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Skewed sex ratios in a newly established osprey population

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Abstract

With recent increases in the numbers of reintroduction projects, it has become crucial to know the main factors that allow colonization of new areas and prevent the extinction of small and reintroduced populations. Dispersal is one of the most important phenomena in population biology with consequences to the proportion of individuals that keep breeding in the natal population and the number of individuals that move to other populations to breed. We studied changes in offspring sex ratio and differences in dispersal patterns between the sexes in a reintroduced population of Osprey (*Pandion haliaetus*). Results showed that at the beginning of the colonization process breeding pairs produced more males, which dispersed shorter distances and were more philopatric than females. However, with increasing breeding population size over the years, the offspring production was skewed to females, which dispersed longer distances from their natal area and tended to breed in different areas. Here we suggest that changes in offspring sex ratio during colonization processes, together with differences in dispersal pattern between sexes could influence colonization rate and the probability of success of future reintroduction projects.

Introduction

Offspring sex-ratio variation, and its possible consequences to populations, is a debated concept in population demography (Mayr 1939; Trivers and Willard 1973; Blank and Nolan 1983; Gowaty 1993; Becker et al.2008; Benito et al. 2013; Ferrer et al. 2013; Katzner et al. 2014). According to Fisher (1930) whenever the sex ratio of a population deviates from equilibrium, any genetic disposition to produce the rare sex will be favored by selection and the ratio will eventually return to equilibrium. In consequence, by natural selection sex ratios tend strongly to stick to the 1:1 ratio. Subsequent studies have identified numerous factors that can bias the sex ratio from 1:1, including local mate competition (Hamilton 1967), maternal condition (Trivers and Willard 1973), parent–offspring conflicts (Trivers 1974; Trivers and Hare 1976), and other unusual life history strategies or sex determination systems (Hardy 2002). Shyu and Caswell (2016) summarized which factors may modify the primary sex ratio, including differential offspring costs by sexes, mortality of offspring or parent mortality.

In sexually dimorphic species of raptors, differences in dispersal distances between sexes are often associated with differences in body size, (Newton 2008), affecting the capacity to connect with other populations (Muriel et al. 2016). In consequence, the dispersal patterns shown by populations of dimorphic species could be influenced by prevailing offspring sex ratios (Dale 2001).

Dispersal is one of the most important phenomena in population biology (Gadgil 1971), and may affect many aspects of demography in birds, influencing population dynamics and potential range of expansion (Newton 1998). Phylopatric behavior could benefit an animal in several ways, including pre-existing knowledge of the local environment and awareness that the area concerned can support a breeding population, however, it can also increases the risk of inbreeding (Ferrer et al. 2015).

In sexually dimorphic species, determining trends in sex ratios of patchy distributed populations becomes important in understanding population trends. Some studies show how differences in nestling sex ratios are correlated to population density (Santoro et al. 2015; Ferrer et al. 2009) or the availability of resources (Johnson et al. 2001; Arroyo 2002). Other studies have explored the effects of short or long term deviations in sex ratio for population dynamics (Gerlach and Le Maitre 2001; Ferrer et

al. 2009; Ferrer et al. 2013; Lambertucci et al. 2013). Dispersal and metapopulation connectivity are key components of population dynamics. Connectivity affect significantly the risk of extinction, particularly in small populations (Newton 1998; Penteriani and Delgado 2009; Whitfield et al. 2009; Muriel et al. 2015). Reintroduced populations, with all individuals monitored since the beginning of the colonization, provide rare opportunities to examine the dispersal patterns in a colonization process and to analyze differences among individuals, population size and ages of breeders during different stages of the colonization process. If offspring sex ratio is biased in some stages of the colonization process, and the dispersal distances vary between sexes, that could have consequences in the metapopulation structure, and subsequently in the colonization success of the reintroduced population. According to that, some authors demonstrate that reintroduction programs may be less effective if the sex ratios of the released individuals are not considered (Dzialak et al. 2006; Bosé et al. 2007; Lenz et al. 2007; Lambertucci et al. 2013).

In the present study, we analysed trends in offspring sex ratios and natal dispersal patterns in both sexes in a reintroduced population of Ospreys (*Pandion haliaetus*) in southern Spain. For this marked population, information is available for all released individuals and surviving chicks hatched within the project since its inception.

