The first winter influences lifetime wintering decisions in a partially migrant bird

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20   In facultative partial migration, flexibility of the wintering behaviour throughout the birds'

21   lifetime (switching between the migrant and resident tactics, and vice versa) may be

22   considered as an advantage because it allows individuals to cope with environmental

23   conditions. Quantifying the extent of flexibility of the wintering behaviour, and identifying

24   the related factors (environmental and individual variables) are crucial issues. The present

25   study addresses these questions in a European subpopulation of a shorebird species, the pied

26   avocet (*Recurvirostra avosetta*), that displays three wintering tactics: strictly resident, locally

27   resident, and migrant. We explored tactic fidelity over consecutive years since the birds' first

28   winter by notably testing the influence of age and estimating more specifically the long-term

29   consistency of the first wintering tactic. We also explored tactic-related survival. Based on a

30   10-year ringing study carried out on five French colonies and on capture-recapture modelling

31   (558 birds with a known first-winter tactic), we showed that birds were highly faithful to their

32   first wintering tactic over consecutive years (probabilities ranged from 0.78 to 0.98 depending

33   on tactic and age), and when a tactic change occurred, it mainly consisted in wintering in the

34   French Atlantic area. Besides, we found a moderate decrease in fidelity to the migrant tactic

35   over consecutive years with bird age. Complementarily, the fidelity of locally resident and

36   migrant individuals to their first wintering site was remarkably high. Finally, survival over

37   winters was particularly high (≥ 0.90) and non-dependent on tactic. At the individual scale,

38   the flexibility of the wintering tactic was therefore limited over the study period. Despite a

39   slight age effect, other biological information resulted in invalidating two hypotheses

40   commonly suggested to explain age-differential migration. Additional biological

41   interpretations including the absence of harsh winters, habitat quality, and advantages of site

42   familiarity can be put forward to interpret the main results.

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45 **KEYWORDS**

46 Arrival-time hypothesis

47 Capture-recapture modelling

48 Dominance hypothesis

49 Facultative partial migration

50 Fidelity

51 Pied avocet

52 *Recurvirostra avosetta*

53 Site-fidelity index

54 Survival

55 Wintering tactic

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62   The wintering behaviour can arise in different ways in birds (Newton, 2008). Typically, in

63   partially migrant populations, some individuals overwinter within their breeding region

64   (namely resident birds) while others display a migratory behaviour (migrant birds) to reach

65   distant wintering quarters (Lack, 1943; Newton, 2008; Dingle, 2014). In such systems, the

66   coexistence of these wintering behaviours may increase the heterogeneity of the

67   environmental conditions experienced by individuals in wintering sites, with possible

68   significant consequences at both the individual and population levels (Newton, 2008;

69   Chapman, Brönmark, Nilsson, & Hansson, 2011). Indeed, travel costs (i.e. the energy

70   expense) and wintering conditions (e.g. climatic conditions, food resources) are known to

71   affect subsequent reproductive success (Norris et al., 2004; Sedinger et al., 2006), survival

72   (Peach, Baillie, & Underhill, 1991; Schaub, Kania, & Köppen, 2005), and ultimately

73   population growth rates (Sæther & Bakke, 2000; Rockwell et al., 2017).

74   In partially migrant populations, the flexibility of the wintering behaviour and site

75   selection throughout the birds' lifetime may highly modulate all these consequences

76   (Bearhop, Hilton, Votier, & Waldron, 2004; Gunnarsson et al., 2005; Iverson & Esler, 2006).

77   The control of partial migration (see Chapman, Brönmark, Nilsson, & Hansson, 2011 for a

78   review) is generally positioned along a continuum. At one end is a strong genetic basis

79   leading to two 'wintering strategies' that remain stable throughout the individuals' lifetime

80   (commonly called obligate partial migration; Biebach, 1983; Lundberg, 1988; Berthold,

81   2001). At the other end is a combination of environmental (e.g. winter harshness) and

82   individual (e.g. body size and condition) factors leading to two flexible 'wintering tactics' that

83   can alternate throughout the birds' lifetime (facultative partial migration; Ketterson & Nolan,

84   1983; Lundberg, 1988; Alcock, 2013). In the case of facultative partial migration, the birds'

85   age is assumed to influence the wintering behaviour. Young birds often exhibit different

86   wintering distributions and site-fidelity patterns than older birds (Cristol, Baker, & Carbone,

87 1999; Marchi et al., 2010; Lok, Overdijk, Tinbergen, & Piersma, 2011). Several hypotheses

88 have been suggested to explain age-differential migration in birds. The 'dominance

89 hypothesis' assumes that migration constitutes the best option for subordinate young

90 individuals to avoid the costs related to conspecific competition (notably resource requisition

91 by more dominant adults; Gauthreaux, 1978; Townshend, 1985; Schwabl & Silverin, 1990).

92 In return, young migrant birds have to cope with putative costs associated with migration (i.e.

93 travel costs and conditions in wintering grounds; Lok, Overdijk, Tinbergen, & Piersma, 2011;

94 Lok, Overdijk, & Piersma, 2015). As a result, the likelihood for a bird to migrate is expected

95 to decrease with age. The 'arrival-time hypothesis' suggests that adults benefit from

96 overwintering nearby breeding grounds (e.g. access to better quality mates and nesting

97 places), and hence predicts a shift towards wintering closer to the breeding grounds with age

98 until sexual maturity (Ketterson & Nolan, 1983). Such pattern is notably expected for

99 territorial individuals (i.e. a sex-biased pattern). The predictions deriving from the two

100 hypotheses mentioned above are very similar. In this context, the dominance would

101 proximately influence the wintering behaviour (Gauthreaux 1982). More generally,

102 quantifying the extent of flexibility of the wintering behaviour throughout the individuals'

103 lifetime and the study of the associated correlates constitute a relevant way to address the

104 issue of the control of partial migration.

105   However, investigating partial migration at the individual scale over a long-term

106 period represents a challenging field work because collecting individual data in large and

107 distant wintering quarters is difficult and requires a huge amount of time. To date, only very

108 few studies have focused on the issue of the flexibility of the wintering behaviour and on the

109 related consequences (see for instance Sanz-Aguilar et al., 2012). In the present work, we

110 specifically addressed these issues in the partially migrant French subpopulation of pied

111 avocets, *Recurvirostra avosetta*. In a companion paper (Chambon et al., 2018), we found that

112   three wintering tactics coexist in first-year pied avocets from this subpopulation: (i)

113   overwintering within the natal colony site (ʿstrictly resident tacticʾ, SR), (ii) overwintering in

114   sites located at a relatively short distance from the natal colony (at few dozen kilometres)

115   along the French Atlantic coast (ʿlocally resident tacticʾ, LR), or (iii) reaching farther

116   wintering quarters, mainly in the Iberian Peninsula, through migration (ʿmigrant tacticʾ, M).

