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REVIEW

Migratory connectivity of Palearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis

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Running head: Serial residency and migratory connectivity

19 In most long-distance migratory birds, juveniles migrate without their parents, and so are likely to lack
20 detailed knowledge of where to go. This suggests the potential for stochasticity to affect their choice
21 of wintering area at a large scale (>1000km). Adults, in contrast, may re-use non-breeding sites that
22 promote their survival, so removing uncertainty from their subsequent migrations. I review the
23 evidence for large scale stochastic juvenile site selection followed by adult site fidelity, and then
24 develop a 'serial-residency' hypothesis based on these two traits as a framework to explain both the
25 migratory connectivity and population dynamics of migrant birds and how these are affected by
26 environmental change. Juvenile stochasticity is apparent in the age-dependent effects of weather or
27 experimental displacement on the outcome of migration and in the very wide variation in the
28 destinations of individuals originating from the same area. Adults have been shown to be very faithful
29 to their wintering grounds and even to staging sites. The serial residency hypothesis predicts that
30 migrants that show these two traits will rely on an individually unique but fixed series of temporally
31 and spatially linked sites to complete their annual cycle. As a consequence, migratory connectivity
32 will be apparent at a very small scale for individuals, but only a large scale for a population, and
33 juveniles are predicted to occur more often at less suitable sites than adults, so that survival will be
34 lower for juveniles. Migratory connectivity will arise only through spatial and temporal autocorrelation
35 with local environmental constraints, particularly on passage, and the distribution and age structure of
36 the population may reflect past environmental constraints. At least some juveniles will discover
37 suitable habitat that they may re-use as adults, thus promoting overall population level resilience to
38 environmental change, and suggesting value in site-based conservation. However, because migratory
39 connectivity only acts on a large scale, any population of a migrant will contain individuals that
40 encounter a change in suitability somewhere in their non-breeding range, so affecting average
41 survival. Differences in population trends will therefore reflect variation in local breeding output added
42 to average survival from wintering and staging areas. The latter is likely to be declining given
43 increasing levels of environmental degradation throughout Africa. Large scale migratory connectivity
44 also has implications for the evolutionary ecology of migrants generally because this is likely to lead to
45 selection for generalist traits.

46

47 The causes of current population declines of many migrant species in the Palearctic are likely to be
48 both species- and population-specific (Vickery *et al.* 2014), yet a general decline in most migrant
49 species has been recorded over large areas of the Palearctic (European Bird Census Council 2012).
50 If declines in migrants are species- and population-specific, then some characteristics such as their
51 life history strategy or environmental conditions in Africa are likely to be causing the decline recorded
52 across species (Sanderson *et al.* 2006). Here I propose two traits of migrants that may help to explain
53 these population dynamics. First, in most long-distance migrant birds, juveniles migrate without their
54 parents, and most likely lack detailed knowledge of where to go, suggesting the potential for
55 stochasticity to affect their choice of wintering area on a large scale (>1000km). Second, adults then
56 show very high fidelity to these sites, re-using sites that secured their survival as juveniles and so
57 removing uncertainty from their subsequent migrations and location of wintering sites. Here I review
58 the evidence for stochastic juvenile site selection at a large spatial scale, and adult site fidelity, and
59 develop from this a 'serial-residency' hypothesis based on these two traits that forms a framework to
60 explain both the connectivity of migrant species to their wintering grounds and their population
61 dynamics, and how both may vary with environmental change.

62 **STOCHASTIC LOCATION OF WINTERING SITES BY JUVENILES**

63 The demonstrated ability of migratory birds to return exactly 'home', quickly and efficiently, after a
64 considerable experimental spatial displacement (Mewaldt 1964, Akesson 2003) indicates that birds
65 can be considered to have the equivalent of a GPS system (Thorup *et al.* 2007a, Thorup & Holland
66 2009). Navigation can only take place, however, when the final destination is known but there is no
67 evidence to date of genetic programs that provide naïve migrants with instructions on how to reach
68 wintering sites at a specific location on a small (<100 km) or medium scale (100 – 1000 km). Genetic
69 control of migratory direction in juveniles has been shown to operate only on a very large scale at the
70 level of migratory divides, such as south-west through Iberia or south-east through the Middle East
71 (Perez-Tris *et al.* 2004, Ilieva *et al.* 2012), or with respect to the approximate timing of encounter with
72 barriers which require pauses for refuelling or very major shifts in direction (e.g. Chernetsov *et al.*
73 2008). Migration departure directions are sufficiently variable within individuals to result in large
74 differences in destinations over journeys of several thousand kilometres (Thorup *et al.* 2007b) and
75 within populations (Karlsson *et al.* 2010), and juveniles do not usually use environmental cues to

76 contradict their basic 'compass and clock' program (e.g. Deutschlander *et al.* 2012, Holland & Helm
77 2013). Even when they do (e.g. magnetic cues; Kullberg *et al.* 2003), this is again variable across
78 individuals in timing and direction.

79 Lacking innate small or medium-scale location information, a juvenile bird can only head in the
80 direction of migration and encounter sites stochastically along its line of travel, although as sites are
81 encountered, their location can be learned and so used or avoided in subsequent migrations. Some
82 birds may use social learning to locate suitable passage and wintering sites. Long-lived migrants, for
83 example, will have greater opportunities for removing stochasticity in site selection, leading to extreme
84 cases where social learning may be involved to ensure the same, best sites are always used even by
85 first-year birds (Mueller *et al.* 2013). Some shorter-lived passerine migrants that migrate diurnally in
86 flocks, such as Barn Swallows *Hirundo rustica*, might also use social learning or public information to
87 locate good passage sites and roosts. However, many species show no association between
88 juveniles and adults in the migration period, and indeed many adults migrate before juveniles, so
89 precluding any chance of social learning of destinations from parents. Such species, including almost
90 all passerines where this is known, migrate at night, often singly or in associations formed by
91 bottlenecks on the migration route, but without any coherent, coordinated group behaviour that might
92 suggest some individuals are following others, or have the potential systematically to follow others
93 (Berthold 2001). Although grouping, for whatever reason, must provide an opportunity for individuals
94 to follow one another, we know of no mechanisms whereby such grouping leads to coordinated site
95 selection at medium or small scales. Adults tend to have a different moult and migration phenology,
96 with juveniles travelling more slowly (e.g. Strandberg *et al.* 2008, Hope *et al.* 2011), so making the
97 option of following adults difficult. Nonetheless, studies on the use of cues such as flight calls and
98 adult presence and density, during and at the end of migration, are needed to determine the degree to
99 which any stochasticity might be offset by social information.

100 ***Evidence for stochastic site selection by juveniles***

101 Juveniles, unlike adults, do not correct for experimental displacement during migration, thus ending
102 up in atypical wintering areas, whereas adults are able to make corrections and so reach their usual
103 winter quarters (Perdeck 1958, 1967, Wolff 1970). A recent meta-analysis of orientation in caged
104 juvenile birds after displacement has confirmed that any corrections by juveniles in autumn are

105 approximate and even these are probably reliant on star positions in clear skies, whereas juveniles
106 returning in the spring correct more coherently as if heading back to their known breeding grounds
107 (Thorup & Rabøl 2007). Experienced birds, in contrast, use 'true navigation' whereby celestial and
108 magnetic cues along with site-specific experience allow for precise orientation and correction after
109 displacement (Wiltschko & Wiltschko 1999).

110 Many migrants may use favourable tailwinds during migration (Erni *et al.* 2005). This implies that
111 change in wind direction during a migration flight, or slight differences in starting wind directions, can
112 influence destinations. Although compensation for this wind drift can occur, it is species- and context-
113 specific (Liechti 2006) and can result, after strong, sustained and unexpected winds, in very large
114 numbers of birds, notably passerines, being displaced from their usual migration paths (Elkins 1983).
115 Passerines, in particular, may also migrate without favourable tailwinds because they are time-
116 constrained and so are likely to be subject to small changes in direction as a result of wind drift
117 throughout every night of their long-distance migrations (Karlsson *et al.* 2011). Consequently, even if
118 genetic orientation mechanisms of juveniles were more precise, accumulated small deviations over a
119 long migration will result in destinations that vary on a country-wide scale (Mouritsen 2003).

120 Wintering locations of individuals are now becoming better known from light-based geolocators and
121 satellite telemetry, and this evidence suggests that there is wide variation in the wintering destinations
122 of individuals originating from the same population (Table 1). The wintering distributions of individuals
123 from the same small breeding area in Europe may extend over thousands of kilometres in Africa.
124 However, the measurement of migratory tracks of small passerine species from such tags is in its
125 infancy, and hence biased against finding connectivity because of the stochasticity inherent in small
126 sample sizes. Many more data are needed and will emerge as tagging capability and programs
127 expand.

128 Further evidence that juveniles reach their wintering sites stochastically is that they occur commonly
129 in any habitat that is minimally suitable (e.g. Nevoux *et al.* 2008), and not always in the best habitats.
130 Evidence is limited, but one study of Eurasian Spoonbills *Platalea leucorodia* has been able to
131 examine this over a convincing scale that accounted for dispersal as well as survival, finding that
132 Spoonbills were highly faithful to winter sites despite others being available that would result in higher
133 survival (Lok *et al.* 2011). There same has been found for Icelandic Black-tailed Godwits *Limosa*
134 *limosa islandica* wintering in Western Europe (Gunnarsson *et al.* 2005). Similar evidence comes from

135 a lack of correlation between settlement patterns of migrants and the quality of sites (e.g. Johnson *et*
136 *al.* 2009, 2011).

137 ***Post-migration sampling of sites to compensate for stochasticity***

138 On arrival, subsequent movements may then occur so that the stochasticity of migration can be
139 mitigated by finding better sites locally. Although little is known about the degree of local, post-
140 migratory sampling undertaken by juvenile birds (Mettke-Hofmann & Greenberg 2005), we may gain
141 some insight by examining dispersal distances from the natal site on return at after the first complete
142 migration. Although these distances are likely to be underestimated in many studies (e.g. c. 1-10 km,
143 Sutherland *et al.* 2000), mean distances analysed from population demographic methods for
144 passerines are of the order of 15-95 km (Tittler *et al.* 2009). This scale is compatible with the
145 stochastic nature of juvenile migratory destinations at a medium to large scale. Any migrant, when
146 necessary, may carry out site selection at larger scales to compensate for stochasticity (e.g. Honey
147 Buzzards *Pernis apivorus* Strandberg *et al.* 2012). Nevertheless this does not mean that many do,
148 because the advantages of locating the best site may not outweigh the costs of moving on a large
149 scale or delaying site selection.

150 Key to understanding the stochasticity involved in selection of a wintering site by juveniles are the
151 relative costs and benefits of moving. If these are high and low respectively, then juveniles should
152 invest little time and energy in sampling sites and stay roughly where they initially settle in Africa
153 (Switzer 1993). There is some evidence that costs of moving between sites are high. Migration itself
154 incurs a survival cost (Strandberg *et al.* 2010), whereas juveniles that have become resident on a site
155 for the winter have the same survival as adults (Silllett & Holmes 2002), suggesting that movement
156 between sites results in lower survival than residency. Mechanisms for increased cost are likely to
157 include increased predation risk in unfamiliar surroundings (e.g. Clarke *et al.* 1993, Yoder *et al.* 2004)
158 and increased encounter rates with new parasites (Møller & Szep 2011).

159 There is also some evidence to suggest that the benefits of switching sites at a large scale may be
160 low, at least for Palearctic passerine migrants wintering in Africa because suitable, unoccupied habitat
161 is widespread. First, the absence of Palearctic migrants from certain wintering habitats is well
162 predicted by habitat models but, within suitable habitat, presence is poorly predicted, suggesting that
163 much suitable habitat is unoccupied (Wilson & Cresswell 2006, Cresswell *et al.* 2007, Hulme &

164 Cresswell 2012). Second, many Palearctic terrestrial migrant species occur in a wide range of
165 habitats (Rabøl 1987, Leisler 1990, Morel & Morel 1992, Pearson & Lack 1992, Salewski & Jones
166 2006). Some studies in the Neotropics suggest the opposite, with clear survival differences between
167 habitats and evidence of exclusion of age and sex classes (Strong & Sherry 2000, Marra & Holmes
168 2001). However, habitat limitation, and indeed many factors which affect migrants, may act differently
169 in the Neotropics because many species winter in Central America and on Caribbean islands where
170 the availability of land is limited (Jones & Cresswell 2010).