Methods

Study species

The Osprey breeds on all continents except Antarctica, being resident in some areas and migratory in others (Poole 1989). It is a specialist fish-eating raptor; with a breeding dispersion ranging from solitary to loosely colonial (Poole 1989). Over the years, it has suffered heavily from various human impacts, becoming extinct over large areas due to human persecution in the late 19th and early 20th centuries (Poole 1989; Saurola 1997). In mainland Spain, after a continuing decline in the number of breeding pairs at least from the 1960s, the last breeding attempt took place in the province of Alicante in 1981 (Urios et al. 1991).

To re-establish the species, a reintroduction program was undertaken in Andalusia province, during the years 2003-12. Over this period, 180 young Ospreys were

123   released by means of hacking (Dzialak et al. 2006) at two locations 125 km apart, a

124   reservoir in the province of Cádiz and a coastal marshland in the province of Huelva (Fig.

125   1). The first breeding pair became established in 2005 in the province of Cádiz (Muriel

126   et al. 2006) and the first successful pair reared a brood in 2009 in the same territory

127   (Muriel et al. 2010).

128   The Iberian Peninsula is an important passage area for migratory Ospreys

129   travelling between Europe and wintering areas in Africa, and a small number of northern

130   European birds winter in southern Spain (Saurola 1997; Schmidt-Rothmund et al. 2014).

131   Because of this, reintroduced populations in southern Spain are in regular contact with

132   migratory individuals from other populations, being a partial migratory population with

133   some of the breeding birds staying all year

134

135   **Data collection**

136   All released individuals were ringed with metal and PVC colour rings. They were

137   obtained as chicks from populations further north in Europe, including Scotland (27),

138   Germany (144) and Finland (20). We surveyed the study area at the beginning of each

139   breeding season (January–February, during the courtship and nest site selection period;

140   Poole 1989) to find any pairs that had settled and established territories. Nests were

141   visited to ring the young when they reached 40 days old, providing information about

142   the secondary sex ratio. In addition, the identity of every breeder was determined from

143   the ring number. Non-ringed breeders were captured at the beginning of the breeding

144   cycle using a dho-gaza mist net and an owl to attract the individual to the net; all

145   individuals captured were ringed to allow individual identification thereafter. Some

146   unringed individuals were identified over the years by their unique pattern of spots on

147   the head feathers (Bretagnolle et al. 1994).

148   For our sex ratio analysis, we considered population size (as the total number of

149   breeding pairs that year in each of the two release areas), age of breeders and sex ratio

150   of all broods from 2009 (the year of first successful breeding) to 2016. The secondary

151   sex ratio among young was expressed as the number of males per total number of

152   nestlings in all broods at ringing, including only those broods composed of non-

153   translocated (locally produced) nestlings. In all, sex was determined for 86 wild-hatched

154   nestlings in 39 different broods, using molecular analysis of feather samples (Ellegren

155   1996).

156   As the usual age of first breeding is considered as 3-4 years in Europe and the

157   Mediterranean region (Dennis 2015), we considered as "young" any pair with at least

158   one member younger than 5 years old.

159   In order to study the dispersal pattern of the population we analyzed data from

160   23-ringed breeding adults and assessed their natal dispersal distance (NDD; the distance

161   between the breeding site and the natal nest). All territorial adults since 2005 were used

162   in this analysis, including those released by hacking, considering the release site (hacking

163   tower) as the natal location.

164

165   **Statistical analysis**

166   We conducted two analyses, one examining factors affecting variation in nestling sex

167   ratio in the population since the first breeding pair in 2009, and another one examining

168   factors affecting the dispersal distances among breeders.

169   Analyses were conducted using the STATISTICA 13.3 package (Statsoft Inc., Tulsa,

170   USA) and R. First, we used a GLM analysis with sex ratio on the brood level as response

171   variable and population size as continuous predictor to test correlation between them.

