Influence of age and sex on winter site fidelity of sanderlings *Calidris alba* (#11188)

First submission

Please read the **Important notes** below, and the **Review guidance** on the next page.
When ready **submit online**. The manuscript starts on page 3.

Important notes

Editor and deadline

Patricia Gandini / 7 Jul 2016

Files	1 Raw data file(s) 1 Other file(s) Please visit the overview page to **download and review** the files not included in this review pdf.
Declarations	**Involves vertebrate animals.**

Review guidelines

Please in full read before you begin

How to review

When ready **submit your review online**. The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this **pdf** and upload it as part of your review

To finish, enter your editorial recommendation (accept, revise or reject) and submit.

BASIC REPORTING

- Clear, unambiguous, professional English language used throughout.
- Intro & background to show context. Literature well referenced & relevant.
- Structure conforms to **PeerJ standard**, discipline norm, or improved for clarity.
- Figures are relevant, high quality, well labelled & described.
- Raw data supplied (See **PeerJ policy**).

EXPERIMENTAL DESIGN

- Original primary research within **Scope of the journal**.
- Research question well defined, relevant & meaningful. It is stated how research fills an identified knowledge gap.
- Rigorous investigation performed to a high technical & ethical standard.
- Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- Data is robust, statistically sound, & controlled.
- Conclusion well stated, linked to original research question & limited to supporting results.
- Speculation is welcome, but should be identified as such.

The above is the editorial criteria summary. To view in full visit **https://peerj.com/about/editorial-criteria/**

Influence of age and sex on winter site fidelity of sanderlings *Calidris alba*

Pedro M Lourenço Corresp., [1] , **José A Alves** [2, 3] , **Jeroen Reneerkens** [4] , **Jelle Loonstra** [4] , **Peter M Potts** [5] , **José P Granadeiro** [1] , **Teresa Catry** [1]

[1] Centro de Estudos do Ambiente e do Mar (CESAM), Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal
[2] Centro de Estudos do Ambiente e do Mar (CESAM), Universidade de Aveiro, Aveiro, Portugal
[3] South Iceland Research Centre, University of Iceland, Selfoss, Iceland
[4] Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands
[5] Farlington Ringing Group, Southampton, United Kingdom

Corresponding Author: Pedro M Lourenço
Email address: p.m.g.lourenco@gmail.com

Many migratory bird species show high levels of site fidelity to their wintering sites, which confers advantages due to prior knowledge, but may also limit the ability of individual to move away from degrading sites or to detect alternative foraging opportunities. Winter site fidelity often varies among age groups, but sexual differences have seldom been recorded in birds.

We studied a population of individually colour-marked sanderlings wintering in and around the Tejo estuary, a large estuarine wetland on the western coast of Portugal. For 160 individuals, sighted a total of 1249 times between November 2009 and March 2013, we calculated the probability that they moved among five distinct wintering sites and how this probability is affected by distance between them. To compare site fidelity among age classes and sexes, as well as within the same winter and over multiple winters, we used a Site Fidelity Index (SFI). Birds were sexed using a discriminant function based on biometrics of a large set of molecularly sexed sanderlings (n = 990) with data from. The vast majority of birds were observed at one site only, and the probability of the few detected movements between sites was negatively correlated with the distance among each pair of sites. Hardly any movements were recorded over more than 15 km, suggesting small home ranges. SFI values indicated that juveniles were less site-faithful than adults which may reflect the accumulated knowledge and/or dominance of older animals. Among adults, females were significantly less site faithful than males. A sexual difference in winter site fidelity is unusual in shorebirds. SFI values show site-faithfulness is lower when multiple winters were considered, and most birds seem to chose a wintering site early in the season and use that site throughout the winter. Sanderlings show a very limited tendency to explore alternative wintering options, which might have implications

for their survival when facing habitat change or loss (e.g. like severe beach erosion as can be the case at one of the study sites).

Manuscript for *PeerJ* (dd. 6 June 2016)

Influence of age and sex on winter site fidelity of sanderlings *Calidris alba*

Pedro M. Lourenço[1], José A. Alves[2,3], Jeroen Reneerkens[4], Jelle Loonstra[4], Pete M. Potts[5], José P. Granadeiro[1] & Teresa Catry[1]

[1]Centro de Estudos do Ambiente e do Mar (CESAM), Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal

[2] Centro de Estudos do Ambiente e do Mar (CESAM), Universidade de Aveiro, Campus Universitário de Santiago, 3180-193, Aveiro, Portugal

[3] South Iceland Research Centre, University of Iceland, Tryggvagata 36, IS-800 Selfoss, Iceland

[4]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

[5]Peter M Potts (Farlington Ringing Group) c/o Solent Court Cottage, Chilling Lane, Warsash, Southampton, Hampshire, SO31 9HF, England, UK

Corresponding author:

P.M. Lourenço, email: p.m.g.lourenco@gmail.com, tel: (+351) 938468585

Abstract

Many migratory bird species show high levels of site fidelity to their wintering sites, which confers advantages due to prior knowledge, but may also limit the ability of individual to move away from degrading sites or to detect alternative foraging opportunities. Winter site fidelity often varies among age groups, but sexual differences have seldom been recorded in birds.

We studied a population of individually colour-marked sanderlings wintering in and around the Tejo estuary, a large estuarine wetland on the western coast of Portugal. For 160 individuals, sighted a total of 1249 times between November 2009 and March 2013, we calculated the probability that they moved among five distinct wintering sites and how this probability is affected by distance between them. To compare site fidelity among age classes and sexes, as well as within the same winter and over multiple winters, we used a Site Fidelity Index (SFI). Birds were sexed using a discriminant function based on biometrics of a large set of molecularly sexed sanderlings (n = 990) with data from. The vast majority of birds were observed at one site only, and the probability of the few detected movements between sites was negatively correlated with the distance among each pair of sites. Hardly any movements were recorded over more than 15 km, suggesting small home ranges. SFI values indicated that juveniles were less site-faithful than adults which may reflect the accumulated knowledge and/or dominance of older animals. Among adults, females were significantly less site faithful than males. A sexual difference in winter site fidelity is unusual in shorebirds. SFI values show site-faithfulness is lower when multiple winters were considered, and most birds seem to chose a wintering site early in the season and use that site throughout the winter. Sanderlings show a very limited tendency to explore alternative wintering options, which might have implications for their survival when facing habitat change or loss (e.g. like severe beach erosion as can be the case at one of the study sites).

Introduction

Although migratory birds are extremely mobile, they are often remarkably site-faithful to their breeding (e.g. Harvey et al. 1979; Jackson 1994), wintering (e.g. Burton & Evans 1997; Catry et al. 2003; Leyrer et al. 2006) and staging sites (Gudmundsson & Lindström 1992; Kruckenberg & Borbach-Jaene 2004, Loonstra et al. 2016), both within the same season and among years. Such high levels of site fidelity are likely to confer advantages related to prior ownership of territories, previous knowledge of foraging locations, potential nest sites and local predators, and maintenance of social position within local dominance structures (Greenwood & Harvey 1982; Alerstam 1990; Snell-Rood & Cristol 2005).

