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4 **Long-distance travellers stopover for longer: a case study with spoonbills staying in North Iberia**

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20 **Abstract** Long-distance migration is widespread among birds, connecting breeding and wintering areas
21 through a set of stopover localities where individuals refuel and/or rest. The extent of the stopover is critical in
22 determining the migratory strategy of a bird. Here, we examined the relationship between minimum length of
23 stay of PVC-ringed birds in a major stopover site and the remaining flight distance to overwintering area in
24 the Eurasian spoonbill (*Platalea l. leucorodia*) during four consecutive autumn migrations. We also analysed
25 the potential effect of timing (arrival date), as well as the role of experience in explaining stopover duration of
26 spoonbills. Overall, birds wintering in Africa, and facing a long-distance travel from the stopover site (ca.
27 3,000 km), stay for longer (2.7 ± 0.4 days) than Iberian winterers (1.5 ± 0.2 days) that perform a much shorter
28 migration (ca. 800 km). These differences were consistent between years. Stopover duration was not
29 significantly affected by the age of the bird. However there is a significant reduction as migration advanced.
30 Our results suggest that spoonbills develop different stopover strategies depending on the expected distance to
31 the wintering grounds. Adults, especially long-distance migratory ones, could reduce the potential negative
32 effects of density-dependence processes by avoiding stopover at the end of the migration period. These
33 findings are of significant relevance for understanding differences in migratory behaviour within single
34 populations, especially for declining waterbirds, as well as stress the relevance of preserving stopover
35 localities for the conservation of intraspecific diversity in migratory species.

36

37 **Keywords:** Experience · intraspecific competition · migratory strategies · spoonbill · stopover duration ·
38 timing.

39 **Introduction**

40

41 Many animals undertake seasonal movements from the breeding to the wintering grounds, which are regarded
42 primarily as an adaptation for exploiting the best conditions in food availability throughout the year (Alerstam
43 et al. 2003; Newton 2008). Long-distance migration is a costly process that consists in sequential movements
44 interrupted by stopovers for resting and/or refuelling, and is widespread in many animal groups such as
45 mammals, birds, fish and insects (Alerstam et al. 2003).

46 Migrating birds spend most of the time at stopover sites (Schaub et al. 2001), that are usually discrete and
47 far apart for many long-distance migratory species, especially waterbirds (Pennycuik and Battley 2003;
48 Battley et al. 2005; Gill et al. 2005; Piersma et al. 2005). Stopover duration is the most important factor
49 determining the total length of a migratory journey and the total amount of energy load (Alerstam et al. 2003).
50 Considering the energy-optimisation theory, individuals should stay in a stopover until enough fuel is stored
51 to reach the next stopover site, independently of the rate of fuel deposition (Alerstam and Lindström 1990;
52 Hedenström and Alerstam 1997). On the other hand, in the context of the time-minimisation theory,
53 individuals should be sensitive to the rate of fuel deposition, adjusting their departure fuel load to their fuel
54 deposition rate (Alerstam and Lindström 1990; Hedenström and Alerstam 1997). In terms of energy turnover
55 rate, associated costs may appear in the short- and/or long-term (Schmidt-Wellenburg 2007). Therefore,
56 timing and conditions experienced at stopover sites may affect not only the success of the migration, but also
57 the future individual reproduction and survival, with potential consequences for population dynamics (Newton
58 2006).