171 A further key issue in understanding the net costs of sampling and moving between sites lies in the
172 concept of predictability of foraging and management of hazard such as predation risk (Cuadrado
173 1997), both of which rely on local information. The information needed to allow prediction of foraging
174 gain and management of starvation and predation risks can only be gained through experience of a
175 site. Therefore the value of a site increases with greater residence in it (Piper 2011). This concept
176 perhaps explains why migration for first-year birds (and adults that have their migratory routes
177 disrupted by weather) carries greater survival costs (see below). Each step means that a new site
178 must be sampled and assessed, to gain knowledge of local food sources, competitor densities,
179 predators and the location of refuges, which will interact to determine predation risks and foraging
180 predictability (Lind & Cresswell 2006, Cresswell 2011). The process of gaining experience of a site
181 may itself increase energetic costs, reduce foraging time and increase predation risk for migrants (see
182 Robinson & Merrill 2013 for a mammalian example of this). If much of the cost of shifts between sites
183 in wintering areas is a consequence of imperfect information, then we would predict that birds select
184 wintering sites according to a threshold of minimum acceptability to reduce the time to locate a site
185 (see Oring 1982 for this argument applied to breeding territories). This is made more compelling by
186 considering that the energy requirements of a passerine in the tropics are relatively low outside
187 migration periods and foraging may only need to occur for a few hours every day (Brandt & Cresswell
188 2009). A migrant in a poor site might choose simply to feed for longer during the day rather than risk
189 seeking a better site.

190 A further consideration in determining the scale at which winter site selection is stochastic is the
191 degree to which juveniles use the presence of adults in an area to locate suitable habitats. Once a
192 juvenile arrives in a potential wintering area it may then locate suitable wintering sites at a finer scale
193 using local enhancement, whereby the presence of adult conspecifics indicates suitable and probably

194 high quality habitat. Conspecific attraction certainly occurs in choice of breeding site when the
195 confounding effect of habitat quality itself is experimentally removed (e.g. Hahn & Silverman 2006,
196 Betts *et al.* 2008, Theriault *et al.* 2012). We know nothing of whether birds use local enhancement to
197 locate suitable wintering areas, but it seems reasonable that they would do so and consequently
198 aggregate depending on a pre-existing distribution.

199

200 **NON-BREEDING SITE FIDELITY IN ADULTS**

201 There is much convincing evidence of site fidelity to the main non-breeding sites (wintering sites
202 where individuals spend more than a few days) for many of the migrant species for which data are
203 available (Table 2 and Newton 2008). Site fidelity in birds generally seems to vary along a continuum
204 from highly site-faithful even at a small spatial scale, to virtually no fidelity at any scale, depending on
205 year-to-year predictability in food-supplies (Newton 2008). Serial residency and its associated
206 predictions will have much less relevance to any population that specialises on spatially unpredictable
207 food supplies or ephemeral habitats (Newton 2012) such as White Storks *Ciconia ciconia* (Berthold *et al.*
208 *al.* 2002). However, there is no evidence that any Palearctic-African passerine migrant is nomadic (i.e.
209 sudden appearances in non-usual areas of large numbers of individuals), and in non-passerines such
210 as raptors and storks nomadism is perhaps much more noticeable and easier to demonstrate than
211 serial residency. This is distinct from the use made by individuals of several species of more than one
212 wintering site (or prolonged staging sites) in Africa (Jones 1995). These typically reflect large-scale
213 movements in response to worsening dry season conditions as a consequence of intra-annual rainfall
214 and primary productivity patterns (Tottrup *et al.* 2012, Lemke *et al.* 2013). There is no logical reason
215 to suppose that use of several wintering sites would affect fidelity to any one of these sites, but there
216 are no data available to examine this.

217 Fidelity to passage sites, where individuals may only spend a few days refuelling before continuing
218 migration, has not been as well demonstrated for passerines. Fidelity to staging sites may be lower
219 because it is harder for birds to assess the quality of a particular staging site given that they only
220 sample it for a short period of time, and there may be greater short-term temporal variation in
221 competitor numbers at staging sites than at over-wintering sites (G. Ruxton pers. comm.).

222 Nevertheless, some geese, shorebirds and raptors have high site fidelity to passage sites (Table 2

223 and Newton 2008), even though apparent site fidelity may be inflated by limited availability of suitable
224 staging sites. Most passerines probably do not have site fidelity for passage sites (Catry *et al.* 2004),
225 but it does occur in some species (Table 2, Newton 2008).

226 What is known about wintering site fidelity is entirely consistent with what we know about breeding
227 site fidelity. Breeding and natal site fidelity at a very small scale (hundreds of metres) in most adult
228 birds, and at a slightly larger scale (<10 km) in juveniles, has been long established (Greenwood &
229 Harvey 1982). Although there are many exceptions, and the degree of site fidelity is dependent on
230 many ecological factors, most birds tend breed close to their natal site. Much of the contention about
231 whether or not species are site-faithful is actually about the scale of dispersal (Cilimburg *et al.* 2002,
232 Hosner & Winkler 2007). Natal and breeding site fidelity of migrants in particular is well established
233 and tends to be similar to that of non-migratory populations or species (Greenwood & Harvey 1982,
234 Sandercock & Jaramillo 2002, Middleton *et al.* 2006, Foerschler *et al.* 2010) and between migrants
235 occupying different habitats (Schlossberg 2009).

236 What we know about wintering and breeding site fidelity predicts that an individual migrant is likely to
237 occupy the same sites for breeding and wintering throughout its life, even over many years (hence
238 'serial' residency), and this may also extend to the passage stop-over sites between them. This does
239 not, however, rule out an individual abandoning sites or adopting new sites, or using multiple
240 wintering sites but, on average, if sites remain available and suitable, the prediction is that they will be
241 used again. Site fidelity is expected to decrease with increase in variation at sites due to changes in
242 weather, climate, habitat and competition, or the ability of a migrant species to find and move to better
243 sites. As with juveniles, the key to understanding adult site fidelity is therefore the cost of changing
244 habitat and the scale over which site changes occur (see Møller & Szep 2011 for an example
245 involving the costs of parasitism leading to selection for winter site fidelity). However, there is little
246 information available to examine how frequently and why adult birds change their wintering sites.

247 We have much better information for change of breeding site, and it may be that similar rules apply for
248 shifts to new wintering sites. Adult birds tend not to change breeding sites, particularly as they get
249 older and more experienced (Middleton *et al.* 2006, Sergio *et al.* 2009, Bernard *et al.* 2011), and when
250 they do so movements are generally <100km. Many studies show shifts in breeding sites over
251 relatively small distances (of the order of <1-10km) and usually only females move in response to
252 reduced reproductive success (Sedgwick 2004, Eeva *et al.* 2008, Schaub & von Hirschheydt 2009).

253 However, many studies that show such correlations between site shifts and reproductive success are
254 confounded by increasing reproductive success with age. Thus, when experimental manipulations of
255 reproductive success are carried out these tend not to lead to site shifts (e.g. Howlett & Stutchbury
256 2003, Shutler & Clark 2003, but see Hoover 2003). Studies that experimentally manipulate habitat
257 quality to induce movements to new areas have not been carried out for any migrant species on the
258 wintering grounds in Africa, and there are real biases towards not identifying species that have low
259 site fidelity because of the scale of study necessary. Nevertheless the expectation of high adult site
260 fidelity on even a small scale seems the most parsimonious for wintering passerines.

261 **THE SERIAL RESIDENCY HYPOTHESIS**

262 Traits whereby large (>1000 km) and probably medium (>100 km) scale location of passage and
263 wintering sites is stochastic by juveniles on first migration, but then surviving adults have high site
264 fidelity to the wintering and possibly also staging sites in subsequent migrations, form the basis of a
265 novel 'serial residency' hypothesis. This hypothesis generates testable predictions in three areas:

- 266 (i) ***Age-dependent site use and survival.*** Juveniles are predicted to show greater
267 variance of migration routes and number of stop-over sites in time and space, and greater
268 occurrence than adults at less suitable sites, so that survival is higher for adults than
269 juveniles.
- 270 (ii) ***Migratory connectivity.*** This will arise only through spatial and temporal autocorrelation
271 of local environmental constraints, particularly on passage, and the distribution and age
272 structure of the population may reflect past environmental constraints.
- 273 (iii) ***Population resilience.*** At least some juvenile birds will discover suitable habitat that can
274 be re-used when the birds are adults, allowing overall population level resilience to
275 environmental change and giving value to site-based conservation.

276 The serial residency hypothesis is most likely to apply to species in those orders of birds (e.g.
277 Passeriformes) of smaller body size, lower flight range and lower ability to maintain migration and
278 orientation in adverse weather. Such birds are subject to events during migration that cannot be
279 predicted or compensated for, and end up distributed over a wider area when they reach their
280 wintering grounds. The hypothesis will apply less to those orders with characteristics such as large

281 body size, high flight speeds and large flight ranges such as shorebirds, swifts and terns, or with
282 social learning, such as wildfowl and cranes. In these cases, most species may use initial large scale
283 sampling of sites or public information to end up in targeted areas.

284 Under the serial residency hypothesis, stochastic site selection, site fidelity and resultant migratory
285 connectivity are all scale-dependent. At a small scale – within a few hundred metres to less than 10
286 kilometres – any species may sample or use social information to choose sites in a non-random
287 fashion and this may even extend to 10 – 100 km. However sampling of or ability to choose sites on a
288 larger scale (greater than 100 km) is much less likely to occur, so at this scale, site choice may be
289 stochastic. Similarly, at a very large scale (greater than 1000 km) there is always migratory
290 connectivity (i.e. western Europe to west Africa).

291 ***Age-dependent site use and survival***

292 Juveniles are predicted to show greater variance of migration routes and number of stop-over sites in
293 time and space, and greater occurrence at lower quality sites, because they lack knowledge and
294 migration arrival location is stochastic. The degree to which a migrant will show predictable site re-use
295 in time and space across years within a species is also then modified by its age. As birds age we
296 expect them to become more site faithful, both because of natural selection removing those that have
297 not located suitable sites and because the value of a site probably increases with experience of it.
298 Moreover, any necessary shifts in sites have already been made earlier in life. Survival is therefore
299 predicted to be higher for adults than juveniles. Juvenile survival has been universally found to be
300 lower than adult survival in migrants (e.g. Sæther 1989, Donovan *et al.* 1995, Sæther & Bakke 2000),
301 but the underlying mechanisms predicted by the serial residency hypothesis remain to be tested.

302 ***Migratory connectivity***

303 Migratory connectivity is predicted to arise through spatial autocorrelation because populations from
304 the same area experience similar local constraints and so follow the same migration routes (Fig. 1).
305 Although selection of wintering sites for juveniles is predicted to be stochastic, local environmental
306 factors will constrain survivable routes and so influence and limit the potential outcomes. For example
307 a terrestrial migrant cannot find a wintering site if it ends up migrating too far to the west into the
308 Atlantic. Consequently we predict migratory connectivity as a consequence of these limitations (e.g.
309 Cano & Telleria 2013). This is particularly relevant to any comparisons between the Nearctic and

310 Palearctic migration systems because of the much smaller land availability in the former system:
311 migratory connectivity will be very much greater in the Nearctic even if the serial residency hypothesis
312 applies equally.

