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**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.

43

44

45	KEYWORDS
46	Arrival-time hypothesis
47	Capture-recapture modelling
48	Dominance hypothesis
49	Facultative partial migration
50	Fidelity
51	Pied avocet
52	<i>Recurvirostra avosetta</i>
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,

1999; Marchi et al., 2010; Lok, Overdijk, Tinbergen, & Piersma, 2011). Several hypotheses have been suggested to explain age-differential migration in birds. The ‘dominance hypothesis’ assumes that migration constitutes the best option for subordinate young individuals to avoid the costs related to conspecific competition (notably resource requisition by more dominant adults; Gauthreaux, 1978; Townshend, 1985; Schwabl & Silverin, 1990). In return, young migrant birds have to cope with putative costs associated with migration (i.e. travel costs and conditions in wintering grounds; Lok, Overdijk, Tinbergen, & Piersma, 2011; Lok, Overdijk, & Piersma, 2015). As a result, the likelihood for a bird to migrate is expected to decrease with age. The ‘arrival-time hypothesis’ suggests that adults benefit from overwintering nearby breeding grounds (e.g. access to better quality mates and nesting places), and hence predicts a shift towards wintering closer to the breeding grounds with age until sexual maturity (Ketterson & Nolan, 1983). Such pattern is notably expected for territorial individuals (i.e. a sex-biased pattern). The predictions deriving from the two hypotheses mentioned above are very similar. In this context, the dominance would proximately influence the wintering behaviour (Gauthreaux 1982). More generally, quantifying the extent of flexibility of the wintering behaviour throughout the individuals’ lifetime and the study of the associated correlates constitute a relevant way to address the issue of the control of partial migration.

However, investigating partial migration at the individual scale over a long-term period represents a challenging field work because collecting individual data in large and distant wintering quarters is difficult and requires a huge amount of time. To date, only very few studies have focused on the issue of the flexibility of the wintering behaviour and on the related consequences (see for instance Sanz-Aguilar et al., 2012). In the present work, we specifically addressed these issues in the partially migrant French subpopulation of pied avocets, *Recurvirostra avosetta*. In a companion paper (Chambon et al., 2018), we found that

three wintering tactics coexist in first-year pied avocets from this subpopulation: (i) overwintering within the natal colony site ('strictly resident tactic', SR), (ii) overwintering in sites located at a relatively short distance from the natal colony (at few dozen kilometres) along the French Atlantic coast ('locally resident tactic', LR), or (iii) reaching farther wintering quarters, mainly in the Iberian Peninsula, through migration ('migrant tactic', M). In addition, we highlighted the influence of context-dependent and individual factors on the choice of the wintering tactic for first-year birds. Accordingly, we speculated the existence of facultative partial migration in this subpopulation.

The present study is based on a 10-year ringing survey involving field re-sightings data collected in Western Europe in winter. We addressed several issues related to partial migration in this shorebird species. We explored whether wintering tactics were fixed since the birds' first winter or were flexible throughout the birds' lifetime. We particularly investigated whether and how tactic fidelity and tactic change over consecutive winters were influenced by age. Under the two hypotheses described above, we predicted a strong decrease of fidelity to the migrant tactic with bird age in the early years of life. Additionally, we predicted similar high fidelity to the two resident tactics, irrespective of age, given the relatively short distance between natal sites (used by SR birds) and the other French wintering grounds (used by LR birds). We also tested whether the wintering tactic influenced individual survival. This parameter is considered as both a good indicator of wintering habitat suitability (Peach, Baillie, & Underhill, 1991; Schaub, Kania, & Köppen, 2005) and the most influential fitness component of population growth rates, as suggested in long-lived species (Crone, 2001).