59 During migration, many bird species or populations with similar migratory patterns and/or trophic
60 requirements may use the same stopover sites to refuel and/or rest (Newton 2004). Density-dependent
61 processes may thus be promoted at stopovers, and interspecific and/or intraspecific competition could increase
62 (Alerstam and Hedenström 1998, Newton 2006). In this context, early arrival should be under high positive
63 selection since feeding resources may be fewer, or even depleted, when later birds arrive at a single stopover
64 (Newton 2006; Nolet et al. 2006). Therefore, experience accumulated along years/migrations could play a

65 significant role to achieve an optimal migration (Hedenström 2008), and allows the development of different
66 stopover strategies within a population (Scheiffarth et al. 2002; Drent et al. 2003). For long-lived migratory
67 birds, such as cranes and storks, experience (i.e. age of the birds) could be a sign of consistent migration
68 success (Berthold 2001). Accumulated experience may be crucial to achieve a ‘dominant competitive status’
69 to be able to outcompete conspecifics at stopover and/or wintering localities (Alerstam et al. 2003),
70 especially in species without apparent sexual dimorphism. Experienced birds should be able to reach required
71 fuel-loads faster than inexperienced ones, and thus reducing stopover duration (Newton 2008). Nevertheless,
72 to date, empirical data about ecological factors affecting stopover duration are scarce, and most frequently
73 involves a reduced number of individuals (Schaub et al. 2001; Salewski and Schaub 2007).

74 Decisions on the necessity for stopover and its duration may depend on the expected length of the
75 migratory bout (Schaub et al. 2001), but to the best of our knowledge no empirical studies have corroborated
76 this hypothesis. A previous study addressed this question, but looking at two different subspecies of the
77 Northern wheatear *Oenanthe oenanthe* (Dierschke and Delingat 2001) and potentially including some
78 confounding factors (i.e. differential ecological/energetic requirements between subspecies). Therefore, the
79 remaining distance to the wintering area has not been fully considered yet as a main factor explaining stopover
80 duration in birds. In this study, we examined the relationship between the length of stay at a major stopover
81 site in Northern Iberia and the overwintering area (Africa or South Iberia) in migrating Eurasian spoonbills
82 (*Platalea l. leucorodia*). We predicted that adult spoonbills travelling to overwinter in Africa will stopover for
83 longer in North Iberia than birds overwintering in South Iberia, and that experience (age) of the birds will play
84 a significant role in explaining stopover duration.

85

86 **Methods**

87

88 The Eurasian spoonbill (*Platalea l. leucorodia*) maintains a small breeding population in Western Europe
89 (4,800 pairs; Triplet et al. 2008), catalogued as “Rare” (BirdLife 2004). Less than 2,000 pairs breed in
90 northern latitudes, the so-called North-Atlantic population, most (1,600 pairs) in the Netherlands (Triplet et al.

91 2008; see Figure 1). These birds spend the winter in two distant geographic areas: about 20% of the birds in
92 the Iberian Peninsula, most of them in the Southwest (Lorenzo and De le Court 2007), and the rest of the
93 population in North-Western African wetlands, mainly Mauritania and Senegal (Bauchau et al. 1998; Figure
94 1). Around 35-40% of the North-Atlantic spoonbill population make a strategic stopover in the Santoña
95 Marshes Natural Park (43°30'N 3°30'W; Fig. 1) during autumn migration (Navedo 2006a), where ca. 80% of
96 these birds came from the Wadden Sea islands, 15% from inland Netherlands, and 5% from France (Navedo
97 2006a). On average, 90% of the spoonbills using Santoña make their stopover during September (Navedo
98 2006a).

99 Santoña marshes is an estuarine area located in the northern coast of the Iberian Peninsula with
100 semidiurnal tides exposing the intertidal zone (roughly 1,200 ha.) daily for 5.5--6.5 h. (Navedo and Masero
101 2007). This estuary is strategically located within the route of the North-Atlantic spoonbill population (Figure
102 1), just before the geographical barrier of the Cantabrian Mountains, and about 800 km far away from the next
103 main suitable stopover areas at the southern coasts of Iberia (Algarve, Odiel and Doñana). Spoonbill habitat
104 use is invariably driven by the tides, feeding in the intertidal channels during the low tide period and resting at
105 high tide in a supratidal area (Navedo 2006a). Tidal amplitude at Santoña ranges from ca. 2.5 m during neap
106 tides up to ca. 4.5 m during spring ones (mean 3.5 m; Navedo, 2006b), so it potentially has a great influence in
107 available foraging possibilities, with periods of spring tides significantly enlarging potential spatial and time
108 foraging budget.

