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Migration strategies revealed by satellite tracking among descendants of a population of European White Stork (*Ciconia ciconia*) reintroduced to Belgium.

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1   **Abstract**

2   Migration in the European white stork (*Ciconia ciconia*) has historically described a

3   predictable annual cycle. The white stork is extensively distributed across continental Europe

4   which diverges to eastern and western wintering flyways. Within the western European

5   population some ring recovery and anecdotal information suggests that birds are giving up

6   their traditional wintering grounds in the Sahel and remaining in alternative sites in the

7   Iberian Peninsula. Here we report on long-term satellite tracking of juvenile and adult stork

8   collected between 2000 and 2011whose natal site is in Belgium, in the northern range of the

9   western migration path. We identified three distinct migration patterns, two of which diverged

10   from traditional expectations. Juvenile birds showed unique migration profiles both

11   individually across migration cycles and when compared to one another, whereas adults

12   showed consistent migrations but failed to migrate to Africa in any of the years surveyed.

13   Stopover and wintering locations within Iberia were strongly associated with refuse sites or

14   modified agricultural land. Overall, non-traditional migration movements appeared linked

15   most strongly to artificial food sources rather than alternate drivers such as climate or habitat.

16

17   **Keywords:** *Ciconia ciconia*, satellite tracking, western migration route, migration distance.

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19

20   **Zusammenfassung**

21   **Durch Satellitenverfolgung aufgezeigte Zugstrategien von Nachfahren einer Population**

22   **von in Belgien wieder eingeführten europäischen Weißstörchen (*Ciconia ciconia*)**

23   Der Zug des europäischen Weißstorchs (*Ciconia ciconia*) ist historisch einem vorhersagbaren

24   Jahreszyklus gefolgt. Der Weißstorch ist in Kontinentaleuropa weit verbreitet, und hier gibt es

25   einen östlichen und einen westlichen Zugweg. Innerhalb der westeuropäischen Population

26   deuten einige Ringfunde sowie Einzelberichte darauf hin, dass die Vögel ihre traditionellen

27   Überwinterungsgebiete in der Sahelzone aufgeben und in alternativen Gebieten auf der

28   Iberischen Halbinsel verbleiben. Hier berichten wir von Langzeit-Satellitenverfolgung

29   juveniler und adulter Störche, die in Belgien geboren wurden, zwischen 2000 und 2011, im

30   nördlichen Gebiet des westlichen Zugwegs. Wir identifizierten drei verschiedene Zugmuster,

31   von denen zwei von den traditionellen Erwartungen abwichen. Juvenile Vögel zeigten

32   einzigartige Zugprofile, sowohl individuell über Zugzyklen als auch im Vergleich zueinander,

33   während Altvögel konsistente Zugmuster aufwiesen, aber in keinem der Untersuchungsjahre

34   nach Afrika zogen. Rast- und Überwinterungsgebiete auf der Iberischen Halbinsel waren stark

35   mit Müllkippen oder abgewandeltem Agrarland assoziiert. Insgesamt schienen nicht-

36   traditionelle Zugbewegungen am stärksten mit künstlichen Nahrungsquellen in Verbindung

37   zu stehen und nicht mit alternativen Faktoren wie Klimawandel oder Habitat.

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Introduction

Phenological shifts in species distribution, migration strategy and other life history traits are attracting increasing research attention, particularly in light of altered climate regimes and ongoing habitat alteration (Visser et al. 2009; Barbet-Massin et al. 2011; Moussus et al. 2011; Singh and Milner-Gulland 2011; Gordo et al. 2013). Both habitat and climate have been implicated in the modification of established migration ecologies (Evans et al. 2011).

Among avian species, cues to migrate are complex, strongly linked to food availability (Alerstam 1993), breeding cycles and weather conditions (Shamoun-Baranes et al. 2003; Mitchell et al. 2012). The choice to migrate is not without risk, and among long-distance migrants mortality risks can be high, particularly given that conditions along the migration route, and on the wintering grounds, are unknown at the time of departure (Bauer et al. 2008).

Migration in the European white stork (*Ciconia ciconia*) has historically described a predictable annual cycle (Gordo et al. 2013). The white stork is extensively distributed across continental Europe as far east as Belarus and Ukraine, and as far north as southern Scandinavia to St. Petersburg, Russia. South of the Mediterranean there are breeding populations in northern Algeria, Morocco and Tunisia (Schulz 1998; Huntley et al. 2007). The European population diverges to eastern and western wintering flyways, though these populations are not genetically partitioned based on neutral genetic markers (Shephard et al. 2013). Western individuals migrate across the Straits of Gibraltar to wintering areas in the Sahel region in west Africa, and eastern birds follow a path through the Bosphorus to wintering areas in east and South Africa.

70 Typical foraging habitat consists of wet grasslands, agricultural and natural lowlands, shallow

71 lakes and marshes (Elliot 1992; Carrascal et al. 1993). Storks especially favour freshly

72 ploughed fields (Carrascal et al. 1993) or mown meadows (Johst et al. 2001). Their diet

73 consists of a wide variety of invertebrates, fish, rodents, reptiles and amphibians (Elliot

74 1992).Their nesting place includes high trees, and frequently man-made structures like roofs,

75 chimneys and purpose built nesting platforms including modified and unmodified electricity

76 poles (Elliot 1992; Tryjanowski et al. 2009a).