117   In addition, we highlighted the influence of context-dependent and individual factors on the

118   choice of the wintering tactic for first-year birds. Accordingly, we speculated the existence of

119   facultative partial migration in this subpopulation.

120   The present study is based on a 10-year ringing survey involving field re-sightings

121   data collected in Western Europe in winter. We addressed several issues related to partial

122   migration in this shorebird species. We explored whether wintering tactics were fixed since

123   the birds' first winter or were flexible throughout the birds' lifetime. We particularly

124   investigated whether and how tactic fidelity and tactic change over consecutive winters were

125   influenced by age. Under the two hypotheses described above, we predicted a strong decrease

126   of fidelity to the migrant tactic with bird age in the early years of life. Additionally, we

127   predicted similar high fidelity to the two resident tactics, irrespective of age, given the

128   relatively short distance between natal sites (used by SR birds) and the other French wintering

129   grounds (used by LR birds). We also tested whether the wintering tactic influenced individual

130   survival. This parameter is considered as both a good indicator of wintering habitat suitability

131   (Peach, Baillie, & Underhill, 1991; Schaub, Kania, & Köppen, 2005) and the most influential

132   fitness component of population growth rates, as suggested in long-lived species (Crone,

133   2001).

134   **METHODS**

135   *Data Collection and Selection*

136   The birds originated from five of the major breeding colonies located along the French

137   Atlantic coast (Fig. 1a): (i) the gulf of Morbihan, (ii) the marshes of Mesquer, (iii) the

138   marshes of Guérande, (iv) the bay of Bourgneuf, including the island of Noirmoutier, and (v)

139   the island of Ré. All details on the fieldwork, data selection, and bird categorisation in relation

140   to their wintering tactic are provided in Chambon et al. (2018). In short, they were ringed as

141   chicks with a unique combination of plastic colour-rings fixed on their two tiobiotarsi (plus a

142   metal ring from the French ringing scheme – C.R.B.P.O.), from 2006 to 2015. Given the lack

143   of sexual dimorphism, the gender of chicks was not determined. Furthermore, the ˙arrival-

144   time hypothesis˙ could be tested on all birds, irrespective of the gender, since both members

145   of a breeding pair actively prospect for nesting places, then build and defend the nest (males

146   being not more territorial than females; Adret, 1983; Cramp & Simmons, 1983).

147   From winter 2006/2007 to winter 2016/2017, a large network of professional

148   ornithologists and amateur bird-watchers routinely observed ringed pied avocets, in few

149   typical coastal grounds used by the species (e.g. inter-tidal mudflats), across the Atlantic coast

150   of Western Europe. The re-sighting effort during winter was considered as relatively more

151   intensive in France (see Chambon et al., 2018 for more details). Based on our full database

152   and given the range of migratory timing, individuals re-sighted in France from 20th December

153   to 25th February were defined as resident birds, and individuals re-sighted from 1st November

154   to 31st March in distant areas were considered as migrant birds (Chambon et al., 2018). In

155   cases of multiple re-sightings per bird and year, the closest location to the middle of the

156   wintering period (i.e. 15th January) was selected in order to attribute to each bird a single

157   wintering location and tactic per year.

158   As we were notably interested in the long-term consistency of the first tactic, we only

159   focused on individuals whose first tactic was known (Chambon et al., 2018). We

160   discriminated between migrant birds wintering in the Iberian Peninsula and those wintering

161   northwest Europe because of putative differences in wintering conditions that might bias

162   survival estimates. Nevertheless, owing to numerical issues, birds wintering in northwest

163   Europe were excluded from the dataset (only 16 individuals re-sighted in northwest Europe

164   during their first winter, and one individual re-sighted in northwest Europe as adult but not

165   during its first winter). Ultimately, we analysed a re-sighting database of 558 ringed pied

166   avocets that were re-sighted in their first winter, and for which 364 individuals were re-

167   sighted in subsequent winters, totalling 889 additional bird-winters (see Table 1). Overall,

168   resident and migrant birds were re-sighted in 12 distinct French sites and 6 Iberian sites,

169   respectively (Fig. 1a, b).

170   *Multisite Capture-Recapture Modelling*

171   The re-sighting database was converted into individual encounter histories to perform capture-

172   recapture (CR) analyses. Consequently, each year of the study period constituted an occasion.

173   For each occasion and individual, it was specified whether the bird considered was re-sighted

174   – with the attribution of its wintering tactic (coded as 1, 2 and 3 for SR, LR and M,

175   respectively) – or not (coded as 0). For each individual, the first tactic mentioned in its

176   encounter history referred to the tactic displayed during its first winter. In the CR analyses,

177   the three tactics were considered as three different sites, and we therefore used a multisite

178   (specific case of multistate) CR modelling approach (Arnason, 1973; Brownie et al., 1993;

179   Schwarz, Schweigert, & Arnason, 1993). We particularly followed the method proposed by

180   Grosbois & Tavecchia (2003), allowing the decomposition of a multi-step process expressed

181   as the product of elementary probability matrices (see Appendix 1). Concretely, based on the

182   individual encounter histories, this method allowed us to distinguish and to provide estimated

183   probabilities of several parameters of interest for the present study: bird survival (S) from time

184   i to $i + 1$, then conditional on survival, fidelity (F) to the wintering tactic adopted at time i

185   between time i to $i + 1$, and conditional on infidelity ($1 - F$), tactic change (C) from time i to

186   time $i + 1$, while taking the re-sighting probability (R) into account. Therefore, all these

187   parameters were estimated together for each pair of consecutive occasions in a multi-

188   parameter CR model.

189   Each parameter can be modelled as a function of several variables (leading to different

190   candidate functions per parameter, thereafter called 'structures'), allowing to explore different

191   hypotheses through a model selection procedure. The initial model used in the model

192   selection procedure was the Jolly Move (JMV) model that allows S, F, C, and R probabilities

193   to vary with site (tactic in our case) and time (years). Based on our full re-sighting database,

194   we noted that bird survival associated to the first tactic would be strongly underestimated by

195   CR modelling because a fraction of the birds was never re-sighted during the subsequent

196   winters while being still alive (Table 1). Moreover, even if the survival probability estimated

197   by CR modelling should be considered as local (Lebreton, Burnham, Clobert, & Anderson,

198   1992), data exploration indicated that estimated survival would tend more to mirror true

199   survival for birds re-sighted in subsequent winters. Accordingly, we allowed the S parameter

200   of the initial model to also vary between two age classes: survival from the first to the second

201   winter of birds, and survival between two consecutive winters since their second winter. This

202   two-age-classes variable typically accounted for variation in survival between newly and

203   previously encountered birds (transience effect; Choquet et al., 2005; Pradel, Gimenez, &

204   Lebreton, 2005). Then, we tested the goodness-of-fit (GOF) of the initial model to ensure that

205   it fitted well our CR data, using the U-CARE programme, version 2.3.4 (Choquet et al.,

206   2005). We removed the 3G.SR subcomponent of the GOF tests (linked to the transience

207   effect; see Pradel, Gimenez, & Lebreton, 2005 for details), and the adjusted level of

208   overdispersion was 1.30 (see Appendix 1).