109 We have estimated stopover duration of spoonbills in Santoña during September in four consecutive
110 years (2002-2005) on the base of PVC-ringed birds. Every day from 1st to 28th of September, and throughout
111 diurnal low tide period, two experienced observers carefully checked foraging flocks from a boat looking for
112 PVC-ringed birds. Observers were connected by walkie-talkies with people in two little hills overlooking the
113 estuarine area, which informed them about the localisation of all foraging spoonbills in the intertidal channels.
114 Thus, we assumed that almost all the spoonbills using the estuary (mean daily number at low tide was 69.4
115 birds; J.G. Navedo unpubl. data) were checked on a daily basis. When a PVC-ringed bird was located, the
116 boat was slightly beached to identify the code of the PVC-ring with the help of a 20x-60x telescope (mean

117 observation distance: 120 m.). Approximately 15% of the north-atlantic spoonbill population was currently
118 marked with individual PVC ring codes (O. Overdijk, unpubl. data).

119 Minimum stopover duration was defined as the time elapsed between first location and last relocation of
120 a bird in the estuary. Since resighting probability of birds that stopover three days or more (n=74) was $0.89 \pm$
121 0.01 , and it was not significantly different between years ($F_{3,70} = 0.81$; $p = 0.5$), it approaches real stopover
122 duration. Overall, we read 974 PVC-rings during the study (277, 209, 312 and 176; in 2002, 2003, 2004, and
123 2005, respectively), comprising 263 accurately identified PVC-ringed spoonbills [69 yearlings (1st year-cal);
124 39 immatures (2nd and 3rd year-cal) and 155 adult birds (4th year-cal or more)]. Of these birds, 38 were
125 located during more than one autumn at Santoña, corresponding to 34 adults and 4 immatures, all of them 3rd
126 year-cal at the time of their first observation (Dutch Spoonbill Working Group Database). Despite most PVC-
127 ringed yearlings were not resighted during its first wintering season, many PVC-ringed birds identified in
128 Santoña were resighted in its major wintering areas a few months later (data obtained from the Dutch
129 Spoonbill Working Group database). Nonetheless, as this population shows high fidelity to wintering area (De
130 Voogd 2004), data was used even if wintering area was not known for the specific year for which stopover
131 duration was recorded. In these cases, only birds for which wintering area is known, and remained constant
132 for three years during 2002-2008, were included in the analyses. Under these premises, we analysed
133 information about stopover duration and wintering area for a total of 127 birds (17 yearlings, 17 immatures
134 and 93 adults)

135 Spoonbills resighted during November and December at Algarve (Portugal), Odiel and Doñana (Spain)
136 were grouped into the Iberian-wintering class (43% of the PVC-ringed birds), whereas spoonbills resighted at
137 that time at Banc d'Arguin (Mauritania) and Senegal Delta (Senegal) were grouped into the African-wintering
138 class (57% of the PVC-ringed birds).

139

140 Statistical analysis

141

142 Some spoonbills ($n = 38$) were resighted on more than one migration at Santoña. Therefore, effects of year
143 and wintering area on minimum stopover duration of spoonbills were analysed by fitting a Linear Mixed
144 Model with individual (ring code) as random effect. Wintering area and year were respectively included into
145 the model as two-level (Iberia/Africa) and four-level (2002/2003/2004/2005) fixed factors, respectively.
146 Arrival date, defined as days elapsed from August 31st, was introduced as a potential predictive covariable
147 since timing could significantly affect migratory behaviour (Newton 2008). Similarly, age as well as within-
148 site experience (i.e. number of previous years registered at the area during the study period) were both
149 included as potential predictive variables into the model. Tidal amplitude at arrival, defined as a coefficient
150 ranging from 20 to 120, a measure directly correlated with the height of the tide, was also examined as a
151 predictive covariable due to its potential influence in migratory decisions (Piersma et al. 1990). As arrival date
152 and tidal amplitude were correlated we have tested their effects separately (not in the same model). However,
153 tidal amplitude was not finally included into the model since it was not correlated with the dependent variable
154 (Spearman $r = -0.06$; $p > 0.05$).

