). Ten hours of observation accounted for 69% of the average daily hours

130 of light (14 h 55') for Bearded Vulture and 66% of the average hours of light (15 h 06') for Golden Eagle. We made

131 observations using 20-60x telescopes from vantage points, which allowed good visibility of the nest and of the

132 surrounding area, located at a distance large enough to prevent any potential disturbance to breeding birds. According to

133 the topography and accessibility of different locations, the average distance between observation points and nests for

134 Bearded Vulture was 1251 ± 430 m (range 1000-2510 m), whereas for Golden Eagle it was 1071 ± 677 m (range 300-

135 2250 m).

136 After observing the position of partners during copulatory behaviour and during pair flights, the sex identification for

137 both species was based on (1) the individual features of the plumage thanks to the long-term process of moulting and

138 the different shapes of pectoral bands, (2) reverse sexual size dimorphism (Bertran and Margalida 1999). The latter is

139 more striking in Golden Eagle, with females much larger than males (Newton 1979; Watson 2010), than in Bearded

140 Vulture, which shows a less clear dimorphism with females only slightly larger than males (Margalida and Bertran

141 2000). When it was not possible to distinguish between the two sexes (usually because of the unfavourable weather

142 conditions), data were discarded from analyses.

143 To describe the partner behaviour during focal sampling, we recorded activities (subdividing them in continuous and

144 dichotomous behaviours), and whether they occurred intra-nest (or in patch 1) or extra-nest (within all other patches).

145 The visible area from observation points was divided into polygons (patches) to get a spatial location of all the activities

146 carried out by pair members. Patch 1 was defined as the polygon where the active nest was located.

147 Patches were respectively of 1.2 km2 for Bearded Vulture, SD = 0.4 km2 and 1 km2 for Golden Eagle, SD = 0.6 km2.

148 The continuous activities recorded (as minutes spent in a given activity) were: (1) egg incubation and nestling brooding

149 (including when adults with opened wings protected chicks from excessive sunlight); (2) no incubation (the adult was in

150 the nest, but it did not spend time in incubation); (3) flight; (4) surveillance of the nest (when an adult was placed

151 outside the nest, but inside patch 1); (5) not detected (when an adult was not observed in the monitored area); (6) adult

152 feeding in the nest; (7) nestling fed by adults; (8) autonomous nestlings' feeding (we also considered the phase of the

153 prey (or remains) preparation according to Margalida and Bertran (2000); (9) perching on a dominant position by an

154 adult; (10) direct flight, consisting in a straight flight with semi-closed or slightly bent wings, with a gradual loss of

155 altitude; (11) intra/inter-specific interactions; (12) undulating territorial flight (for Golden Eagle only).

156 Dichotomous activities recorded were: (13) provision of food; (14) nest maintenance (branches brought to the nest) and

157 (15) changeovers at nest. Dichotomous activities were expressed as daily frequency.

158 To analyse the contribution of the two sexes to parental tasks and thus to quantify the sex-specific involvement in

159 parental cares and nesting activities during the different periods, we considered two main behaviours (calculated as the

160 daily ratio between the amount of minutes of the specific recorded behaviour and the total minutes of observation in that

161 day): (1) daily percentage of time spent in egg incubation and nestling brooding and (2) daily percentage of time spent

162 in nest attendance, i.e. time invested in surveillance and nest defence (observation of the breeding individuals inside

163 nest or patch 1 and displaying one of the above continuous activities except for incubation/brooding). Nest attendance

164 indicates how much time is invested in parental activity by two sexes besides incubation and brooding behaviour. To

165 test the relationship between parental investment, sex and period of the reproduction, we related the % time spent in

166 incubation and the % time spent in nest attendance to the breeding period and the sex of the pairs' members by means of

167 linear mixed effect models. The potential predictors were thus sex and breeding period (factors) and their interaction.

168 Pair identity and year of observation were entered as random factors in the models to correct for non-independence due

169 to repeated observations of the same pairs and to the potential year effect.

170 Then, we adopted an information-theoretic approach (Burnham and Anderson 2002), and ranked all possible models

171 according to the value of the Akaike Information Criterion corrected for small sample sizes (AICc). Given that the

172 difference between the most supported and all the other models (ΔAICc) was higher than 6 in all cases, we selected the

173 most supported model as the best one (Burnham et al. 2011).