172   Effect sizes and confidence intervals were also calculated. Then, in order to detect

173   factors involved in sex ratio deviations, we used mixed models (GLMMs); with age of

174   breeders (older or younger than 5 years) and released areas (Cadiz or Huelva) as fixed

175   factors and population size as a covariate. The response variable (nestling sex) was

176   binary, (1) male or (0) female. Therefore, we fitted GLMMs with a binomial error

177   structure and logit link using the lmer function in R (Bates and Maechler 2010), adding

178   brood identity as a random effect in the model (Krackow and Tkadlec 2001; Laaksonen

179   et al. 2004; Katzner et al. 2014). In some cases, the age of the parent would not be

180   determined, decreasing the sample size to 72 (instead of 86 used in analyses excluding

181   age of the parents). Population size was expressed as number of pairs in each of the

182   studied areas (Cadiz and Huelva) each year.

183   A generalized linear model GLM was used to check for differences in philopatry

184   among the 23-ringed breeders. In this case, we used the logarithms of the dispersal

185   distances to achieve normality. Logarithm of NDD was taken as the response variable,

186   while sex and reintroduction (separating between reintroduced n = 19, and wild

187   individuals n = 4) were included as fixed factors in the analysis.

188

Results

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191   By 2016, the breeding population in southern Spain reached 23 pairs (13 pairs in Cadiz

192   and 10 in Huelva). Throughout the study period (2009–2016), fledgling sex ratio was not

193   found different from 1:1 (40 males, 46 females, χ2 = 0.707, p = 0.998). However, intra-

194   brood offspring sex ratio was significantly affected by population size (GLM with sex

195   ratio on the brood level as response variable and population size as continuous

196   predictor; Wald statistic=6.577, p=0.010, Table 1), explaining 47% of the variance

197   (R^2=0.473). We found more production of males when population density was low and

198   more production of females as density increases (24 males and 10 females in the period

199   2009-2012 vs. 16 males and 36 females in the period 2013-2016, Figure 2).

200   Offspring sex ratio was related to population size, but not to parental age. When

201   the size of the breeding population increased, offspring sex ratio was increasingly biased

202   toward females (Table 2). No differences between the Cádiz and Huelva populations

203   were found (Table 2). From 2009, when the first two pairs bred successfully in southern

204   Spain, until 2016, when the population reached 23 territorial pairs, the proportion of

205   males declined from 0.8 to 0.26 (Figure 2). The total males and females produced over

206   the study period were 40 and 46 respectively, but 78% of the total females and 40% of

207   the total males were produced in the last 3 years (2014 to 2016).

208   The 23 ringed adults (10 females and 13 males) whose natal dispersal distances

209   were known included 19 individuals released during the reintroduction project, 2

210   individuals coming from other populations (Morocco and Balearic Islands) and 2 hatched

211   in the reintroduced populations. Interestingly, all the males (6 in Cadiz and 7 in Huelva)

212   but only 3 females bred in their natal area (2 in Cadiz and 1 in Huelva), whereas 7 females

213   but no males bred in a different area (4 females from Cadiz were found breeding in

214   Huelva, 1 female from Huelva was found breeding in Cadiz, and 2 females each from

215   Morocco and Balearic Islands were found breeding in Cadiz and Huelva, Fig 3). The

216   differences between the sexes in natal dispersal distances were statistically significant

7

217 (Table 3). Females showed higher natal dispersal distances than males, median values

218 for NDD were 9. 6 km in males and 183. 6 km in females

219

220 **Discussion**

221

222 As previous studies suggest, the probability of a bird starting to breed in its own natal

223 population depends largely on the chance of its finding a mate on an appropriate

224 territory (Dale 2001; Lenz et al. 2007). For that reason, in breeding populations the

225 optimal offspring sex-ratio is the one that balances the adult sex ratio, maximizing the

226 number of breeding pairs and giving the highest population growth rate (Dale 2001;

227 Lambertucci et al. 2013).

228   In a metapopulation context, the likelihood of individual dispersal between

229 populations of different sizes and degrees of isolation is of central importance in

230 understanding extinction and colonization dynamics. Our results showed a differential

231 natal dispersal between males and females, as already shown in other studies of birds

232 (Newton 1979, 2008; Greenwood and Harvey 1982) including Ospreys(Martell et al.