155 Statistical analyses were performed using STATISTICA v6.1 (StatSoft Inc. 2002). In all cases we used a
156 0.05 level of significance. Values are presented as means \pm SE.

157

158 **Results**

159

160 Individuals wintering in Africa spent more time (2.7 ± 0.4 days; $n = 72$) at Santoña marshes during the autumn
161 migration than those wintering in south Iberia (1.5 ± 0.2 days; $n = 55$) (Table 1; Figure 2). Minimum stopover
162 duration was similar between years, and longer stays for birds wintering in Africa were always recorded even
163 during the year with the shortest length of stay (2004, Figure 2). As migration period progresses minimum
164 stopover duration decreased significantly (Table 1; Figure 3). However, nor age neither within-site experience
165 did have a significant effect in explaining stopover duration of spoonbills.

166

167 **Discussion**

168

169 This study empirically shows that stopover duration in a long-distance migratory bird as the Eurasian
170 spoonbill was influenced by the remaining flight distance to the overwintering area. According to our
171 prediction, spoonbills wintering in Africa, and consequently facing a long-distance travel from a crucial
172 stopover site, stay for longer than those birds wintering in south Iberia that performed a shorter migration.
173 Although there are alternative reasons to stay at a stopover site than refuelling (e.g. resting, foraging for
174 maintenance or waiting for favorable winds to continue migration, e.g. Weber et al. 1998), spoonbills were
175 foraging most of the available time during stopover (J.G.Navedo pers obs). Therefore, longer stopover
176 duration would reflect higher energy-loads for spoonbills staying at the study area.

177 Birds wintering in south Iberia seem to minimise the time spent at the stopover locality, flying after a
178 short refuelling. Without large energy requirements, the need to arrive to the best foraging grounds in these
179 short-distance wintering areas ahead of other conspecifics may be the driving force explaining the fast
180 stopover of Iberian-wintering spoonbills. Moreover, as birds wintering in Southern Iberia are close to their
181 destination, they could be less dependent on the foraging conditions at this stopover to successfully complete
182 their migration. Inversely, birds wintering in Africa need to adjust their stopover duration at Santoña Marshes
183 to the requirements of a high energy-demanding flight and the prospects for a longer migratory trip (Alerstam
184 and Lindström 1990), thus refuelling for longer. Furthermore, at least some birds might take advantage of the
185 high energy load to 'skip' those south Iberian wetlands (Piersma 1987), where their conspecifics overwinter,
186 to perform a non-stop bout from Santoña to north western African wetlands.

187 Eurasian spoonbills consistently stopover for less time as migration period progressed. Prey consumption
188 at stopover areas would reduce food availability for migratory birds and even depleted them (Gudmundsson et
189 al. 1991; Prop et al. 2003; Nolet et al. 2006). Although we have not measured food availability in our study
190 area (main prey for spoonbills are little fishes and shrimps; J.G. Navedo unpubl. data), a significant decrease
191 of food resources for waterbirds occurs in estuaries around north Iberian coasts during autumn migration, and
192 extending to the winter season (Boileau et al. 2001; Viegas et al. 2007). If food is limited, an increase in
193 intraspecific competition resulting from a particular good breeding season (i.e. high number of breeding pairs

194 and productivity) may have measurable consequences in the migratory performance within a given population
195 (Alerstam et al. 2003), specially for experienced adults (Berthold 2001). The reduced stopover duration
196 observed during 2004 could have been affected by the highest population size during the study period reached
197 in that year (a high number of breeding pairs achieving a high reproductive success; O. Overdijk unpubl.
198 data), which also coincided with the maximum number of spoonbills that stopover at Santoña marshes during
199 the study period (Navedo 2006a).