METHODS

Data Collection and Selection

The birds originated from five of the major breeding colonies located along the French Atlantic coast (Fig. 1a): (i) the gulf of Morbihan, (ii) the marshes of Mesquer, (iii) the marshes of Guérande, (iv) the bay of Bourgneuf, including the island of Noirmoutier, and (v) the island of Ré. All details on the fieldwork, data selection, and bird categorisation in relation to their wintering tactic are provided in Chambon et al. (2018). In short, they were ringed as chicks with a unique combination of plastic colour-rings fixed on their two tibiotarsi (plus a metal ring from the French ringing scheme – C.R.B.P.O.), from 2006 to 2015. Given the lack of sexual dimorphism, the gender of chicks was not determined. Furthermore, the ‘arrival-time hypothesis’ could be tested on all birds, irrespective of the gender, since both members of a breeding pair actively prospect for nesting places, then build and defend the nest (males being not more territorial than females; Adret, 1983; Cramp & Simmons, 1983).

From winter 2006/2007 to winter 2016/2017, a large network of professional ornithologists and amateur bird-watchers routinely observed ringed pied avocets, in few typical coastal grounds used by the species (e.g. inter-tidal mudflats), across the Atlantic coast of Western Europe. The re-sighting effort during winter was considered as relatively more intensive in France (see Chambon et al., 2018 for more details). Based on our full database and given the range of migratory timing, individuals re-sighted in France from 20th December to 25th February were defined as resident birds, and individuals re-sighted from 1st November to 31st March in distant areas were considered as migrant birds (Chambon et al., 2018). In cases of multiple re-sightings per bird and year, the closest location to the middle of the wintering period (i.e. 15th January) was selected in order to attribute to each bird a single wintering location and tactic per year.

As we were notably interested in the long-term consistency of the first tactic, we only focused on individuals whose first tactic was known (Chambon et al., 2018). We discriminated between migrant birds wintering in the Iberian Peninsula and those wintering

northwest Europe because of putative differences in wintering conditions that might bias survival estimates. Nevertheless, owing to numerical issues, birds wintering in northwest Europe were excluded from the dataset (only 16 individuals re-sighted in northwest Europe during their first winter, and one individual re-sighted in northwest Europe as adult but not during its first winter). Ultimately, we analysed a re-sighting database of 558 ringed pied avocets that were re-sighted in their first winter, and for which 364 individuals were re-sighted in subsequent winters, totalling 889 additional bird-winters (see Table 1). Overall, resident and migrant birds were re-sighted in 12 distinct French sites and 6 Iberian sites, respectively (Fig. 1a, b).

Multisite Capture-Recapture Modelling

The re-sighting database was converted into individual encounter histories to perform capture-recapture (CR) analyses. Consequently, each year of the study period constituted an occasion. For each occasion and individual, it was specified whether the bird considered was re-sighted – with the attribution of its wintering tactic (coded as 1, 2 and 3 for SR, LR and M, respectively) – or not (coded as 0). For each individual, the first tactic mentioned in its encounter history referred to the tactic displayed during its first winter. In the CR analyses, the three tactics were considered as three different sites, and we therefore used a multisite (specific case of multistate) CR modelling approach (Arnason, 1973; Brownie et al., 1993; Schwarz, Schweigert, & Arnason, 1993). We particularly followed the method proposed by Grosbois & Tavecchia (2003), allowing the decomposition of a multi-step process expressed as the product of elementary probability matrices (see Appendix 1). Concretely, based on the individual encounter histories, this method allowed us to distinguish and to provide estimated probabilities of several parameters of interest for the present study: bird survival (S) from time i to $i + 1$, then conditional on survival, fidelity (F) to the wintering tactic adopted at time i between time i to $i + 1$, and conditional on infidelity ($1 - F$), tactic change (C) from time i to

time $i + 1$, while taking the re-sighting probability (R) into account. Therefore, all these parameters were estimated together for each pair of consecutive occasions in a multi-parameter CR model.

