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

3

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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 ( $\geq 0.90$ ) 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 ('strictly resident tactic', 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 ('locally resident tactic', LR), or (iii) reaching farther  
116 wintering quarters, mainly in the Iberian Peninsula, through migration ('migrant tactic', 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 tibiotarsi (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 20<sup>th</sup> December  
153 to 25<sup>th</sup> February were defined as resident birds, and individuals re-sighted from 1<sup>st</sup> November  
154 to 31<sup>st</sup> 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. 15<sup>th</sup> 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 ( $\hat{c}$ ) 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,  $\pm$  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 ('Centre de Recherches sur la Biologie des Populations d'Oiseaux – C.R.B.P.O.' from the  
270 French 'Muséum 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):  $S_{a(1)+a(2:10)} F_{a(1),f+a(2:10),f,Tactic} C_{f,to} R_{f,t}$

284 *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  $0.90 \pm 0.01$   
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 ( $0.98 \pm 0.02$ ), intermediate  
289 for LR birds ( $0.88 \pm 0.03$ ), and the lowest for SR birds ( $0.78 \pm 0.05$ ; 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 ( $0.91 \pm 0.05$ ). 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):  $0.96 \pm 0.01$  for LR birds ( $N =$   
306  $163$ ), and  $0.96 \pm 0.01$  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).

## 310 **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 ( $\geq 0.90$ ) 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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643 **Appendix 1**

644 *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 \*.

$$IS = \begin{matrix} & SR & LR & M \\ I & I & I & * \end{matrix}$$

$$S = \begin{matrix} & & SR & LR & M & † \\ SR & S & - & - & - & * \\ LR & - & S & - & - & * \\ M & - & - & S & - & * \\ † & - & - & - & - & * \end{matrix}$$

$$F = \begin{matrix} & & FiSR & LeSR & FiLR & LeLR & FiM & LeM & † \\ SR & F & * & - & - & - & - & - & - \\ LR & - & - & - & F & * & - & - & - \\ M & - & - & - & - & - & F & * & - \\ † & - & - & - & - & - & - & - & * \end{matrix}$$

$$C = \begin{matrix} & & SR & LR & M & † \\ FiSR & * & - & - & - & - \\ LeSR & - & C & * & - & - \\ FiLR & - & * & - & - & - \\ LeLR & * & - & C & - & - \\ FiM & - & - & * & - & - \\ LeM & C & * & - & - & - \\ † & - & - & - & - & * \end{matrix}$$

			0	SR	LR	M
		SR	*	R	-	-
		LR	*	-	R	-
R	=	M	*	-	-	R
		†	*	-	-	-

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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

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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	$\Delta$ QAICc	Akaike Weight
<i>S</i>	a(1)+a(2:10)	93	4 574.52	3 717.78	0.00	0.71
<i>S</i>	a(1)+a(2:10).f(1 2,3)	94	4 575.24	3 720.63	2.85	0.17
<i>S</i>	a(1)+a(2:10).f	95	4 573.22	3 721.36	3.58	0.12
<i>F</i>	a(1).f+a(2:10).f.Tactic	75	4 582.09	3 683.00	0.00	0.80
<i>F</i>	f	66	4 614.13	3 687.74	4.74	0.07
<i>F</i>	a(1,2,3:10).f	72	4 597.20	3 687.96	4.96	0.07
<i>F</i>	a(1,2:10).f	69	4 607.65	3 689.36	6.36	0.03
<i>C</i>	f.to	48	4 600.76	3 638.41	0.00	0.63
<i>C</i>	a(1,2:10).f.to	51	4 595.36	3 640.70	2.28	0.20
<i>C</i>	a(1,2,3:10).f.to	54	4 588.11	3 641.58	3.17	0.13
<i>C</i>	a(1,2,3,4:10).f.to	57	4 583.31	3 644.38	5.97	0.03
<i>C</i>	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  $\Delta$ QAICc < 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	$\chi^2$	p	df	$\hat{c}$
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