200 Age-related differences in timing of migration at stopover sites are common in many bird species (e.g.
201 Restani 2000; Ueta and Higuchi 2002; Hake et al. 2003; Meissner 2007; Lee et al. 2008). In our case, a
202 preliminary study addressed that the majority of adult spoonbills (ca. 70%) had currently used the area before
203 the arrival of the majority of yearlings (ca. 60%) at the last week of September (Navedo 2008), when overall
204 stopover duration has markedly decreased. Therefore, yearlings that stopover at the last part of the migration
205 period without knowledge about remaining distance to wintering areas, associated energy demands, and/or
206 suitability of stopover areas, may reduce their probability of survive during a long migration (Newton 2006),
207 which could be viewed as an evolutionary issue regulating long-distance migratory bird populations
208 (Schekkerman et al. 2003). Inversely, adults could minimise the effects derived from density-dependent
209 processes by avoiding stopover at the end of the migration period, in particular African wintering birds
210 dealing with a fairly narrow time window to satisfy their higher energy demands (Skagen and Knopf 1994),
211 that overall arrive a few days earlier (mode: 13th September) than Iberian ones (mode: 17th September).

212 Notwithstanding the lack of prey surveys and fuelling rates (Hedenström and Alerstam 1997), our
213 findings suggest that spoonbills may experience a high intraspecific competition during stopover that could
214 result in the different strategies observed (Drent et al. 2003). However, further studies are needed to clarify
215 this point and to evaluate potential differences between sexes (Cristol et al. 1999), as well as the role of
216 experience (age) within sexes in these long-lived bird (Berthold 2001), especially for African-wintering
217 spoonbills that refuel for longer.

218 To sum up, this study provides empirical evidence of different stopover duration in a natural bird
219 population in function of the remaining migratory distance to overwintering area, and remarks the relevance
220 of stopover places for determining migratory route and pace in long-distance migratory birds.

221

222 **Zusammenfassung**

223

224 **Langstreckenzieher rasten länger: eine Fallstudie an in Nordiberien rastenden Löfflern**

225

226 Langstreckenzug ist bei Vögeln weit verbreitet und verbindet die Brut- und Überwinterungsgebiete durch eine
227 Serie von Rastplätzen, wo Individuen auftanken und/oder ruhen. Das Ausmaß der Rast ist entscheidend für die
228 Zugstrategie eines Vogels. Hier haben wir die Beziehung zwischen der minimalen Aufenthaltsdauer von
229 PVC-beringten Löfflern (*Platalea l. leucorodia*) an einem Hauptrastplatz und der verbleibenden
230 Flugentfernung zum Überwinterungsgebiet während vier aufeinander folgender Herbstzüge untersucht. Wir
231 haben auch den potenziellen Einfluss von Timing (Ankunftsdatum) und die Rolle von Erfahrung analysiert,
232 um die Rastdauer von Löfflern zu erklären. Insgesamt bleiben Vögel, die in Afrika überwintern und vom
233 Rastplatz aus eine längere Strecke ziehen (ca. 3000 km), länger ($2,7 \pm 0,4$ Tage) als Vögel, die in Iberien
234 überwintern und eine deutlich kürzere Strecke (ca. 800 km) ziehen ($1,5 \pm 0,2$ Tage). Diese Unterschiede
235 waren über den untersuchten Zeitraum beständig. Die Rastdauer wurde nicht signifikant vom Alter des Vogels
236 beeinflusst. Sie verringerte sich jedoch signifikant mit dem Fortschreiten des Zuges. Unsere Ergebnisse deuten
237 darauf hin, dass Löffler unterschiedliche Raststrategien entwickeln, abhängig von der erwarteten Entfernung
238 zum Überwinterungsgebiet. Altvögel, insbesondere solche, die lange Strecken ziehen, könnten mögliche
239 negative Effekte dichteabhängiger Prozesse reduzieren, indem sie Rasten am Ende des Zuges vermeiden.
240 Diese Ergebnisse sind von signifikanter Bedeutung für das Verstehen von Unterschieden im Zugverhalten
241 innerhalb einzelner Populationen, insbesondere für in ihrem Bestand abnehmende Wasservögel, und betonen
242 die Bedeutung des Schutzes von Rastplätzen für die Bewahrung innerartlicher Diversität bei Zugvögeln.