313 Distribution patterns in Africa (and so migratory connectivity) may also reflect past history,
314 environmental and cohort events. Initially, stochasticity and the costs of finding the best sites may
315 lead to selection of non-optimal sites by juveniles. Then inter-annual or decadal changes in local
316 climatic conditions on the wintering grounds – well recorded in Africa (Nicholson 2001) - may lead to
317 changes in the quality of these sites for the returning adults, which may return to the same site for
318 several years (Fig. 1). Consequently bird-habitat associations on the wintering grounds may be weak
319 (e.g. Wilson & Cresswell 2006, Cresswell *et al.* 2007, Hulme & Cresswell 2012). Furthermore, in years
320 in which the best sites for winter survival change there will be a greater proportion of juveniles
321 surviving to breed the following year, because adults become concentrated where conditions were
322 suitable previously (due to differential survival) whereas juveniles always end up over a wider area
323 (Fig. 1, panels iii & iv). For example, the serial residency hypothesis would predict that there would
324 have been a greater proportion of juvenile Common Whitethroats *Sylvia communis* returning to
325 western Europe in 1969, after the likely major change in typical habitat conditions in the Sahel during
326 the previous winter caused a >50% reduction in the size of the returning population (Winstanley *et al.*
327 1974).

328 A further possible influence on connectivity may arise through the use of more than one main
329 wintering site in Africa. Although stochasticity in initial site selection will apply independently of the
330 number of wintering sites, we know little about whether shifts between wintering sites are a gradual
331 drift south as conditions worsen (e.g. Cresswell *et al.* 2009), or represent a single-step flight (e.g.
332 Lemke *et al.* 2013). Gradual shifts southward would be more likely lead to fine scale optimal habitat
333 selection which would be perhaps more significant for the end of the winter when body condition
334 needs to be prioritised for migration back to Europe. Increased population level connectivity might
335 then result as birds concentrate in the best areas later in the winter. In contrast, intra-African migration
336 during the winter to a new site would be likely to lead to further stochasticity (again juveniles will not
337 know where they are going) and so further reduce population level connectivity. It is interesting to
338 note that the one Palearctic passerine migrant species that has been shown to have an intra-African
339 migration during the wintering period has also been shown to have the largest spread in wintering

340 destinations from a single breeding site and so the lowest migratory connectivity (Lemke *et al.* 2013,
341 Table 1).

342 ***Population resilience***

343 If a migrant bird shows serial residency, then it will rely on a series of individually unique, connected
344 sites in both space and time. The dependence on a chain of sites makes an individual migrant
345 relatively more vulnerable to change because the probability that any one site is affected by
346 environmental change increases with the number of sites used - 'multiple jeopardy' (Newton 2004).
347 Populations in which individuals have more stop-over sites will therefore be more likely to show
348 declines than those with fewer. The average number of stop-over sites for most species is unknown
349 and, although migration distance may be a proxy, inter-specific variation in migratory capability and
350 the availability of stop-over sites due to variation in average routes will confound this. Both passerine
351 and non-passerine species with longer migration distances to Africa have been shown to have
352 suffered larger declines (Sanderson *et al.* 2006, Møller 2008, Jones & Cresswell 2010), but
353 regardless of the number of sites used, loss of one may have the same effect, so that even shorter-
354 distance migrants will be affected by the loss of key sites. It is also important to note that there may
355 be circumstances when use of multiple sites increases fitness in a migrant, because it might allow
356 better adjustment of migratory timing (see below) or a bet-hedging strategy in the context of optimal
357 migration (Alerstam *et al.* 1990, Alerstam 2011).

358 The serial residency hypothesis, however, modifies the predictions of the 'multiple jeopardy'
359 hypothesis because it predicts that there will be intraspecific spatial and temporal variation in which
360 stop-over sites are used rather than simply just considering their number. Because initial discovery
361 and use of each site by juveniles is largely stochastic and untargeted except at a broad spatial scale,
362 each adult is likely to have a different series of linked sites. Therefore increased resilience at a
363 population level emerges as a prediction, for any given average number of sites used by a migrant
364 species. At least some first-year birds will discover functional links that can be re-used as adults,
365 including protected areas. These links will be different even within populations so that environmental
366 change will usually only affect some individuals of the population in any one year. Therefore, the
367 serial residency hypothesis predicts that populations with greater first-year stochasticity in route

368 finding will be more resilient to larger scale change (i.e. there will always be some first-year
369 individuals that find a functional linked chain of sites). These predictions have not been tested to date.
370 The extent of population resilience engendered by serial residency is however dependent on whether
371 environmental conditions limit availability of passage sites at any stage (i.e. migratory bottlenecks)
372 and on the spatial scale of environmental change. Populations that are concentrated at sites because
373 of bottlenecks will be more susceptible to anthropogenic change even if they otherwise follow the
374 predictions of the serial residency hypothesis. Large population declines have been shown to be
375 associated with bottlenecks (Baker *et al.* 2004, Verkuil *et al.* 2012), but in most cases we do not know
376 the degree to which most populations are concentrated into bottlenecks. Habitat specialisation will be
377 a proxy for this however, and species that are habitat specialists have been shown to have suffered
378 larger declines (Siriwardena *et al.* 1998, Gregory *et al.* 2004, 2007, Hewson *et al.* 2007). Additionally,
379 where change is operating over a large spatial scale, such as climate change, then most individuals in
380 a population might be affected, despite a wide spatial separation in sites and routes.

381 **Understanding and managing Palearctic passerine migrant declines**

382 Testing the predictions of the serial residency hypothesis will allow us better to understand why many
383 European passerine migrant bird species are declining, but in a very population-specific way. If there
384 is initial stochasticity of juvenile site selection on the wintering grounds such that there is only
385 migratory connectivity on a very large scale, then conditions throughout the wintering grounds affect
386 all breeding populations of a species (Taylor & Norris 2010). Some juveniles from a population end up
387 in good sites and others in poor sites, with average survival reflecting the relative availability of good
388 and poor sites across the African wintering range. Average juvenile survival over a very large scale is
389 then added to the breeding productivity of a population in an area of Europe being monitored on a
390 much smaller scale to give overall population change. Thus whether a particular breeding population
391 is declining, static or increasing may depend on the quality of the environment on the scale that the
392 population is being monitored in Europe, but the proportion of local populations that are declining,
393 static or increasing, may depend on the average quality of the environment over the whole wintering
394 area (Fig. 2). So as average environmental quality throughout Africa decreases (e.g. Lutz & Samir
395 2010), so the overall population trend for a migrant species is predicted to become more negative at
396 larger (e.g. European) scales. Consequently we may have highly variable population dynamics for

397 migrant species within Europe depending on country or area in which they breed, but an overarching
398 effect of quality of the wintering ground. Furthermore, because birds from specific wintering sites are
399 spread over a wide range of breeding sites, local wintering populations have some resilience against
400 destruction of specific breeding sites. Limiting factors which act locally (like piecemeal habitat
401 destruction) may then have less immediate impact on overall populations than factors, such as
402 climatic influences, that act simultaneously over wide areas.

403 The lack of small- or medium-scale migratory connectivity then has profound implications for any
404 hypotheses about where population limitation in Palearctic migrants occurs (e.g. Newton 2004, Taylor
405 & Norris 2010). Without large-scale connectivity, factors that affect breeding populations for any
406 relatively local scale breeding population monitored in Europe will always have a stronger effect than
407 factors measured at a local scale on the wintering ground. This is because any local detrimental
408 change in Africa will affect a population in Europe by reducing survival of only those individuals that
409 winter in the affected area, so these decreases will be diluted by the many individuals wintering in
410 other areas of Africa not affected by the local change. However, any detrimental change on the
411 breeding grounds in Europe will affect all individuals being monitored, so giving a stronger average
412 effect. The converse would apply if we monitored a wintering population. Any conclusion about the
413 relative strength of population limitation on the breeding and wintering grounds will therefore be
414 influenced by the location and the scale of the study from which it comes (Foppen *et al.* 1999,
415 Morrison *et al.* 2013b). For example, Willow Warblers *Phylloscopus trochilus* in Britain have very
416 different regional population trends (Morrison *et al.* 2010) but have the same wintering regions and
417 habitat requirements (Morrison *et al.* 2013a). Only by comparison of populations, species or functional
418 groups that differ fundamentally in their wintering habitats in Africa (e.g. Sahel vs forest) or have
419 different wintering areas on a very large geographical scale (e.g. east vs west Africa) will population
420 trend differences emerge that can be related to their wintering grounds (e.g. Sanderson *et al.* 2006,
421 Ockendon *et al.* 2012).

422 We would therefore predict that local breeding parameters would correlate more often, or more
423 strongly, with local breeding population trends than wintering parameters. Taking the ten most
424 declining migrant species in Europe and searching the most recent 150 papers or papers published
425 over a 10-year period on Web of Science using the keywords 'species name' and 'breeding' or
426 'wintering', eight species were the subject of studies that examined the relative effect of drivers of

427 local breeding population change. Almost all of these show local breeding parameters as a main
428 driver of local population change, including European Turtle Dove *Streptopelia turtur* (Browne &
429 Aebischer 2004), Wood Warbler *Phylloscopus sibilatrix* (Mallord *et al.* 2012), Willow Warbler (Hogstad
430 2005), Whinchat *Saxicola rubetra* (Grubler *et al.* 2008), European Pied Flycatcher *Ficedula hypoleuca*
431 (Both *et al.* 2006a), Eurasian Reed Warbler *Acrocephalus scirpaceus* (Harrison & Whitehouse 2012)
432 and Garden Warbler *Sylvia borin* (Widmer 1996). In contrast, only one study showed the dominance
433 of wintering conditions on local population dynamics, in Northern Wheatear (Arlt *et al.* 2008). But it is
434 again important to note that the importance of scale in this argument. As the geographic size of the
435 breeding population considered increases, so the importance of wintering conditions as drivers of
436 breeding population dynamics increases (Baillie & Peach 1992, Thingstad *et al.* 2006).

437 Stochastic site selection by juveniles at a large scale also has implications for the importance of
438 phenological mismatch (Jones & Cresswell 2010) in driving population dynamics of passerine
439 migrants. Critical to this hypothesis, whereby population declines are predicted because climate
440 change occurs disproportionately in the wintering and the breeding areas such that migrants arrive to
441 breed later than the local food peak, is that cues on the wintering ground may inform breeding arrival
442 times (e.g. Both *et al.* 2006b). If there is little migratory connectivity then it is unlikely that selection
443 can act for the use of winter climate cues to time migration. Only cues that correlate well with habitat
444 suitability across the entire wintering range can have a selective effect (e.g. Saino *et al.* 2007, van
445 Wijk *et al.* 2012). It seems likely therefore that selection will have acted on migrants to use timing
446 mechanisms independent of local climate cues, long before anthropogenic climate change may have
447 disrupted them. Only populations that have clear migratory bottlenecks, or that have greater migratory
448 connectivity because of common wintering or passage sites relatively close to the breeding ground,
449 might be expected to show migratory timing changes in response to breeding climate change (Both &
450 te Marvelde 2007, Both 2010, Rubolini *et al.* 2010, Tottrup *et al.* 2010).

451 The serial residency hypothesis has clear conservation implications. First, maintenance of a network
452 of protected areas on the wintering grounds will always protect some individuals from all populations
453 in Europe because juveniles redistribute annually, and so this will be the case even with climate
454 change, as long as the network of protected areas overall still embraces suitable habitat (Fig. 2).
455 Second, species with high stochasticity in initial site selection will also have diverse migration routes
456 promoting resilience and the effectiveness of a large network of conserved sites, regardless of

457 location. Third, any actions which promote the carrying capacity of habitats for such migrants
458 anywhere in Africa will benefit a large range of breeding populations in Europe, although these
459 actions would have to be very widespread to have detectable effects. In contrast, if a species has low
460 stochasticity in site selection then specific local solutions on the wintering grounds will be needed to
461 affect specific local European breeding populations, and identification, management and protection of
462 key wintering sites is then of utmost importance. Such species are also likely to have specific
463 migration routes with key bottleneck passage sites that require identification and conservation, with
464 alternative sites also conserved to insure against future anthropogenic and climate change. These
465 species will therefore be much more susceptible to anthropogenic climate and habitat change but will
466 also respond quickly to targeted local conservation initiatives.