209   The modelling procedure consisted in testing different structures on S, F, and C to

210   explore our biological hypotheses. Following Lok, Overdijk, Tinbergen, & Piersma (2011),

211 we divided our modelling procedure into three steps and based it on the initial model. In step

212 1, we kept F and C structures as they were in the initial model, and we tested several

213 structures on S by comparing these structures and selecting the most competitive one. In step

214 2, we tested several structures on F while keeping the most competitive S structure from step

215 1, and keeping the C structure as in the initial model. Finally, we tested several structures on

216 C in step 3 while keeping the most competitive S and F structures from the previous steps. We

217 always maintained the R structure of the initial model to adjust the estimates of the other three

218 parameters, according to potential variation in the observation effort. Furthermore, all the

219 structures tested on S included the previously described two-age-classes variable. We fixed

220 the survival value of the first age class to the unique rate of 0.93 (mean value when

221 considering resident and migrant birds, tending towards true survival estimate; see Table 1).

222 The effects of candidate variables on S were only tested on the second age class.

223   Concretely speaking, in step 1, we tested whether the S structure of the initial model

224 was better supported when using a two-tactic categorisation (resident versus migrant) for the

225 tactic variable, instead of the three tactics. If this structure was retained, it would indicate that

226 survival was influenced by different wintering conditions between the French and Iberian

227 areas. In addition, we tested the influence of tactic and year on survival by removing one of

228 these two variables or both of them (keeping only the two-age-classes variable in this latter

229 case) on all S structures tested. In step 2, to investigate variations in tactic fidelity with age,

230 we tested whether the F structure of the initial model was better supported when tactic fidelity

231 was additionally allowed to vary with a two-, three- or four- age-classes variable (i.e.

232 distinguishing: second- and >second-winter birds; second-, third- and >third-winter birds; or

233 second-, third-, fourth- and >fourth-winter birds, respectively). These different age classes

234 rely on knowledge of the age of recruitment of pied avocets in the French subpopulation

235 (from 1 to 3 years old; Watier & Fournier, 1980; Touzalin, 2017). We tested additional

236   structures by including the first tactic of the birds as a group covariate on the previous F

237   structures (on all age classes except the first one), to assess the influence of the birds' first

238   tactic on their fidelity to each tactic in the subsequent winters (e.g. higher fidelity rate in

239   consecutive years to the first tactic in comparison to a newly displayed tactic). Once more, we

240   tested the influence of tactic and year on tactic fidelity by removing one of these two variables

241   or both of them (keeping only the age variable in this latter case) on all F structures tested. In

242   step 3, we tested whether the C structure of the initial model was better supported when tactic

243   change was additionally allowed to vary with a two-, three- or four-age-classes variable (as

244   defined above). Then, we tested whether these structures were better supported when

245   considering supplementary variation according to the birds' first tactic (group covariate for all

246   age classes except the first one). The aim was to explore the preferential tactic change

247   between two consecutive winters according to the birds' age and first tactic. Finally, we tested

248   the influence of year on tactic change by removing this variable on all C structures. The

249   complete list of structures tested for each parameter is provided in Appendix 1.

250   We used the E-SURGE programme, version 2.1.3 (Choquet, Rouan, & Pradel, 2009),

251   to build the elementary probability matrices, and to build and compare the different structures

252   tested on the S, F, and C parameters. For each parameter, the comparison of the different

253   structures tested was performed using the quasi Akaike information criterion corrected for

254   both overdispersion and small sample sizes (QAICc; Burnham & Anderson, 2002). The

255   adjusted level of overdispersion (ĉ) from the GOF test was taken into account for the

256   calculation of the QAICc. A model was considered to be more competitive than the others

257   when its QAICc was at least two units lower. Final estimates of all parameters (means ranging

258   from 0 to 1, ± SE when available) came from the model retained in step 3.

259   Since we suspected a large fraction of re-sighted birds to exhibit a high fidelity to the

260   tactic displayed during their first winter, on the basis of data exploration (Table 1), we

261 complementarily assessed their fidelity to their first wintering site. It was performed on LR

262 and M birds (see Catry et al., 2012; and Appendix 2 for more details on the calculation of the

263 site-fidelity index).

264 *Ethical Note*

265 This paper is based on re-sightings of ringed wild birds. Capture, ringing, and observations

266 were carried out with minimal disturbance (more details are available in Chambon et al.,

267 2018). Permit for the research programme and ringing permits for ringers involved in the

268 study were provided by the organisation managing birds' capture and ringing in France

269 (ˊCentre de Recherches sur la Biologie des Populations d'Oiseaux – C.R.B.P.O.' from the

270 French ˊMuséum National d'Histoire Naturelle').

271 # RESULTS

272 *Final Multi-Parameter Model*

273 The most competitive structure on survival supported in step 1 of the CR analyses only

274 included a two-age-classes variable distinguishing survival between the first and second

275 winters (fixed value), and survival between consecutive winters in older birds (Table 2, and

276 see Appendix 1 for details on the model selection). Then, for the tactic-fidelity parameter

277 (step 2), the largely most competitive structure considered different tactic-dependent fidelity

278 probabilities for second-, and >second-winter birds in consecutive years, with a variation

279 according to the tactic adopted during the first winter for this last age class (Table 2). For step

280 3, the most competitive structure considered different tactic-change probabilities according to

281 the tactic abandoned and to the tactic subsequently adopted (Table 2). The resulting final

282 multi-parameter model obtained was therefore (see Appendix 1 for details on the language

283 used): $S_{a(1)+a(2:10)} \, F_{a(1).f+a(2:10).f.Tactic} \, C_{f.to} \, R_{f.t}$

Estimates

285   From the final multi-parameter CR model described above, survival estimates were very

286   similar according to birds' age: 0.93 between the first and second winter, and 0.90 ± 0.01

287   between two consecutive winters in older birds. Conditional on survival, the fidelity to a

288   given tactic for second-winter birds was the highest for M birds (0.98 ± 0.02), intermediate