233 2002, Monti et al. 2014), with longer dispersal distances in females than in males. In

234 Ospreys and other raptors, males are the smaller, more philopatric sex, while females

235 are bigger and more liable to disperse further and breed in a different population. Under

236 this scenario, the proportion of males in a new population is expected to limit local

237 population growth, due to their reluctance to disperse large distances, reducing the

238 probability to incorporate males coming from neighboring populations. We cannot

239 discard that the higher NDD found in females is consequence of a sex-differential

240 response to disturbance due to the reintroduction project. However previous studies

241 showed that dispersal patterns of hacked birds are similar to those of non-hacked birds

242 (Amar et al. 2000) and where differences were found in juvenile dispersal distances

243 between reintroduced and hacked birds, differences were related to nutritional

244 condition (Muriel et al. 2015), having similar effects in both sexes (Ferrer and Morandini

245 2017).

246   Even if the specific causes that create differences in biased offspring sex ratio

247 during a colonization process are not being analyzed in our study, as Shyu and Caswell

248 (2016) highlighted, there are sex-specific differences that can affect the offspring sex

249 ratio, for example male and female offspring may differ in how they affect future

250 parental reproduction. The philopatric sex that breeds closer to their parents tends to

251 increase competition with its parents (Trivers 1985). According to that, a biased

252 offspring sex ratio toward females will reduce the competition with her own parents in

253 high-density populations. Nevertheless, our study populations seem to be still far from

254 high density situation, consequently these potential benefits are not yet operating.

255 Other factors might play a critical role in offspring sex ratio deviations, including seasonal

256 effects, trade-off between resource availability, individual quality and the differential

257 costs to produce the sex that enhances fitness the most (Wiebe et al. 1992; Dzus et al.

258 1996; Clout et al. 2002; Griffith et al. 2003; Szekély et al. 2004).

259 From an evolutionary viewpoint, producing more males at the beginning of the

260 colonization process would have some benefits for the parents. At low densities, when

261 high quality territories are available and competition for various resources is likely to be

262 low, the philopatric sex would be favored (Ferrer and Donazar 1996; Kokko et al. 2004;

263 Ferrer et al. 2008; Krüger et al. 2012). Later in the colonization process, when

264 competition for territories is high, the dispersive sex should be favored, leaving them in

265 a better position to find a nesting opportunity away from the natal area in another

266 population with lower density.

267 In line with theory, we found changes in offspring sex ratios related to population

268 size (Figure 2), with a tendency of breeders to produce more males at the beginning of

269 the colonization process and more females when population size increased. It is

270 important to point that in our study, we cannot separate the correlation between

271 population size and *"time"*, as the population tended to increase over the studied

272 period, avoiding the possibility to compare a situation advanced in time but with a

273 smaller population situation.

274 A similar study in the Spanish Imperial Eagle, also in southern Spain, showed a

275 similar trend, with more of the smaller, cheaper sex (males) produced when population

276 density was low and more of the larger female offspring when density increased (Ferrer

277 et al. 2009). In this case, variations in nestling sex ratio were associated with changes in

278 the proportions of immature breeders, which tended to produce more males. As the

279 proportion of breeders in immature plumage is density-dependent (Ferrer et al. 2003),

280 it was not possible to discard an underlying effect of density on nestling sex ratio. Our

281 Osprey population being in the early stages of establishment, tended to have a high

282 proportion of young pairs and an absence of old birds. For this reason, findings

283 concerning the relationship between sex ratio and parental age should be treated with

284 caution. It is not possible in either study to eliminate the possibility that sex ratios

285 changed through time for some very different reason, unrelated to either population

286 density or age-composition of breeders. In addition, we only evaluated secondary, not

287 primary sex ratio variation; therefore, we cannot determine mechanisms to achieve it

288 (Bowers et al. 2013; Morandini and Ferrer 2015). Only further studies will help to

289 separate these confounding factors, including the possibility of facultative brood

290 reduction affecting secondary sex ratio.

291 Previous studies with Spanish imperial eagles, have also explored the

292 relationship between nutritional conditions, presence of adults in the natal area and

293 dispersal distances (Ferrer 1993b; Muriel et al. 2016; Morandini and Ferrer 2017).

294 Individuals may be attracted by the presence of other breeders for settling (social

295 attraction); in this sense, individuals released without adults in the area will tend to

296 disperse longer distances than young with adults in their natal area do. In addition,

297 under the "wandering hypothesis", individuals in better nutritional conditions will

298 disperse longer distances than individuals in poor conditions, independently of

299 availability of territories or the presence of adults in the area (Muriel et al. 2015; Muriel

300 et al. 2016). If ospreys behave like imperial eagles, we would expect that reintroduced

301 populations would show higher dispersal distances than established populations,

302 regardless of changes in offspring sex ratios.