77

78 Survivorship is strongly affected by weather in both the breeding and wintering areas

79 (Kanyamibwa et al. 1993; Schaub et al. 2005; Saether et al. 2006; Gimenez et al. 2009;

80 Tryjanowski et al. 2009b). In particular drought in the Sahel region is suspected to have

81 contributed to extensive declines in the western population in the early 1900's (Bairlein 1991;

82 Senra and Alés 1992; Schulz 1999).

83

84 Although considered a species of least concern (LC) globally (IUCN 2011), the western

85 population of white stork was subject to significant levels of decline with some country

86 specific extirpations since the late 19th century (Bairlein 1991; Senra and Alés 1992; Schulz

87 1999). These have been attributed to habitat alteration including wetland drainage and

88 agricultural intensification, but also to factors such as: hunting, overhead power lines, heavy

89 rain during the breeding season and drought in the wintering areas (Bairlein 1991; Barbraud et

90 al. 1999; Infante and Peris 2003; Saether et al. 2006; Thomsen and Hötker 2006; Grosbois et

91 al. 2008; Nevoux et al. 2008a; Nevoux et al. 2008b; Tryjanowski et al. 2009a; Kaługa et al.

92 2011). In response to these declines, intensive reintroduction programmes that began in 1948,

93 have returned white storks to much of their former range, and census sizes continue to rise

94 (NABU 2006).

95

96   Storks have a long association with human settlement. Scavenging, supplementary feeding as

97   part of reintroduction programmes, the prevalence of waste disposal sites as alternate foraging

98   habitats and the invasive red swamp crayfish (*Procambus clarkii*) as an additional food

99   source, have all been linked to suspected changes in migration strategy (Doligez et al. 2004;

100   Massemin-Challet et al. 2006; Olsson 2007); though notably crayfish consumption has been

101   shown to be comparatively low during winter, at least in Portugal (Correia 2001).

102

103   Satellite tracking studies in the eastern population have shown birds to be remarkably

104   consistent in their migration direction across repeated years, though their choice of wintering

105   site may vary (Berthold et al. 2001; Berthold et al. 2004; Schaub et al. 2005).

106   In western Europe there is significant anecdotal and ring recovery evidence (e.g. Barbraud et

107   al. 1999) to suggest that storks from the northern distribution that use the western migration

108   route (Berthold et al. 1992b) are giving up their traditional wintering grounds in the Sahel

109   region of West Africa and remaining in alternative sites in the Iberian peninsula. This has led

110   to speculation that long-term interference with migration ecology could lead to permanent

111   disruption of historical migration routes and overall migration distance as demonstrated in

112   other European migrants (e.g. Evans et al. 2011).

113

114   Here we report on the first long-term satellite tracking of juvenile, pre-adult and adult storks

115   whose natal site is in the northerly range of the western migration path. Specifically we were

116   interested in: 1) the variation in migration movement within an individual between different

117   migration cycles, 2) variation in migration movement between individuals in each migration

118   cycle, 3) differences in migration strategy between pre-breeding (juvenile and pre-adult) and

119   adult birds, and 4) assessing the effects of age and sex and the amount of time spent

120   migrating, breeding and wintering.

121   **Methods**

122   Satellite data were collected from 12 storks between the years 1999 and 2011. A total of

123   eleven transmitters were used in the study. In one instance two birds carried the same

124   transmitter in consecutive years (PTT15258a and b). In this instance the first bird died, and

125   the transmitter was recovered and placed on a new bird. Individuals were tagged as pre-

126   fledged juveniles prior to their first migration (n = 6), or as pre-adult (n = 1) and adult birds (n

127   = 4). Adults were already breeding and pre-adults had already migrated, but had not shown

128   breeding behaviour yet. One bird was of unknown age; all other birds were ringed prior to

129   fledging so were of known age. Some birds were tracked across multiple years and may have

130   fitted different age classes across the full term of the study. Birds were part of the

131   Planckendael colony, descendants of an intensively managed reintroduction group started in

132   1978 (n = 14) within the grounds of Wild Animal Park Planckendael, Mechelen, Belgium

133   (51°00'N, 4°31' E). The original founder group comprised captive birds (pinioned) sourced

134   from zoos in Paris, Warsaw and Budapest. Between 1978 and 1990 supplementary food was

135   supplied to the colony which was housed in the open, such that free-flying storks were able to

136   join the colony, and birds were able to breed naturally and follow natural migration cycles. As

137   at 2013 the colony contained 53 breeding pairs and functions as a wild colony attracting new

138   free-flying wild birds annually. Both ringed and non-ringed birds have joined the colony.

139   According to ring data, some of these have dispersed from the eastern flyway (J. Shephard,

140   pers. obs.). Significant scavenging opportunities exist within the grounds of the park.

