

Mechanisms driving phenological and range change in migratory species

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Author-supplied statements

Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:

This article does not present research with ethical considerations

Statement (if applicable):

CUST_IF_YES_ETHICS :No data available.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:

Yes

Statement (if applicable):

All data are presented and accessible in the figures

Conflict of interest

I/We declare we have no competing interests

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All three authors conceived and designed the study and generated the data. JAG conducted the analyses and all three authors contributed to the writing of the manuscript.

Mechanisms driving phenological and range change in migratory species

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Summary

Many migratory systems are changing rapidly in space and time, and these changes present challenges for conservation. Changes in local abundance and site occupancy across species' ranges have raised concerns over the efficacy of existing protected area networks, while changes in phenology can potentially create mismatches in the timing of annual events with the availability of key resources. These changes could arise either through individuals shifting in space and time or through generational shifts in the frequency of individuals using different locations or on differing migratory schedules. Using a long-term study of a migratory shorebird in which individuals have been tracked through a period of range expansion and phenological change, we show that these changes occur through generational shifts in spatial and phenological distributions, and that individuals are highly consistent in space and time. Predictions of future rates of changes in range size and phenology, and their implications for species conservation, will require an understanding of the processes that can drive generational shifts. We therefore explore the developmental, demographic and environmental processes that could influence generational shifts in phenology and distribution, and the studies that will be needed to distinguish among these mechanisms of change.

Keywords: avian, climate change, migration, mismatch

Introduction

Migratory populations throughout the world are changing rapidly, with declines in abundance being reported on all major flyways [1-3] and driving international calls for action [4]. Identifying the causes of population changes in migratory species is inherently complex because of the range of sites and conditions experienced by individuals on their

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3 38 annual journeys. Changing conditions in any or all parts of migratory ranges could drive
4 39 changes in abundance and distribution. For example, changes in local conditions could
5 40 influence local demography and thus alter relative abundances and site occupancy
6 41 anywhere within a migratory range. However, the effects of local changes in one part of a
7 42 range can also cascade through to influence abundance and distribution across a range
8 43 [5,6]. This potential for interactions between local environmental conditions, demography,
9 44 individual development and range-wide distribution and phenology make migratory systems
10 45 complex, and designing conservation actions to halt and reverse declines in migratory
11 46 species is therefore a major challenge.

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16 47 Recent changes in abundance of migratory species have been linked to their distribution
17 48 and phenology. For example, phenological change is most commonly observed as shifts in
18 49 the timing of migration to breeding grounds, and the magnitude of these shifts can vary
19 50 greatly among species. Among European breeding birds, declines have been more frequent
20 51 in species for which advances in spring arrival dates have not occurred [7], and species with
21 52 non-overlapping breeding and wintering ranges are both more likely to be declining and less
22 53 likely to have shown advances in spring arrival [2]. A lack of advance in spring arrival dates
23 54 can potentially increase the impact of any trophic mismatch resulting from climate-driven
24 55 changes in the timing of availability of key food resources for breeding [8,9]. Declining
25 56 species with little or no phenological change are often assumed to be constrained from
26 57 responding to changing climatic conditions in breeding areas (for example because they
27 58 migrate to more distant non-breeding locations), but the nature of any such constraint is
28 59 unknown. Identifying the mechanisms through which phenological change occurs, and thus
29 60 the factors constraining or facilitating these changes, may therefore be key to designing and
30 61 targetting conservation actions to mitigate the effects of trophic mismatch.

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36 62 Changes in the distribution of breeding and non-breeding ranges have also occurred in
37 63 many migratory species, with polewards range shifts being particularly prevalent [10, 11].
38 64 Concerns have consequently arisen over the efficacy of existing protected area networks
39 65 [5, 12]. Range change is often interpreted as a response to changes in the suitability of
40 66 environmental conditions (eg colonisation of areas that were previously unsuitable and/or
41 67 contraction from areas of declining suitability). However, the mechanisms driving changes in
42 68 the distribution of individuals across a range are rarely known.