However, when confronted with a rapidly changing environment, the regular use of the same set of sites over the years may expose individuals to increasingly poorer conditions and habitats (Battin 2004), when a traditionally used site suffers negative changes over time (e.g. Porzig et al. 2014) e.g. through a limitation in the use of all available habitat (Matthiopoulos et al. 2005). Therefore, the ability of animals to disperse and/or sample new areas can be of critical importance for highly site faithful species, under the current fast pace of global environmental change. Unfortunately, evaluating the use of multiple sites over large areas by the same individuals requires intensive effort to repeatedly detect marked individuals, which hinders the possibility of expanding efforts over large areas and impedes the detection of dispersion over longer distances. In addition, the traditionally low rate of movement among sites hinders the use of remote tracking techniques due to the need for very large sample sizes (e.g. Nathan et al. 2003; Hobson 2005).

Site fidelity may be influenced by age, as juvenile animals of most species exhibit dispersive and/or exploratory behaviours during which they search for places to ultimately settle (Clobert et al. 2001). However, few studies have focused on age effects in winter site fidelity in migratory birds, and the available studies have reported conflicting results in this issue. Juvenile western sandpipers *Calidris mauri* showed larger home ranges and weaker homing behaviour than adults in winter

(Warnock & Takekawa 1996; Baccetti et al. 1999), and younger white-fronted geese *Anser albifrons* were more likely to move among wintering sites than older birds (Wilson et al. 1991). However, there were no differences in winter site fidelity among different age groups of either pink-footed geese *Anser brachyrhynchus* (Fox et al. 1994) or American black ducks *Anas rubripes* (Diefenbach et al. 1988).

Sex can also influence site fidelity. Most research on site fidelity in migratory birds has focused on the breeding season, generally showing that males tend to be more site-faithful and disperse over shorter distances between years than females (Clarke et al. 1997, Gunnarsson et al. 2012). Such a pattern has been explained by the increased fitness benefits of prior knowledge of the local environment for the sex that establishes territories (Greenwood 1980; Gienapp & Merilä 2011). Also, in both sexes site fidelity is often also influenced by previous breeding success (e.g. Haas, 1998; Vergara et al. 2006). This stronger territoriality and site fidelity in males observed in a reproductive context could lead to a similar tendency in the wintering areas, resulting in a higher predisposition for site-fidelity even in a gregarious (wintering) context. On the other hand, sexual dimorphism or behavioural differences between sexes may imply different ecological requirements during winter (e.g. Alves et al. 2013) which could also drive sexual differences in site fidelity if required resources are heterogeneous in space. However, sexual differences in winter site fidelity have seldom been recorded in birds, being mostly restricted to species that frequently move during winter following spatial variation in food resources or that have family group composition affect their winter distribution (e.g. Roberts & Cook 1999; Wunderle et al. 2014). Studies in highly site-faithful long distance migrants, such as waders, have not shown sexual differences thus far (e.g. Warnock & Takekawa 1996; Catry et al. 2012).

Over the years, waders have been the focus of many individual-based studies, providing a significant source of information regarding site fidelity and individual movements. When faced with short-term changes in habitat quality/availability, some waders seem to be able to respond by moving up to over 100 km to more favourable areas (e.g. Kirby & Lack 1993; Takekawa et al.

2002; van Gils et al 2006, Lourenço et al. 2010), while others continue to use degraded/changed habitats (Connolly & Colwell 2005; Taft et al. 2008) apparently due to limited ability to increase or change home ranges (Taft et al. 2008). Understanding the level of site fidelity exhibited by individuals at a small spatial-scale (e.g. among sites within a single wetland) and, by opposition, the predisposition to disperse over increasing distances under stable conditions may provide some insights into the general ability of wader species to explore potential new areas or respond to short-term changes in their environment.

Sanderlings are common and widespread waders in coastal areas worldwide (Grond et al. 2015; Conklin et al. 2016). They are mainly associated with coarse sediment habitats, such as sandy beaches and sand or muddy-sand flats, which are particularly prone to quick changes through sediment migration and coastal erosion (Pethick 2001) and often affected by human disturbance (e.g. Burger 1991; Thomas et al. 2003). Sanderlings have been described as very site faithful and seem to have small home ranges at both wintering and staging areas (review in Reneerkens et al. 2009). In this study we use a dataset of observations of colour-marked sanderlings wintering in and around a large estuarine wetland to compare the level of winter site fidelity, within a single winter and among multiple winters, between sexes and age groups, and estimating the probability of these birds naturally dispersing over increasing distances under relatively stable conditions.

Materials and Methods

Study area

Field work was carried out in the Tagus estuary, Portugal, one of the largest tidal wetlands in Western Europe, and comprised five sites known to harbour sanderlings during winter. Three of the sites are located within the estuarine area (Alcochete, Samouco and Seixal), and two are located on the oceanic coast near the mouth of the Tejo river (Caparica and Oeiras; Fig 1). The minimum distance between a pair of sites is 3.1 km (Alcochete and Samouco), and the maximum is 29.8 km (Alcochete and Oeiras; Figs. 1). All study sites include foraging and roosting areas, the former located in the intertidal flats and the later situated above the high water mark. In Alcochete birds also roost on a saltpan located near the beach, which was also routinely monitored during the study. All sites harbour sanderling flocks throughout the winter with average counts of 75-126 individuals per site (more details regarding the study area in Lourenço et al. 2015).

<u>Study population and data analysis</u>

A total of 374 sanderlings were captured and ringed with individual colour-ring combinations in all three sites within the Tejo estuary in five consecutive non-breeding seasons between 2008/9 and 2012/13. Some birds were caught during late August and thus could still have been passage migrants, but since the re-sighting data refers only to the wintering period, this will not affect our winter site fidelity analysis. At capture, all birds were aged based on plumage characteristics, being classified as either first winter (hereafter referred as juveniles) or adults. Biometric data (wing length and tarsus length measured to the nearest mm; bill length and total head length measured to the nearest 0.1 mm) were also collected for most individuals. The protocol was approved by the responsible ethical and legal authority, the Portuguese Institute of Nature Conservation and Forests (ICNF) and performed under official permits 385/2013/CAPT, 386/2013/CAPT and 387/2013/CAPT.

Sex of measured birds was determined based on a function derived from a generalised linear model (GLM) of biometric data from 990 molecularly sexed sanderlings captured in Mauritania and Ghana in a concurrent study (see appendix for details). Since juvenile sandpipers can have shorter wing lengths than adults (Yosef & Meissner 2006), which is also true for sanderlings captured in the Tejo estuary (juveniles: 125.0±0.3 mm, n=89; adults: 127.1±0.2 mm, n=212; t_{299}=5.03, p<0.001), we only sexed adult birds through this method as wing is a key biometric sexing parameter. The GLM correctly assigned the sex of a large proportion of birds (84%; see appendix), but to minimize the risk of incorrect assignments all birds with a sex assignment probability below 75% (i.e. $0.25 \leq P_{(male)} \leq 0.75$; n=24) were excluded from the sex-related fidelity analysis. This resulted in 102 sexed birds, 64 males and 38 females.