174 To check for consistency of the effects of sex and phase, we re-run the above models according to an alternative

175 approach, which integrated into the dependent variable the information about investment and time of observation.

176 Therefore, we used a binomial model, which dependent variable had as numerator the time of incubation or nest

177 attendance, respectively, and as the binomial denominator the time of observation. We performed this analysis by means

178 of Generalized Linear Mixed Models fitted via Penalized Quasi-Likelihood (glmmPQL), as the standard GLMM

179 procedure led to severely overdispersed models.

180 All analyses were performed using the software R 3.3.0 (R Development Core Team 2016) and the packages 'MuMIn',

181 'mass', 'lme4' and 'nlme' (Venables and Ripley 2002; Pinheiro et al. 2010; Bartoń 2014; Bates et al. 2015).

182

183 **Results**

184 **Time in parental activities**

185 Considering the overall period investigated (incubation + post hatching + partial dependence), the mean time dedicated

186 to egg incubation and nestling brooding behaviour was 50.9 ± 14.8% for Bearded Vulture (males 20.1 ± 22.3%, range:

187 0-80.6%; females 30.9 ± 29.2%, range: 0-100%) and 43.2 ± 18.7% for Golden Eagle (males: 12.7 ± 20.1, range: 0-

188 88.8%; females 30.5 ± 32.3%, range: 0-100%). Percentages of time dedicated to egg incubation and nestling brooding

189 behaviour for each period of the reproduction, species and sex are reported in Table 1, and the parental contribution in

190 the two species during the three different breeding periods is summarised in Fig. 1.

191 Linear mixed models and penalized quasi-likelihood (binomial) models provided fully coherent results, with the partial

192 exception of the effect of the interaction between sex and period, which provided different (and generally non

193 significant) estimates according to the two methods for females during the pre-fledging period (for both species).

194 Therefore, we showed results of the linear mixed models only (for which the estimated interaction between sex and

195 period is fully consistent with the observed pattern, see Fig. 1). Notably, all linear models' residuals approached a

196 normal distribution. For both species the model including sex, period and their interaction was the most supported one

197 (ΔAICc > 6), both for egg incubation and nestling brooding and for nest attendance. In both Bearded Vulture and

198 Golden Eagle (Table 2), time spent in incubation/brooding was higher in females, declined with the progression of the

199 breeding phase, and was relatively lower in females during the last period, i.e. pre-fledging. In addition, in Golden

200 Eagle females during the post-hatching period, the time spent in incubation/brooding was higher than expectable on the

201 basis of the overall effect of sex and period.

202 The time spent in nest attendance varied according to a pattern generally similar to that affecting incubation and

203 brooding. In both species, time spent in nest attendance was higher in females than in males, declined with the

204 progression of the breeding phase, and was relatively higher in females during the post hatching period (Table 3). The

205 drop in nest attendance with the season progression was particularly marked in Golden Eagles (see Table 3 and Fig. 1).

206 **Changeovers**

207 The maximum frequency of nest changeovers for both species took place during the middle of the day (Fig. 2). Overall,

208 166 changeovers were observed for Bearded Vulture (1.2 changeovers/day of observation), of which 69 occurred during

209 the incubation period (1.6 changeovers/day of observation), 36 during the post-hatching period (from hatching to the

210 fifth week of life of the nestling; 1.6 changeovers/day of observation) and 61 in the pre-fledging period (from the sixth

211 week of life of the nestling until the flegding; 0.8 changeovers/day of observation). For the Golden Eagle, we observed

212 a total of 126 changeovers (0.9 changeovers/day of observation), with an average of 2.5 changeovers/day during the

213 incubation period (n = 87) and 1.1 changeovers/day during the post-hatching period (n = 39). No changeovers were

214 observed during the pre-fledging period.

215 **Food provision**

216 In the Bearded Vulture, we observed a total of 35 food deliveries to the nest: the male and female contributed 45.1%

217 and 54.9% of deliveries respectively (0.24 prey/day of observation; 0.03 prey/hour of observation). No significant

218 differences were recorded between the sexes (male 0.011 ± 0.033 prey items/hour, range: 0-0.167; female 0.014 ± 0.041

219 prey items/hour, range: 0-0.2; z = -1.845, p = 0.065). No food provision was observed during the incubation period.