Each parameter can be modelled as a function of several variables (leading to different candidate functions per parameter, thereafter called 'structures'), allowing to explore different hypotheses through a model selection procedure. The initial model used in the model selection procedure was the Jolly Move (JMV) model that allows S , F , C , and R probabilities to vary with site (tactic in our case) and time (years). Based on our full re-sighting database, we noted that bird survival associated to the first tactic would be strongly underestimated by CR modelling because a fraction of the birds was never re-sighted during the subsequent winters while being still alive (Table 1). Moreover, even if the survival probability estimated by CR modelling should be considered as local (Lebreton, Burnham, Clobert, & Anderson, 1992), data exploration indicated that estimated survival would tend more to mirror true survival for birds re-sighted in subsequent winters. Accordingly, we allowed the S parameter of the initial model to also vary between two age classes: survival from the first to the second winter of birds, and survival between two consecutive winters since their second winter. This two-age-classes variable typically accounted for variation in survival between newly and previously encountered birds (transience effect; Choquet et al., 2005; Pradel, Gimenez, & Lebreton, 2005). Then, we tested the goodness-of-fit (GOF) of the initial model to ensure that it fitted well our CR data, using the U-CARE programme, version 2.3.4 (Choquet et al., 2005). We removed the 3G.SR subcomponent of the GOF tests (linked to the transience effect; see Pradel, Gimenez, & Lebreton, 2005 for details), and the adjusted level of overdispersion was 1.30 (see Appendix 1).

The modelling procedure consisted in testing different structures on S , F , and C to explore our biological hypotheses. Following Lok, Overdijk, Tinbergen, & Piersma (2011),

we divided our modelling procedure into three steps and based it on the initial model. In step 1, we kept *F* and *C* structures as they were in the initial model, and we tested several structures on *S* by comparing these structures and selecting the most competitive one. In step 2, we tested several structures on *F* while keeping the most competitive *S* structure from step 1, and keeping the *C* structure as in the initial model. Finally, we tested several structures on *C* in step 3 while keeping the most competitive *S* and *F* structures from the previous steps. We always maintained the *R* structure of the initial model to adjust the estimates of the other three parameters, according to potential variation in the observation effort. Furthermore, all the structures tested on *S* included the previously described two-age-classes variable. We fixed the survival value of the first age class to the unique rate of 0.93 (mean value when considering resident and migrant birds, tending towards true survival estimate; see Table 1). The effects of candidate variables on *S* were only tested on the second age class.

Concretely speaking, in step 1, we tested whether the *S* structure of the initial model was better supported when using a two-tactic categorisation (resident versus migrant) for the tactic variable, instead of the three tactics. If this structure was retained, it would indicate that survival was influenced by different wintering conditions between the French and Iberian areas. In addition, we tested the influence of tactic and year on survival by removing one of these two variables or both of them (keeping only the two-age-classes variable in this latter case) on all *S* structures tested. In step 2, to investigate variations in tactic fidelity with age, we tested whether the *F* structure of the initial model was better supported when tactic fidelity was additionally allowed to vary with a two-, three- or four- age-classes variable (i.e. distinguishing: second- and >second-winter birds; second-, third- and >third-winter birds; or second-, third-, fourth- and >fourth-winter birds, respectively). These different age classes rely on knowledge of the age of recruitment of pied avocets in the French subpopulation (from 1 to 3 years old; Watier & Fournier, 1980; Touzalin, 2017). We tested additional

structures by including the first tactic of the birds as a group covariate on the previous *F* structures (on all age classes except the first one), to assess the influence of the birds' first tactic on their fidelity to each tactic in the subsequent winters (e.g. higher fidelity rate in consecutive years to the first tactic in comparison to a newly displayed tactic). Once more, we tested the influence of tactic and year on tactic fidelity by removing one of these two variables or both of them (keeping only the age variable in this latter case) on all *F* structures tested. In step 3, we tested whether the *C* structure of the initial model was better supported when tactic change was additionally allowed to vary with a two-, three- or four-age-classes variable (as defined above). Then, we tested whether these structures were better supported when considering supplementary variation according to the birds' first tactic (group covariate for all age classes except the first one). The aim was to explore the preferential tactic change between two consecutive winters according to the birds' age and first tactic. Finally, we tested the influence of year on tactic change by removing this variable on all *C* structures. The complete list of structures tested for each parameter is provided in Appendix 1.