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46 69 Both range change and phenological change could arise through individual plasticity in use
47 70 of space and time. For example, range change may occur through individual movement to
48 71 locate suitable conditions, while changes in timing of migration could arise through
49 72 individual decisions on departure timings or time spent on migratory journeys varying
50 73 between years. By contrast, these changes could also result from generational shifts in the
51 74 frequency of individuals that use different locations or migrate at specific times.
52 75 Generational shifts would not require individual plasticity but would require changes in the
53 76 conditions determining the frequency of individuals within a population with different
54 77 phenologies or probabilities of occupying different parts of a range, such that the spatial
55 78 and temporal distribution of recruits to the population would differ from their predecessors.
56 79 For example, changes in distribution could arise through shifts in the conditions influencing
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3 80 the probability of occupancy of different locations by new recruits, and/or by shifts in the
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5 81 survival rates achieved within different locations. Similarly, shifts in timing of migration
6 82 could occur through changes in the conditions influencing adoption of migration schedules
7 83 by new recruits (or survival rates associated with different schedules) altering the frequency
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9 84 of individuals on different schedules within a population [13].

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11 85 Individual plasticity in spatial distribution and migratory timings would facilitate relatively
12 86 rapid responses to changing environmental conditions. However, generational shifts would
13 87 likely result in slower responses to environmental changes, particularly in long-lived species,
14 88 as the direction and magnitude of the changes would depend on the proportion of annual
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16 89 recruits within a population and the proportion of those recruits experiencing changing
17 90 drivers of use of space and time. If individual variation in migratory destination or timing has
18 91 a genetic component, then generational shifts could drive microevolutionary change.
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20 92 However, genetic change is not an inevitable consequence of generational shifts, as
21 93 individual destinations or timings could also be determined by environmental or social cues.

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23 94 Changes in range size or migration phenology of populations as a result of individual
24 95 plasticity in use of space and time has not been demonstrated, and a growing number of
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26 96 individual tracking studies are reporting high levels of repeatability in individual migratory
27 97 destinations and timings [13-20]. If generational shifts are the more likely driver of
28 98 population changes in space and time, then our focus should be on understanding drivers of
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30 99 settlement and phenology of recruits, as well as their subsequent survival and recruitment.

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32 100 Identifying the relative contributions of generational shifts and individual plasticity requires
33 101 model systems in which individuals can be tracked across space and time, through periods
34 102 of shifts in range and phenology. Such large-scale, long-term tracking data are rare but one
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36 103 system that provides all of these elements is the Icelandic black-tailed godwit, *Limosa*
37 104 *limosa islandica*, which has been the subject of intensive individual and population studies
38 105 since the mid-1990s [21-23]. In common with many migratory bird species at temperate and
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40 106 subarctic latitudes, advances in the phenology of spring migration have occurred in the
41 107 Icelandic godwit population in recent decades [24]. Iceland supports very large breeding
42 108 populations of several shorebird populations which migrate south to locations ranging from
43 109 temperate Europe to sub-Saharan Africa [25]. The first recorded arrival dates of these
44 110 species into south Iceland in spring have advanced over the last three decades, with godwits
45 111 showing one of the most rapid advances (~2 weeks earlier now than in the 1990s; [24]). In
46 112 addition, this godwit population has shown sustained increases in number for over a
47 113 century, likely as a consequence of warming conditions in Iceland facilitating earlier and
48 114 more successful breeding and recruitment [6,26,27]. This population growth has been
49 115 accompanied by range expansion in both the breeding and non-breeding ranges; in Iceland,
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51 116 godwits have expanded from a breeding range that was confined to the south-west corner
52 117 of the country around 1900, to occupy progressively more northerly and easterly locations
53 118 [27]. In the non-breeding range, which spans coastal areas of north-west Europe from
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55 119 Britain and Ireland to Iberia and northern Morocco, colonisation and population increases
56 120 have primarily occurred in the northern part of the range (east and north-west England,
57 121 Scotland and east Ireland) since the 1970s, when surveys began [21,28].
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122 In the mid-1990s, a programme of population-wide and life-long tracking of individual
123 godwits was initiated [21,29]. Across the breeding and non-breeding ranges, godwits have
124 been caught and marked with unique combinations of coloured leg-rings, and ~1-2% of the
125 population (which numbers ~50,000 individuals; [30]) is marked. A citizen science network
126 of >2000 observers across Europe regularly report marked individuals, allowing the locations
127 of individuals to be repeatedly tracked within and across years [31]. Here, we use this range-
128 wide tracking of an expanding (in space) and advancing (in time) migratory shorebird, to
129 explore whether individual plasticity or generational shifts are likely to have caused these
130 changes in space and time, and to consider the evidence for potential developmental,
131 environmental and demographic drivers of such changes.