220   For the Golden Eagle, we observed 58 food deliveries, 55.2% by males and 44.8% by females (0.40 prey/day of

221   observation; 0.051 prey/hour of observation). No significant difference was found between the sexes (male $0.023 \pm$

222   0.054 prey items/hour, range: 0-0.2; female 0.025 ± 0.056 prey items/hour, range: 0-0.33; $z = -1.416$, $p = 0.157$).

223   **Nestling feeding duration**

224   In both species, from hatching to fledging, the time invested in nestling feeding differed between the sexes, as females

225   spent much time than their partners in feeding young (Bearded Vulture: male 33.0%; female 67.0%; Mann-Whitney U-

226   test: $z = -2.483$, $p = 0.013$; Golden Eagle: male 17.1%; female 82.9%; Mann-Whitney U-test: $z = -4.159$, $p < 0.001$).

227

228   **Discussion**

229   **General and species-specific patterns**

230   Our study contributed to the description of parental activities in two large raptor species, which have received little

231   attention until now despite their widespread distribution. In particular, we provided the first information for a

232   reintroduced population of Bearded Vulture, and we investigated partner time investments in an area characterized by a

233   very high densities of wild ungulates, providing abundant natural trophic resources for vultures and eagles.

234   Both species incubated the eggs continuously until hatching, while after this event, the percentage of nestling warming

235   behaviour progressively decreased. After a mean of respectively 130 days (Bearded Vulture) and 93 days (Golden

236   Eagle) since egg laying, nestlings were brooded for less than 5% of the time.

237   In both species, females spent more time both in incubation/brooding and in nest attendance, the differences being

238   particularly striking in brooding Golden Eagles during the post hatching period (Fig. 1 and Table 2).

239   Significant differences between periods were observed both in egg incubation-nestling brooding and in nest attendance

240   behaviour in both raptors, although with some species- and sex-specific patterns. From incubation to the early stages of

241   the post-hatching period, partners of both species continuously covered the clutch, with the exception of time spent for

242   changeovers, turning the eggs and re-arranging the nest. The regular presence of one of the adults at the nest during the

243   early phase is necessary to protect eggs or chicks from extreme cold temperatures and from predation by Ravens *Corvus*

244   *corax* (Margalida and Bertran 2000) and Golden Eagles.

245   On the other side, the frequent adult absence of the last breeding phase coincides with an increase in the energy

246   requirements of the nestlings (Newton 1979). Bearded Vultures may thus need to explore larger feeding areas, moving

247   over larger distance from the nest, and Golden Eagles may need to intensify hunting activity within their territories to

248   gather more food.

249   In general, Bearded Vultures spent more time in parental activities than Golden Eagles due to the longer breeding cycle,

250   to different physical adaptations to parental cares (Deeming 2002) and probably also because of the different feeding

ecology (Pedrini and Sergio 2001; Margalida et al. 2009). The entire breeding cycle, from egg laying to fledging, required an average of 176 days (range 162-193) for Bearded Vulture and 117 days (range 111-129) for Golden Eagle (Diana et al. 2013). The time invested in parental cares was similar for both species during the incubation period, whereas during the post-hatching and pre-fledging periods Bearded Vulture invested more time than the Golden Eagle in parental activities (Fig. 1). The higher time spent by vultures at nest sites may be related also to the higher risk of food stealing. Several kleptoparasitic events (food stealing) were observed at Bearded Vulture nests, carried out by corvids, such as Raven *Corvus corax* (n = 4), Alpine Chough *Pyrrhocorax graculus* (n = 13) and Nutcracker *Nucifraga caryocatactes* (n = 1), and by Squirrel *Sciurus vulgaris* (n = 1). No kleptoparasitic events were observed against Golden Eagle nests or food. Also Margalida and Bertran (2003) observed many kleptoparasitic actions at the expense of Bearded Vultures, but only one for Golden Eagles.

In the Pyrenees, Ravens can negatively impact on Bearded Vultures by increasing the energetic cost of nest defence, and by disturbance generated by kleptoparasitic attempts at the nest, in ossuaries, in flight and on perching sites (Bertran and Margalida 2004). Adult presence in nest proximity may thus reduce or prevent the loss of food from the nesting area (Margalida and Bertran 2005).