We used the E-SURGE programme, version 2.1.3 (Choquet, Rouan, & Pradel, 2009), to build the elementary probability matrices, and to build and compare the different structures tested on the *S*, *F*, and *C* parameters. For each parameter, the comparison of the different structures tested was performed using the quasi Akaike information criterion corrected for both overdispersion and small sample sizes (QAICc; Burnham & Anderson, 2002). The adjusted level of overdispersion ($\hat{c}$) from the GOF test was taken into account for the calculation of the QAICc. A model was considered to be more competitive than the others when its QAICc was at least two units lower. Final estimates of all parameters (means ranging from 0 to 1, $\pm$ SE when available) came from the model retained in step 3.

Since we suspected a large fraction of re-sighted birds to exhibit a high fidelity to the tactic displayed during their first winter, on the basis of data exploration (Table 1), we

complementarily assessed their fidelity to their first wintering site. It was performed on LR and M birds (see Catry et al., 2012; and Appendix 2 for more details on the calculation of the site-fidelity index).

Ethical Note

This paper is based on re-sightings of ringed wild birds. Capture, ringing, and observations were carried out with minimal disturbance (more details are available in Chambon et al., 2018). Permit for the research programme and ringing permits for ringers involved in the study were provided by the organisation managing birds' capture and ringing in France ('Centre de Recherches sur la Biologie des Populations d'Oiseaux – C.R.B.P.O.' from the French 'Muséum National d'Histoire Naturelle').

RESULTS

Final Multi-Parameter Model

The most competitive structure on survival supported in step 1 of the CR analyses only included a two-age-classes variable distinguishing survival between the first and second winters (fixed value), and survival between consecutive winters in older birds (Table 2, and see Appendix 1 for details on the model selection). Then, for the tactic-fidelity parameter (step 2), the largely most competitive structure considered different tactic-dependent fidelity probabilities for second-, and >second-winter birds in consecutive years, with a variation according to the tactic adopted during the first winter for this last age class (Table 2). For step 3, the most competitive structure considered different tactic-change probabilities according to the tactic abandoned and to the tactic subsequently adopted (Table 2). The resulting final multi-parameter model obtained was therefore (see Appendix 1 for details on the language 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 ± 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

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

DISCUSSION

Studying partial migration and more precisely the extent of flexibility of the wintering behaviour throughout the lifetime of individuals represents a great challenge. Nevertheless, this issue is of particular importance because animals, especially birds, must face global changes bound to increase in the future (e.g. Pearce-Higgins & Green, 2014). One additional key question is to identify the factors controlling partial migration. Addressing all these questions requires long-term data on the encounter history of marked individuals. The present work faced a typical difficulty in such a survey-based study, i.e. a low sample size for migrant birds (see Table 1). Even if interpretations should be made with caution in such circumstances, we are confident about our results concerning migrant birds overwintering in the Iberian Peninsula because they were relatively homogenous within this bird group. Furthermore, the number of re-sighted birds we studied resulted from the fact that we were interested in exploring the long-term consistency of the first wintering behaviour which forced us to only select individuals whose first wintering behaviour was known; but this number properly reflected the low proportion of French migrant birds wintering in the Iberian Peninsula (Chambon et al., 2018). To date, flexibility of the wintering behaviour over lifetimes has been extremely poorly documented in partially migrant birds (but see for instance Sanz-Aguilar et al., 2012).

The first major finding of the present study is that pied avocets originating from the French Atlantic subpopulation displayed high fidelity to their first wintering tactic over a long-term period. This result is consistent with the work of Sanz-Aguilar et al. (2012). These authors indeed found that wintering greater flamingos (*Phoenicopterus roseus*) were highly

faithful to their first wintering area (they wintered either in their French natal area, in the Iberian Peninsula, in Italy, or in Africa) across years. Such a result suggests that the first winter experienced by birds largely influences their wintering decisions in later life.