From 2009/10 to 2012/13, during the sanderling wintering period (November-March), the study sites were visited frequently by us and many volunteer observers and the presence and identity of colour-marked birds was recorded. A total of 317 marked individuals were sighted, including 302 birds ringed locally and another 15 marked elsewhere (Greenland, Iceland and The Netherlands). The full dataset included 2358 sightings. Since the dataset includes many sightings obtained during haphazard visits of volunteers (21% of all individual sightings used in the analysis), we do not know whether the searching effort was similar for all sites, because volunteer observers will not have contacted us when they did not find a colour-ringed sanderling during their visits. We also suspect that the sites outside the estuary are likely to have been visited less often than the sites located within the estuary. For the same reason, sightings are not evenly spread over each winter and over different winters (Table 1).

In order to minimize the risk of having incorrect readings affecting our analyses, we limited our analysis to include birds that had been sighted a minimum of three times in a given area/year which resulted in 160 individuals (36 juveniles and 124 adults) for which we had a total of 1249 sightings (Table 1). For 101 of these individuals we had data over multiple years (65 seen in 2 winters, 28 seen in three winters and 8 seen in 4 winters). For each study site we calculated the proportion of individuals that were recorded only locally, and the proportion also recorded in other sites, both within a single winter (using the average of all four winters) and over multiple winters. To evaluate how the probability of dispersal varies with distance we used Generalized Linear Mixed-effects Models (GLMM) with logit link functions to relate a binomial variable indicating whether an individual sighted at a given site was later seen at each of the other sites, or only seen at the first site (movement distance = 0 km), to the distance among each pair of sites. Individual was used as a random factor in the GLMMs. This analysis was performed to assess inter-annual site fidelity (i.e.

data from multiple winters), using all available sightings of each individual, and also intra-annual site fidelity in which case we used data available for each individual each year and used year as covariate. The GLMM analysis were performed using package lme4 v1.1-11 in R (R Core Team 2014).

In order to test differences in site fidelity between sexes and age classes, as well as differences in the site fidelity within a single winter and over multiple winters we calculated a site fidelity index (SFI) described by Catry et al. (2012). This index takes into account the number of sites used, the number of observed changes between sites and the total number of sightings for each individual:

$$SFI = 1 - \left[\left(\frac{n_i - 1}{n - 1}\right) \times \left(\frac{p_i}{o_i - 1}\right)\right]$$

where n_i is the number of sites used by individual i, n is the total number of sites surveyed, p_i is the observed number of changes between sites performed by individual i and o_i is the total number of sightings of individual i. SFI ranges from zero (no site fidelity) to one (complete site fidelity). For each individual, SFI values were calculated within each winter (intra-annual SFI) and for all winters combined (inter-annual SFI).

To investigate sex differences in site fidelity, we compared both intra-annual and inter-annual SFI values for males and females. For birds with multiple winters of data we used the average intra-annual SFI, and in both cases we used Mann-Whitney tests to compare SFI scores. Two approaches were used to compare site fidelity among age classes. One compared the intra-annual SFI values for juvenile and adult birds for the winter when each individual was ringed/aged, through a Mann-Whitney test; the other used only birds ringed as juveniles and sighted over multiple winters, in which case we made a pair-wise comparison of intra-annual SFI values calculated for each juvenile in their first winter and in the subsequent winter (when adult) with the most sightings of that particular individual, using a Wilcoxon matched pairs test.

Finally, in order to compare site fidelity within the same winter and over multiple winters, we made a pair-wise comparison of intra and inter-annual SFI values for all adult birds sighted over multiple years using a Wilcoxon matched pairs test. There could be some biases when comparing inter-annual SFI of individuals with different numbers of sightings in each winter, but this problem would only affect comparisons among individuals and not pair-wise comparisons for each individual. Note that birds ringed as juveniles were excluded from this analysis because the tests described above showed that sanderlings are less site faithful in their first winter (see below). Data are presented as average ± SE.

Results

The majority of individuals (93.6± 0.7%, n=4 winters with an average 73±25 individuals/winter) were always sighted at the same site within a given winter (Fig. 1). The same pattern was observed for multiple winters (Fig. 1) but the proportion of birds that were only observed at a single site decreased with the number of winters considered, with 81.5% (n=65) for 2 winters, 67.9% (n=28) for 3 winters and 62.5% (n=8) for 4 winters. Bird movements were more likely to occur between sites in close proximity, namely between Alcochete and Samouco, between Samouco and Seixal and between Seixal and Caparica (Fig. 1).

In fact, the GLMMs indicated that the probability of movement was negatively affected by distance, with lower probabilities of dispersal between sites further away both within one winter (β=-0.609±0.071, z=8.61, $p<0.001$) and over multiple winters (β=-0.278±0.026, z=10.57, $p<0.011$; Fig. 2). In the analysis for a single winter the covariable 'year' had no effect on the probability of movement (z=0.45, $p>0.5$). In fact, there was only a single case of dispersal between sites located at a distance of over 20 km. No marked birds were ever detected at Oeiras even though the site was frequently used by non-marked sanderlings.

Females exhibited significantly lower intra-annual SFI values than males (intra-annual SFI_{male}=0.999±0.001, n=64; intra-annual SFI_{female}=0.991±0.005, n=38; Z=2.15, $p<0.05$; Fig. 3A), while there was no significant difference in inter-annual SFI values between sexes (inter-annual SFI_{male}=0.989±0.004, n=42; inter-annual SFI_{female}=0.979±0.007, n=31; Z=1.40, p>0.1; Fig. 3B). Juvenile birds had significantly lower intra-annual SFI values than adults in the winter when they were ringed/aged (intra-annual SFI_{adult}=0.997±0.003, n=126; intra-annual $SFI_{juvenile}$=0.975±0.009, n=34; Z=3.56, p<0.001; Fig. 3C). The intra-annual SFI values of birds ringed as juveniles increased in subsequent winters (intra-annual $SFI_{first\ winter}$=0.977±0.009, n=24; intra-annual $SFI_{subsequent\ winter}$=0.995±0.005, n=24; Z=1.99, p<0.05; Fig. 3D). For adult birds, inter-annual SFI values were significantly lower than intra-annual SFI values (intra-annual SFI =0.995±0.003, n=101; inter-annual SFI =0.985±0.004, n=101; Z=2.59, p<0.01; Fig. 3E).

Discussion

Despite some movements among sites, our data show high levels of short-scale winter site fidelity in sanderlings wintering in the Tejo estuary region, especially if we consider that the study sites are located in close proximity, with a minimum distance of just 3.1 km between sites. Such high level of site fidelity is remarkable for a long-distance migrant accustomed to fly thousands of kilometres, and which disperses over a huge latitudinal range during the winter, but it is in line with previous studies both on sanderlings (Evans et al. 1980; Myers et al. 1990; Gudmundsson & Lindström 1992) and other waders (e.g. Burton & Evans 1997; Leyrer et al. 2006; Catry et al. 2012).