Females of both species spent more time in parental care. In raptors characterized by reversed sexual size dimorphism, this could be explained by a better defence of the nest due to the larger female size and less efficient incubation of eggs by the smaller male (Margalida et al. 2007; Watson 2010). Newton (1979) reported that vultures are the only raptors in which both sexes invest similar time in incubation and foraging activities, most probably due to the reduced size dimorphism and to the peculiar feeding ecology. This was confirmed for Bearded Vultures in the Pyrenees, where both sexes attended the clutch in equal proportion (males: $48 \pm 6.6\%$; range: 35-57%; females: $52 \pm 6.6\%$; range: 43-65%), but not by our results, which suggested indeed a lower contribution by the male (see Cramp and Simmons 1980). Such a remarkable difference might be due to the high food predictability experienced by the Catalan population (Margalida and Bertran 2000), where vultures benefit from the presence of 7 feeding stations from November to April (Margalida et al. 2009). In this context, food sources are easily predictable thanks to feeding stations, which may shorten the time needed to collect food and consequently increase male's contribution to parental tasks. In fact, pre-adult individuals in the Pyrenees seems to forage over smaller areas than individuals from other subpopulations as a consequence of the network of supplementary feeding sites (Margalida et al. 2013). Although non-adults showed higher attendance at feeding stations than adults (Margalida et al. 2011), the latter mostly frequented them during mating-incubation (December-March) and nestling rearing (April-July) periods (Moreno-Opo et al. 2015), with remarkable chances to store food in the typical ossuaries (Margalida and Bertran 2001).

In addition, also the colder climate of the Alpine region (the average of minimum temperature recorded during 2009-2011 in our study area in fact was 4.7 °C lower than that recorded in the Pyrenees by Margalida and Bertran 2000) could promote a greater investment by Alpine vulture females, with their larger size enabling them to better tolerate extreme temperatures and thus to incubate for longer bouts than males.

Individual traits of the pair members, such as age, experience and personality, could also affect behavioural differences. In addition, the breeding adult turnover was rather high, with 2 pairs that changed respectively 1 and 3 individuals during three different breeding seasons, and also a temporary trio (made by one male and two females in one breeding season) occurred. Genetic analyses on feather samples collected below the nests confirmed the identities of the breeders for each monitored Bearded Vulture pair (Hefti-Gautschi 2013). Bearded Vultures have a deferred maturity (Antor et al. 2007); within the four territories, the overall mean age of the breeders was similar: males 13 years (n = 12) and females 12.4 years (n = 13, Jenny and Bassi *unpubl. data*). Nevertheless, such a similarity was not mirrored within pairs: in pair 1, mean male age 10 y, mean female age 10 y; in pair 2, mean male age 13 y, mean female age 10.2 y; in pair 3, mean male age 12 y, mean female age 11.2 y; in pair 4, mean male age 17 y, mean female age 19 y.

Considering Golden Eagles, in pairs breeding in the SNP the males spent more time in incubation and nestling brooding than reported in the few available studies from other countries (e.g. Idaho, USA: Collopy 1984; Japan: Aoyama et al. 1988; UK: Everett 1981; Jenny 1992). These studies reported an average male investment corresponding to 6-18.4% of male presence during the incubation period, but just Collopy (1984) spent nearly 700 h at 11 nests during incubation in 1977-79, whereas Aoyama et al. (1988) reported the results of one single nest continuously monitored by video recorder in which the female incubated for more than 90% of daylight hours. Also Everett (1981), reporting results from only one eyrie, found that the female did most of the incubation and brooding, although the male relieved her on most days and accounted for some 6% of the whole incubation period. On the contrary, Gordon (1955) observed one pair over 8 breeding seasons and reported that the incubation duties were equally shared by both adults. Watson (2010) considered Gordon's findings exceptional and the behaviour described by Collopy (1984) was thought to be the species' typical one across most of its range. In territories where carrions are scarce and prey must be actively hunted, either the male must bring food to the eyrie or the female must spend longer time away from the nest, with a corresponding increase in the incubation duties of the male (Watson 2010). In our study area, the male's contribution to incubation was notably higher also than in the Swiss Alps, where Jenny (1992) recorded a male investment of 18.4% ± 15.5. A higher male contribution could be potentially related to several factors such as age, individual ability and experience, territory size and female behaviour, as the latter sometimes does not allow male to access the nest, or by male reluctance to incubate (Ricau and Decorde 2009).