We also showed a moderate age effect on tactic fidelity when distinguishing second-winter and >second-winter birds. This effect varied among wintering tactics. Birds displaying a migrant tactic in their first winter were relatively less faithful to their first tactic beyond the second winter as compared to younger (second-winter) birds, unlike individuals that firstly displayed one of the two resident tactics. In addition, second-winter birds were more faithful to the migrant tactic than to the other two resident tactics. At first sight, these results tend to support the dominance hypothesis. Nevertheless, this hypothesis predicts that fidelity to the migrant tactic strongly decreases with age due to the subordinate status of young birds (Gauthreaux, 1978, 1982). Based on the relatively slight variation of fidelity to the migrant tactic with age, our findings do not really support this. Rejection of this hypothesis appears consistent with the low proportion of migrant birds in the French pied avocet subpopulation (12% of first wintering birds in the present study, and around 14% in Chambon et al., 2018), whereas we could expect it to be very high under the dominance hypothesis. In addition, the gregarious behaviour of wintering pied avocets (Cramp & Simmons, 1983), and the few agonistic interactions observed in winter highly contrast with what is outlined in the dominance hypothesis. Under the arrival hypothesis, immature individuals are assumed to shift towards wintering closer to breeding grounds (i.e. a strong decreasing fidelity to the migrant tactic) to take fitness advantages from arriving earlier in breeding grounds until sexual maturity (see Ketterson & Nolan, 1983), as suggested in the black-backed gull (*Larus fuscus*; Marques, Sowter, & Jorge, 2010), and in the greater flamingo (Sanz-Aguilar et al., 2012). However, our results do not support this prediction. The relatively low variation in fidelity to the migrant tactic with age in French pied avocets could be explained by the fact

that the costs linked to the migrant tactic probably do not affect individual reproductive success. Nevertheless, Hötker (1998, 2002) suggested that breeders from the strictly migrant German subpopulation of pied avocets would benefit from overwintering in closer areas to breeding grounds. Therefore, further investigations addressing seasonal interactions (e.g. the effects of wintering ground selection on the date of arrival at breeding sites and the related consequences on reproductive success; Lundberg, 1988, Norris & Marra, 2007; Gillis, Green, Middleton, & Morrissey, 2008) would be needed to investigate this point in our subpopulation.

Furthermore, winter conditions probably contributed to the high rates of tactic fidelity estimated across years. Winter weather conditions are known to modulate bird behaviour; harsh winters trigger bird migration in response to lower habitat suitability, notably in food availability (Lundberg, 1988; Newton, 2008). German and Danish pied avocets are more exposed to harsh wintering conditions than birds from regions located at lower latitudes; this factor probably forces them to display a strictly migrant pattern (Salvig, 1995; Hötker, 1998, 2002). In addition, Hötker (1998) showed that first-year German pied avocets mainly overwintered in France during mild winters, otherwise further south, in the Iberian Peninsula (Hötker, 1998). Hötker (1998) speculated that most birds were subsequently faithful to their first wintering region, but this assumption has remained untested over a long period and requires the control of winter weather conditions (i.e. year effect) in the assessment of fidelity to a wintering region. Since relatively mild winters occurred in France over our study period (see more information in Touzalin, 2017), we cannot rule out that harsh weather conditions would have significant consequences on tactic fidelity and the other biological parameters of interest we studied. In accordance with the absence of harsh winters during the study period, the year effect was not retained in the model selection.

Fidelity to the first wintering site (conditional on fidelity to the first tactic) was remarkably high, as found in German pied avocets (Hötter, 1998). Site fidelity over successive winters is also commonly reported in other shorebirds (e.g. Burton & Evans, 1997; Colwell, 2010; Buchanan et al., 2012; Lourenço et al., 2016; Murphy, Virzi, & Sanders, 2017). The high fidelity to a wintering site may indicate that experience-related knowledge of wintering grounds (e.g. the amount of food resources, the level of disturbance, the predation risk) is important for individuals, as suggested in sanderlings (*Calidris alba*; Lourenço et al., 2016). This interpretation highlights the advantages of site familiarity in winter, much more commonly admitted during breeding (Greenwood, 1980; Brown & Bomberger Brown, 1996; Yoder, Marschall, & Swanson, 2004; Brown, Brown, & Brazeal, 2008). Further investigations are therefore required to test whether site fidelity and consequently tactic fidelity are triggered by wintering habitat suitability and predictability (as notably proposed by Robertson & Cooke, 1999), and whether site familiarity significantly influences certain fitness components of individuals.