467 Overall, the most important population implication of the serial residency hypothesis is perhaps that
468 we should expect average changes in conditions across African wintering grounds at a large scale to
469 more or less affect all European passerine migrant populations such that decadal changes in rainfall
470 or habitat change will cause groups of species sharing the same wintering habitats to show consistent
471 population changes. Some of these changes may reflect natural variation in rainfall patterns such as
472 periods of wet and dry in the Sahel, whereas others may reflect long term anthropogenic degradation
473 of wooded and savannah wintering habitats, or key passage sites. Any natural change or
474 conservation action that increases carrying capacity for migrants in suitable habitat in Africa will
475 positively affect Palearctic passerine migrant populations by increasing juvenile survival. However, if
476 the surrounding environment is degraded these local positive effects may be swamped by greater
477 large scale effects on juvenile survival. Therefore we need sustainable development solutions that
478 minimise the large scale average impact that the increasing human population in Africa has on its
479 habitats for migrant birds.

480 **Conclusion: passerine migrants must be generalists**

481 Serial residency may well be the consequence of selection to provide passerine migrants with a
482 mechanism to deal with the environmental change that we know occurs in Africa on a decadal, and
483 indeed, often an inter-annual basis, due to major variation in rainfall patterns (Nicholson 2001).
484 Therefore we should expect corresponding changes in juvenile survival to affect overall population
485 trends in Europe as part of this 'natural' dynamic system. For example, coincident with reduced

486 rainfall in the Sahel we have observed declines in Sahelian wintering species and these have now
487 reversed as Sahelian rainfall has increased through the last decade. In contrast, species wintering in
488 the Guinea savanna are now considered to have greater declines, where widespread anthropogenic
489 habitat modification is likely to be increasing (Thaxter *et al.* 2010, Ockendon *et al.* 2012). Much of the
490 variation we see in European migrant populations may therefore reflect 'normal' readjustment of the
491 distribution of migrants to climate variation in Africa. This does not mean that we should not be
492 concerned about migrant declines, because any anthropogenic degradation of the environment will
493 always affect European populations. But it does mean that we should always expect some migrant
494 populations to be increasing and some to be decreasing with decadal and even longer term changes
495 in climatic conditions (mainly rainfall variation) across Africa. We should also expect large decadal
496 changes in the distribution of Palearctic migrants in Africa to reflect these decadal changes in climatic
497 conditions. This may well be the case, as is hinted at by likely changes in distribution of the main
498 wintering and staging areas of Common Whitethroats during the last 40 years (Winstanley *et al.* 1974,
499 Vickery *et al.* 1999, Wilson & Cresswell 2006), although our information on distribution in west Africa
500 is at such poor temporal and spatial resolution that we would be unlikely to detect even very large
501 scale changes in distribution.

502 The serial residency hypothesis has implications for the evolutionary ecology of passerine migrants
503 generally, because if migratory connectivity only occurs at a large scale, then this is likely to lead to
504 selection for generalist traits. Those individuals in a population that are able to exploit a wide range of
505 habitats and conditions on the wintering grounds or during migration will be at a selective advantage
506 because their initial post-migration sites are likely to be more suitable than those of specialists. As has
507 been discussed above, there is evidence to suggest only weak co-variation of Palearctic migrant
508 density with habitat quality in Africa, and studies that have explored foraging or inter-specific
509 competition in Palearctic migrants in Africa have by and large described generalist traits (Salewski *et al.*
510 *et al.* 2003, Wilson & Cresswell 2007, Jones *et al.* 2010, Wilson & Cresswell 2010). There will also be
511 selection with respect to ability to deal with the increased range of environmental conditions
512 encountered (e.g. Møller & Szep 2011). Finally it has been suggested that higher within-clutch
513 variation of migratory orientation compared to within-clutch homogeneity may yield higher geometric
514 mean fitness in migratory populations (Reilly & Reilly 2009) suggesting that a generalist 'bet-hedging'
515 strategy in migrants is fundamental.

516 The degree to which a migrant species has fidelity to a site initially located stochastically, and the
517 scale at which the stochasticity operates, will determine whether the predictions outlined here apply.
518 Therefore there is a clear priority for research to enable identification of those species to which the
519 serial residency hypothesis applies. In general, we would expect it to apply wherever a species is
520 generalist and associated with wintering habitats that shift in space and time over a period of
521 decades. Then, the key research area is juvenile site selection and survival. Currently, these
522 parameters are inadequately monitored because variable natal site fidelity confounds estimates of
523 true survival of birds over the first winter. Nevertheless, losses between fledging and the following
524 breeding season, when estimated, have been shown to be important in the population dynamics of
525 many migrant species (Baillie & Peach 1992, Newton 1998). In particular, we need studies of how the
526 initial degree of stochasticity in site selection by juveniles affects survival and how wintering habitat
527 quality affects survival of migrants in their wintering area.

528 In conclusion, the serial residency hypothesis provides a framework to explain many of the population
529 dynamics of passerine migrant birds, and perhaps those of many non-passerines. Two simple rules
530 that are reasonably supported by empirical evidence lead to a large number of predictions that are,
531 when they have actually been tested, supported by further empirical evidence. But perhaps the most
532 important implication is that serial residency is a migratory strategy that must have evolved to deal
533 with environmental change: it allows some individuals from a brood to survive even in spatially
534 unpredictable environments. Therefore we might always expect high levels of variation in migrant
535 population trends and their distribution, particularly within the highly dynamic context of environmental
536 change in Africa.

537

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542

543 **References**

- 544 **Akesson, S.** 2003. Avian long-distance navigation: experiments with migratory birds. In Berthold, P., Gwinner, E.
545 & Sonnenschein, E. (eds.) *Avian Migration*: 471-492. Berlin: Springer-Verlag.
- 546 **Alerstam, T.** 2011. Optimal bird migration revisited. *J. Ornith.* **152**: 5-23.
- 547 **Alerstam, T., Hake, M. & Kjellen, N.** 2006. Temporal and spatial patterns of repeated migratory journeys by
548 ospreys. *Anim. Behav.* **71**: 555-566.
- 549 **Alerstam, T., Lindstrom, A. & Gwinner, E.** 1990. Optimal bird migration: the relative importance of time, energy
550 and safety. In Gwinner, E. (eds.) *Bird Migration: physiology and ecophysiology*: 331-351. Berlin:
551 Springer-Verlag.
- 552 **Arlt, D., Forslund, P., Jeppsson, T. & Part, T.** 2008. Habitat-Specific Population Growth of a Farmland Bird.
553 *PLoS ONE DOI: 10.1371/journal.pone.0003006*.
- 554 **Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J.W., Afanasyev, V. & Liechti, F.** 2010. Year-
555 Round Tracking of Small Trans-Saharan Migrants Using Light-Level Geolocators. *PLoS ONE DOI:*
556 **10.1371/journal.pone.0009566**: e9566.
- 557 **Baillie, S.R. & Peach, W.J.** 1992. Population limitation in Palearctic-African passerine migrants. *Ibis* **134 (suppl.**
558 **1)**: 120-132.
- 559 **Baker, A.J., Gonzalez, P.M., Piersma, T., Niles, L.J., do Nascimento, I.D.S., Atkinson, P.W., Clark, N.A.,**
560 **Minton, C.D.T., Peck, M.K. & Aarts, G.** 2004. Rapid population decline in red knots: fitness
561 consequences of decreased refuelling rates and late arrival in Delaware Bay. *P. Roy. Soc. Lond. B Bio.*
562 **271**: 875-882.
- 563 **Beckett, S.R. & Proudfoot, G.A.** 2011. Large-scale movement and migration of northern saw-whet owls Eastern
564 North America. *Wilson J. Ornithol.* **123**: 521-535.
- 565 **Benvenuti, S. & Ioalè, P.** 1980. Homing experiments with birds displaced from their wintering ground. *J.*
566 *Ornithol.* **121**: 281-286.
- 567 **Bernard, M.J., Goodrich, L.J., Tzilkowski, W.M. & Brittingham, M.C.** 2011. Site fidelity and lifetime territorial
568 consistency of ovenbirds (*Seiurus aurocapilla*) in a contiguous forest. *Auk* **128**: 633-642.
- 569 **Berthold, P.** 2001. *Bird Migration: A general survey*. Oxford: Oxford University Press.
- 570 **Berthold, P., Bossche, W., Jakubiec, Z., Kaatz, C., Kaatz, M. & Querner, U.** 2002. Long-term satellite tracking
571 sheds light upon variable migration strategies of White Storks (*Ciconia ciconia*). *J. Ornithol.* **143**: 489-
572 493.
- 573 **Betts, M.G., Hadley, A.S., Rodenhouse, N. & Nocera, J.J.** 2008. Social information trumps vegetation structure
574 in breeding-site selection by a migrant songbird. *P. Roy. Soc. Lond. B Bio.* **275**: 2257-2263.
- 575 **Both, C.** 2010. Flexibility of Timing of Avian Migration to Climate Change Masked by Environmental Constraints
576 En Route. *Curr. Biol.* **20**: 243-248.
- 577 **Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E.** 2006a. Climate change and population declines in a
578 long-distance migratory bird. *Nature* **441**: 81-83.
- 579 **Both, C., Sanz, J.J., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuizen, A.J., Enemar, A., Javinen, A.,**
580 **Nyholm, N.E.I., Potti, J., Ravussin, P.A., Silverin, B., Slater, F.M., Sokolov, L.V., Visser, M.E.,**
581 **Winkel, W., Wright, J. & Zang, H.** 2006b. Pied Flycatchers *Ficedula hypoleuca* travelling from Africa to
582 breed in Europe: differential effects of winter and migration conditions on breeding date. *Ardea* **94**: 511-
583 525.
- 584 **Both, C. & te Marvelde, L.** 2007. Climate change and timing of avian breeding and migration throughout Europe.
585 *Clim. Res.* **35**: 93-105.