However, sanderlings do visit other sites and, after four winters, roughly one third of all birds had already been sighted in at least two sites. The very high intra-annual SFI values and the significantly lower inter-annual SFI values suggest that movements rarely occur during winter, but rather that birds may change wintering location between winters. These data also support the idea that movements are probably not influenced by stress caused by our catching events. Although we did not have the statistical power to analyse how the probability of movement changes over the course of the winter, the majority of sanderlings seem to select a wintering site early after arrival from their High Arctic breeding areas and remain faithful to that site over the rest of the winter. When sanderlings' wintering sites have reached their carrying capacity, individuals were forced to use other non-preferred sites (Ntiamoa-Baidu et al. 2014). Hence, the first arriving birds in autumn are more likely to return to previously used winter sites. Given that juveniles arrive later in the wintering areas than adults (e.g. Lemke et al. 2012), the juveniles would be more prone to be forced to non-preferred sites.

Both age and sex influenced the level of site fidelity of sanderlings. However, since we did not sex juveniles, we cannot determine if there is any interaction between these two variables. The lower site fidelity exhibited by juveniles seems to be in line with evidence from other avian species where younger birds show larger home ranges (Warnock & Takekawa 1996) and are more likely to switch roosting and feeding locations (Rehfisch et al. 1996) during winter. In fact, an experimental study involving displacement of dunlins *Calidris alpina* showed that site fidelity of juveniles seems to increase even within their first winter with birds moved later in the winter being more likely to show "homing" behaviour (Baccetti et al. 1999). Although this age effect is not observed in all bird species (e.g. Diefenbach et al. 1988; Fox et al. 1994; Monsarrat et al. 2013), such differences may reflect the fact that, as age increases, birds may be using accumulated knowledge of site specific characteristics or past experiences to develop preferences for particular sites, while dominance can also play a role with juveniles being more easily displaced by older, more dominant individuals (e.g. Groves 1978). Consequently, older animals with presumably greater knowledge of wintering site characteristics and more past experiences may show increased fidelity to wintering sites which they found to be profitable and/or safe, similarly to what is known for breeding site fidelity (e.g. Serrano et al. 2001).

Unlike previous studies, which did not find sexual differences in winter site fidelity of waders (e.g. Warnock & Takekawa 1996; Catry et al. 2012), we detected significantly lower site fidelity in females within a single winter. It must be noted that this difference is quite small, with the vast majority of birds of both sexes remaining faithful to their wintering site throughout the winter. This small difference may have hampered its detection in previous studies using different methods. In the breeding areas, many bird species show higher site fidelity in the sex that establishes territories (Greenwood 1980; Gienapp & Merilä 2011). Sanderlings can also be territorial in winter (Myers et al. 1979) so we cannot rule out that territoriality may play a role here, but since sanderlings are also gregarious and frequently change group composition within the same foraging site (Myers 1983; Roberts & Evans 1993) this seems unlikely. Lower site fidelity could indicate that females have less benefits from prior knowledge of their foraging or roosting sites, or more benefits from exploring alternative foraging sites if for instances their preferred prey has a different distribution than that from the males (Alves et al. 2013). However, since sanderlings shows little sexual dimorphism (Engelmoer & Roselaar 1998; supplementary information to this study), there is no evidence for differences in energetic costs or foraging behaviour that could drive the observed sexual difference. In fact, the few cases in which sexual differences in winter site fidelity have been reported in bird species which make frequent movements during winter following changes in food availability, or species in which pair bonds or family group composition affect wintering distributions (e.g. Roberts & Cook 1999; Wunderle et al. 2014). Further studies will be required to confirm whether the sexual trend in winter site fidelity we observed is a general feature in sanderlings, and potentially other site-faithful long-distance migrants.

Overall, and despite the discussed sexual and age differences, sanderlings are highly site faithful to their wintering sites. Also, the observed movements are mostly on a small scale and there was only a single case of a bird moving between sites located further than 20 km apart. As is the case for most studies focusing on animal dispersal (Nathan et al. 2003), our study is also hampered by the impossibility to sample all potential areas past a limited distance. The maximum distance between our study sites was 29.8 km, which is a very considerable distance and larger than in many similar studies (e.g. Evans et al. 1980; Groen 1993; Burton & Evans 1997; Leyrer et al. 2006), but we still may be failing to detect movements to areas located further away. There is also the possibility that within this 30 km radius birds could use other sites within and in the vicinity of the estuary that were not monitored, although the relatively rare occurrence of sandy substrates in the Tejo estuary and the known preference sanderlings show for these substrates suggest this is unlikely (Lourenço et al. 2015). Also, since ringing only took place in the three sites within the estuary, and not on the furthest sites located outside the estuary, while the latter were probably visited less often, there might be a bias against detecting movements over larger distances.

Still, even when considering these biases and limitations, there is a clear pattern of site fidelity and decreasing chance of movements over increasing distances. The few birds ever detected outside the estuary originated from the sites nearer the mouth of the estuary (mainly the nearest, Seixal), and never from the site located the furthest (Alcochete) even though this was the site with the largest number of individual birds ringed and sighted. The few sightings elsewhere along the Portuguese coast of sanderlings that were colour-marked in other countries than Portugal, suggest similar site fidelity: from 37 sightings of 12 individuals (average sightings per individual: 3.1±2.0), each observed in a single winter, only one was observed at two locations which were separated by less than 4 km (Póvoa de Varzim 41º23'N/8º46'W and Vila do Conde 41º21'N/8º45W).

Altogether, our data suggest that sanderlings in and around the Tejo estuary rarely move among wintering sites located at distances of more than 15 km. Such a level of site fidelity during winter is likely to confer advantages related to previous knowledge of foraging locations, potential predation risks, and social interactions with other individuals using the same areas (e.g. Alerstam 1990; Snell-Rood & Cristol 2005), but may also limit the ability of these birds to detect new areas of favourable habitat that may become available for colonization (Matthiopoulos et al. 2005) or even of avoiding the consequences of any degradation to their traditional wintering sites (e.g. Porzig et al. 2014).

In the Netherlands, individually recognisable sanderlings have been observed to move over tens of kilometres in response to a sudden increase in food availability generated by a storm washing up large amounts of American Jack knife clam *Ensis americanus* on the shore (J. Reneerkens *unpubl. data*), suggesting that sanderlings are able to react to the availability of new foraging opportunities. Also, in the Solent estuary, UK, marked sanderlings seem to move regularly among feeding sites located 15-20 km apart (P.M. Potts *unpubl. data*). There is no evidence that any of the three areas we studied within the Tejo estuary suffered significant changes during the course of this study, so we cannot predict whether the birds would move if there was any decline in habitat quality. However, at Caparica, the beaches are known to be suffering from severe coastal erosion and are estimated to be retreating inland at an average rate of 7 $m.year^{-1}$ as a result of river damming and dredging, inadequate coastal management and urban pressure, and sea-level rise (Ferreira & Matias 2013). These beaches only persist there due to intense artificial sediment nourishment (Ferreira & Matias 2013) which can result in severe ecological impacts and loss of biodiversity (Schlacher et al. 2007). In fact, data collected in parallel to this study indicate both food availability and sanderling intake rates are currently lower in Caparica than in the sites within the estuary (Lourenço et al. 2015). Despite this, sanderlings continue to use this site and the few birds ringed in the estuary that were sighted in Caparica continued to use the site throughout the winter. This may indicate that site fidelity is a stronger driver of habitat selection for sanderlings than foraging habitat quality (as far as we can measure it) with potentially negative consequences for birds using areas suffering fast human-mediated changes such as the case of many coastal areas worldwide (Zhang et al. 2004; Schlacher et al. 2007).