Tactic changes mainly resulted in wintering on the French Atlantic coast. This result is consistent with the mild conditions described above in the French wintering area over the study period, which limited the need to adopt a migrant behaviour to cope with wintering conditions. Furthermore, given the high tactic-fidelity rate over consecutive years, tactic-change events were relatively limited at the individual scale for most of the birds; they may be partly linked to the shift to the mate's wintering site as suggested in the greenland white-fronted goose (*Anser albifrons flavirostris*; Marchi et al., 2010). The pied avocet is indeed a monogamous mating species in which pairing may likely last for more than one season (Cramp & Simmons, 1983; Chambon et al., unpublished data), making this hypothesis plausible.

The survival estimate was particularly high (≥ 0.90) and did not differ among wintering tactics (i.e. the tactic effect was not retained by the model selection). These values are consistent with the high life expectancy of the species (Cramp & Simmons, 1983; personal obs.). Furthermore, survival can be viewed as a proxy of wintering site quality (Peach, Baillie, & Underhill, 1991; Schaub, Kania, & Köppen, 2005). In this case, most of the wintering sites in France and in the Iberian Peninsula that hosted pied avocets over the study period can be qualified as suitable. Lok, Overdijk, Tinbergen, & Piersma (2011) and Sanz-Aguilar et al. (2012) reached the same conclusion based on high survival estimates for spoonbills (*Platalea leucorodia leucorodia*), and greater flamingos, respectively, which also winter in Iberian sites. The absence of harsh winters during the study period may explain both the high survival estimates and the fact that year effect was not retained in the model selection related to the survival parameter. In accordance with this explanation, Sanz-Aguilar et al. (2012) showed that punctual harsh winters may strongly affect bird survival.

To conclude, based on a 10-year ringing study, we showed very high fidelity of pied avocets to their first-wintering tactic (SR, LR, or M), slightly influenced by age. Even if flexibility in tactic fidelity at the individual level was limited, it supports the facultative partial migration hypothesis (Lundberg, 1987; Chapman, Brönmark, Nilsson, & Hansson, 2011; Alcock, 2013). Moreover, in a companion study (Chambon et al., 2018), we highlighted the combined influence of context-dependent (natal colony as a proxy of habitat quality in winter, and hatching date) and intrinsic (body condition) variables on the probability for first-year pied avocets to exhibit one of the three wintering tactics in their first winter; this also supports the hypothesis of facultative partial migration. We also assume that individual behavioural flexibility would be higher under harsher wintering conditions. Additional factors known to influence the choice of the wintering tactic, and ultimately tactic fidelity throughout the birds' lifetime (e.g. density-dependence, immune function, personality: Chapman, Brönmark,

Nilsson, & Hansson, 2011; Vélez-Espino, McLaughlin, & Robillard, 2013; Hegemann, Marra, & Tieleman, 2015) could play a role in the case of pied avocets. Investigating the relative importance of possible genetic factors would be of interest. The threshold model of migration advocates that (i) the mechanisms involved in the control of partial migration imply a genetic basis, and (ii) that environmental factors may modify the threshold that determines whether the genetic predisposition to migrate is expressed or not (Pulido, 2011). For instance, assessing whether only migrant birds physiologically prepare for migration (e.g. levels of baseline corticosterone; Fudickar et al., 2013) would be an interesting perspective in this 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 *.

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

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

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

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

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

Table A1, A2 and A3 summed up the results of the goodness-of-fit test of the initial model, the complete list of structures tested on each parameter of interest (survival, tactic fidelity and tactic change), and the results of the model selection at each step of the modelling procedure, respectively.