289   for LR birds (0.88 ± 0.03), and the lowest for SR birds (0.78 ± 0.05; Fig. 2a). For >second-

290   winter birds, the fidelity to one of the two resident tactics in two consecutive winters was, on

291   average, higher for birds that exhibited the focal tactic in their first winter than for birds that

292   displayed another tactic as first wintering behaviour: 0.89–0.93 against 0.69–0.77 depending

293   on the focal tactic and first tactic displayed by the birds (Fig. 2b, c). Fidelity to the M tactic

294   for >second-winter birds was also influenced by their first wintering tactic (Fig. 2d); it was

295   particularly high for birds that displayed a M behaviour as first tactic (0.91 ± 0.05). However,

296   fidelity to the M tactic was also very high for birds originally exhibiting a SR tactic ($0.92 \pm$

297   0.08). Additionally, birds exhibiting a M tactic during their first winter were relatively less

298   faithful to it in consecutive winters beyond the second winter when compared to younger

299   birds (second-winter birds; differences in estimates between the two age classes: -0.07; Fig

300   2a, d). Birds exhibiting one of the two resident tactics as first wintering behaviour were

301   relatively more faithful to it in consecutive winters beyond their second winter (differences in

302   estimates between the two age classes: +0.11 and +0.05 for SR and LR, respectively; Fig 2a,

303   b, c). Furthermore, the fidelity of individuals to their first wintering site (conditional on the

304   fidelity to the first wintering tactic) was very high for the two bird groups for which it was

305   calculated (see the calculation of this index in Appendix 2): 0.96 ± 0.01 for LR birds ($N =$

306   163), and 0.96 ± 0.01 for M birds ($N = 27$). Finally, conditional on tactic change between two

307   consecutive winters, and regardless of bird age, individuals displaying one of the two resident

308   tactics predominantly shifted to the other resident tactic (Fig. 3a, b), and M birds mainly

309   became SR birds (Fig. 3c).

DISCUSSION

311   Studying partial migration and more precisely the extent of flexibility of the wintering

312   behaviour throughout the lifetime of individuals represents a great challenge. Nevertheless,

313   this issue is of particular importance because animals, especially birds, must face global

314   changes bound to increase in the future (e.g. Pearce-Higgins & Green, 2014). One additional

315   key question is to identify the factors controlling partial migration. Addressing all these

316   questions requires long-term data on the encounter history of marked individuals. The present

317   work faced a typical difficulty in such a survey-based study, i.e. a low sample size for migrant

318   birds (see Table 1). Even if interpretations should be made with caution in such

319   circumstances, we are confident about our results concerning migrant birds overwintering in

320   the Iberian Peninsula because they were relatively homogenous within this bird group.

321   Furthermore, the number of re-sighted birds we studied resulted from the fact that we were

322   interested in exploring the long-term consistency of the first wintering behaviour which

323   forced us to only select individuals whose first wintering behaviour was known; but this

324   number properly reflected the low proportion of French migrant birds wintering in the Iberian

325   Peninsula (Chambon et al., 2018). To date, flexibility of the wintering behaviour over

326   lifetimes has been extremely poorly documented in partially migrant birds (but see for

327   instance Sanz-Aguilar et al., 2012).

328   The first major finding of the present study is that pied avocets originating from the

329   French Atlantic subpopulation displayed high fidelity to their first wintering tactic over a

330   long-term period. This result is consistent with the work of Sanz-Aguilar et al. (2012). These

331   authors indeed found that wintering greater flamingos (*Phoenicopterus roseus*) were highly

332   faithful to their first wintering area (they wintered either in their French natal area, in the

333   Iberian Peninsula, in Italy, or in Africa) across years. Such a result suggests that the first

334   winter experienced by birds largely influences their wintering decisions in later life.

335   We also showed a moderate age effect on tactic fidelity when distinguishing second-

336   winter and >second-winter birds. This effect varied among wintering tactics. Birds displaying

337   a migrant tactic in their first winter were relatively less faithful to their first tactic beyond the

338   second winter as compared to younger (second-winter) birds, unlike individuals that firstly

339   displayed one of the two resident tactics. In addition, second-winter birds were more faithful

340   to the migrant tactic than to the other two resident tactics. At first sight, these results tend to

341   support the dominance hypothesis. Nevertheless, this hypothesis predicts that fidelity to the

342   migrant tactic strongly decreases with age due to the subordinate status of young birds

343   (Gauthreaux, 1978, 1982). Based on the relatively slight variation of fidelity to the migrant

344   tactic with age, our findings do not really support this. Rejection of this hypothesis appears

345   consistent with the low proportion of migrant birds in the French pied avocet subpopulation

346   (12% of first wintering birds in the present study, and around 14% in Chambon et al., 2018),

347   whereas we could expect it to be very high under the dominance hypothesis. In addition, the

348   gregarious behaviour of wintering pied avocets (Cramp & Simmons, 1983), and the few

349   agonistic interactions observed in winter highly contrast with what is outlined in the

350   dominance hypothesis. Under the arrival hypothesis, immature individuals are assumed to

351   shift towards wintering closer to breeding grounds (i.e. a strong decreasing fidelity to the

352   migrant tactic) to take fitness advantages from arriving earlier in breeding grounds until

353   sexual maturity (see Ketterson & Nolan, 1983), as suggested in the black-backed gull (*Larus*

354   *fuscus*; Marques, Sowter, & Jorge, 2010), and in the greater flamingo (Sanz-Aguilar et al.,

355   2012). However, our results do not support this prediction. The relatively low variation in

356   fidelity to the migrant tactic with age in French pied avocets could be explained by the fact

357   that the costs linked to the migrant tactic probably do not affect individual reproductive

358   success. Nevertheless, Hötker (1998, 2002) suggested that breeders from the strictly migrant

359   German subpopulation of pied avocets would benefit from overwintering in closer areas to

360   breeding grounds. Therefore, further investigations addressing seasonal interactions (e.g. the

361   effects of wintering ground selection on the date of arrival at breeding sites and the related

362   consequences on reproductive success; Lundberg, 1988, Norris & Marra, 2007; Gillis, Green,

363   Middleton, & Morrissey, 2008) would be needed to investigate this point in our

364   subpopulation.