- 586 **Brandt, M.J. & Cresswell, W.** 2009. Diurnal foraging routines in a tropical bird, the rock finch *Lagonosticta*
587 *sanguinolondorsalis*: how important is predation risk? *J. Av. Biol.* **40**: 90-94.
- 588 **Browne, S.J. & Aebischer, N.J.** 2004. Temporal changes in the breeding ecology of European Turtle Doves
589 *Streptopelia turtur* in Britain, and implications for conservation. *Ibis* **146**: 125-137.
- 590 **Buchanan, J.B., Salzer, L.J., Wiles, G.J., Brady, K., Desimone, S.M. & Michaelis, W.** 2011. An investigation
591 of Red Knot *Calidris canutus* spring migration at Grays Harbor and Willapa Bay, Washington. *Wader*
592 *Study Group Bull.* **118**: 97-104.
- 593 **Cano, L.S. & Telleria, J.L.** 2013. Migration and winter distribution of Iberian and central European black storks
594 *Ciconia nigra* moving to Africa across the Strait of Gibraltar: a comparative study. *J. Av. Biol.* **44**: 189-
595 197.
- 596 **Catry, P., Encarnacao, V., Araujo, A., Fearon, P., Fearon, A., Armelin, M. & Delaloye, P.** 2004. Are long-
597 distance migrant passerines faithful to their stopover sites? *J. Av. Biol.* **35**: 170-181.
- 598 **Chernetsov, N., Kishkinev, D., Gashkov, S., Kosarev, V. & Bolshakov, C.V.** 2008. Migratory programme of
599 juvenile pied flycatchers, *Ficedula hypoleuca*, from Siberia implies a detour around Central Asia. *Anim.*
600 *Behav.* **75**: 539-545.
- 601 **Chevallier, D., Le Maho, Y., Brossault, P., Baillon, F. & Massemin, S.** 2011. The use of stopover sites by
602 Black Storks (*Ciconia nigra*) migrating between West Europe and West Africa as revealed by satellite
603 telemetry. *J. Ornith.* **152**: 1-13.
- 604 **Cilimburg, A.B., Lindberg, M.S., Tewksbury, J.J. & Hejl, S.J.** 2002. Effects of dispersal on survival probability
605 of adult yellow warblers (*Dendroica petechia*). *Auk* **119**: 778-789.
- 606 **Clarke, M.F., Dasilva, K.B., Lair, H., Pocklington, R., Kramer, D.L. & McLaughlin, R.L.** 1993. Site familiarity
607 affects escape behavior of the eastern chipmunk, *Tamias striatus*. *Oikos* **66**: 533-537.
- 608 **Conklin, J.R. & Battley, P.F.** 2012. Carry-over effects and compensation: late arrival on non-breeding grounds
609 affects wing moult but not plumage or schedules of departing bar-tailed godwits *Limosa lapponica*
610 *baueri*. *J. Av. Biol.* **43**: 252-263.
- 611 **Cresswell, B. & Edwards, D.** 2012. Geolocators reveal wintering areas of European Nightjar (*Caprimulgus*
612 *europaeus*). *Bird Study* **60**: 77-86.
- 613 **Cresswell, W.** 2011. Predation in bird populations. *J. Ornith.* **152**: 251-263.
- 614 **Cresswell, W., Boyd, M. & Stevens, M.** 2009. Movements of Palearctic and Afrotropical bird species during the
615 dry season (November-February) within Nigeria. In Harebottle, D.M., Craig, A.J.F.K., Anderson, M.D.,
616 Rakotomanana, H. & Muchai (eds.) *Proceedings of the 12th Pan African Ornithological Congress, 2008*:
617 18-28. Cape Town: Animal Demography Unit.
- 618 **Cresswell, W., Wilson, J.M., Vickery, J., Jones, P. & Holt, S.** 2007. Changes in densities of Sahelian bird
619 species in response to recent habitat degradation. *Ostrich* **78**: 247-253.
- 620 **Cuadrado, M.** 1997. Why are migrant robins (*Erithacus rubecula*) territorial in winter?: The importance of anti-
621 predatory behaviour. *Ethol. Ecol. Evol.* **9**: 77-88.
- 622 **Deutschlander, M.E., Phillips, J.B. & Munro, U.** 2012. Age-dependent orientation to magnetically-simulated
623 geographic displacements in migratory Australian silvereyes (*Zosterops lateralis*). *Wilson J. Ornithol.*
624 **124**: 467-477.
- 625 **Donovan, T.M., Thompson, F.R., III, Faaborg, J. & Probst, J.R.** 1995. Reproductive Success of Migratory
626 Birds in Habitat Sources and Sinks. *Cons. Biol.* **9**: 1380-1395.
- 627 **Eeva, T., Ahola, M., Laaksonen, T. & Lehikoinen, E.** 2008. The effects of sex, age and breeding success on
628 breeding dispersal of pied flycatchers along a pollution gradient. *Oecologia* **157**: 231-238.
- 629 **Elkins, N.** 1983. *Weather and Bird Behaviour*. Calton, England: T & AD Poyser.

- 630 **Erni, B., Liechti, F. & Bruderer, B.** 2005. The role of wind in passerine autumn migration between Europe and
631 Africa. *Behav. Ecol.* **16**: 732-740.
- 632 **European Bird Census Council.** 2012. Trends of common birds in Europe, 2012 update.
633 <http://www.ebcc.info/index.php?ID=485>.
- 634 **Faaborg, J. & Arendt, W.J.** 1984. Population Sizes and Philopatry of Winter Resident Warblers in Puerto Rico.
635 *J. Field Ornithol.* **55**: 376-378.
- 636 **Ferreira Rodrigues, A.A., Lyra Lopes, A.T., Goncalves, E.C., Silva, A. & Cruz Schneider, M.P.** 2007.
637 Philopatry of the Semipalmated Sandpiper (*Calidris pusilla*) on the Brazilian Amazonian coast. *Ornitol.*
638 *Neotrop.* **18**: 285-291.
- 639 **Foerschler, M.I., del Val, E. & Bairlein, F.** 2010. Extraordinary high natal philopatry in a migratory passerine. *J.*
640 *Ornith.* **151**: 745-748.
- 641 **Foppen, R., ter Braak, C.J.F., Verboom, J. & Reijnen, R.** 1999. Dutch sedge warblers *Acrocephalus*
642 *schoenobaenus* and West-African rainfall: empirical data and simulation modelling show low population
643 resilience in fragmented marshlands. *Ardea* **87**: 113-127.
- 644 **Gavashelishvili, A., McGrady, M., Ghasabian, M. & Bildstein, K.L.** 2012. Movements and habitat use by
645 immature Cinereous Vultures (*Aegypius monachus*) from the Caucasus. *Bird Study* **59**: 449-462.
- 646 **Greenwood, P.J. & Harvey, P.H.** 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* **13**: 1-
647 21.
- 648 **Gregory, R.D., Noble, D.G. & Custance, J.** 2004. The state of play of farmland birds: population trends and
649 conservation status of lowland farmland birds in the United Kingdom. *Ibis* **146**: 1-13.
- 650 **Gregory, R.D., Vorisek, P., Van Strien, A., Meyling, A.W.G., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P.**
651 **& Burfield, I.J.** 2007. Population trends of widespread woodland birds in Europe. *Ibis* **149**: 78-97.
- 652 **Grubler, M.U., Schuler, H., Muller, M., Spaar, R., Horch, P. & Naef-Daenzer, B.** 2008. Female biased mortality
653 caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow
654 bird. *Biol. Cons.* **141**: 3040-3049.
- 655 **Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M. & Sutherland, W.J.** 2005. Seasonal matching of habitat
656 quality and fitness in a migratory bird. *P. Roy. Soc. Lond. B Bio.* **272**: 2319-2323.
- 657 **Hahn, B.A. & Silverman, E.D.** 2006. Social cues facilitate habitat selection: American redstarts establish
658 breeding territories in response to song. *Biol. Lett-UK* **2**: 337-340.
- 659 **Harrison, N. & Whitehouse, M.** 2012. Drivers of songbird productivity at a restored gravel pit: Influence of
660 seasonal flooding and rainfall patterns and implications for habitat management. *Agric. Ecosyst.*
661 *Environ.* **162**: 138-143.
- 662 **Heckscher, C.M., Taylor, S.M., Fox, J.W. & Afanasyev, V.** 2011. Veery (*Catharus fuscescens*) wintering
663 locations, migratory connectivity, and a revision of its winter range using geolocator technology. *Auk*
664 **128**: 531-542.
- 665 **Hedenström, A., Bensch, S., Hasselquist, D., Lockwood, M. & Ottosson, U.** 1993. Migration, stopover and
666 moult of the great reed warbler *Acrocephalus arundinaceus* in Ghana, West Africa. *Ibis* **135**: 177-180.
- 667 **Hewson, C.M., Amar, A., Lindsell, J.A., Thewlis, R.M., Butler, S., Smith, K. & Fuller, R.J.** 2007. Recent
668 changes in bird populations in British broadleaved woodland. *Ibis* **149**: 14-28.
- 669 **Hinnebusch, D.M., Therrien, J.F., Valiquette, M.A., Robertson, B., Robertson, S. & Bildstein, K.L.** 2010.
670 Survival, site fidelity, and population trends of American kestrels wintering in southwestern Florida.
671 *Wilson J. Ornithol.* **122**: 475-483.
- 672 **Hogstad, O.** 2005. Numerical and functional responses of breeding passerine species to mass occurrence of
673 geometrid caterpillars in a subalpine birch forest: a 30-year study. *Ibis* **147**: 77-91.

- 674 **Holland, R.A. & Helm, B.** 2013. A strong magnetic pulse affects the precision of departure direction of naturally
675 migrating adult but not juvenile birds. *J. Roy. Soc. Interface* **10**: 20121047.
- 676 **Hoover, J.P.** 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* **84**: 416-
677 430.
- 678 **Hope, D.D., Lank, D.B., Smith, B.D. & Ydenberg, R.C.** 2011. Migration of two calidrid sandpiper species on the
679 predator landscape: how stopover time and hence migration speed vary with geographical proximity to
680 danger. *J. Av. Biol.* **42**: 522-529.
- 681 **Hosner, P.A. & Winkler, D.W.** 2007. Dispersal distances of Tree Swallows estimated from continent-wide and
682 limited-area data. *J. Field Ornithol.* **78**: 290-297.
- 683 **Howlett, J.S. & Stutchbury, B.J.M.** 2003. Determinants of between-season site, territory, and mate fidelity in
684 hooded warblers (*Wilsonia citrina*). *Auk* **120**: 457-465.
- 685 **Hulme, M.F. & Cresswell, W.** 2012. Density and behaviour of Whinchats *Saxicola rubetra* on African farmland
686 suggest that winter habitat conditions do not limit European breeding populations. *Ibis* **154**: 680-692.
- 687 **Ilieva, M., Toews, D.P.L., Bensch, S., Sjöholm, C. & Akesson, S.** 2012. Autumn migratory orientation and
688 displacement responses of two willow warbler subspecies (*Phylloscopus trochilus trochilus* and *P. t.*
689 *acredula*) in South Sweden. *Behav. Process.* **91**: 253-261.
- 690 **Iverson, S.A. & Esler, D.** 2006. Site fidelity and the demographic implications of winter movements by a
691 migratory bird, the harlequin duck *Histrionicus histrionicus*. *J. Av. Biol.* **37**: 219-228.
- 692 **Iverson, S.A., Esler, D. & Rizzolo, D.J.** 2004. Winter philopatry of Harlequin Ducks in Prince William Sound,
693 Alaska. *Condor* **106**: 711-715.
- 694 **Jahn, A.E., Cueto, V.R., Cecilia Sagario, M., Maria Mamani, A., Quillen Vidoz, J., Lopez de Casenave, J. &**
695 **Di Giacomo, A.G.** 2009. Breeding and winter site fidelity among eleven neotropical austral migrant bird
696 species. *Ornitol. Neotrop.* **20**: 275-283.
- 697 **Johnson, E.I., DiMicali, J.K., Stouffer, P.C. & Brooks, M.E.** 2011. Habitat use does not reflect habitat quality
698 for Henslow's sparrows (*Ammodramus henslowii*) wintering in fire-managed longleaf pine savannas.
699 *Auk* **128**: 564-576.
- 700 **Johnson, E.I., DiMiceli, J.K. & Stouffer, P.C.** 2009. Timing of migration and patterns of winter settlement by
701 Henslow's sparrows. *Condor* **111**: 730-739.
- 702 **Jones, P., Salewski, V., Vickery, J. & Mapaure, I.** 2010. Habitat use and densities of co-existing migrant Willow
703 Warblers *Phylloscopus trochilus* and resident eremomelas *Eremomela* spp. in Zimbabwe. *Bird Study* **57**:
704 44-55.
- 705 **Jones, P.J.** 1995. Migration strategies of Palearctic passerines in Africa. *Israel J. Zool.* **41**: 393-406.
- 706 **Jones, T. & Cresswell, W.** 2010. The phenology mismatch hypothesis: are declines of migrant birds linked to
707 uneven global climate change? *J. Anim. Ecol.* **79**: 98-108.
- 708 **Karlsson, H., Backman, J., Nilsson, C. & Alerstam, T.** 2010. Exaggerated orientation scatter of nocturnal
709 passerine migrants close to breeding grounds: comparisons between seasons and latitudes. *Behav.*
710 *Ecol. Sociobiol.* **64**: 2021-2031.
- 711 **Karlsson, H., Nilsson, C., Backman, J. & Alerstam, T.** 2011. Nocturnal passerine migration without tailwind
712 assistance. *Ibis* **153**: 485-493.
- 713 **King, J.M.B. & Hutchinson, J.M.C.** 2001. Site fidelity and recurrence of some migrant bird species in The
714 Gambia. *Ringing & Migration* **20**: 292-302.
- 715 **Kochert, M.N., Fuller, M.R., Schueck, L.S., Bond, L., Bechard, M.J., Woodbridge, B., Holroyd, G.L., Martell,**
716 **M.S. & Banasch, U.** 2011. Migration patterns, use of stopover areas, and austral summer movements
717 of Swainson's Hawks. *Condor* **113**: 89-106.