Appendix 2

Site Fidelity Index

We investigated site fidelity since the first winter of the birds, conditional on fidelity to the first wintering tactic. Site fidelity was estimated independently for the locally resident (LR) and migrant (M) tactics. For this purpose, we only selected the occasions for which re-sightings matched the first tactic of the birds. For each bird, we calculated a site-fidelity index (SFI), as described in Catry et al. (2012):

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

This index, ranging from 0 (no fidelity) to 1 (complete fidelity), takes into account the number of sites (ni) used by individual i , the total number of surveyed sites (n), the number of site change (pi) performed by individual i and the total number of sightings (oi) of individual i . In our case, for each bird qualified as LR in its first winter, n was set to 11 (i.e. the 12 French wintering sites involved in the present study minus one site – natal site – corresponding to the strictly resident tactic for each bird; Fig. 1a), and oi was the total number of occasions that matched the LR tactic. For each bird qualified as M in its first winter, n was set to 6 (i.e. the 6 Iberian wintering sites involved in the present study; Fig. 1b), and oi was the total number of occasions that matched the M tactic. The SFI was calculated for 163 and 27 birds displaying a LR or M tactic as first wintering behaviour, respectively. Lastly, oi ranged from 2 to 9 (with a median value of 3), and systematically included the first occasion (winter).

TABLES

Table 1. Summary of the individual encounter histories of the pied avocets studied ($N = 558$)

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

The table should be read as follows: from the 212 birds exhibiting a strictly resident wintering behaviour (SR: wintering in the natal site) in their first winter, 99 kept the same behaviour, 34 changed to a locally resident behaviour (LR: wintering in another French Atlantic site; at a variable age), 2 changed to a migrant behaviour (M: wintering in the Iberian Peninsula; also at a variable age), and 14 exhibited variable wintering behaviours (called 'Multiple') throughout their individual encounter history. For the rest of the birds adopting a SR behaviour in their first winter, 53 were subsequently re-sighted in the breeding and post-nuptial periods (therefore considered as alive after the first winter), and 10 were never re-sighted irrespective of the period of the annual cycle ('NA'). Consequently, true survival rate related to the first winter for SR birds was close to 0.95.

Table 2. Model selection at each step of the modelling procedure from E-SURGE programme

Parameter	Structure	k	Deviance	QAICc	Δ 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

Step 1: survival parameter (*S*), step 2: tactic-fidelity parameter (*F*), and step 3: tactic-change parameter (*C*). For each parameter, only structures with Δ QAICc < 10 were reported in the table. The description of the E-SURGE language used to build the different structures, and the complete list of structures tested are available in Appendix 1.

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	$\hat{c}$
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

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).

Table A2. List of all the different structures tested on survival (*S*, step1), tactic-fidelity (*F*, step 2) and tactic-change (*C*, step 3) parameters

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)	

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

775 **Table A3.** Details of the model selection result at each step of the modelling procedure
776 from E-SURGE programme
777

Parameter	Structure	k	Deviance	QAICc	Δ QAICc	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

Figure 1. Location of the wintering sites used by the 558 ringed pied avocets of the study: (a) the 12 French sites used by resident birds (following decreasing latitudes: the Ria of Pont l'Abbé, the Gulf of Morbihan – Mo, the Estuary of la Vilaine and Pénérf, the marshes of Mesquer – Me, the marshes of Guérande – Gu, the Loire Estuary, the Bay of Bourgneuf – Bo, the marshes of Olonne, the Bay of Aiguillon, the island of Ré – Re, the marshes of Moëze-Oléron, and the Arcachon Bay), including the five colony sites (empty circles) from the birds originated, and (b) the 6 sites used by migrant individuals in the Iberian Peninsula (following the coast from North to South: the Tagus Estuary, the Sado Estuary, the marshes of Tavira, the marshes of Odiel, the marshes of the Guadalquivir river, the Bay of Cádiz).

Figure 2. Estimates ($\pm$ SE) of fidelity to: (a) the first wintering tactic displayed by pied avocets between their first and second winters (second-winter birds), then (b) the SR (strictly resident), (c) the LR (locally resident), and (d) the M (migrant) tactics between two consecutive winters in older birds ($>$ second-winter birds) in relation to the wintering tactic adopted during their first winter. Grey circles represent the estimate obtained when the focal tactic matched with the first wintering tactic of the birds.

Figure 3. Estimate ($\pm$ SE when available) of each tactic-change probability between two wintering tactics (arrows), conditional on infidelity to a given tactic (grey circles) in two consecutive winters: (a) from the strictly resident tactic (SR), (b) from the locally resident tactic (LR), and (c) from the migrant tactic (M).