Acknowledgements

We would like to thank all the observers who voluntarily sent us sightings of our colour-marked birds, including several members of the Farlington Ringing Group who routinely visit the Tejo estuary and provided great help in catching, marking and re-sighting sanderlings. Particularly, Ruth Croger, Anne de Poitier and Mark Fletcher visited our study areas each winter and were an important help in the field. We would also like to thank Afonso Rocha, Sara Pardal and Miguel Braga for help in catching and marking sanderlings.

References

Alerstam, T. 1990. *Bird migration*. Cambridge University Press. Cambridge, UK.

Alves, J.A., Gunnarsson, T.G., Potts, P.M., Sutherland, W.J. & Gill, J.A. 2013. Sex differences in distribution and resource use at different spatial scales in a sexually dimorphic migratory shorebird. *Ecology & Evolution* 3: 1079-1090.

Baccetti, N., Serra, L., Cherubini, G. & Magnani, A. 1999. Timing of attachment to wintering site as revealed by experimental displaced dunlins (*Calidris alpina*). *Journal of Ornithology* 140: 309-317.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology* 18: 1482-1491.

Burton, N.H.K. & Evans, P.R. 1997. Survival and winter site-fidelity of turnstone *Arenaria interpres* and purple sandpiper *Calidris maritima* in northeast England. *Bird Study* 44: 35-44.

Catry, P., Catry I., Catry, T. & Martins, T. 2003. Within and between-year winter site fidelity in chiffchaffs *Phylloscopus collybita*. *Ardea* 91: 213-220.

Catry, T., Alves, J.A., Gill, J.A., Gunnarsson, T.G. & Granadeiro, J.P. 2012. Sex promotes spatial and dietary segregation in a migratory shorebird during the non-breeding season. *PLoS ONE* 7: e33811. doi:10.1371/journal.pone.0033811.

Clarke, A.L., Sæther, B.-E- & Røskaft, E. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* 79: 429-438.

Clobert, J., Danchin, É., Dhondt, A.A. & Nichols, J. Dispersal. Oxford University Press. Oxford, UK.

Conklin J.R., Reneerkens J., Verkuil Y.I., Tomkovich P., Palsbøll P.J. & Piersma T. 2016. Low genetic differentiation between Greenlandic and Siberian Sanderling populations implies a different phylogeographic history than found in Red Knots. *Journal of Ornithology* 157: 325-332.

Connolly, L.M. & Colwell, M.A. 2005. Comparative use of longline oysterbeds and adjacent tidal flats by waterbirds. *Bird Conservation International* 15: 237-255.

Haas, C.A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. Auk 115: 929-936.

Diefenbach, D.R., Nichols, J.D. & Hines, J.E. 1988. Distribution patterns during winter and fidelity to wintering areas of American black ducks. *Canadian Journal of Zoology* 66: 1506-1513.

Evans, P.R., Breary, D.M. & Goodyer, L.R. 1980. Studies on sanderling at Teesmouth, NE England. *Wader Study Group Bulletin* 30: 18–20.

Engelmoer, M. & Roselaar, C.S. 1998. *Geographic variation in waders*. Kluwer Academic Publishers. Dordrecht. The Netherlands.

Ferreira, Ó. & Matias, A. 2013. Portugal. In: Pranzini, E. & Williams, A. (eds.) *Coastal erosion and protection in Europe*. Routledge, Oxfordshire. pp. 275-293.

Fox, A.D., Mitchell, C., Stewart, A., Fletcher, J.D., Turner, J.V.N., Boyd, H., Shimmings, P., Salmon, D.G., Haines, W.G. & Tomlinson, C. 1994. Winter movements and site fidelity of pink-footed geese *Anser brachyrhynchus* ringed in Britain, with particular emphasis on those marked in Lancashire. *Bird Study* 41: 221-234.

Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B. & Page, G. 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. *Waterbirds* 25: 173-183.

Gienapp, P. & Merilä, J. 2011. Sex-specific fitness consequences of dispersal in Siberian jays. *Behavioral Ecology and Sociobiology* 65: 131-140.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behavior* 28: 1140-1162.

Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13: 1-21.

Groen, N.M. 1993. Breeding site tenacity and natal philopatry in the black-tailed godwit *Limosa l. limosa*. *Ardea* 81: 107-113.

Grond, K., Ntiamoa-Baidu, Y., Piersma, T. & Reneerkens, J. 2015. Prey type and foraging ecology of Sanderlings *Calidris alba* in different climate zones: are tropical areas more favourable than temperate sites ? *PeerJ* 3: e1125.

Groves, S. 1978. Age-related differences in ruddy turnstone foraging and aggressive behaviour. *Auk* 95: 95-103.

Gudmundsson, G.A. & Lindström, Å. 1992. Spring migration of sanderling *Calidri alba* through SW Iceland: wherefrom and whereto. *Ardea* 80: 315-326.

Gunnarsson, T.G., Sutherland, W.J., Alves, J.A., Potts, P.M. & Gill, J.A. 2012. Rapid changes in phenotype distribution during range expansion in a migratory bird. *Proceedings of the Royal Society B* 279: 411-416.

Harvey, P.H., Greenwood, P.J., Perrins, C.M. 1979. Breeding area fidelity of great tit (*Parus major*). *Journal of Animal Ecology* 48: 305-313.

Hobson, K.A. 2005. Using stable-isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions* 11: 157-164.

Jackson, D.B. 1994. Breeding dispersal and site-fidelity in three monogamous wader species in the Western Isles, U.K. *Ibis* 136: 463-473.

Kirby, J.S. & Lack, P.C. 1993. Spatial dynamics of wintering lapwings and golden plovers in Britain and Ireland, 1981/82 to 1983/84. *Bird Study* 40: 38-50.

Kruckenberg, H. & Borbach-Jaene, J. 2004. Do greylag geese (*Anser anser*) use traditional roosts? Site fidelity of colour-marked Nordic greylag geese during spring migration. *Journal of Ornithology* 145: 117-122.

Lemke, H.W., Bowler, J. & Reneerkens J. 2012. Establishing the right period to estimate juvenile proportions of wintering Sanderlings via telescope scans in western Scotland. *Wader Study Group Bulletin* 119: 129-132.

Leyrer, J., Spaans, B., Camara, M. & Piersma, T. 2006. Small home ranges and high site fidelity in red knots (*Calidris c. canutus*) wintering on the Banc d’Arguin, Mauritania. *Journal of*

Ornithology 147: 376-384.

Lourenço, P.M., Mandema, F.S., Hooijmeijer, J.C.E.W., Granadeiro, J.P. & Piersma, T. 2010. Site selection and resource depletion in black-tailed godwits *Limosa l. limosa* eating rice during northward migration. *Journal of Animal Ecology* 79: 522-528.

Lourenço, P.M., Alves, J.A., Catry, T. & Granadeiro, J.P. 2015. Foraging ecology of sanderlings *Calidris alba* wintering in estuarine and non-estuarine intertidal areas. *Journal of Sea Research* 104: 33-40.