365   Furthermore, winter conditions probably contributed to the high rates of tactic fidelity

366   estimated across years. Winter weather conditions are known to modulate bird behaviour;

367   harsh winters trigger bird migration in response to lower habitat suitability, notably in food

368   availability (Lundberg, 1988; Newton, 2008). German and Danish pied avocets are more

369   exposed to harsh wintering conditions than birds from regions located at lower latitudes; this

370   factor probably forces them to display a strictly migrant pattern (Salvig, 1995; Hötker, 1998,

371   2002). In addition, Hötker (1998) showed that first-year German pied avocets mainly

372   overwintered in France during mild winters, otherwise further south, in the Iberian Peninsula

373   (Hötker, 1998). Hötker (1998) speculated that most birds were subsequently faithful to their

374   first wintering region, but this assumption has remained untested over a long period and

375   requires the control of winter weather conditions (i.e. year effect) in the assessment of fidelity

376   to a wintering region. Since relatively mild winters occurred in France over our study period

377   (see more information in Touzalin, 2017), we cannot rule out that harsh weather conditions

378   would have significant consequences on tactic fidelity and the other biological parameters of

379   interest we studied. In accordance with the absence of harsh winters during the study period,

380   the year effect was not retained in the model selection.

381   Fidelity to the first wintering site (conditional on fidelity to the first tactic) was

382   remarkably high, as found in German pied avocets (Hötker, 1998). Site fidelity over

383   successive winters is also commonly reported in other shorebirds (e.g. Burton & Evans, 1997;

384   Colwell, 2010; Buchanan et al., 2012; Lourenço et al., 2016; Murphy, Virzi, & Sanders,

385   2017). The high fidelity to a wintering site may indicate that experience-related knowledge of

386   wintering grounds (e.g. the amount of food resources, the level of disturbance, the predation

387   risk) is important for individuals, as suggested in sanderlings (*Calidris alba*; Lourenço et al.,

388   2016). This interpretation highlights the advantages of site familiarity in winter, much more

389   commonly admitted during breeding (Greenwood, 1980; Brown & Bomberger Brown, 1996;

390   Yoder, Marschall, & Swanson, 2004; Brown, Brown, & Brazeal, 2008). Further investigations

391   are therefore required to test whether site fidelity and consequently tactic fidelity are triggered

392   by wintering habitat suitability and predictability (as notably proposed by Robertson &

393   Cooke, 1999), and whether site familiarity significantly influences certain fitness components

394   of individuals.

395   Tactic changes mainly resulted in wintering on the French Atlantic coast. This result is

396   consistent with the mild conditions described above in the French wintering area over the

397   study period, which limited the need to adopt a migrant behaviour to cope with wintering

398   conditions. Furthermore, given the high tactic-fidelity rate over consecutive years, tactic-

399   change events were relatively limited at the individual scale for most of the birds; they may be

400   partly linked to the shift to the mate's wintering site as suggested in the greenland white-

401   fronted goose (*Anser albifrons flavirostris*; Marchi et al., 2010). The pied avocet is indeed a

402   monogamous mating species in which pairing may likely last for more than one season

403   (Cramp & Simmons, 1983; Chambon et al., unpublished data), making this hypothesis

404   plausible.

405   The survival estimate was particularly high (≥ 0.90) and did not differ among

406   wintering tactics (i.e. the tactic effect was not retained by the model selection). These values

407   are consistent with the high life expectancy of the species (Cramp & Simmons, 1983; personal

408   obs.). Furthermore, survival can be viewed as a proxy of wintering site quality (Peach, Baillie,

409   & Underhill, 1991; Schaub, Kania, & Köppen, 2005). In this case, most of the wintering sites

410   in France and in the Iberian Peninsula that hosted pied avocets over the study period can be

411   qualified as suitable. Lok, Overdijk, Tinbergen, & Piersma (2011) and Sanz-Aguilar et al.

412   (2012) reached the same conclusion based on high survival estimates for spoonbills (*Platalea*

413   *leucorodia leucorodia*), and greater flamingos, respectively, which also winter in Iberian sites.

414   The absence of harsh winters during the study period may explain both the high survival

415   estimates and the fact that year effect was not retained in the model selection related to the

416   survival parameter. In accordance with this explanation, Sanz-Aguilar et al. (2012) showed

417   that punctual harsh winters may strongly affect bird survival.

418   To conclude, based on a 10-year ringing study, we showed very high fidelity of pied

419   avocets to their first-wintering tactic (SR, LR, or M), slightly influenced by age. Even if

420   flexibility in tactic fidelity at the individual level was limited, it supports the facultative partial

421   migration hypothesis (Lundberg, 1987; Chapman, Brönmark, Nilsson, & Hansson, 2011;

422   Alcock, 2013). Moreover, in a companion study (Chambon et al., 2018), we highlighted the

423   combined influence of context-dependent (natal colony as a proxy of habitat quality in winter,

424   and hatching date) and intrinsic (body condition) variables on the probability for first-year

425   pied avocets to exhibit one of the three wintering tactics in their first winter; this also supports

426   the hypothesis of facultative partial migration. We also assume that individual behavioural

427   flexibility would be higher under harsher wintering conditions. Additional factors known to

428   influence the choice of the wintering tactic, and ultimately tactic fidelity throughout the birds'

429   lifetime (e.g. density-dependence, immune function, personality: Chapman, Brönmark,

430   Nilsson, & Hansson, 2011; Vélez-Espino, McLaughlin, & Robillard, 2013; Hegemann, Marra,

431   & Tieleman, 2015) could play a role in the case of pied avocets. Investigating the relative

432   importance of possible genetic factors would be of interest. The threshold model of migration

433   advocates that (i) the mechanisms involved in the control of partial migration imply a genetic

434   basis, and (ii) that environmental factors may modify the threshold that determines whether

435   the genetic predisposition to migrate is expressed or not (Pulido, 2011). For instance,

436   assessing whether only migrant birds physiologically prepare for migration (e.g. levels of

437   baseline corticosterone; Fudickar et al., 2013) would be an interesting perspective in this

438   context.

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Appendix 1

Multisite Capture-Recapture Modelling Process

645 The elementary probability matrices (*IS*: initial state probabilities – the probability for an

646 individual observed for the first time to adopt one of the three wintering tactics, *S*: survival, *F*:

647 tactic fidelity, *C*: tactic change, and *R*: re-sighting) were defined in E-SURGE programme

648 (GEPAT module) version 2.1.3 as described below to build the different models to be tested.

649 Respectively, 'Fi' and 'Le' mean fidelity to a given tactic and leaving the focal tactic. The

650 'dead' state and 'not seen' event are represented by † and 0, respectively. Estimates are

651 represented by letters within the matrices (I, S, C, T and R), and complements (1 minus

652 estimate) are represented by *.