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The 3G.SR subcomponent was removed to adjust the global level of overdispersion ( $\hat{c}$  of the Global test\*) in accordance with the *S* structure of the initial model used in the model selection procedure. The meanings of all subcomponents are described in Choquet et al. (2005) and Pradel, Gimenez, & 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	$\Delta$ QAICc	Akaike Weight
<i>S</i>	<b>a(1)+a(2:10)</b>	<b>93</b>	<b>4 574.52</b>	<b>3 717.78</b>	<b>0.00</b>	<b>0.71</b>
<i>S</i>	a(1)+a(2:10).f(1 2,3)	94	4 575.24	3 720.63	2.85	0.17
<i>S</i>	a(1)+a(2:10).f	95	4 573.22	3 721.36	3.58	0.12
<i>S</i>	a(1)+a(2:10).t	101	4 566.34	3 729.89	12.11	0.00
<i>S</i>	a(1)+a(2:10).f(1 2,3).t	110	4 561.49	3 747.12	29.34	0.00
<i>S</i>	a(1)+a(2:10).f.t	119	4 553.68	3 762.35	44.57	0.00
<i>F</i>	<b>a(1).f+a(2:10).f.Tactic</b>	<b>75</b>	<b>4 582.09</b>	<b>3 683.00</b>	<b>0.00</b>	<b>0.80</b>
<i>F</i>	f	66	4 614.13	3 687.74	4.74	0.07
<i>F</i>	a(1,2,3:10).f	72	4 597.20	3 687.96	4.96	0.07
<i>F</i>	a(1,2:10).f	69	4 607.65	3 689.36	6.36	0.03
<i>F</i>	a(1,2,3,4:10).f	75	4 592.69	3 691.16	8.16	0.01
<i>F</i>	a(1,2:10)	65	4 623.09	3 692.43	9.43	0.01
<i>F</i>	a(1,2,3:10)	66	4 620.44	3 692.59	9.59	0.01
<i>F</i>	a(1,2,3,4:10)	67	4 620.31	3 694.70	11.70	0.00
<i>F</i>	a(1).f+a(2,3:10).f.Tactic	84	4 578.06	3 700.07	17.07	0.00
<i>F</i>	a(1).f+a(2,3,4:10).f.Tactic	93	4 553.59	3 701.69	18.69	0.00
<i>F</i>	t	73	4 613.15	3 702.45	19.45	0.00
<i>F</i>	a(1).f.t+a(2:10).f.Tactic.t	102	4 545.54	3 716.20	33.20	0.00
<i>F</i>	f.t	93	4 574.52	3 717.78	34.78	0.00
<i>F</i>	a(1,2:10).t	82	4 608.13	3 718.69	35.69	0.00
<i>F</i>	a(1).f.t+a(2,3:10).f.Tactic.t	111	4 530.75	3 725.82	42.82	0.00
<i>F</i>	a(1,2,3:10).t	90	4 597.74	3 728.81	45.81	0.00
<i>F</i>	a(1).f.t+a(2,3,4:10).f.Tactic.t	120	4 530.46	3 746.87	63.87	0.00
<i>F</i>	a(1,2:10).f.t	120	4 535.63	3 750.85	67.85	0.00
<i>F</i>	a(1,2,3:10).f.t	144	4 505.92	3 786.16	103.16	0.00
<i>F</i>	a(1,2,3,4:10).t	97	4 672.36	3 802.22	119.22	0.00
<i>F</i>	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	$\Delta$ QAICc	Akaike Weight
<i>C</i>	<b>f.to</b>	<b>48</b>	<b>4 600.76</b>	<b>3 638.41</b>	<b>0.00</b>	<b>0.63</b>
<i>C</i>	a(1,2:10).f.to	51	4 595.36	3 640.70	2.28	0.20
<i>C</i>	a(1,2,3:10).f.to	54	4 588.11	3 641.58	3.17	0.13
<i>C</i>	a(1,2,3,4:10).f.to	57	4 583.31	3 644.38	5.97	0.03
<i>C</i>	a(1).f.to+a(2:10).f.to.Tactic	57	4 586.59	3 646.90	8.49	0.01
<i>C</i>	a(1).f.to+a(2,3:10).f.to.Tactic	66	4 574.61	3 657.34	18.93	0.00
<i>C</i>	a(1).f.to+a(2,3,4:10).f.to.Tactic	75	4 563.43	3 668.65	30.23	0.00
<i>C</i>	f.to.t	75	4 581.91	3 682.86	44.45	0.00
<i>C</i>	a(1,2:10).f.to.t	102	4 554.90	3 723.40	84.99	0.00
<i>C</i>	a(1,2,3:10).f.to.t	126	4 542.09	3 770.16	131.75	0.00
<i>C</i>	a(1).f.to.t+a(2:10).f.to.Tactic.t	140	4 527.75	3 793.12	154.70	0.00
<i>C</i>	a(1,2,3,4:10).f.to.t	147	4 530.28	3 812.33	173.92	0.00
<i>C</i>	a(1).f.to.t+a(2,3:10).f.to.Tactic.t	187	4 510.86	3 899.74	261.33	0.00
<i>C</i>	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

778 Step 1: survival parameter (*S*), step 2: tactic-fidelity parameter (*F*), and step 3: tactic-  
779 change parameter (*C*). The model corresponding to the most competitive structure for  
780 each parameter of interest is in bold. Each model was run three times with different initial  
781 parameter values to ensure convergence to the lowest deviance (Lebreton & Pradel,  
782 2002). Overall, the best model can be written as follows:  $S_{a(1)+a(2:10)} F_{a(1).f+a(2:10).f.Tactic} C_{f.to}$   
783  $R_{f,t}$   
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793 **FIGURE LEGENDS**

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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).