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133 Methods

134 *Phenological change: repeated measures of individual spring arrival dates*

135 Black-tailed godwits return to Iceland between mid-April and mid-May and, on arrival, flocks
136 congregate on a small number of arrival sites [32]. Since 1999, standardised surveys of
137 arrival sites in south and west Iceland have taken place from mid-April to early May, with
138 the identities of all individually-marked birds at all study locations being recorded every 1-3
139 days [13,32]. Between 1999 and 2018, arrival dates were recorded in at least three years for
140 85 individuals (Fig. 1). In order to quantify (a) the trends in arrival dates of individuals, we
141 constructed a GLM with each individual arrival date (in Julian days) as the dependent
142 variable, and year and individual as fixed effects (an extension of the model reported in Gill
143 et al. 2014 for a smaller sample). In order to then quantify (b) whether individual trends in
144 arrival dates have changed in magnitude or (c) whether the frequency of individuals with
145 differing arrival dates has changed over the 16-year survey period, we then constructed two
146 further GLMs with the (b) trend in arrival date and (c) mean arrival date for each individual
147 as the dependent variable, and the year of first spring arrival (ie the first year in which each
148 individual was observed on arrival in Iceland) observation as a fixed effect.

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150 *Range change: non-breeding locations of marked individuals*

151 Locations of individually-marked godwits across the migratory range have been recorded by
152 a network of citizen scientists since the mid-1990s. Here we use all recorded non-breeding
153 locations (ie excluding records within Iceland) of 631 individuals marked at the main post-
154 breeding moult location in east England during the autumns of 1995-2014, and the winter
155 (mid-Oct to mid-Feb) records of the 419 of these individuals observed during that period. To
156 assess the role of individual movement in driving the northward range expansion, we use
157 these sightings to quantify the total number of non-breeding locations (individual estuaries
158 and wetlands), regions and countries (Table 1) used by individuals tracked for differing
159 numbers of years. To quantify the contribution of generational shifts in the frequency of
160 individuals using different locations to the northwards range expansion, we then use these
161 sightings to assess whether individuals marked in more recent years (which will be younger,

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4 162 on average, than previously marked individuals) are more likely to use recently colonised
5 163 locations. We constructed generalised linear models with a binomial structure and a logit
6 164 link, with the number of individuals marked in consecutive 5-year time periods since 1995
7 165 that winter in sites (a) colonised before or after the 1960s and (b) north and south of 52°N
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9 166 (most of the recently colonised sites are north of 52°N; [31,33]) as the dependent variable,
10 167 and time period as a fixed effect.

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13 14 169 **Results**

15 16 170 *Mechanisms driving phenological change: individual plasticity or generational shifts*

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18 171 Although first spring observations of godwits in South Iceland have advanced by more than
19 172 two weeks in the last two decades [24], trends in arrival dates of 85 marked individuals over
20 173 the last 16 years vary significantly among individuals but show no consistent advances in
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22 174 individual arrival date (Table 2a), and no change in individual arrival trends over the survey
23 175 period (Fig. 2a, Table 2b). However, the distribution of arrival dates of marked individuals
24 176 has changed over time, with individuals first observed in more recent years tending to arrive
25 177 earlier than individuals first recorded in the late 1990s/early 2000s (Fig. 2b, Table 2c). Thus,
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27 178 while the arrival dates of individuals have not advanced, the frequency of early-arriving
28 179 individuals has increased over this time period.

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31 32 181 *Mechanisms driving range change: individual plasticity or generational shifts*

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34 182 Repeated tracking of individual godwits across the migratory range for up to 23 years
35 183 indicates a remarkably low level of individual plasticity in site use throughout their lives. On
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37 184 average, individuals are recorded on a total of only ~4 (± 2.5 SE) non-breeding locations,
38 185 regardless of the number of years for which they have been tracked (Fig. 3). In addition,
39 186 these few locations are spread across, on average, 2.5 (± 1.5) regions in 1.5 (± 0.8) countries.
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41 187 Individuals are therefore highly restricted and consistent in their use of a small number of
42 188 passage and winter locations, and these can be spread across the migratory range.
43 189 However, over the two decades of continuous marking and tracking, with newly marked
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45 190 individuals being added to the population each year, the relative frequency of individuals
46 191 using 'new' (colonised since the 1960s, Table 1) winter sites has increased (Fig. 4a), and this
47 192 is primarily through increased numbers of individuals using more northerly sites (Fig. 4b,
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49 193 Table 1).