	SR	LR	M
IS =	I	I	*

	SR	LR	M	†
SR	S	-	-	*
LR	-	S	-	*
S = M	-	-	S	*
†	-	-	-	*

	FiSR	LeSR	FiLR	LeLR	FiM	LeM	†
SR	F	*	-	-	-	-	-
LR	-	-	F	*	-	-	-
F = M	-	-	-	-	F	*	-
†	-	-	-	-	-	-	*

	SR	LR	M	†
FiSR	*	-	-	-
LeSR	-	C	*	-
FiLR	-	*	-	-
C = LeLR	*	-	C	-
FiM	-	-	*	-
LeM	C	*	-	-
†	-	-	-	*

$$R = \begin{array}{c|cccc} & 0 & SR & LR & M \\ SR & * & R & - & - \\ LR & * & - & R & - \\ M & * & - & - & R \\ \dagger & * & - & - & - \end{array}$$

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654   Table A1, A2 and A3 summed up the results of the goodness-of-fit test of the initial model,

655   the complete list of structures tested on each parameter of interest (survival, tactic fidelity and

656   tactic change), and the results of the model selection at each step of the modelling procedure,

657   respectively.

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670 **Appendix 2**

671 *Site Fidelity Index*

672 We investigated site fidelity since the first winter of the birds, conditional on fidelity to the

673 first wintering tactic. Site fidelity was estimated independently for the locally resident (LR)

674 and migrant (M) tactics. For this purpose, we only selected the occasions for which re-

675 sightings matched the first tactic of the birds. For each bird, we calculated a site-fidelity index

676 (SFI), as described in Catry et al. (2012):

$$SFI = 1 - \frac{ni - 1}{n - 1} \times \frac{pi}{oi - 1}$$

677   This index, ranging from 0 (no fidelity) to 1 (complete fidelity), takes into account the

678 number of sites (ni) used by individual i, the total number of surveyed sites (n), the number

679 of site change (pi) performed by individual i and the total number of sightings (oi) of

680 individual i. In our case, for each bird qualified as LR in its first winter, n was set to 11 (i.e.

681 the 12 French wintering sites involved in the present study minus one site – natal site –

682 corresponding to the strictly resident tactic for each bird; Fig. 1a), and oi was the total number

683 of occasions that matched the LR tactic. For each bird qualified as M in its first winter, n was

684 set to 6 (i.e. the 6 Iberian wintering sites involved in the present study; Fig. 1b), and oi was

685 the total number of occasions that matched the M tactic. The SFI was calculated for 163 and

686 27 birds displaying a LR or M tactic as first wintering behaviour, respectively. Lastly, oi

687 ranged from 2 to 9 (with a median value of 3), and systematically included the first occasion

688 (winter).

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691   **TABLES**

692   **Table 1.** Summary of the individual encounter histories of the pied avocets studied ($N = 558$)
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Tactic	1st Winter	Subsequent Winters					
		Re-Sighted				Non-Resighted	
		SR	LR	M	Multiple	Alive	NA
SR	212	99	34	2	14	53	10
LR	279	29	142	2	11	81	14
M	67	3	1	24	3	30	6

694
695   The table should be read as follows: from the 212 birds exhibiting a strictly resident wintering
696   behaviour (SR: wintering in the natal site) in their first winter, 99 kept the same behaviour, 34
697   changed to a locally resident behaviour (LR: wintering in another French Atlantic site; at a
698   variable age), 2 changed to a migrant behaviour (M: wintering in the Iberian Peninsula; also at
699   a variable age), and 14 exhibited variable wintering behaviours (called ´Multiple´) throughout
700   their individual encounter history. For the rest of the birds adopting a SR behaviour in their
701   first winter, 53 were subsequently re-sighted in the breeding and post-nuptial periods
702   (therefore considered as alive after the first winter), and 10 were never re-sighted irrespective
703   of the period of the annual cycle (´NA´). Consequently, true survival rate related to the first
704   winter for SR birds was close to 0.95.
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717 **Table 2.** Model selection at each step of the modelling procedure from E-SURGE programme
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Parameter	Structure	k	Deviance	QAICc	ΔQAICc	Akaike Weight
S	a(1)+a(2:10)	93	4 574.52	3 717.78	0.00	0.71
S	a(1)+a(2:10).f(1 2,3)	94	4 575.24	3 720.63	2.85	0.17
S	a(1)+a(2:10).f	95	4 573.22	3 721.36	3.58	0.12
F	a(1).f+a(2:10).f.Tactic	75	4 582.09	3 683.00	0.00	0.80
F	f	66	4 614.13	3 687.74	4.74	0.07
F	a(1,2,3:10).f	72	4 597.20	3 687.96	4.96	0.07
F	a(1,2:10).f	69	4 607.65	3 689.36	6.36	0.03
C	f.to	48	4 600.76	3 638.41	0.00	0.63
C	a(1,2:10).f.to	51	4 595.36	3 640.70	2.28	0.20
C	a(1,2,3:10).f.to	54	4 588.11	3 641.58	3.17	0.13
C	a(1,2,3,4:10).f.to	57	4 583.31	3 644.38	5.97	0.03
C	a(1).f.to+a(2:10).f.to.Tactic	57	4 586.59	3 646.90	8.49	0.01

719
720 Step 1: survival parameter (*S*), step 2: tactic-fidelity parameter (*F*), and step 3: tactic-change
721 parameter (*C*). For each parameter, only structures with ΔQAICc < 10 were reported in the
722 table. The description of the E-SURGE language used to build the different structures, and the
723 complete list of structures tested are available in Appendix 1.
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Table A1. Results of the different subcomponents of goodness-of-fit (GOF) test of the Jolly Move (JMV) model, using U-CARE programme (version 2.3.4)

Test	χ^2	p	df	ĉ
WBWA	43.82	0.00	16	2.74
3G.SR	-	-	-	-
3G.SM	62.47	0.83	74	0.84
M.ITEC	26.08	0.02	13	2.01
M.LTEC	9.24	0.16	6	1.54
Global test*	141.61		109	1.30

735
736 The 3G.SR subcomponent was removed to adjust the global
737 level of overdispersion (ĉ of the Global test*) in accordance
738 with the *S* structure of the initial model used in the model
739 selection procedure. The meanings of all subcomponents are
740 described in Choquet et al. (2005) and Pradel, Gimenez, &
741 Lebreton (2005).
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755 **Table A2.** List of all the different structures tested on survival (S, step1), tactic-fidelity
756 (F, step 2) and tactic-change (C, step 3) parameters