141   Throughout the study period supplementary food was supplied by the park keepers. Storks

142   could choose to eat this food or forage in the surrounding semi-rural area and township. The

143   same amount of food support was supplied throughout the year. Birds were fitted with solar

144   charged PTT-100 transmitters (Microwave Telemetry, http://www.microwavetelemetry.com;

145   and North Star, http://www.northstarst.com). Transmitters were attached using teflon and

146   nylon harnesses and weighed between 20 and 30 grams representing between 0.6 and 1.5% of

147   total body weight depending on sex (determined genetically), which is considered well within

148   recommended range loads (Kenward 2001).

149

150   **Data processing**

151   Data were collected via the ARGOS satellite based positioning system. Transmitters were set

152   to a 24hr duty cycle with a maximum of eight locations received per transmitter per day, and

153   included all measurements. However, reliable fixes were not received on all days, most likely

154   due to cloud cover or associated weather conditions. ARGOS accuracy classes (LC): 3 (<

155   250m), 2 (250m < < 500m), 1 (500m < < 1500m), 0 (> 1500m) were analysed and were

156   determined by four or more satellite messages (CLS 2007-2014). Any locations based on

157   three or less satellite messages were deleted. LC0 locations were included as we were

158   interested in gross rather than fine scale movement patterns (Bradshaw et al. 2007). Data were

159   checked by eye and locations considered implausible, such as those over open water (other

160   than the Straits of Gibraltar), were removed. Data were visualized in a GIS (ArcView 3.2,

161   ESRI 1996). Raw ARGOS data were imported using the 'Argos-tools' add-on (Potapov and

162   Dubinin 2005).

163

164   **Treatment of the data**

165   Data were treated in two ways. Firstly, all available data (n = 12; 1999 - 2011) were used to

166   describe the overall pattern in all migration events and to determine the location of stopover

167   sites. To test whether the number of days on spring and autumn migration, time spent

168 breeding, and time spent wintering were influenced by age and/or sex, we used Generalized

169 Estimating Equations (GEE; Hardin et al. 2012) with a Poisson distribution in SPSS (IBM

170 Corp.Released 2012). This method was applied because per subject repeated measures were

171 done; the same birds were measured repeatedly (in different years). In the GEE analysis, the

172 score test statistic (generalised score option) is used as it has been shown to be more robust

173 than the Wald test statistic (Molenberghs and Verbeke 2007). An independent correlation

174 matrix was used, assuming independence of the results for each year. Running the model

175 using an unstructured-correlation matrix showed that some correlations between the years

176 could be estimated; however, these models showed a higher Quasi-AIC (QIC), indicating a

177 poorer performance. The response (the number of days) was counts. We used a fixed value of

178 1 for the scale parameter. We checked for overdispersion, by estimating the scale parameter

179 using models with Deviance and Pearson. Four separate models were run, each for the

180 different responses (spring migration - SM, autumn migration - AM, time breeding - TB, and

181 time wintering - TW). For the models for SM and TB, the estimated scale parameters were 1.0

182 and 1.3 respectively, which suggests that a fixed value of 1 was plausible. For the models for

183 AM and TW, scale parameters were estimated to be approximately 5.6-5.9 and 9.4-9.5

184 respectively, suggesting overdispersion. Applying a negative binomial model did not lead to

185 different conclusions on the effects of age and time on any of the outcome variables.

186 Applying this model also did not lead to a significantly improved model fit.

187   The subject in each model was the bird, the within subject factor was year, which means that

188 the same birds were followed during several migration cycles over consecutive years and that

189 year is the repetition within each bird. Predictors were age and sex, and an interaction term

190 (age*sex) was included in the model. In this way we determined the relation between age and

191 sex, and days of the different migration phases of the birds. Model selection was done by

192 removing insignificant effects and comparing the QIC of the different models, so that the

193   model with the best goodness of fit was found. Age was calculated in years and was treated as

194   a continuous variable. The within-subject factor is not considered a random factor, since we

195   do not consider the years in this research as a random sample of all years. The bird of

196   unknown age was omitted from the analysis. The model was validated by plotting the

197   residuals against the predicted values of each response. No patterns were found in these

198   graphs.

199

200   In the second analysis, variation in migration pattern was compared between three juvenile

201   (prior to reproductive maturity), and three adult birds, over three consecutive migration

202   cycles. Non-continuous or missing data precluded the inclusion of more birds. Birds used in

203   this study displayed breeding behaviour at three years of age. Juvenile birds had their

204   transmitters affixed in the first year of life and were tracked until their fourth year of life.

205   Adult birds were tagged in either the fourth or sixth year of life and were tracked until their

206   seventh or ninth year of life. In each case they showed breeding behaviour during at least one

207   of the migration cycles. Breeding status could only be determined if the bird returned to

208   Planckendael colony and was observed at an active nest.

209

210   A full migration cycle describes the autumn migration (in a southward direction) in Year 1,

211   and the spring return migration (normally in a northerly direction) in Year 2. For both juvenile

212   and adult comparisons, the third cycle contains a final autumn migration. Transmitters failed

213   after this time preventing further data collection.