311 We suppose that the higher investment shown by male eagles in our study area is potentially due to the high availability

312 of both live preys and ungulate carrions in late winter, up to May. This could enhance males to spend less time in

313 hunting and foraging, resulting in more time spent at nest. Raptors showing a high specialization on a small number of

314 prey species reportedly increase foraging efficiency and have higher reproductive success (Katzner et al. 2005; Watson

315 2010), but a broader diet is not necessarily disadvantageous (Whitfield et al. 2009). In our study area, Golden Eagles

316 mostly forage on Marmots (*Marmota marmota*), Bovidae, alpine Galliformes and Leporidae (respectively accounting

317 for 34.7%, 17.6%, 12.5% and 10.2%) during the reproductive period (Bassi and Gambarin, unpubl. data). Marmots,

318 occurring over all the area at high densities (6.9 burrows or 56-62 individuals/km^2; SNP unpubl. data.), were abundantly

319 found in all the 16 Golden Eagle nests we investigated. Our study population thus has a generalist diet, even if Marmots

320 tend to predominate in the diet. The long protection history of the study area (SNP is one of the most ancient protected

321 areas of Western Europe) results in abundant ungulate populations, with plenty of carrions (from winter to May)

322 available to raptors.

323 It is therefore possible that such favourable trophic conditions (coupled with a possible slight specialization on the very

324 abundant Marmots) enhance hunting efficacy of Golden Eagles, reducing the time needed to collect food and thus

325 favouring male investment in nest activities. Notably, the incubation period coincides with the peak in carrion

326 availability, during March-May, and this period is also the one in which the time invested by the male in parental cares

327 (38.1%) is highest. The lack of difference between the sexes in food provision could also be linked to the high

328 availability of prey, which allow females to collect food despite the higher investment in nest activities.

329 **Other behaviours**

330 The pattern of changeovers occurrence we found (Fig. 2) was fully coherent with results from the Pyrenean populations,

331 where changeovers for both species mostly took place in the central hours of the day (Margalida and Bertran 2000),

332 when breeders activity and temperatures are at their maximum.

333 No difference in food provisioning was observed between the sexes of the two species. These findings are consistent

334 with previous information available for Bearded Vultures (Brown 1990; Margalida and Bertran 2000), but not for

335 Golden Eagles, for which the available studies reported more food items brought to the nest by males (Collopy 1984;

336 Watson 2010). The observed differences could be potentially related with the high prey availability and/or the slight

337 specialization in marmot hunting, which could allow the female to not strictly depend on male's food provisioning.

338 In both species, females spent more time in feeding nestlings. In the last weeks nestlings become progressively more

339 skilled and most of the food consumed is self-fed (Watson 2010).

340   In conclusion, our work provided new information about breeding behaviour of two widespread species, which have

341   been widely studied in their breeding ecology and distribution, but received surprisingly little attention for what

342   concerns their nesting behaviour. The patterns we reported were basically similar across Bearded Vulture and Golden

343   Eagle, even if some differences occurred, and revealed a female-biased investment (rather unexpected for the vulture),

344   although males significantly contributed to nest behaviour, especially during the incubation period (which was

345   unexpected for eagles). The large amount of natural preys and carrion in the study area may be an important factor,

346   contributing to shape the nest behaviour of these large raptors.

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349 Table 1. Percentage of time spent by Bearded Vulture (BV) and Golden Eagle (GE) in incubation and chick brooding
350 behavior according to different reproductive periods. Days and hours of focal sampling activity are reported.