303 Breeding pairs occupying high quality territories in low density situations would

304 be expected to provide better nutritional conditions to their offspring, with lower

305 variance between occupied territories than in established populations in which both

306 high and low quality territories are occupied (Ferrer and Donazar 1996; Ferrer et al.

307 2006; Ferrer et al. 2008). However, the wandering hypothesis applies only to juvenile

308 dispersal distances in sedentary species. Nothing is known about its potential effect in

309 migratory species and natal dispersal after migration. According to the social attraction

310 hypothesis we expect longer dispersal distances in young Ospreys released without

311 adults in the area (at the beginning of the reintroduction program), and no differences

312 in the other two possibilities (i.e. released young with adults already breeding in the

313 area and wild young). Further studies would be necessary to separate potential effects

314 of social attraction and nutritional conditions, when the reintroduced population

315 increases in density. Using the same population with different densities, we can avoid

316 problems related to differences in spatial distribution and landscape features when

317 comparing data from different populations (Morandini and Ferrer 2017).

318 In reintroduction and reinforcement programs of species with sex-biased

319 dispersal, the sex ratio of released individuals may influence the rate of population

320 establishment. In spite of the difficulty of assigning a cause to changes in offspring sex

321 ratios, consequences of a biased sex ratio seem to be associated with a differential

322 dispersal behavior in a growing population. On this basis, when re-establishing a new

323 population in a metapopulation context, our suggestion is to release mainly the most

324 philopatric gender initially in order to attract conspecifics of the wandering sex.

325 Depending on the possibilities of immigration from other populations, a large number

326 of males during the first years of releases would be likely to increase the growth rate of

327 the new Osprey population. However, different strategies could be carried out,

328 depending on the distribution of other populations and the chances of immigration. We

329 anticipate that our results could form a starting point for simulation models to predict

330 the viability of connected small populations, taking account of sex differences in

331 dispersal.

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Table 1: Result of GLM analysis with sex ratio on the brood level as response variable
and population size as continuous predictor to test correlation between them.
Confidence intervals were also calculated.

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Effect	Estimate	Standard Error	Wald Stat.	Lower CL 95.0%	Upper CL 95.0%	p
Intercept	-0.0575	0.2734	0.0444	-0.5935	0.4782	0.8329
territorial pairs	-0.0523	0.0204	6.5776	-0.0924	-0.0123	0.0103

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Table 2: Result of binomial GLMM considering the sex of an individual (probability of being male) as the response variable (N=72). Age of parents ("young" and "old") and population identity (Cádiz or Huelva) were analyzed as fixed factors. Annual population size, expressed as number of pairs in each of the studied areas (Cadiz and Huelva) each year, was included as covariate. Confidence intervals (95%) are also presented (estimates are in log scale in a binomial model), and R^2 marginal (fixed effects) and conditional (fixed and random effects together).

	Estimate	Std. Error	z value	P value
Intercept	5.969	2.958	2.018	0.0436
Age	-0.946	0.762	-1.241	0.2147
Population identity	-1.233	0.863	-1.429	0.1531
Population size	-0.316	0.129	-2.436	0.0149

Random effects:

Groups Name	Variance	Std.Dev.
Brood (Intercept)	0.249	0.498

Confidence interval (95%)

	Estimates	2.5%	97.5%
Intercept	5.969	0.669	13.385
Age	-0.946	-2.734	0.552
Population identity	-1.232	-3.323	0.396
Population size	-0.315	-0.644	-0.091

R^2 marginal (fixed effects) and conditional (fixed and random effects together)

Family	Link	Marginal	Conditional
Binomial	logit	0.1891	0.2462

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518 Table3: Result of GLM (normal distribution and identity link function) considering natal

519 dispersal distance (log-transformed) as response variable. Factors included in the

520 analysis were sexes (male or female) and origin (wild or reintroduction).

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Effect	SS	df	MS	F	p
Intercept	1981.679	1	1981.697	1556.271	<0.001
(1) Sex	24.123	1	24.123	18.945	<0.001
(2) Reintroduction	1.172	1	1.172	0.921	0.352

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525   Figure 1: Osprey population in Southern Spain. First nests appeared in Cádiz population and in

526   Huelva population are represented in black, the following nests are represented in gray. Division

527   between populations area represented by the limit of the provinces (Cádiz and Huelva).