214

215   A breeding or nesting ground (or summering ground for non-breeding birds) was defined as

216   the most northerly position occupied by a bird during the summer months, and included

217   foraging movements within a relatively similar latitudinal band (April to August). A bird was

218   considered to be migrating when it moved away from its breeding or natal site in a southern

219   direction and stopped in the wintering ground, where it stayed for a couple of months. A

220   wintering ground was defined as the most southerly point of a migration route where the bird

221   spent the winter months and foraged within a relatively similar latitudinal band (October to

222   January). Similarly, spring migration was defined as a sustained movement away from the

223   wintering site (i.e. a clear movement north of the wintering latitude). Arrival and departure

224   dates were determined based on sustained movement away from either the breeding or

225   wintering ground. Therefore a series of behavior windows were identified and used to

226   calculate the number of days: 1) on spring migration, 2) on autumn migration, 3) spent on the

227   breeding or summering ground, 4) spent in the wintering ground. Data were excluded where a

228   clear break between behavior windows could not be identified.

229

230   Not all birds performed a constant migration. Accordingly, stopover sites were defined as

231   places where migration was interrupted and the direction of flight was scattered over a certain

232   area for a period of five days to one month after which the bird continued to the wintering

233   ground. These were distinct from refueling stops, where a bird may forage for one or two days

234   in an area before continuing. Both time spent at stopover and refueling sites were included in

235   the 'time spent migrating' calculations.

236

237   Migration movements where birds wintered in Europe rather than the Sahel region in west

238   Africa are called 'short-distance migrations' in this paper.

239 **Results**

240 **Overall spatial pattern**

241 11 wintering events, 12 breeding or summering events, 9 spring migration events and 22

242 autumn migration events were recorded. From these, three distinct migration patterns were

243 identified (Fig. 1). In the first, birds completed a full migration with wintering in the Sahel

244 region of West Africa. This pattern describes the traditional migration pattern for the western

245 European population of this species. In the second, birds wintered in the south of Spain

246 without crossing the Strait of Gibraltar . In the third, birds wintered in Madrid, Spain .

247 Stopover sites were identified in France, Spain and Morocco. Recorded stopover sites fell into

248 one of five regional clusters and were associated with either agricultural areas in Saubusse

249 (France), Tudela (Spain), parts of the south of Spain and northern Morocco, or refuse sites

250 around Madrid (Spain) and northern Morocco (Fig. 2). The majority of stopovers (76%) were

251 during the autumn migration. The average number of days spent at stopover sites was 9.5

252 days during the southward autumn migration (range 5 – 19 days; SD 4.2 days; n = 13)

253 compared to 16 days during the return spring migration (range 5-24 days; SD 8.9 days; n = 4).

254

255 None of the GEE models showed an effect of either age or sex on the number of days birds

256 spent on autumn or spring migration, on the breeding or wintering ground (Table 1). Overall,

257 an average 21.8 days (range 6 – 47 days; SD 14.8 days; n = 22) were spent on autumn

258 migration, and an average 28 days (range 13-54 days; SD 12.7 days; n = 9) on spring

259 migration. An average 156 days (range 55 – 200 days; SD 44.4 days; n = 12) were spent on

260 the breeding or summering grounds, while an average 148.2 days (range 103 – 207 days; SD

261 29 days; n = 11) were spent on the wintering grounds.

262

263 **Juvenile movement patterns**

264 The three juvenile birds showed unique migration profiles both individually across migration

265 cycles and when compared to one another (Fig. 1). In cycle 1 (2000-2001) PTT27255 and

266 PTT15256 departed together, became separated during migration, but travelled all the way to

267 the Sahel region in Africa where they remained for the winter. During the spring migration

268 PTT27255 travelled north only as far as Morocco, while PTT15256 continued north to Toledo

269 in Spain to a rubbish dump site where it remained for the summer. In contrast, the third

270 juvenile (PTT27254) migrated only as far as the very south of Spain around Tarifa, near the

271 Strait of Gibraltar where it wintered. In spring it travelled north to Tudela, Spain. In cycle 2

272 (2001-2002) PTT27255 wintered in Morocco, but flew north and returned to the Planckendael

273 colony during the spring migration. PTT15256 returned to the Sahel in Africa to winter then

274 returned to Madrid, Spain during the spring migration. PTT27254 returned to the south of

275 Spain again to winter but returned to the Planckendael colony on spring migration. In cycle 3

276 (2002-2003) PTT27255 migrated in the autumn to the southwest of Argenda Del Ray, Spain,

277 in the vicinity of a major rubbish dump where it wintered. In the spring migration it returned

278 to Belgium, and then again only migrated as far south as Seville, Spain in the following

279 autumn migration. PTT15256 again moved from its summer position near Madrid to the Sahel

280 region to winter. However, no data is available for the spring migration, so either the

281 transmitter failed or the bird died. PTT25254 moved again only as far as southern Spain

282 during the autumn migration, but migrated to spend the following summer in Germany

283 returning to the south of Spain to winter in 2003. Interestingly, both PTT27255 and PT15256

284 displayed strong levels of nomadism while on the wintering ground (Fig. 1).