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S structures (step 1)	F structures (step 2)	C structures (step 3)
a(1)+a(2:10).f.t	f.t	f.to.t
a(1)+a(2:10).f(1 2,3).t	a(1,2:10).f.t	a(1,2:10).f.to.t
a(1)+a(2:10).f	a(1,2,3:10).f.t	a(1,2,3:10).f.to.t
a(1)+a(2:10).f(1 2,3)	a(1,2,3,4:10).f.t	a(1,2,3,4:10).f.to.t
a(1)+a(2:10).t	a(1).f.t+a(2:10).f.Tactic.t	a(1).f.to.t+a(2:10).f.to.Tactic.t
a(1)+a(2:10)	a(1).f.t+a(2,3:10).f.Tactic.t	a(1).f.to.t+a(2,3:10).f.to.Tactic.t
	a(1).f.t+a(2,3,4:10).f.Tactic.t	a(1).f.to.t+a(2,3,4:10).f.to.Tactic.t
	f	f.to
	a(1,2:10).f	a(1,2:10).f.to
	a(1,2,3:10).f	a(1,2,3:10).f.to
	a(1,2,3,4:10).f	a(1,2,3,4:10).f.to
	a(1).f+a(2:10).f.Tactic	a(1).f.to+a(2:10).f.to.Tactic
	a(1).f+a(2,3:10).f.Tactic	a(1).f.to+a(2,3:10).f.to.Tactic
	a(1).f+a(2,3,4:10).f.Tactic	a(1).f.to+a(2,3,4:10).f.to.Tactic
	t	
	a(1,2:10).t	
	a(1,2,3:10).t	
	a(1,2,3,4:10).t	
	a(1,2:10)	
	a(1,2,3:10)	
	a(1,2,3,4:10)	

758 The structures follow the language used in the GEMACO module of E-SURGE
759 programme. *IS* was typically allowed to vary among tactics ('to'), and *R* was allowed to
760 differ among tactics ('f') and years ('t'). For instance, the three-age-classes variable
761 distinguishing tactic fidelity or tactic change for second-, third- and >third-winter birds
762 was coded 'a(1,2,3:10)' (10 'year old' being the older age allowed by our study period;
763 'a(1,2,3:10)' equivalent to 'a(1)+a(2)+a(3:10)', and for instance 'a(1,2,3:10).f' equivalent
764 to 'a(1).f+a(2).f+a(3:10).f',). In steps 2 and 3, 'Tactic' referred to the tactic displayed by
765 birds in their first winter (group covariate). For *C* structure, the site variable involved a
766 variation of the probability of adopting a given tactic between the two possible other
767 ones, according to the tactic abandoned ('f.to'). The structures of the first line
768 corresponded to the initial model: $S_{a(1)+a(2:10).f.t}$ $F_{f.t}$ $C_{f.to.t}$ $R_{f.t}$

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Table A3. Details of the model selection result at each step of the modelling procedure from E-SURGE programme

Parameter	Structure	k	Deviance	QAICc	ΔQAICc	Akaike Weight
S	**a(1)+a(2:10)**	**93**	**4 574.52**	**3 717.78**	**0.00**	**0.71**
S	a(1)+a(2:10).f(1 2,3)	94	4 575.24	3 720.63	2.85	0.17
S	a(1)+a(2:10).f	95	4 573.22	3 721.36	3.58	0.12
S	a(1)+a(2:10).t	101	4 566.34	3 729.89	12.11	0.00
S	a(1)+a(2:10).f(1 2,3).t	110	4 561.49	3 747.12	29.34	0.00
S	a(1)+a(2:10).f.t	119	4 553.68	3 762.35	44.57	0.00
F	**a(1).f+a(2:10).f.Tactic**	**75**	**4 582.09**	**3 683.00**	**0.00**	**0.80**
F	f	66	4 614.13	3 687.74	4.74	0.07
F	a(1,2,3:10).f	72	4 597.20	3 687.96	4.96	0.07
F	a(1,2:10).f	69	4 607.65	3 689.36	6.36	0.03
F	a(1,2,3,4:10).f	75	4 592.69	3 691.16	8.16	0.01
F	a(1,2:10)	65	4 623.09	3 692.43	9.43	0.01
F	a(1,2,3:10)	66	4 620.44	3 692.59	9.59	0.01
F	a(1,2,3,4:10)	67	4 620.31	3 694.70	11.70	0.00
F	a(1).f+a(2,3:10).f.Tactic	84	4 578.06	3 700.07	17.07	0.00
F	a(1).f+a(2,3,4:10).f.Tactic	93	4 553.59	3 701.69	18.69	0.00
F	t	73	4 613.15	3 702.45	19.45	0.00
F	a(1).f.t+a(2:10).f.Tactic.t	102	4 545.54	3 716.20	33.20	0.00
F	f.t	93	4 574.52	3 717.78	34.78	0.00
F	a(1,2:10).t	82	4 608.13	3 718.69	35.69	0.00
F	a(1).f.t+a(2,3:10).f.Tactic.t	111	4 530.75	3 725.82	42.82	0.00
F	a(1,2,3:10).t	90	4 597.74	3 728.81	45.81	0.00
F	a(1).f.t+a(2,3,4:10).f.Tactic.t	120	4 530.46	3 746.87	63.87	0.00
F	a(1,2:10).f.t	120	4 535.63	3 750.85	67.85	0.00
F	a(1,2,3:10).f.t	144	4 505.92	3 786.16	103.16	0.00
F	a(1,2,3,4:10).t	97	4 672.36	3 802.22	119.22	0.00
F	a(1,2,3,4:10).f.t	165	4 482.58	3 820.90	137.90	0.00

Table A3. (continued)

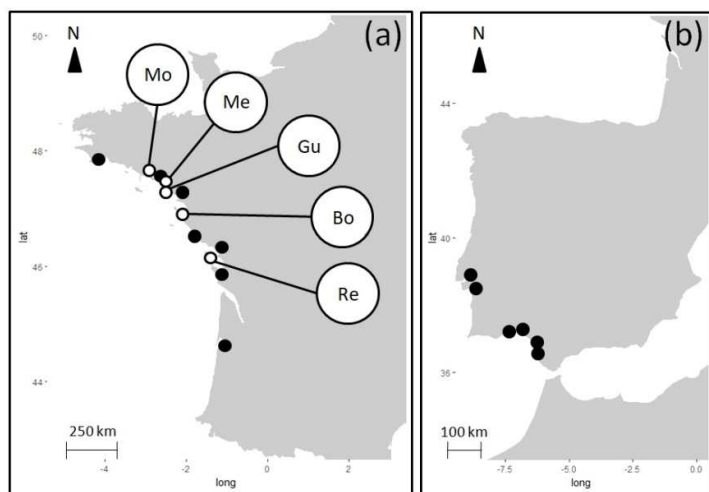| Parameter	Structure	k	Deviance	QAICc	ΔQAICc	Akaike Weight
C	**f.to**	**48**	**4 600.76**	**3 638.41**	**0.00**	**0.63**
C	a(1,2:10).f.to	51	4 595.36	3 640.70	2.28	0.20
C	a(1,2,3:10).f.to	54	4 588.11	3 641.58	3.17	0.13
C	a(1,2,3,4:10).f.to	57	4 583.31	3 644.38	5.97	0.03
C	a(1).f.to+a(2:10).f.to.Tactic	57	4 586.59	3 646.90	8.49	0.01
C	a(1).f.to+a(2,3:10).f.to.Tactic	66	4 574.61	3 657.34	18.93	0.00
C	a(1).f.to+a(2,3,4:10).f.to.Tactic	75	4 563.43	3 668.65	30.23	0.00
C	f.to.t	75	4 581.91	3 682.86	44.45	0.00
C	a(1,2:10).f.to.t	102	4 554.90	3 723.40	84.99	0.00
C	a(1,2,3:10).f.to.t	126	4 542.09	3 770.16	131.75	0.00
C	a(1).f.to.t+a(2:10).f.to.Tactic.t	140	4 527.75	3 793.12	154.70	0.00
C	a(1,2,3,4:10).f.to.t	147	4 530.28	3 812.33	173.92	0.00
C	a(1).f.to.t+a(2,3:10).f.to.Tactic.t	187	4 510.86	3 899.74	261.33	0.00
C	a(1).f.to.t+a(2,3,4:10).f.to.Tactic.t	220	4 496.91	3 978.48	340.06	0.00