Loonstra, A.H.J., Piersma, T. & Reneerkens, J. 2016. Staging duration and passage population size of Sanderlings in the western Dutch Wadden Sea. *Ardea* in press.

Matthiopoulos, J., Harwood, J. & Thomas, L. 2005. Metapopulation consequences of site fidelity for colonially breeding mammals and birds. *Journal of Animal Ecology* 74: 716–727.

Monsarrat, S., Benhamou, S., Sarrazin, F., Bessa-Gomes, C., Bouten, W. & Duriez, O. 2013. How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLoS ONE* 8: e53077. doi:10.1371/journal.pone.0053077.

Myers, J.P. 1983. Space, time and the pattern of individual associations in a group-living species: sanderlings have no friends. *Behavioral Ecology and Sociobiology* 12: 129-134.

Myers, J.P., Connors, P.J. & Pitelka, F.A. 1979. Territory size in wintering sanderlings: the effect of of prey abundance and intruder density. *Auk* 96: 551-561.

Myers, J.P., Sallaberry, M., Ortiz, A.E., Castro, G., Gordon, L.M., Maron, J.L., Schick, C.T., Tabilo, E., Antas, P. & Below, T. 1990. Migration routes of New World sanderlings. *Auk* 107: 172-180.

Nathan, R., Perry, G., Cronin, J.T., Strand, A.E. & Cain, M.L. 2003. Methods for estimating long-distance dispersal. *Oikos* 103: 261-273.

Oring, L.W. & Lank, D. 1982. Sexual selection, arrival time, philopatry and site fidelity in the polyandrous spotted sandpiper. *Behavioral Ecology and Sociobiology* 10: 185-191.

Pethick, J. 2001. Coastal management and sea-level rise. *Catena* 42: 307-322.

Porzig, E.L., Seavy, N.E., Gardali, T., Geupel, G.R., Holyoak, M. & Eadie, J.M. 2014. Habitat suitability through time: using time series and habitat models to understand changes in bird density. *Ecosphere* 5: art12. http://dx.doi.org/10.1890/ES13-00166.1.

Refisch, M.M., Clark, N.A., Langston, R.H.W. & Greenwood, J.J.D. 1996. A guide to the provision of refuges for waders: an analysis of 30 years of ringing data from the Wash, England. *Journal of Applied Ecology* 33: 673-687.

Reneerkens, J., Benhoussa, A., Boland, H., Collier, M., Grond, K., Günther, K., Hallgrimsson, G.T., Hansen, J., Meissner, W., de Meulenaer, B., Ntiamoa-Baidu, Y., Piersma, T., Poot, M., van Roomen, M., Summers, R.W., Tomkovich, P.S. & Underhill, L.G. 2009. Sanderlings using African–Eurasian flyways: a review of current knowledge. *Wader Study Group Bulletin* 116: 2–20.

Roberts, G. & Evans, P.R. 1993. A method for the detection of non-random associations among flocking birds and its application to sanderlings *Calidris alba* wintering in N.E. England. *Behavioural Ecology and Sociobiology* 32: 349-354.

Roberts, G.J. & Cook, F. 1999. Winter philopatry in migratory waterfowl. *Auk* 116: : 20-34.

Schlacher, T.A., Dugan, J., Schoeman, D.S., Lastra, M., Jones, A., Scapini, F., McLachlan, A. & Defeo, O. 2007. Sandy beaches at the brink. *Diversity and Distributions* 13: 556-560.

Serrano, D., Tella, J.L., Forero, M.G. & Donázar, J.A. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of Animal Ecology* 70: 568-578.

Snell-Rood, E.C. & Cristol, D.A. 2005. Prior residence influences contest outcomes in flocks of non-breeding birds. *Ethology* 111: 441-454.

Stroud, D.A., Baker, A., Blanco, D.E., Davidson, N.C., Delany, S., Ganter, B., Gill, R., González, P., Haanstra, L., Morrison, R.I.G., Piersma, T., Scott, D.A., Thorup, O., West, R., Wilson, J. & Zöckler, C. (on behalf of the International Wader Study Group). 2006. The conservation and population status of the world's waders at the turn of the millennium. *In*: Boere, G.C., Galbraith C.A. & Stroud D.A. (eds). *Waterbirds around the world*. The Stationery Office. Edinburgh, UK.

pp. 643-648.
Taft, O.W., Sanzenbacher, P.M. & Haig, S.M. 2008. Movements of wintering dunlin *Calidris alpina* and changing habitat availability in an agricultural wetland landscape. *Ibis* 150: 541–549.
Takekawa, J.Y., Warnock, N., Martinelli, G.M., Miles, A.K. & Tsao, D.C. 2002. Waterbird use of bayland wetlands in the San Francisco Bay estuary: movements of long-billed dowitchers during the winter. *Waterbirds* 25(Sp2): 93-105.
van de Kam, J., Ens, B., Piersma, T. & Zwarts, L. 2004. *Shorebirds. An illustrated behavioural ecology*. KNNV Publishers. Utrecht, The Netherlands.
van Gils, J.A., Piersma, T., Dekinga, A., Spaans, B. & Kraan, C. 2006. Shellfish dresging pushes a flexible avian top predator out of a marine protected area. PLoS Biology 12: e376.
Vergara, P., Aguirre, J.I., Fargallo, J.A. & Dávila, J.A. 2006. Nest-site fidelity and breeding success in White Stork *Ciconia ciconia*. Ibis 148: 672-677.
Warnock, S.E. & Takekawa, J.Y. 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. *Ibis* 138: 160-167.
Wilson, H.J., Norriss D.W., Walsh A., Fox A.D. & Stroud D.A. 1991. Winter site fidelity in Greenland white-fronted geese *Anser albifrons flavirostris*, implications for conservation and management. *Ardea* 79: 287-294.
Wunderle, J.M., Lebow, P.K., White, J.D., Currie, D. & Ewert, D.N. Sex and age differences in site fidelity, food resource tracking, and body condition of wintering Kirtland's warblers (*Setophaga kirtlandii*) in the Bahamas. *Ornithological Monographs* 80: 1-62.
Yosef, R. & Meissner, W. 2006. Seasonal age differences in weight and biometrics of migratory dunlins (*Calidris alpina*) at Eilat, Israel. *Ostrich* 77: 67-72.
Zhang, K., Douglas, B.C. & Leatherman, S.P. 2004. Global warming and coastal erosion. *Climatic Change* 64: 41-58.

Table 1: Details on the data collected for the 160 studied sanderlings, including the number of individuals that were marked and sighted each winter (cumulative number in parenthesis), the number of sighting per individual each winter (average ± SE, range in parenthesis) and the number of visits per site each winter. Number of visits refers only to visits when at least one marked bird was sighted as there is no way of estimating the number of visits made by volunteers when no sightings were reported. Since marked birds were only detected in Caparica in 2012/13, the average only includes this site for that winter.