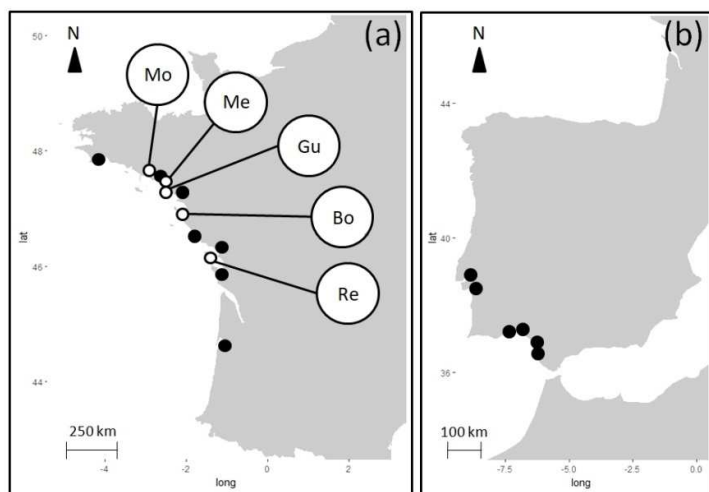


Figure 1.

[1.5-column fitting image]

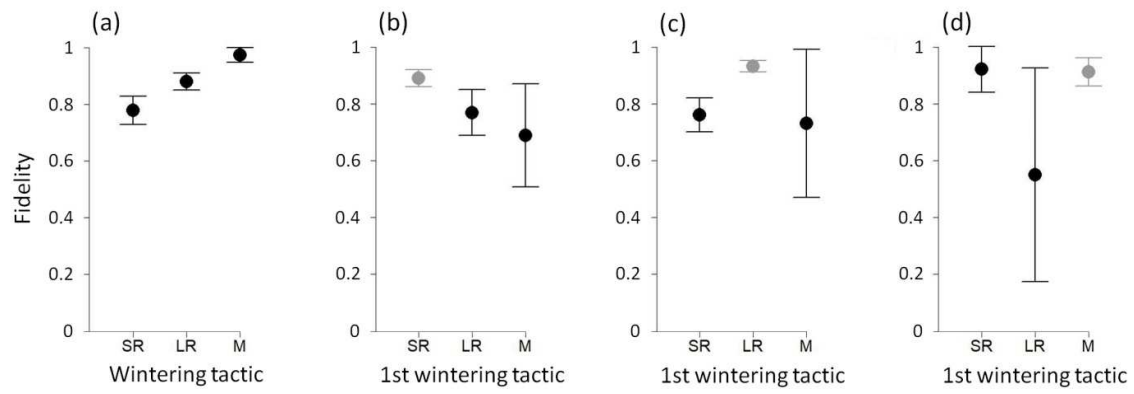


Figure 2.

[2-column fitting image]

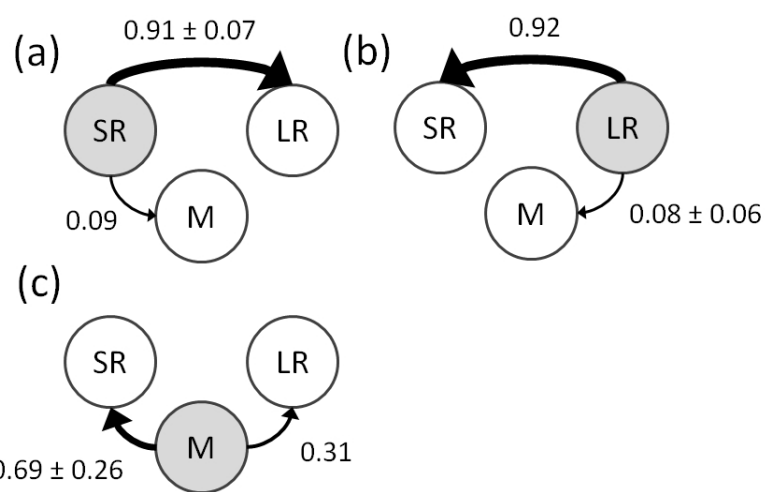


Figure 3.

[1.5-column fitting image]