285

Adult movement patterns

286

287 The three adult birds showed consistent migration behaviours across three full migration

288 cycles, following similar migration paths and using similar stopover sites (Fig. 2 and 3). All

289 birds were reproductively active and in most cases returned to the Planckendael colony to

290 breed. PTT15258a bred in its fifth, sixth and seventh year; PTT15258b bred in its seventh and

291 eighth year, and PTT25254 bred in its seventh year. All birds performed short-distance

292 migrations and wintered in either Seville or Madrid, Spain.

Discussion

294 The traditional route of the western European white stork is to follow the western flyway to

295 the Sahel region of west Africa. In addition to this route, we also identified two quite different

296 migration tracks, relatively uniform in direction, but significantly shorter than expected.

297 These confirm suspicions that storks from the Planckendael colony were consistently

298 performing migrations different to classical expectation.

299

Difference in migration between juvenile and adult birds

301 In the first year of life juvenile storks migrate from their natal site. Two of the three juveniles

302 studied between 2000 and 2003 left Planckendael colony together on their first migration, but

303 followed different migration strategies (Fig. 1) suggesting they joined different flocks for

304 much of the study period. Both genetic (van Noordwijk et al. 2006) and cultural transmission

305 (Chernetsov et al. 2004) have been proposed as mechanisms controlling migration behaviour,

306 and at least one recent study has shown evidence of endogenous programming being

307 overridden due to perceived mortality risk, with inexperienced birds joining experienced

308 migrants, on longer but potentially safer migrations, to wintering areas (Mellone et al. 2011).

309 Among first year migrant storks, Chernetsov et al. (2004) used displacement experiments to

310   show the importance of social interactions. When they forced naïve migrants to rely only on

311   innate orientation mechanisms, many errors in navigation resulted. However, it seems likely

312   that social interaction accounts for the large variation seen both within individual juveniles,

313   and between juveniles across migration periods in this study.

314

315   Two of the three juvenile birds returned to Planckendael colony in their second year of life

316   (Fig. 1) which is consistent with findings elsewhere in both eastern and western populations

317   (e.g. Barbraud et al. 1999; Antczak and Dolata 2006). One of these (PTT27255) started

318   breeding in 2003 and according to demographic records bred every year thereafter until 2008

319   after which it was found dead at the nest. The other juvenile (PTT27254) summered in

320   Belgium in its third year of life, but then migrated to Germany in its fourth year of life. This

321   bird remained in the western flyway, wintering in Spain the next season, and then returned to

322   Planckendael colony in 2004, where according to demographic records it bred until the end of

323   the study period.

324

325   In contrast to the juveniles, adult birds all performed short-distance migrations. Only one of

326   the three birds travelled as far south as Seville, the rest remained in or around Madrid joining

327   previously identified (Blanco 1996) communal roosting and foraging flocks at refuse sites.

328   Some of these sites are populated with storks year round, as well as being stopover locations

329   for birds from throughout the western flyway (Blanco 1996).

330

331   Unfortunately, due to the resampling of individual birds across multiple migration cycles

332   there was insufficient power in the data to confirm statistically significant behaviour

333   differences either between sex or pre-adult and adult birds. Whilst it was tempting to suggest

334   differences based on the raw data, this would have been statistically inappropriate. However,

335   these data suggest that this is worth direct attention in future studies. At least one other long-

336   distance migrant, the black kite (*Milvus migrans*), which often co-occurs in migrating flocks

337   with storks, shows predictable age related variation in migration strategy, with juveniles

338   showing significant variation in all aspects of migration in the first years of life, while adults

339   (> 7 yrs) showed stable and repeatable strategies across years (Sergio et al. 2014).

340

341   **Potential reasons for changes in migration behaviour**

342   Observed changes in migration distance are likely to be driven by a number of factors

343   including habitat and climate. Habitat quality has been implicated in two separate migration

344   consequences. In the first, migration costs are increased as birds are forced to fly further due

345   to poor quality habitat and/or food resources, and in the second migratory ability is lost

346   altogether (Guttal and Couzin 2010).

347

348   The connection between climate and shorter migration distance is less clear. Visser et al.

349   (2009) have found some habitat dependent relationships between climate and migration

350   distance in birds ringed in The Netherlands over the last 70 years. However, most studies have

351   linked climate shifts to changes in arrival and departure times in the eastern and western

352   flyways rather than migration distance in European white stork (Fiedler et al. 2004;

353   Lehikoinen et al. 2004; Vergara et al. 2007; Gordo et al. 2013). Similarly, there is a clear

354   correlation between rainfall and survivorship in wintering areas across Africa (Schaub et al.

355   2005; Saether et al. 2006; Gimenez et al. 2009), and conditions along the migration route are

356   also significant. For example, a major population crash and ultimate extirpation of stork from

357   Sweden is attributed to adverse weather conditions along the migration route during 1856

358   (Cavallin 1999). So, clearly while the impact of reduced habitat quality or climate is not

359   trivial, it appears the strongest driver of migration behavior in this species is food availability.

360   Even in sub-zero temperatures, storks will remain on the breeding ground during the winter if

361   there is adequate food (Authors, unpub. data; N. Chernetsov, pers. comm.).