243

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252

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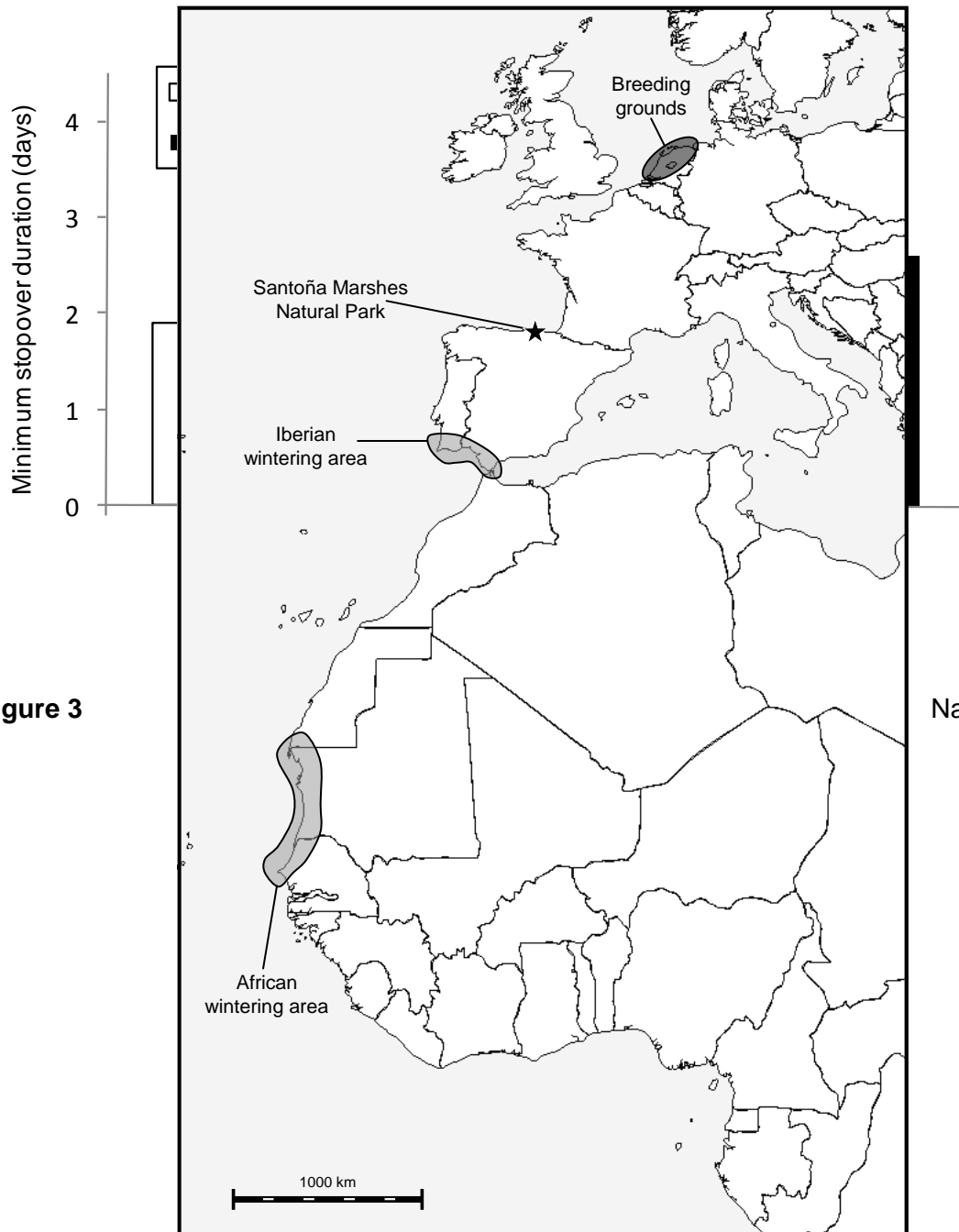
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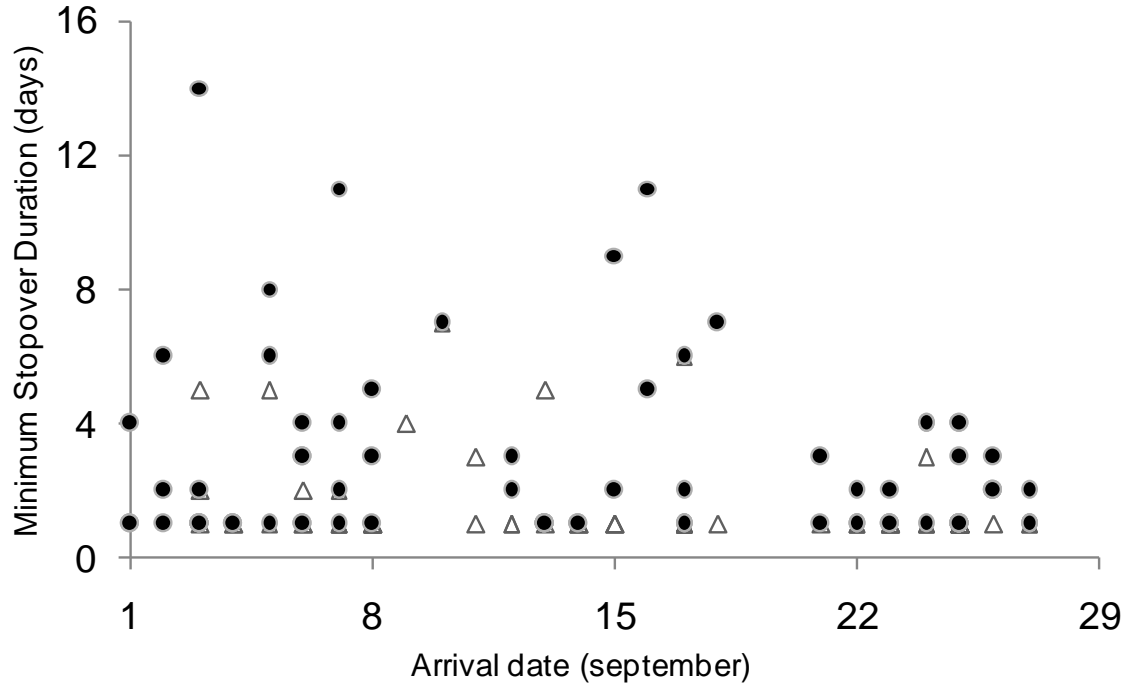
358 **Figure 2** Navedo *et al.*
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362 **Figure 3**
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Navedo *et al.*



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369 **Table 1** Results of a Linear Mixed Model procedure evaluating the effect wintering area and arrival date on
 370 minimum stopover duration (log transformed) of spoonbills (random effect) at Santoña Marshes Natural Park
 371 during autumn migration (2002-2005). Non-significant interactions were sequentially removed from the
 372 model.

Source	Effect	d.f.	F	p
arrival date	Fixed	1	5.80	< 0.02
wintering area	Fixed	1	9.03	< 0.004
ring code	Random	125	1.42	ns

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