Step 1: survival parameter (*S*), step 2: tactic-fidelity parameter (*F*), and step 3: tactic-change parameter (*C*). The model corresponding to the most competitive structure for each parameter of interest is in bold. Each model was run three times with different initial parameter values to ensure convergence to the lowest deviance (Lebreton & Pradel, 2002). Overall, the best model can be written as follows: $S_{a(1)+a(2:10)}$ $F_{a(1).f+a(2:10).f.Tactic}$ $C_{f.to}$ $R_{f.t}$

FIGURE LEGENDS

794

795 **Figure 1.** Location of the wintering sites used by the 558 ringed pied avocets of the study: (a)

796 the 12 French sites used by resident birds (following decreasing latitudes: the Ria of Pont

797 l'Abbé, the Gulf of Morbihan – Mo, the Estuary of la Vilaine and Pénerf, the marshes of

798 Mesquer – Me, the marshes of Guérande – Gu, the Loire Estuary, the Bay of Bourgneuf – Bo,

799 the marshes of Olonne, the Bay of Aiguillon, the island of Ré – Re, the marshes of Moëze-

800 Oléron, and the Arcachon Bay), including the five colony sites (empty circles) from the birds

801 originated, and (b) the 6 sites used by migrant individuals in the Iberian Peninsula (following

802 the coast from North to South: the Tagus Estuary, the Sado Estuary, the marshes of Tavira,

803 the marshes of Odiel, the marshes of the Guadalquivir river, the Bay of Cádiz).

804

805 **Figure 2.** Estimates (± SE) of fidelity to: (a) the first wintering tactic displayed by pied

806 avocets between their first and second winters (second-winter birds), then (b) the SR (strictly

807 resident), (c) the LR (locally resident), and (d) the M (migrant) tactics between two

808 consecutive winters in older birds (>second-winter birds) in relation to the wintering tactic

809 adopted during their first winter. Grey circles represent the estimate obtained when the focal

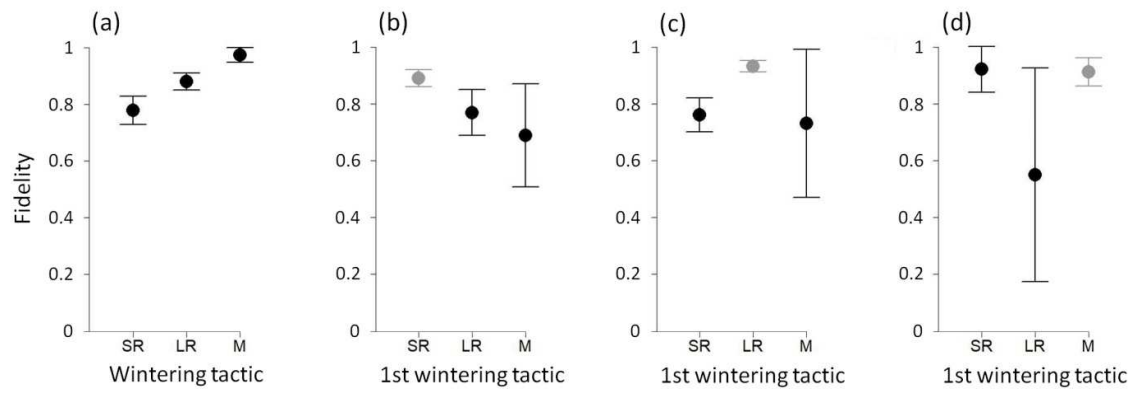810 tactic matched with the first wintering tactic of the birds.

811

812 **Figure 3.** Estimate (± SE when available) of each tactic-change probability between two

813 wintering tactics (arrows), conditional on infidelity to a given tactic (grey circles) in two

814 consecutive winters: (a) from the strictly resident tactic (SR), (b) from the locally resident
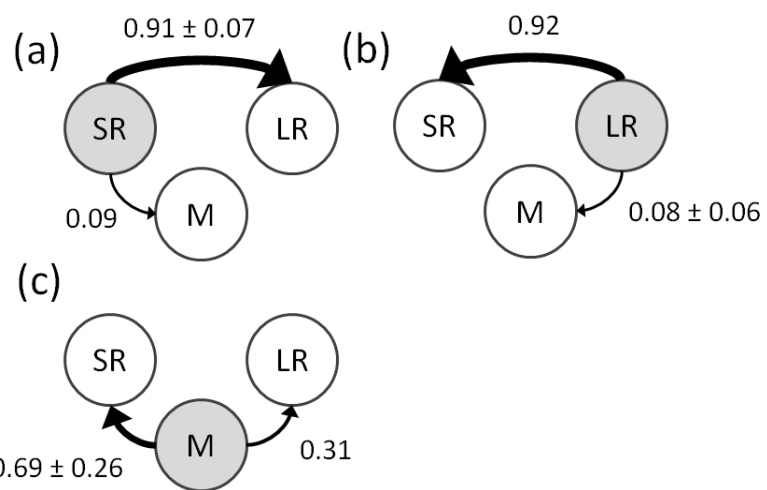
815 tactic (LR), and (c) from the migrant tactic (M).

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817

Figure 1.

[1.5-column fitting image]

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829   **Figure 2.**

830   *[2-column fitting image]*

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(a)

0.91 ± 0.07

SR   LR

0.09   M

(b)

0.92

SR   LR

M   0.08 ± 0.06

(c)

SR   LR

M

0.69 ± 0.26   0.31

Figure 3.

[1.5-column fitting image]