362

363   In some species, the use of urban environments has reduced the need to migrate at all, as both

364   food and temperature requirements are met. Among populations of European blackbird

365   (*Turdus merula*) this has led to ecological divergence in migration behavior (Evans et al.

366   2011). Storks have developed strong associations with human settlements throughout Europe,

367   and in addition to accessing refuse sites, many colonies still benefit from supplementary

368   feeding, as an extension of reintroduction projects, and the provision of artificial nesting

369   platforms. As a consequence, there is mounting evidence among western populations that a

370   certain proportion of birds within colonies remain resident year round. This is the case in the

371   Planckendael colony as well as some colonies in Spain, France and Sweden (Blanco 1996;

372   Massemin-Challet et al. 2006; Olsson 2007).

373

374   None of the adults in this study flew to the Sahel, suggesting that experience also plays a

375   significant role in establishing repeat migration strategies. Though moderated by food supply

376   (Berthold et al. 2002), fidelity to wintering sites is thought to become stronger with age and

377   experience (Barbraud et al. 2003), where knowledge about the predictability of the

378   environment is known (Evans et al. 2011). In particular, one of the juveniles in this study only

379   flew to the Sahel in the first of three full migrations, with a reduction in migration distance in

380   each subsequent migration, suggesting that knowledge gained on previous flights may have

381   guided decision making the following year.

382

Consequences of shorter migration

While shorter migration distances are associated with higher survivorship, and are suggested to provide a competitive advantage facilitating earlier access to the breeding ground and better reproductive outcomes (Visser et al. 2009; Vergara et al. 2010), there is the potential for assortative mating among these birds to drive rapid genetically based selection for offspring displaying these novel migration phenologies. This has already been shown in the Blackcap (*Sylvia atricapilla*) over ecological timescales (Berthold et al. 1992a). In addition, the subsequent cultural transmission of these genetically determined migration routes may hasten the loss of traditional full migration and reinforce shorter migration movements permanently.

While reaction-norms may account for some variation in migration expression (van Noordwijk et al. 2006; Charmantier and Gienapp 2013), it would be interesting to see if there actually is a difference in the genetic profile of short-distance and traditional long-distance stork migrants, particularly as a candidate gene has now been identified in birds (Mueller et al. 2011). The evolution of short-distance migrant behaviour in combination with a reliance on rubbish dumps, may also be of concern as Muñoz-Arnanz et al. (2011) have recently identified the strong imbalance between toxic load in rural versus urban stork colonies. The later use rubbish dumps as a permanent food source in Spain. The impact of pollutants on bird populations is well documented (Ottinger et al. 2009). How broadly toxic impact is replicated among other populations in Europe is unknown and is worthy of significant attention.

Overall, it would seem that artificial food sources play a dominant role in driving both migration behavior and distance in the birds in this study, and suggests the need for additional tracking studies to derive a broader understanding of the extent to which this is occurring elsewhere within the western stork population; as if traditional migration is to be maintained,

408 or at least left to adapt naturally to climate shifts, supplemental feeding, including the

409 availability of rubbish dumps, needs to be curtailed.

410

418 **Tables**

419 Table 1 Significance values in each GEE model for predictors age, sex and interaction term.

420 **Figures**

421

422 Fig. 1 Migration patterns shown by three juvenile storks over a period of three consecutive

423 migration cycles. Confirmed breeding is marked by an oval with year of life below. Autumn

424 and spring migrations are shown with a solid and dashed line respectively.

425

426 Fig. 2 Main stopover sites used by birds in the study, regardless of age and identified in five

427 regional zones: 1) Saubusse, France, 2)Tudela, Spain, both agricultural regions; 3) Madrid,

428 Spain, primarily at refuse sites; 4) south of Spain, 5) northern Morocco, where stopovers were

429   associated with both agricultural regions and refuse sites. Each point represents an individual

430   stopover event.

431

432   Fig. 3 Migration patterns shown by three adult storks over a period of three consecutive

433   migration cycles. Note - PTT15258a was tracked over different years than PTT15258b and

434   PTT27254. Confirmed breeding is marked by an oval with year of life below. Autumn and

435   spring migrations are shown with a solid and dashed line respectively.

436

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633   Table 1 Significance values in each GEE model for predictors age, sex and interaction term.