Period	Species	Observation		Sex	% time	ES	Min	Max
		hours	Days					
Incubation								
	BV	260	44	Tot	96.7	10.9	52.0	100.0
				Males	39.2	18.9	0.0	80.6
				Females	56.7	22.8	1.1	100.0
	GE	197	35	Tot	94.8	11.1	52.2	100.0
				Males	38.1	19.4	5.0	88.8
				Females	57.4	23.7	11.4	100.0
Post hatching								
	BV	130	22	Tot	79.2	22.8	40.3	100.0
				Males	27.3	22.0	0.0	77.5
				Females	52.8	23.7	10.8	99.0
	GE	216	37	Tot	52.6	30.5	0.0	100.0
				Males	12.3	17.9	0.0	71.9
				Females	52.4	30.4	0.0	100.0
Pre-fledging								
	BV	743	78	Tot	16.3	21.1	0.0	100.0
				Males	6.0	9.8	0.0	50.0
				Females	10.2	13.4	0.0	66.0
	GE	719	73	Tot	11.5	23.5	0.0	100.0
				Males	0.9	2.8	0.0	13.9
				Females	9.8	12.7	0.0	53.7

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Table 2. Most supported mixed models for egg incubation and nestling brooding. Reference value for sex is male and for period is incubation.

BEARDED VULTURE	β±SE	P
Intercept	0.387±0.028	
sex: female	0.174±0.036	<0.001
period: post hatching	-0.115±0.045	0.010
period: pre-fledging	-0.329±0.032	<0.001
sex: female*period: post hatching	0.082±0.064	0.198
sex: female*period: pre-fledging	-0.133±0.046	0.004
GOLDEN EAGLE		
(Intercept)	0.411±0.046	
sex: female	0.188±0.043	<0.001
period: post hatching	-0.257±0.043	<0.001
period: pre-fledgling	-0.386±0.038	<0.001
sex: female*period: post hatching	0.119±0.060	0.047
sex: female*period: pre-fledging	-0.104±0.053	0.049

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Table 3. Most supported mixed models for nest attendance. Reference value for sex is male and for period is incubation.

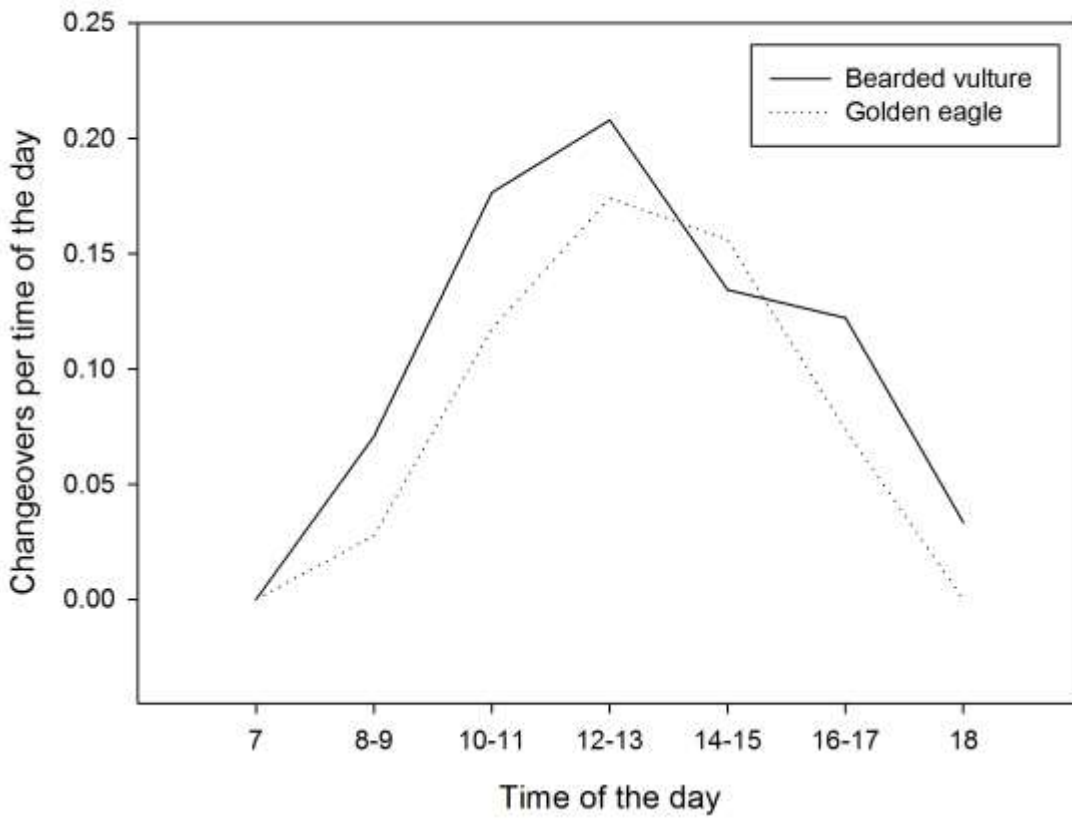| BEARDED VULTURE	β±SE	P
(Intercept)	0.459±0.042	
sex: female	0.131±0.047	0.005
period: post hatching	-0.122±0.058	0.035
period: pre-fledgling	-0.228±0.042	<0.001
sex: female*period: post hatching	0.222±0.081	0.006
sex:female*period: pre-fledging	-0.015±0.059	0.798
GOLDEN EAGLE		
(Intercept)	0.439±0.037	
sex: female	0.158±0.044	<0.001
period: post hatching	-0.282±0.044	<0.001
period: pre-fledgling	-0.372±0.039	<0.001
sex: female*period: post hatching	0.210±0.062	0.001
sex: female*period: pre-fledging	-0.053±0.054	0.322