- 718 **Kristensen, M.W., Tøttrup, A.P. & Thorup, K.** 2013. Migration of the Common Redstart (*Phoenicurus*
719 *phoenicurus*): A Eurasian Songbird Wintering in Highly Seasonal Conditions in the West African Sahel.
720 *Auk* **130**: 258-264.
- 721 **Kullberg, C., Lind, J., Fransson, T., Jakobsson, S. & Vallin, A.** 2003. Magnetic cues and time of season affect
722 fuel deposition in migratory thrush nightingales (*Luscinia luscinia*). *P. Roy. Soc. Lond. B Bio.* **270**: 373-
723 378.
- 724 **Leisler, B.** 1990. Selection and use of habitat of wintering migrants. In Gwinner, E. (eds.) *Bird Migration:*
725 *physiology and ecophysiology*: 156-174. Berlin: Springer-Verlag.
- 726 **Lemke, H.W., Tarka, M., Klaassen, R.H.G., Åkesson, M., Bensch, S., Hasselquist, D. & Hansson, B.** 2013.
727 Annual Cycle and Migration Strategies of a Trans-Saharan Migratory Songbird: A Geolocator Study in
728 the Great Reed Warbler. *PLoS ONE* DOI: [10.1371/journal.pone.0079209](https://doi.org/10.1371/journal.pone.0079209).
- 729 **Leyrer, J., Spaans, B., Camara, M. & Piersma, T.** 2006. Small home ranges and high site fidelity in red knots
730 (*Calidris c. canutus*) wintering on the Banc d'Arguin, Mauritania. *J. Ornith.* **147**: 376-384.
- 731 **Liechti, F.** 2006. Birds: blowin' by the wind? *J. Ornith.* **147**: 202-211.
- 732 **Liminana, R., Soutullo, A., Urios, V. & Reig-Ferrer, A.** 2012. Migration and wintering areas of adult Montagu's
733 Harriers (*Circus pygargus*) breeding in Spain. *J. Ornith.* **153**: 85-93.
- 734 **Lind, J. & Cresswell, W.** 2006. Anti-predation behaviour during bird migration; the benefit of studying multiple
735 behavioural dimensions. *J. Ornith.* **147**: 310-316.
- 736 **Liu, Y., Keller, I. & Heckel, G.** 2012. Breeding site fidelity and winter admixture in a long-distance migrant, the
737 tufted duck (*Aythya fuligula*). *Heredity* **109**: 108-116.
- 738 **Lok, T., Overdijk, O., Tinbergen, J.M. & Piersma, T.** 2011. The paradox of spoonbill migration: most birds
739 travel to where survival rates are lowest. *Anim. Behav.* **82**: 837-844.
- 740 **Lutz, W. & Samir, K.C.** 2010. Dimensions of global population projections: what do we know about future
741 population trends and structures? *Philos. T. Roy. Soc. B* **365**: 2779-2791.
- 742 **Mallord, J.W., Charman, E.C., Cristinacce, A. & Orsman, C.J.** 2012. Habitat associations of Wood Warblers
743 *Phylloscopus sibilatrix* breeding in Welsh oakwoods. *Bird Study* **59**: 403-415.
- 744 **Marra, P.P. & Holmes, R.T.** 2001. Consequence of dominance-mediated habitat segregation in American
745 redstarts during the non-breeding season. *The Auk* **118**: 92-104.
- 746 **McGrady, M.J., Ueta, M., Potapov, E.R., Utekhina, I., Masterov, V., Ladyguine, A., Zykov, V., Cibor, J.,**
747 **Fuller, M. & Seegar, W.S.** 2003. Movements by juvenile and immature Steller's Sea Eagles *Haliaeetus*
748 *pelagicus* tracked by satellite. *Ibis* **145**: 318-328.
- 749 **Merom, K., Yom-Tov, Y. & McCleery, R.** 2000. Philopatry to stopover site and body condition of transient Reed
750 Warblers during autumn migration through Israel. *Condor* **102**: 441-444.
- 751 **Mettke-Hofmann, C. & Greenberg, R.** 2005. Behavioral and cognitive adaptations to long-distance migration. In
752 Greenberg, R. & Marra, P.P. (eds.) *Birds of two worlds: the ecology and evolution of migration*: 114-
753 123. Baltimore, Maryland: John Hopkins University Press.
- 754 **Mewaldt, R.** 1964. California sparrows return from displacement to Maryland. *Science* **146**: 941-942.
- 755 **Middleton, H.A., Morrissey, C.A. & Green, D.J.** 2006. Breeding territory fidelity in a partial migrant, the
756 American dipper *Cinclus mexicanus*. *J. Av. Biol.* **37**: 169-178.
- 757 **Møller, A.P.** 2008. Flight distance and population trends in European breeding birds. *Behav. Ecol.* **19**: 1095-
758 1102.
- 759 **Møller, A.P. & Szep, T.** 2011. The role of parasites in ecology and evolution of migration and migratory
760 connectivity. *J. Ornith.* **152**: 141-150.

- 761 **Moreau, R.E.** 1969. The recurrence in winter quarters (Ortstreue) of trans-Saharan migrants. *Bird Study* **16**: 108-
762 110.
- 763 **Morel, G.J. & Morel, M.Y.** 1992. Habitat use by Palearctic migrant passerines in West Africa. *Ibis* **134 (Suppl.**
764 **1)**: 83-88.
- 765 **Morrison, C.A., Robinson, R.A., Clark, J.A. & Gill, J.A.** 2010. Spatial and temporal variation in population
766 trends in a long-distance migratory bird. *Divers. Distrib.* **16**: 620-627.
- 767 **Morrison, C.A., Robinson, R.A., Clark, J.A., Marca, A.D., Newton, J. & Gill, J.A.** 2013a. Using stable isotopes
768 to link breeding population trends to winter ecology in Willow Warblers, *Phylloscopus trochilus*. *Bird*
769 *Study*: 1-10.
- 770 **Morrison, C.A., Robinson, R.A., Clark, J.A., Risely, K. & Gill, J.A.** 2013b. Recent population declines in Afro-
771 Palaeartic migratory birds: the influence of breeding and non-breeding seasons. *Divers. Distrib.* **19**:
772 1051-1058.
- 773 **Mouritsen, H.** 2003. Spatiotemporal Orientation Strategies of Long-Distance Migrants. In Berthold, P., Gwinner,
774 E. & Sonnenschein, E. (eds.) *Avian Migration*: 493-513. Springer Berlin Heidelberg.
- 775 **Mueller, T., O'Hara, R.B., Converse, S.J., Urbanek, R.P. & Fagan, W.F.** 2013. Social Learning of Migratory
776 Performance. *Science* **341**: 999-1002.
- 777 **Nevoux, M., Barbraud, J.-C. & Barbraud, C.** 2008. Nonlinear impact of climate on survival in a migratory white
778 stork population. *J. Anim. Ecol.* **77**: 1143-1152.
- 779 **Newton, I.** 1998. *Population limitation in birds*. London: Academic Press.
- 780 **Newton, I.** 2004. Population limitation in migrants. *Ibis* **146**: 197-226.
- 781 **Newton, I.** 2008. *The migration ecology of birds*. Oxford: Academic Press.
- 782 **Newton, I.** 2012. Obligate and facultative migration in birds: ecological aspects. *J. Ornith.* **153**: S171-S180.
- 783 **Nicholson, S.E.** 2001. Climatic and environmental change in Africa during the last two centuries. *Clim. Res.* **17**:
784 123-144.
- 785 **Ockendon, N., Hewson, C.M., Johnston, A. & Atkinson, P.W.** 2012. Declines in British-breeding populations of
786 Afro-Palaeartic migrant birds are linked to bioclimatic wintering zone in Africa, possibly via constraints
787 on arrival time advancement. *Bird Study* **59**: 111-125.
- 788 **Oring, L.W.** 1982. Avian Mating Systems. In Farner, D.S. & King, J.R. (eds.) *Avian Biology*: 1-92. New York:
789 Academic.
- 790 **Pearson, D.J. & Lack, P.C.** 1992. Migration patterns and habitat use by passerine and near-passerine migrant
791 birds in eastern Africa. *Ibis* **134 S1**: 89-98.
- 792 **Perdeck, A.C.** 1958. Two types of orientation in migrating starlings, *Sturnus vulgaris* L., and Chaffinches,
793 *Fringilla coelebs* L., as revealed by displacement experiments. *Ardea* **46**: 1-37.
- 794 **Perdeck, A.C.** 1967. Orientation of Starlings after displacement to Spain. *Ardea* **55**: 93-104.
- 795 **Perez-Tris, J., Bensch, S., Carbonell, R., Helbig, A.J. & Telleria, J.L.** 2004. Historical diversification of
796 migration patterns in a passerine bird. *Evolution* **58**: 1819-1832.
- 797 **Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Bennett, V.J.** 2005. Summer distribution and
798 migration of nonbreeding albatrosses: Individual consistencies and implications for conservation.
799 *Ecology* **86**: 2386-2396.
- 800 **Piper, W.H.** 2011. Making habitat selection more "familiar": a review. *Behav. Ecol. Sociobiol.* **65**: 1329-1351.
- 801 **Prochazka, P., Hobson, K.A., Karcza, Z. & Kralj, J.** 2008. Birds of a feather winter together: migratory
802 connectivity in the Reed Warbler *Acrocephalus scirpaceus*. *J. Ornith.* **149**: 141-150.