634

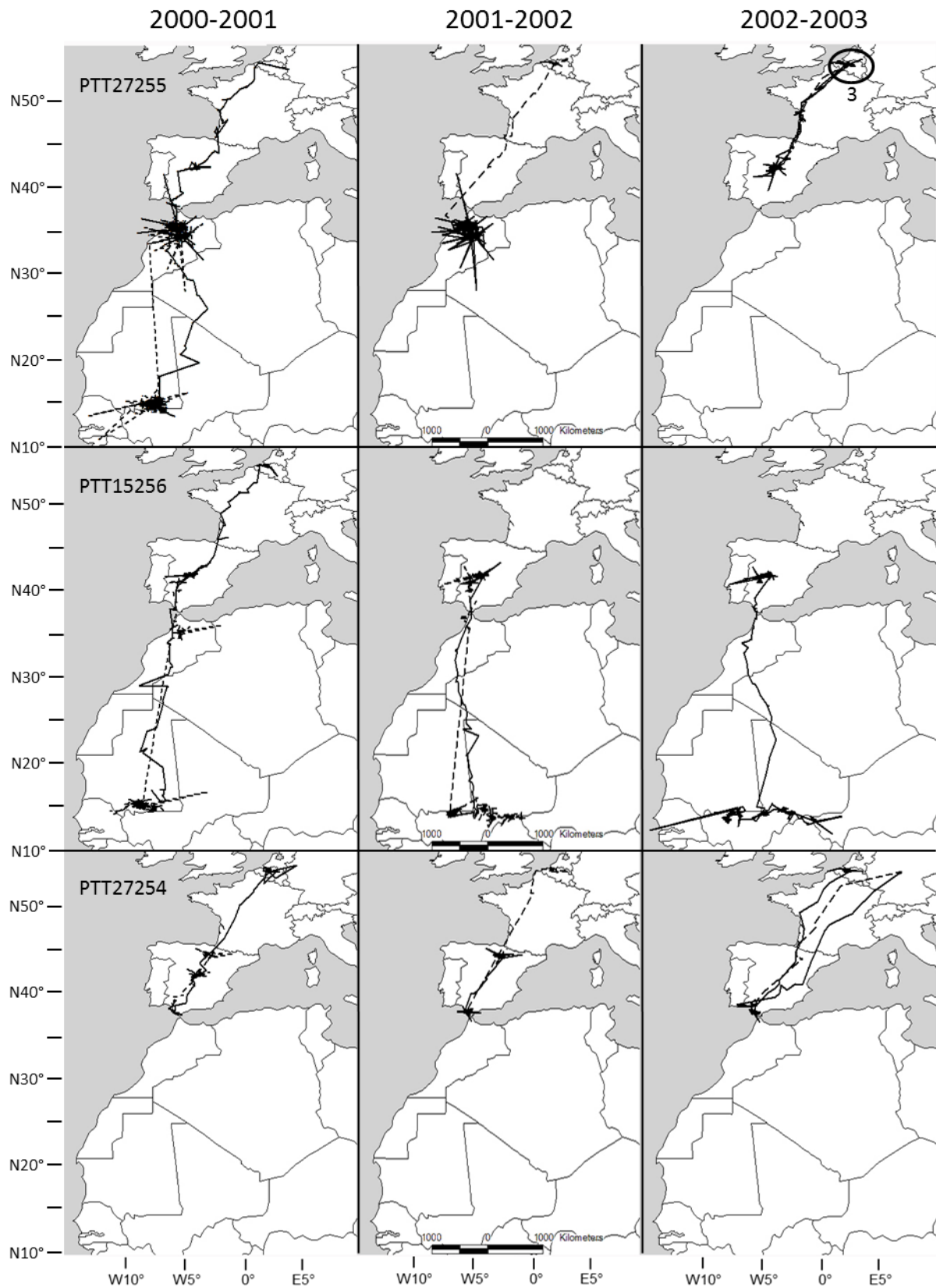|		Test of model effects		
		Age	Sex	Age*Sex
Dependent variable	Summer Migration	0.416	0.081	0.137
	Time Breeding	0.362	0.061	0.265
	Autumn Migration	0.26	0.072	0.299
	Time Wintering	0.416	0.393	0.279

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636

Fig. 1 Migration patterns shown by three juvenile storks over a period of three consecutive migration cycles. Confirmed breeding is marked by an oval with year of life below. Autumn and spring migrations are shown with a solid and dashed line respectively.
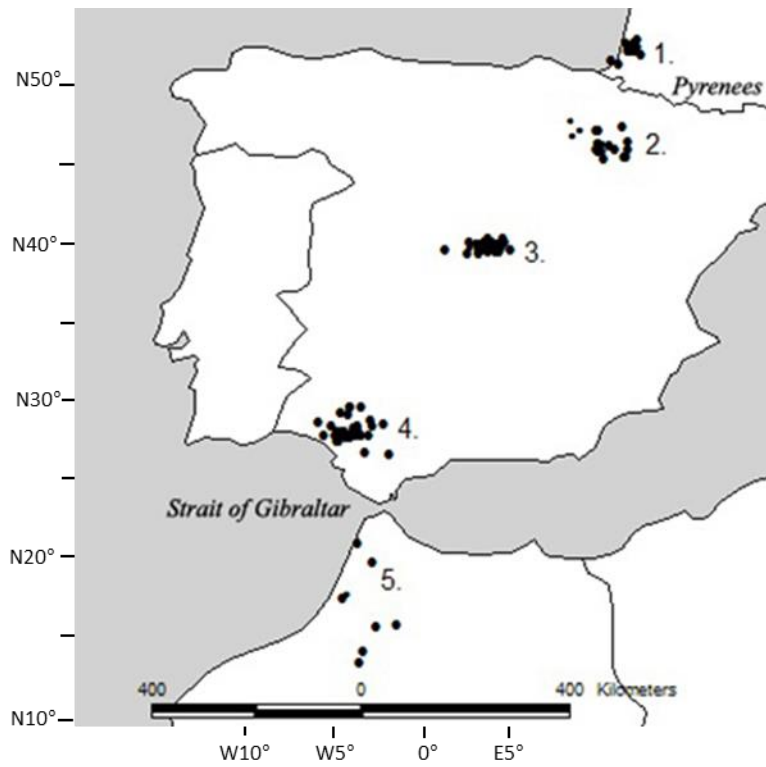
637