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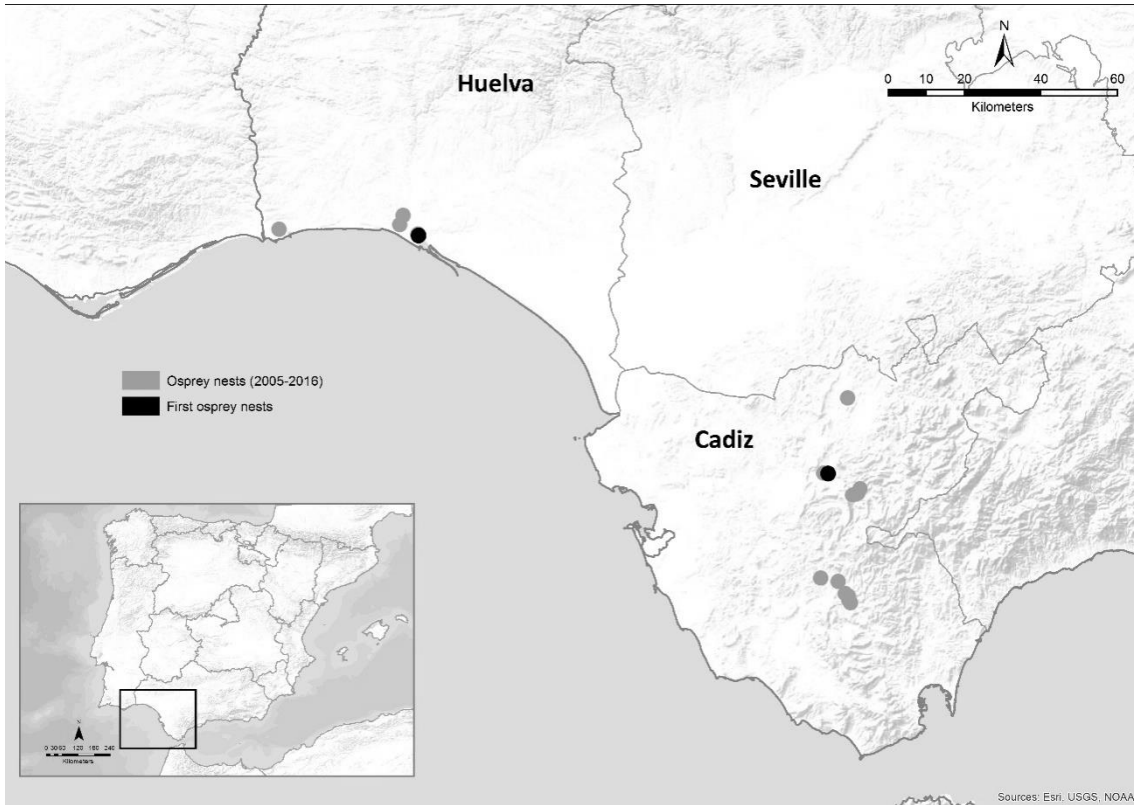
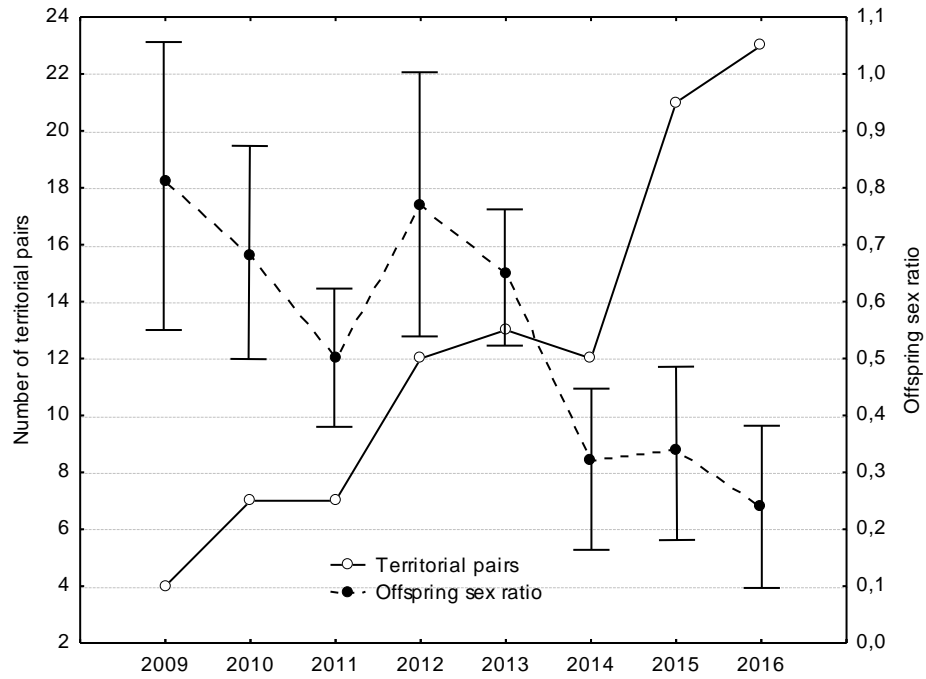
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544 Figure 2: Annual number of pairs and offspring sex ratio (expressed as number of males/total