- 803 **Rabøl, F.** 1987. Coexistence and competition between overwintering willow warblers *Phylloscopus trochilus* and
804 local warblers at Lake Naivasha, Kenya. *Ornis. Scand.* **18**: 101-121.
- 805 **Reilly, J.R. & Reilly, R.J.** 2009. Bet-hedging and the orientation of juvenile passerines in fall migration. *J. Anim.*
806 *Ecol.* **78**: 990-1001.
- 807 **Robinson, B.G. & Merrill, E.H.** 2013. Foraging–vigilance trade-offs in a partially migratory population: comparing
808 migrants and residents on a sympatric range. *Anim. Behav.* **85**: 849-856.
- 809 **Rubolini, D., Saino, N. & Møller, A.P.** 2010. Migratory behaviour constrains the phenological response of birds
810 to climate change. *Clim. Res.* **42**: 45-55.
- 811 **Sæther, B.-E.** 1989. Survival Rates in Relation to Body Weight in European Birds. *Ornis. Scand.* **20**: 13-21.
- 812 **Sæther, B.-E. & Bakke, O.** 2000. Avian Life History Variation and Contribution of Demographic Traits to the
813 Population Growth Rate. *Ecology* **81**: 642-653.
- 814 **Saino, N., Rubolini, D., Jonzen, N., Ergon, T., Montemaggiore, A., Stenseth, N.C. & Spina, F.** 2007.
815 Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan
816 migratory birds. *Clim. Res.* **35**: 123-134.
- 817 **Salewski, V., Bairlein, F. & Leisler, B.** 2003. Niche partitioning of two Palearctic passerine migrants with
818 Afrotropical residents in their West African winter quarters. *Behav. Ecol.* **14**: 493-502.
- 819 **Salewski, V. & Jones, P.** 2006. Palearctic passerines in Afrotropical environments: a review. *J. Ornith.* **147**: 192-
820 201.
- 821 **Sandercock, B.K. & Jaramillo, A.** 2002. Annual survival rates of wintering sparrows: Assessing demographic
822 consequences of migration. *Auk* **119**: 149-165.
- 823 **Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. & van Bommel, F.P.J.** 2006. Long-term population
824 declines in Afro-Palearctic migrant birds. *Biol. Cons.* **131**: 93-105.
- 825 **Schaub, M. & von Hirschheydt, J.** 2009. Effect of current reproduction on apparent survival, breeding dispersal,
826 and future reproduction in barn swallows assessed by multistate capture-recapture models. *J. Anim.*
827 *Ecol.* **78**: 625-635.
- 828 **Schlossberg, S.** 2009. Site fidelity of shrubland and forest birds. *Condor* **111**: 238-246.
- 829 **Seavy, N.E., Humple, D.L., Cormier, R.L. & Gardali, T.** 2012. Establishing the breeding provenance of a
830 temperate-wintering North American passerine, the Golden-Crowned Sparrow, using light-level
831 geolocation. *PLoS ONE* DOI: [10.1371/journal.pone.0034886](https://doi.org/10.1371/journal.pone.0034886).
- 832 **Sedgwick, J.A.** 2004. Site fidelity, territory fidelity, and natal philopatry in willow flycatchers (*Empidonax traillii*).
833 *Auk* **121**: 1103-1121.
- 834 **Sergio, F., Blas, J. & Hiraldo, F.** 2009. Predictors of floater status in a long-lived bird: a cross-sectional and
835 longitudinal test of hypotheses. *J. Anim. Ecol.* **78**: 109-118.
- 836 **Shutler, D. & Clark, R.G.** 2003. Causes and consequences of tree swallow (*Tachycineta bicolor*) dispersal in
837 Saskatchewan. *Auk* **120**: 619-631.
- 838 **Sillett, T.S. & Holmes, R.T.** 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *J.*
839 *Anim. Ecol.* **71**: 296-308.
- 840 **Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D.** 1998. Trends
841 in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census
842 indices. *J. Appl. Ecol.* **35**: 24-43.
- 843 **Somershoe, S.G., Cohrs, D.G. & Cohrs, D.A.** 2009. Stopover-site Fidelity at a Near-coastal Banding Site in
844 Georgia. *Southeast. Nat.* **8**: 537-546.

- 845 **Stanley, C.Q., MacPherson, M., Fraser, K.C., McKinnon, E.A. & Stutchbury, B.J.M.** 2012. Repeat tracking of
846 individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE*
847 **DOI:10.1371/journal.pone.0041818.**
- 848 **Strandberg, R., Hake, M., Klaassen, R.H.G. & Alerstam, T.** 2012. Movements of Immature European Honey
849 Buzzards *Pernis apivorus* in Tropical Africa. *Ardea* **100**: 157-162.
- 850 **Strandberg, R., Klaassen, R.H.G., Hake, M. & Alerstam, T.** 2010. How hazardous is the Sahara Desert
851 crossing for migratory birds? Indications from satellite tracking of raptors. *Biol. Lett-UK* **6**: 297-300.
- 852 **Strandberg, R., Klaassen, R.H.G., Hake, M., Olofsson, P., Thorup, K. & Alerstam, T.** 2008. Complex timing of
853 Marsh Harrier *Circus aeruginosus* migration due to pre- and post-migratory movements. *Ardea* **96**: 159-
854 171.
- 855 **Strandberg, R., Klaassen, R.H.G., Olofsson, P. & Alerstam, T.** 2009. Daily travel schedules of adult Eurasian
856 Hobbies *Falco subbuteo* - variability in flight hours and migration speed along the route. *Ardea* **97**: 287-
857 295.
- 858 **Strong, A.M. & Sherry, T.W.** 2000. Habitat-specific effects of food abundance on the condition of ovenbirds
859 wintering in Jamaica. *J. Anim. Ecol.* **69**: 883-895.
- 860 **Studds, C.E., Kyser, T.K. & Marra, P.P.** 2008. Natal dispersal driven by environmental conditions interacting
861 across the annual cycle of a migratory songbird. *P. Natl. Acad. Sci. USA* **105**: 2929-2933.
- 862 **Sutherland, G.D., Harestad, A.S., Price, K. & Lertzman, K.P.** 2000. Scaling of natal dispersal distances in
863 terrestrial birds and mammals. *Cons. Ecol.* **4**.
- 864 **Switzer, P.V.** 1993. Site fidelity in predictable and unpredictable habitats. *Evol. Ecol.* **7**: 533-555.
- 865 **Taylor, A.R. & Bishop, M.A.** 2008. Stopover site fidelity of a Western Sandpiper on the Copper River Delta,
866 Alaska. *Waterbirds* **31**: 294-297.
- 867 **Taylor, C.M. & Norris, D.R.** 2010. Population dynamics in migratory networks. *Theor. Ecol.* **3**: 65-73.
- 868 **Thaxter, C.B., Joys, A.C., Gregory, R.D., Baillie, S.R. & Noble, D.G.** 2010. Hypotheses to explain patterns of
869 population change among breeding bird species in England. *Biol. Cons.* **143**: 2006-2019.
- 870 **Theriault, S., Villard, M.A. & Hache, S.** 2012. Habitat selection in site-faithful ovenbirds and recruits in the
871 absence of experimental attraction. *Behav. Ecol.* **23**: 1289-1295.
- 872 **Thingstad, P.G., Nyholm, N.E.I. & Fieldheim, B.** 2006. Pied Flycatcher *Ficedula hypoleuca* population
873 dynamics in peripheral habitats in Scandinavia. *Ardea* **94**: 211-223.
- 874 **Thorup, K., Bisson, I.A., Bowlin, M.S., Holland, R.A., Wingfield, J.C., Ramenofsky, M. & Wikelski, M.** 2007a.
875 Evidence for a navigational map stretching across the continental US in a migratory songbird. *P. Natl.*
876 *Acad. Sci. USA* **104**: 18115-18119.
- 877 **Thorup, K. & Holland, R.A.** 2009. The bird GPS - long-range navigation in migrants. *J. Exp. Biol.* **212**: 3597-
878 3604.
- 879 **Thorup, K. & Rabøl, J.** 2007. Compensatory behaviour after displacement in migratory birds - A meta-analysis
880 of cage experiments. *Behav. Ecol. Sociobiol.* **61**: 825-841.
- 881 **Thorup, K., Rabøl, J. & Erni, B.** 2007b. Estimating variation among individuals in migration direction. *J. Av. Biol.*
882 **38**: 182-189.
- 883 **Tittler, R., Villard, M.-A. & Fahrig, L.** 2009. How far do songbirds disperse? *Ecography* **32**: 1051-1061.
- 884 **Tottrup, A.P., Klaassen, R.H.G., Strandberg, R., Thorup, K., Kristensen, M.W., Jorgensen, P.S., Fox, J.,**
885 **Afanasyev, V., Rahbek, C. & Alerstam, T.** 2012. The annual cycle of a trans-equatorial Eurasian-
886 African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *P. Roy.*
887 *Soc. Lond. B Bio.* **279**: 1008-1016.

- 888 **Tottrup, A.P., Rainio, K., Coppack, T., Lehikoinen, E., Rahbek, C. & Thorup, K.** 2010. Local Temperature
889 Fine-Tunes the Timing of Spring Migration in Birds. *Integr. Comp. Biol.* **50**: 293-304.
- 890 **Trierweiler, C., Mullie, W.C., Drent, R.H., Exo, K.-M., Komdeur, J., Bairlein, F., Harouna, A., de Bakker, M. &**
891 **Koks, B.J.** 2013. A Palaearctic migratory raptor species tracks shifting prey availability within its
892 wintering range in the Sahel. *J. Anim. Ecol.* **82**: 107-120.
- 893 **van Wijk, R.E., Kölzsch, A., Kruckenberg, H., Ebbinge, B.S., Müskens, G.J.D.M. & Nolet, B.A.** 2012.
894 Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos* **121**:
895 655-664.
- 896 **Verkuil, Y.I., Karlionova, N., Rakhimberdiev, E.N., Jukema, J., Wijmenga, J.J., Hooijmeijer, J., Pinchuk, P.,**
897 **Wymenga, E., Baker, A.J. & Piersma, T.** 2012. Losing a staging area: Eastward redistribution of Afro-
898 Eurasian ruffs is associated with deteriorating fuelling conditions along the western flyway. *Biol. Cons.*
899 **149**: 51-59.
- 900 **Vickery, J., Rowcliffe, M., Cresswell, W., Jones, P. & Holt, S.** 1999. Habitat selection by Whitethroats *Sylvia*
901 *communis* during spring passage in the Sahel zone of northern Nigeria. *Bird Study* **46**: 348-355.
- 902 **Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J. & Gregory, R.D.** 2014. The
903 decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis* **156**: 1-22.
- 904 **Vogt, D.F., Hopey, M.E., Mayfield, G.R., III, Soehren, E.C., Lewis, L.M., Trent, J.A. & Rush, S.A.** 2012.
905 Stopover Site Fidelity by Tennessee Warblers at a Southern Appalachian High-elevation Site. *Wilson J.*
906 *Ornithol.* **124**: 366-370.
- 907 **Warkentin, I.G. & Hernández, D.** 1996. The conservation implications of site fidelity: A case study involving
908 nearctic-neotropical migrant songbirds wintering in a Costa Rican mangrove. *Biol. Cons.* **77**: 143-150.
- 909 **Widmer, M.** 1996. Phenology, breeding density and population ecology of the garden warbler *Sylvia borin* in a
910 subalpine habitat of the central Swiss Alps. *J. Ornithol.* **137**: 479-501.
- 911 **Wilson, J.M. & Cresswell, W.** 2006. How robust are Palearctic migrants to habitat loss and degradation in the
912 Sahel? *Ibis* **148**: 789-800.
- 913 **Wilson, J.M. & Cresswell, W.** 2010. Densities of Palearctic warblers and Afrotropical species within the same
914 guild in Sahelian West Africa. *Ostrich* **81**: 225-232.
- 915 **Wilson, J.M. & Cresswell, W.R.L.** 2007. Identification of potentially competing Afrotropical and Palaearctic bird
916 species in the Sahel. *Ostrich* **78**: 363-368.
- 917 **Wiltschko, R. & Wiltschko, W.** 1999. The orientation system of birds - III. Migratory orientation. *J. Ornithol.* **140**:
918 273-308.
- 919 **Winstanley, D.R., Spencer, R. & Williamson, K.** 1974. Where have all the whitethroats gone? *Bird Study* **21**: 1-
920 14.
- 921 **Wolff, W.J.** 1970. Goal orientation versus one-direction orientation in Teal, *Anas c. crecca* during autumn
922 migration. *Ardea* **58**: 131-141.
- 923 **Yoder, J.M., Marschall, E.A. & Swanson, D.A.** 2004. The cost of dispersal: predation as a function of
924 movement and site familiarity in ruffed grouse. *Behav. Ecol.* **15**: 469-476.
- 925 **Yohannes, E., Bensch, S. & Lee, R.** 2008. Philopatry of winter moult area in migratory Great Reed Warblers
926 *Acrocephalus arundinaceus* demonstrated by stable isotope profiles. *J. Ornith.* **149**: 261-265.
- 927 **Yohannes, E., Hobson, K.A. & Pearson, D.J.** 2007. Feather stable-isotope profiles reveal stopover habitat
928 selection and site fidelity in nine migratory species moving through sub-Saharan Africa. *J. Av. Biol.* **38**:
929 347-355.
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932

933 **Table 1.** Spread of tagged individuals on their wintering grounds.