Fig. 2 Main stopover sites used by birds in the study, regardless of age and identified in five regional zones: 1) Saubusse, France, 2)Tudela, Spain, both agricultural regions; 3) Madrid, Spain, primarily at refuse sites; 4) south of Spain, 5) northern Morocco, where stopovers were associated with both agricultural regions and refuse sites. Each point represents an individual stopover event.
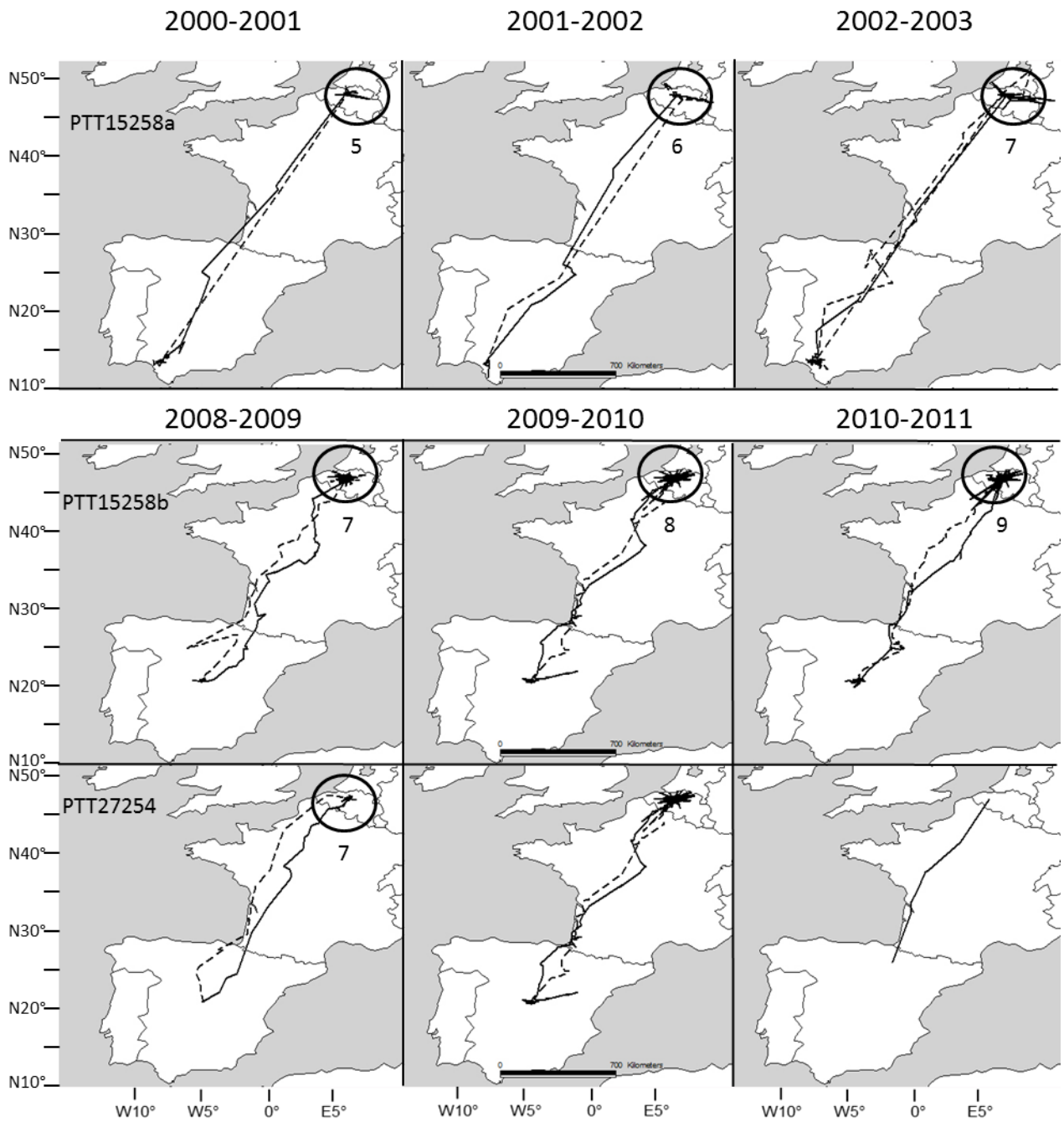
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Fig. 3 Migration patterns shown by three adult stork over a period of 3 consecutive migration cycles. Note - PTT15258a was tracked over different years than PTT15258b and PTT27254. Confirmed breeding is marked by an oval with year of life below. Autumn and spring migrations are shown with a solid and dashed line respectively.

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