545 number of nestlings per year) of the reintroduced Osprey populations in south of Spain from

546 2009 to 2016. The 95% Wilson confidence intervals are included for offspring sex ratios each
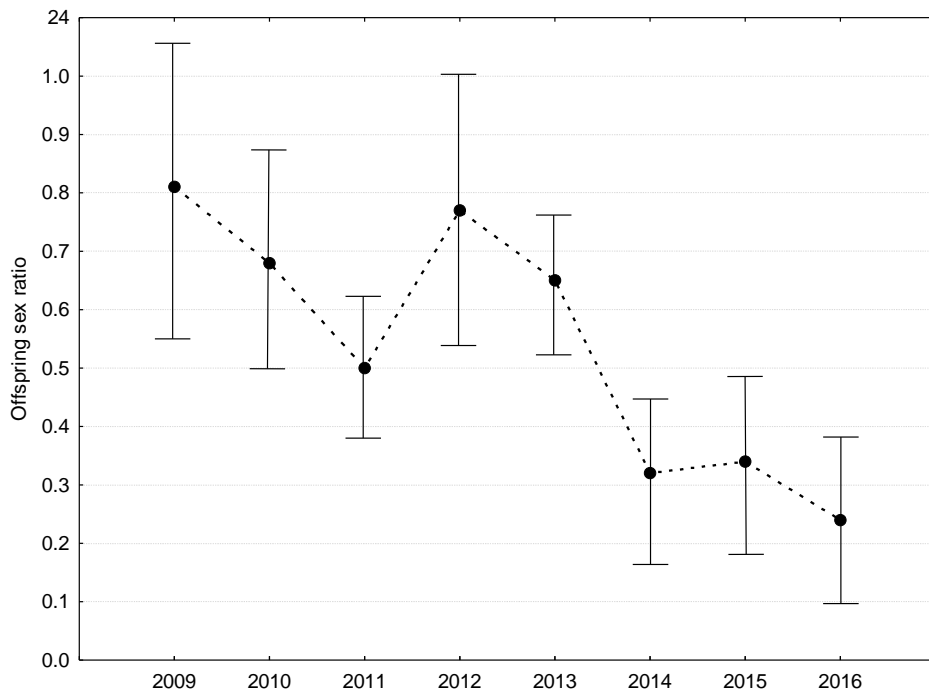
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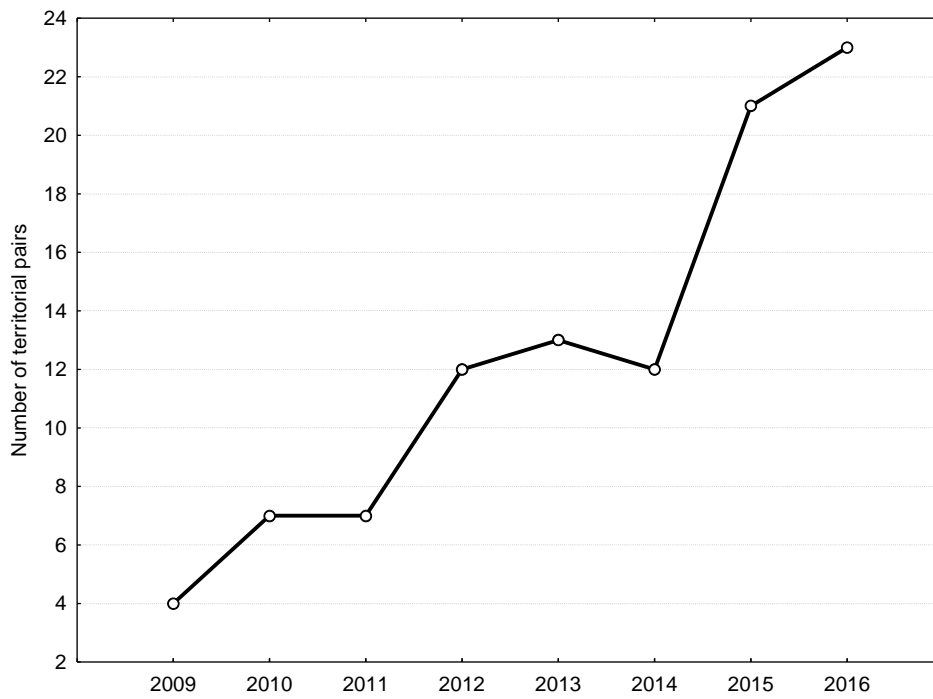
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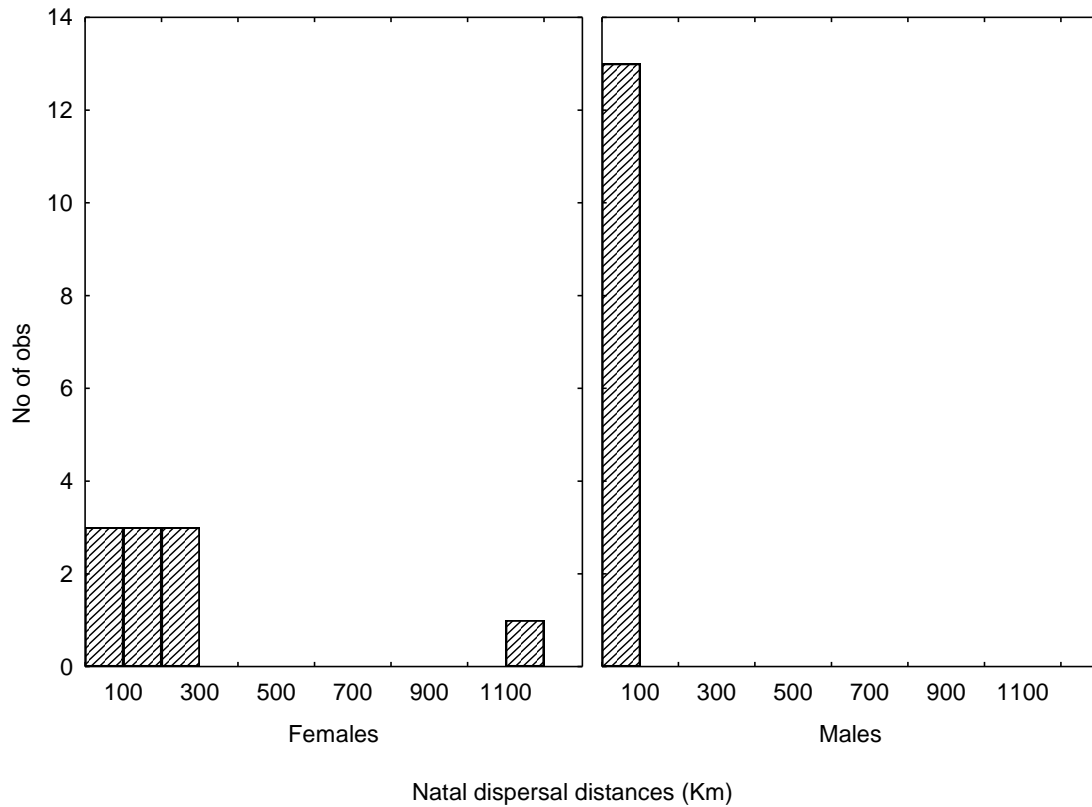
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561   Figure 3: Distribution of breeding dispersal distances of females and males considering the

562   location of the natal nest and the first breeding nest. For individuals released by hacking, the

563   release site (hacking tower) was considered as the natal location

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