Species	Origin	Winter range (km)	Countries (E to W)	N	Study
Black Stork <i>Ciconia nigra</i>	Central Iberia	3200	Senegal Chad	6	(Cano & Telleria 2013)
Cinereous Vulture <i>Aegypius monachus</i>	Caucasus	1400	Saudi Arabia Oman	6	(Gavashelishvili <i>et al.</i> 2012)
Western Marsh Harrier <i>Circus aeruginosus</i>	Sweden	1100	Guinea Bissau Mali	17	(Strandberg <i>et al.</i> 2008)
Eurasian Hobby <i>Falco subbuteo</i>	Sweden	1400	DR Congo Angola	3	(Strandberg <i>et al.</i> 2009)
European Nightjar <i>Caprimulgus europaeus</i>	UK	900	Central Africa	3	(Cresswell & Edwards 2012)
Eurasian Hoopoe <i>Upupa epops</i>	Switzerland	1300	Mauritania Mali	3	(Bächler <i>et al.</i> 2010)
Red-backed Shrike <i>Lanius collurio</i>	Denmark	1400	Angola South Africa	9	(Tottrup <i>et al.</i> 2012)
Common Redstart <i>Phoenicurus phoenicurus</i>	Denmark	1650	Senegal Burkina Faso	6	(Kristensen <i>et al.</i> 2013)
Great Reed Warbler <i>Acrocephalus arundinaceus</i>	Sweden	3250	Guinea CAR	8	(Lemke <i>et al.</i> 2013)

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935 **Table 2.** Examples of studies showing evidence of winter and passage site fidelity for long distance
936 migrant bird taxa. Evidence for wintering (W) site fidelity shown top (pale grey) arranged in order of
937 strength of evidence, followed by passage (P) site fidelity shown below (darker grey) again arranged
938 in order of strength of evidence. Te = Temperate and Tr = Tropical. Further studies of migrants that
939 present evidence prior to 2002 are detailed in Table 17.6 in Newton (2008).

Taxa	Location	Evidence	Source
Passerine	W, Te	Return after experimental displacement	(Mewaldt 1964, Benvenuti & Ioalè 1980)
Passerine	W, Tr & Te	Very high fidelity	(King & Hutchinson 2001, Marra & Holmes 2001, Sillett & Holmes 2002, Seavy <i>et al.</i> 2012)
Waterfowl	W, Te	Most species very high fidelity	(Iverson <i>et al.</i> 2004, Iverson & Esler 2006, Liu <i>et al.</i> 2012)
Spoonbill	W, Tr	Very high fidelity despite non-optimal sites	(Lok <i>et al.</i> 2011)
Raptor	W, Tr	Small, medium and large scale fidelity	(McGrady <i>et al.</i> 2003, Hinnebusch <i>et al.</i> 2010, Kochert <i>et al.</i> 2011, Gavashelishvili <i>et al.</i> 2012, Liminana <i>et al.</i> 2012, Trierweiler <i>et al.</i> 2013)
Seabird	W, SO	Large and medium scale non-breeding fidelity	(Phillips <i>et al.</i> 2005)
Shorebird	W, Tr, Te	Very high small scale fidelity	(Leyrer <i>et al.</i> 2006, Ferreira Rodrigues <i>et al.</i> 2007, Conklin & Battley 2012)
Passerine	W, Tr	Anecdotal fidelity, many species	(Moreau 1969)
Passerine, Raptor	W (P), Tr	Serial fidelity at more than one wintering site during a winter	(Hedenström <i>et al.</i> 1993, Heckscher <i>et al.</i> 2011, Liminana <i>et al.</i> 2012)
Passerine	W, Tr	Several species, high but species-dependent variable fidelity	(Faaborg & Arendt 1984, Warkentin & Hernández 1996, Jahn <i>et al.</i> 2009)
Passerine	W, P, Te, Tr	Migratory connectivity through stable isotopes	(Yohannes <i>et al.</i> 2007, Prochazka <i>et al.</i> 2008, Studds <i>et al.</i> 2008, Yohannes <i>et al.</i> 2008)
Passerine, Shorebirds	P, Te, Tr	High site fidelity on passage sites established	(Merom <i>et al.</i> 2000, Buchanan <i>et al.</i> 2011)
Raptor, Owls	P, Te, Tr	Site fidelity on medium scale	(Strandberg <i>et al.</i> 2008, Beckett & Proudfoot 2011)
Shorebird, Passerine	P, Te,	Possibility of high fidelity demonstrated	(Taylor & Bishop 2008, Somershoe <i>et al.</i> 2009)
Passerine	P, Te, Tr	Several species, little fidelity	(Catry <i>et al.</i> 2004, Stanley <i>et al.</i> 2012, Vogt <i>et al.</i> 2012)
Stork, Raptor	P, Te	No site fidelity on medium scale	(Alerstam <i>et al.</i> 2006, Chevallier <i>et al.</i> 2011, Liminana <i>et al.</i> 2012)

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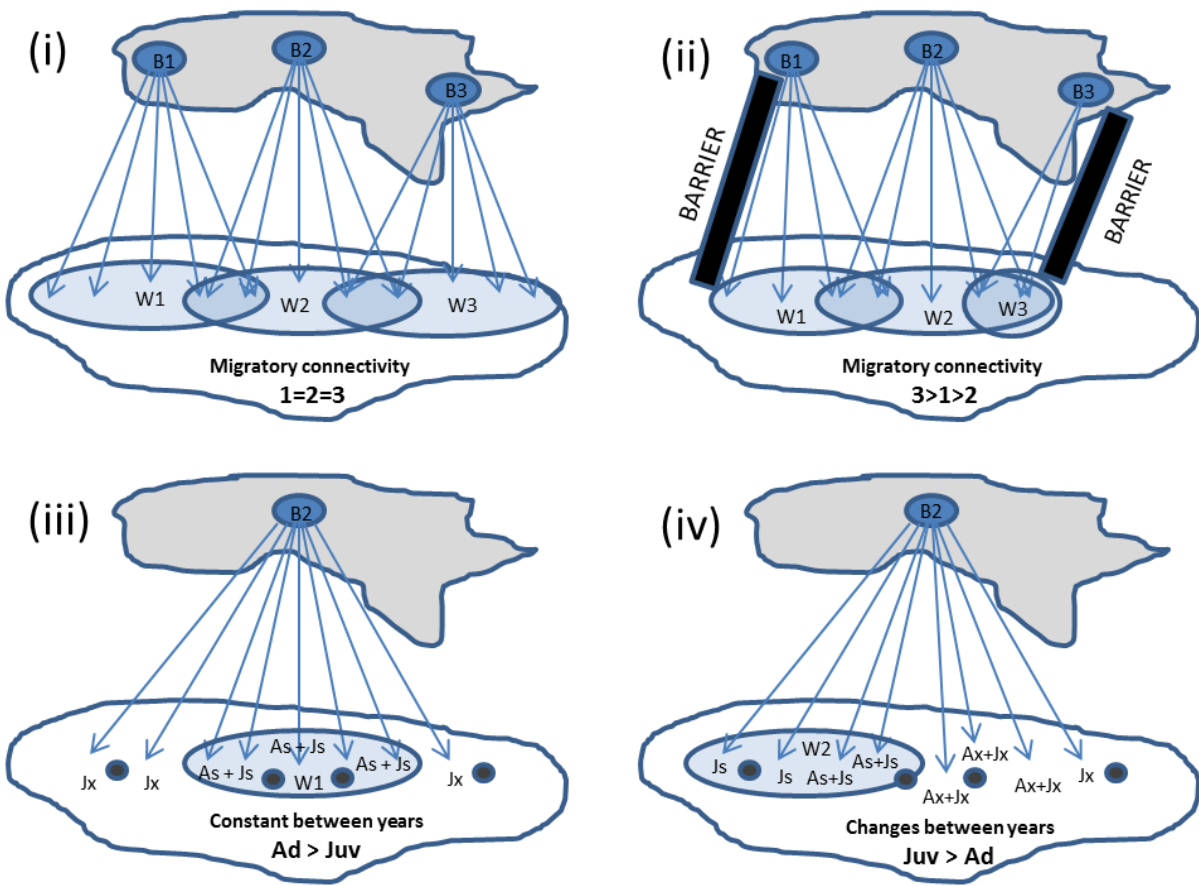
942 **Figure legends**

943 **Figure 1.** Population predictions from the serial residency hypothesis. Diagrams illustrate how
944 migratory connectivity arises through spatial and temporal autocorrelation of local environmental
945 constraints (i & ii), how age structure of the population can change with inter-annual shifts in wintering
946 conditions (iii & iv) and how site-based conservation can function as a strategy despite stochasticity
947 (iii & iv). A hypothetical breeding area (grey and B1-3) and a hypothetical wintering area (white and
948 W1-3) are shown. Wintering migratory pathways are shown as arrows linking the breeding areas with
949 the wintering areas. In (ii) migratory connectivity differences arise because of the presence of barriers
950 constraining wintering migratory pathways. In (iii) adults survive preferentially because they always
951 return to the best areas (W1), while many juveniles end up in poor areas. In (iv) the best areas have
952 shifted between years so many adults return to the now poorer areas and have lower survival
953 whereas juveniles arriving to the new best areas (W2) survive better: consequently the age ratio shifts
954 on the breeding ground the following year. Regardless of the shifting location of ideal conditions (iii &
955 iv), as long as some sites within suitable wintering areas are protected (dark circles) then some
956 juveniles will find the sites and return there as adults.

957 **Figure 2.** A theoretical illustration of how variable conditions on the breeding ground (left hand,
958 summer, graphs showing the effects on population trends through time) add to the uniform, average
959 effects on the wintering ground (middle, winter graphs showing the effects population trends through
960 time) to give the overall population trends over time (right hand graphs). All breeding populations
961 winter right across the southerly wintering grounds and so all will have lower juvenile survival, leading
962 to similarities in trends across these populations, unless these are offset by greater variation in
963 breeding demographics, potentially leading to distinct differences in trends between breeding
964 populations.

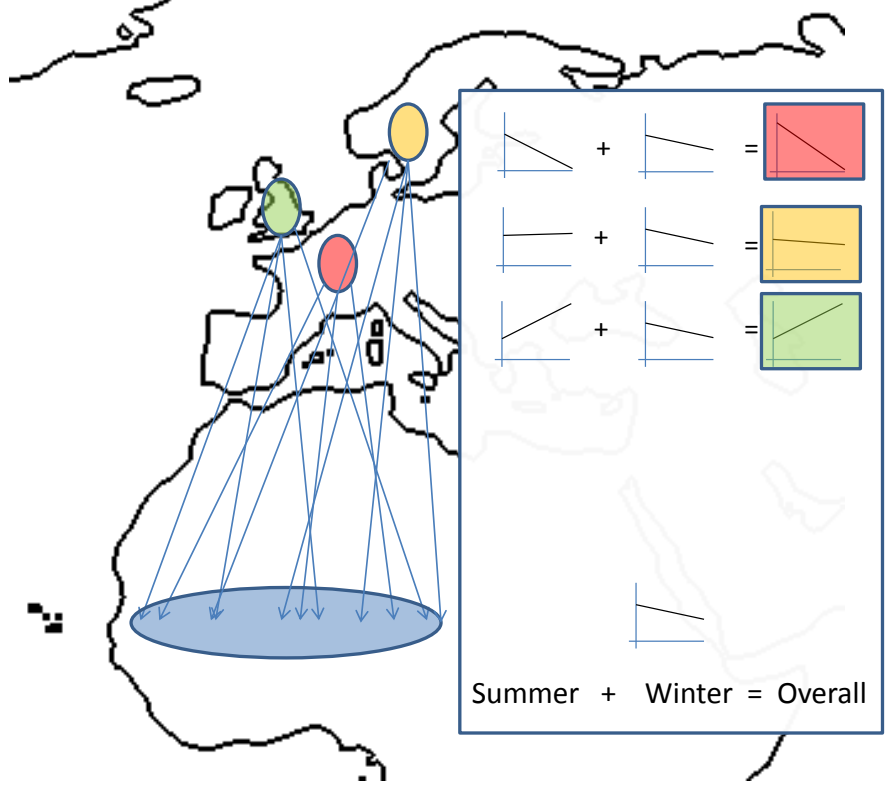
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 967 Fig. 1
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971 Fig. 2
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