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364 **Fig. 1** Tukey's box plots for parental contribution during the three different breeding periods. The line within the box
365 represents the median, the external box lines are first and third quartile (50% of observations are comprised between the
366 two - i.e. in the box). Lines moving from box borders depict intervals including other data up to 1.5 times the
367 interquartile distance. Additional data outside this interval (if any) are shown individually.
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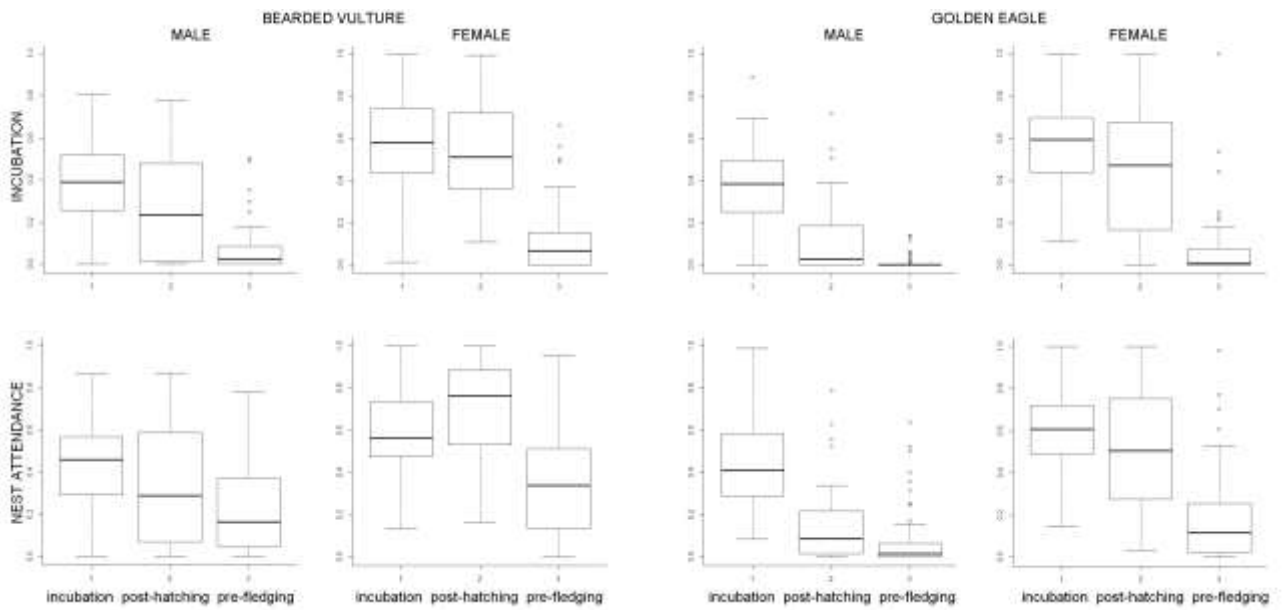
Fig. 2 Pattern of changeovers by Bearded Vulture and Golden Eagle in relation to the time of the day.

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