	2009/10	**2010/11**	**2011/12**	**2012/13**
Marked individuals	44 (44)	28 (72)	42 (114)	46 (160)
Sighted individuals	29	33	71	124
Sightings per individual	4.0±0.2 (3-7)	3.9±0.2 (3-8)	4.4±0.2 (3-14)	5.6±0.23 (3-17)
Visits per site	5.7±1.2 (3 sites)	7.0±1.5 (3 sites)	15.7±1.6 (3 sites)	19.3±4.0 (4 sites)

Figure 1: Map of the study area and proportion of birds sighted in each site that were either only sighted locally or also sighted in other sites. Panel A refers to the average for each winter (4 winters for all sites except Caparica for each we only had sightings of colour-marked birds in 2012-13). Panel B refer to all winters combined. Each site is represented by a different colour (Alcochete: red, Samouco: yellow, Seixal: green, Caparica: blue, Oeiras: pink) and in the pie charts the proportion of birds only sighted locally have the colour of that site and the proportions of birds also sighted elsewhere have the colours of the other sites in which they were sighted. Number of marked individuals (n) that were detected at each site: $n_{Alcochete}$=88, $n_{Samouco}$=42, n_{Seixal}=39 and $n_{Caparica}$=6.

Figure 2: Effect of distance between sites on the probability of movements occurring among them. The grey symbols and GLMM regression line refer to a single winter (average of all four winters), while the black symbols and line refer to multiple winters. Each dot shows the average probability of movement for a given distance. For each pair of sites, the number of marked individuals ranged from 40 (Seixal-Caparica) to 117 (Alcochete-Samouco).

Figure 3: Comparison of Site Fidelity Index (SFI) values between sexes (top line) and age classes (middle), and between a single winter and multiple winters. Panel A represents average intra-annual SFI values for males (n=64) and females (n=38); panel B represents average inter-annual SFI values for males (n=42) and females (n=31); panel C presents average intra-annual SFI values for adults (n=126) and juveniles (n=34) in the winter when they were ringed/aged; panel D presents average intra-annual SFI values of 24 birds ringed as juveniles when considering their first winter (juveniles) and a subsequent winter (adults); and panel E presents average intra and inter-annual SFI values of 101 birds ringed as adults. The black dots represent the mean, the boxes represent standard errors and the whiskers represent the range. * p<0.05, ** p<0.01, *** p<0.001.

Fig. 1

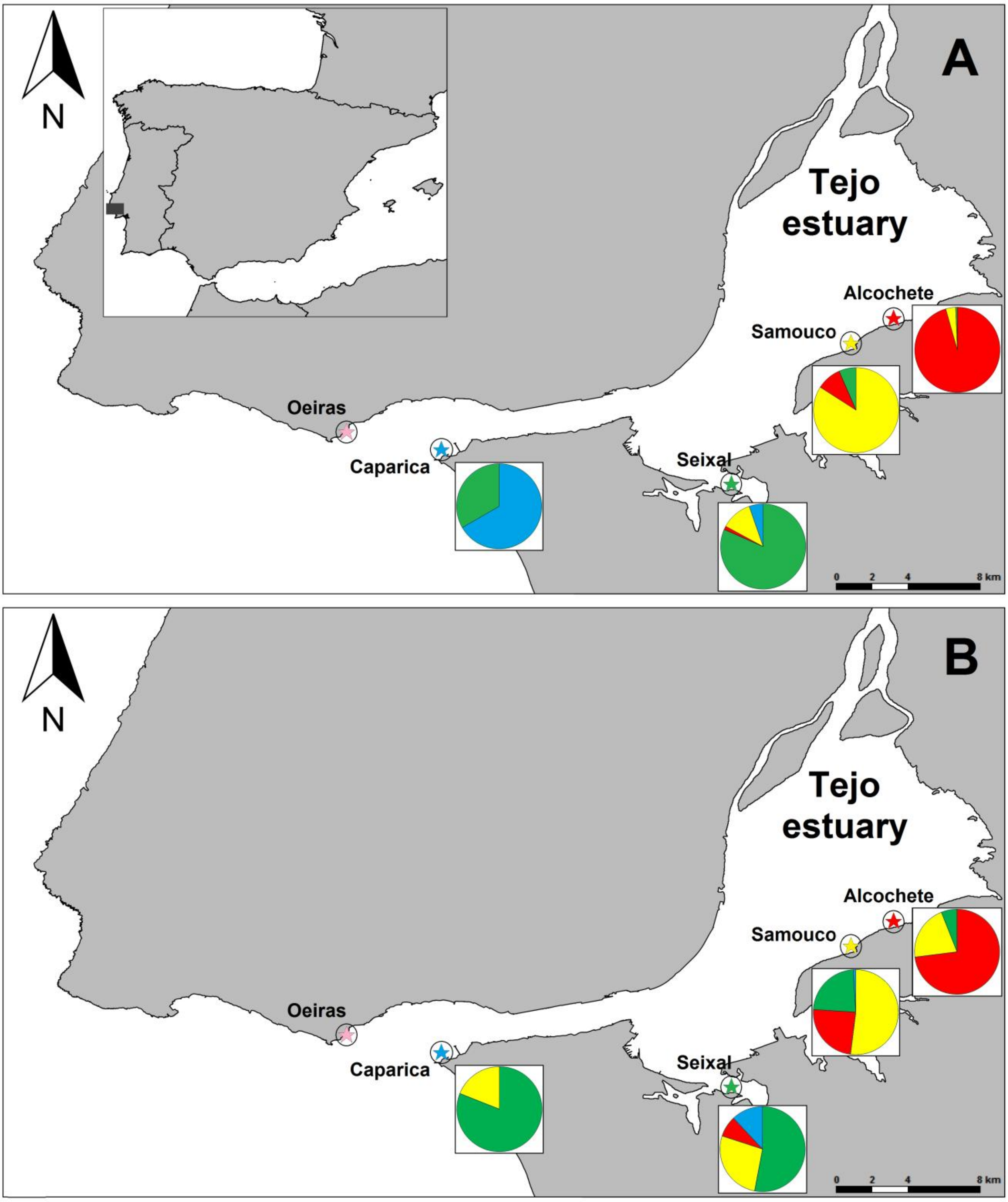

N
A
Tejo
estuary
Alcochete
Samouco
Oeiras
Caparica
Seixal
0 2 4 8 km
N
B
Tejo
estuary
Alcochete
Samouco
Oeiras
Caparica
Seixal
0 2 4 8 km