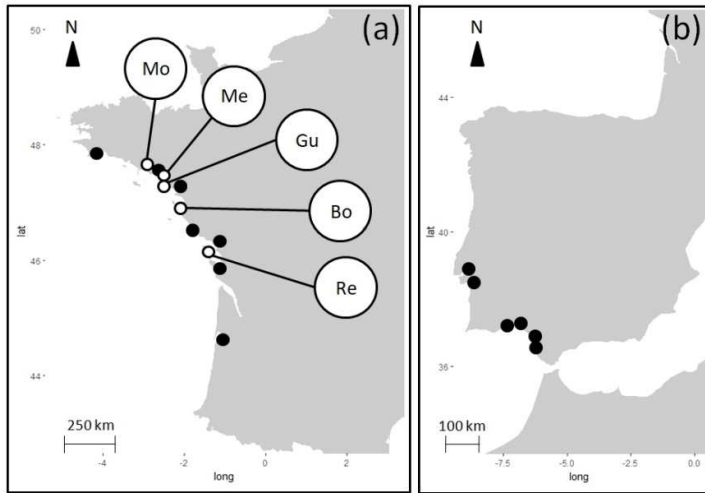
804

805 **Figure 2.** Estimates ( $\pm$  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.

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812 **Figure 3.** Estimate ( $\pm$  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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818 **Figure 1.**

819 *[1.5-column fitting image]*

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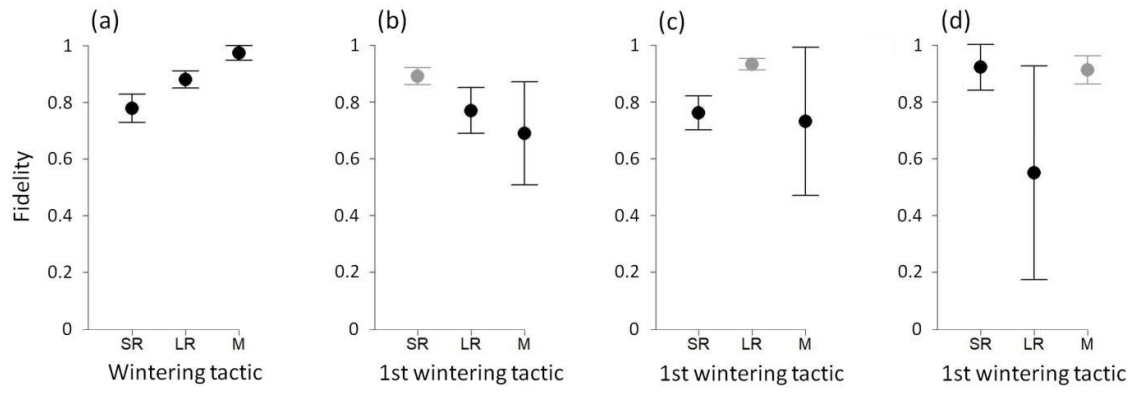
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829 **Figure 2.**

830 *[2-column fitting image]*

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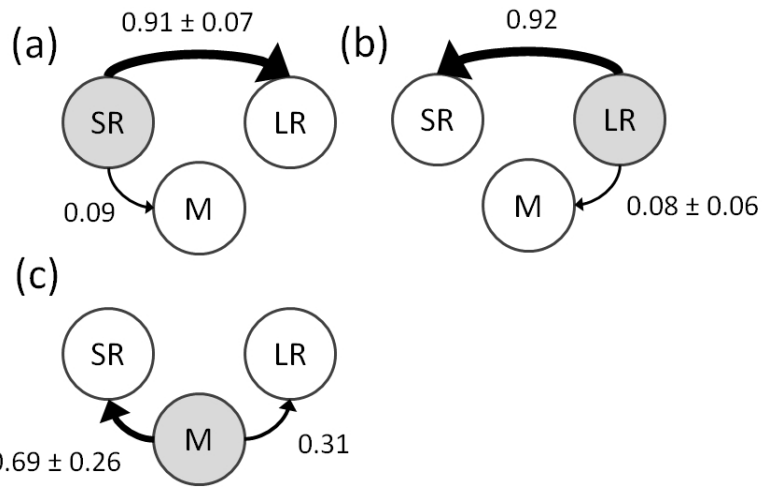
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840 **Figure 3.**

841 *[1.5-column fitting image]*