Fig. 2

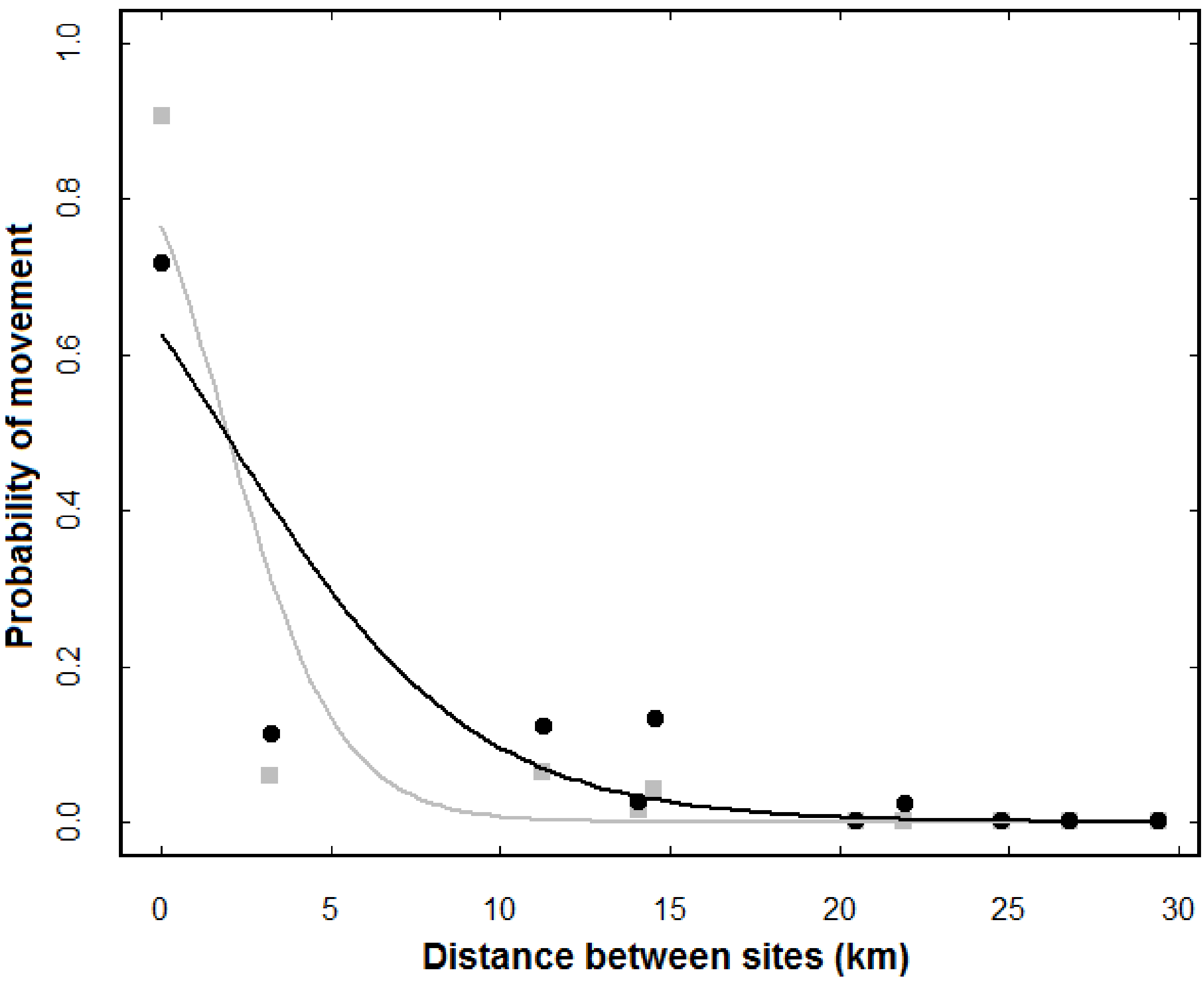
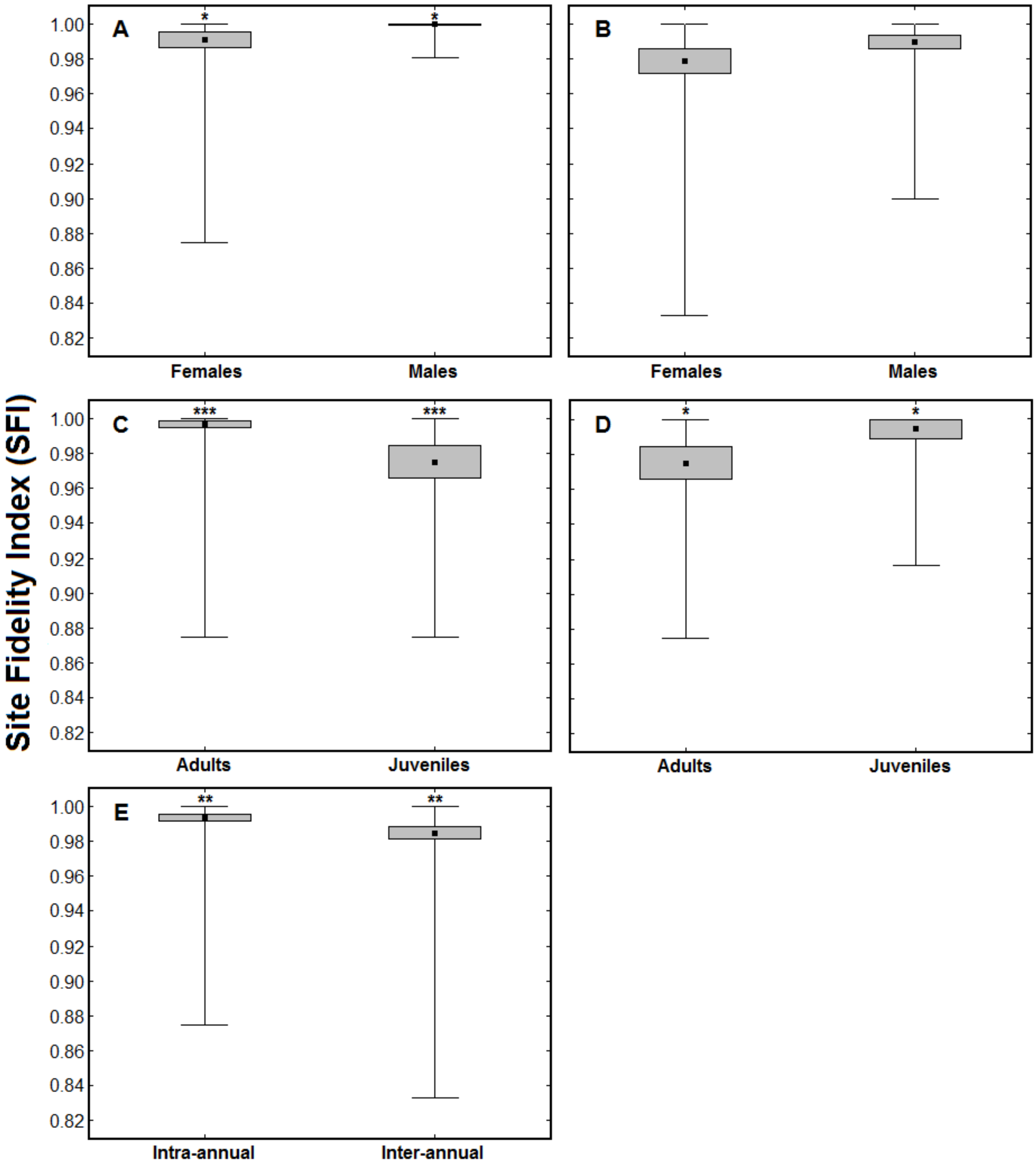

Probability of movement
0.0
0.2
0.4
0.6
0.8
1.0
0
5
10
15
20
25
30
Distance between sites (km)

Fig. 3


Site Fidelity Index (SFI)
A
B
C
D
E
1.00
0.98
0.96
0.94
0.92
0.90
0.88
0.86
0.84
0.82
*
**
***
Females
Males
Adults
Juveniles
Intra-annual
Inter-annual