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52 53 195 **Discussion**

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55 196 The spring arrival dates of godwits in Iceland has advanced [24] and the breeding population
56 197 has expanded northwards in recent decades, with rapid population increases in more
57 198 northerly non-breeding locations [21]. Repeated tracking of individuals in space and time
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59 199 over this period has shown that these expansions and advances are driven by generational
60 200 shifts in the frequency of individuals occupying different locations and migrating at different

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3 201 times, and not by individual plasticity. Individuals show life-long consistency in use of a small
4 202 number of non-breeding locations but the proportion of individuals occupying recently
5 203 colonised sites is greater for more recently-ringed birds. As recently colonised sites are
6 204 primarily (but not exclusively) in the north of the range, and as the network of observers
7 205 recording individual locations has been in operation throughout the 20 year survey period,
8 206 the recorded shift in distribution is unlikely to be influenced by changes in reporting rates
9 207 across the range.

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13 208 The widely reported changes in phenology and distribution of many migratory species in
14 209 recent decades may therefore be likely to result from generational shifts in the frequency of
15 210 individuals with differing phenologies and using different locations. Generational shifts have
16 211 been shown to drive shifts in distribution in other migratory systems. For example, a shift in
17 212 use of spring passage sites by a migratory wader population (continental black-tailed
18 213 godwits, *Limosa limosa limosa*) was driven by new recruits to the population, while adults in
19 214 the population continued to use the site they had always previously occupied [33].
20 215 Quantifying the role of generational shifts requires long-term tracking of individuals, and
21 216 relatively few studies have this information during periods of change. However, tracking
22 217 studies are increasingly being conducted, and studies tracking individuals over multiple
23 218 years are typically reporting high levels of repeatability of individual timings and
24 219 destinations [13-20], suggesting that the benefits of philopatry in use of space and time are
25 220 very strong [34,35]. Thus generational shifts may be the primary mechanism through which
26 221 phenological shifts and range change occur.

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32 222 Identifying the environmental and demographic processes that drive generational shifts in
33 223 space and time is therefore likely to be a critical step in understanding population-level
34 224 responses to environmental change and the associated implications for conservation.
35 225 Generational shifts in distribution or phenology could potentially arise through processes
36 226 occurring at the following points in early life:

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39 227 *1. Developmental drivers of generational shifts*

40 228 Conditions experienced at the natal stage, such as timing of hatching and/or conditions for
41 229 growth and development, could influence the probability of those individuals undertaking
42 230 different subsequent migratory routes and timings. For example, individuals hatched late in
43 231 the season and/or with insufficient resources to fuel rapid growth are likely to migrate later,
44 232 on average, and may thus have less time to locate more distant non-breeding locations. In
45 233 such a case, an increase in the number of later-fledging individuals could drive recruitment
46 234 into non-breeding locations that are closer to the breeding grounds. Similarly, natal
47 235 conditions could potentially influence subsequent migration phenology, either directly
48 236 through impacts on individual condition, or indirectly through impacts on the conditions and
49 237 potential flockmates encountered during the non-breeding season.

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55 239 An important aspect of natal conditions that could potentially influence juvenile distribution
56 240 and migratory timings is the changes in breeding phenology that are widely reported in
57 241 many migratory populations [9,36]. Advances in nesting dates have been reported in many
58 242 species and individual plasticity in nesting dates is common [37,38]. Thus, current evidence

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3 243 suggests that individual timings of arrival of migrants on breeding grounds tend to be
4 244 consistent, but subsequent timings of breeding can vary greatly, and often vary in response
5 245 to local weather conditions [6,39,40]. This changing phenology of natal conditions could
6 246 potentially drive changes in subsequent phenology and distribution of new recruits to the
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8 247 population, if timing of fledging influences subsequent migratory routes and timings. A key
9 248 mechanism that could drive such links is the potential for timing of fledging to influence the
10 249 likely flockmates on migratory journeys, and the destinations to which they are travelling.
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12 250 For example, tracking of adult and juvenile Lesser Spotted Eagles, *Clanga pomarina*, on their
13 251 migratory journeys has shown that juveniles that departed at the same time as adults were
14 252 significantly more likely to take the same routes as adults, and to have higher subsequent
15 253 survival rates, than juveniles who departed without adults [41]. Timing-driven access to
16 254 social cues in migratory flocks could therefore be an important driver of the migratory
17 255 routes and destinations located by juveniles, and changes in timing of fledging could
18 256 therefore drive changes in the non-breeding distribution of migratory species.
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23 258 *2. Environmental effects on generational shifts*

24 259 Changing environmental conditions could directly influence the probability of recruits
25 260 migrating at specific times or locating specific non-breeding locations. For example,
26 261 changing weather conditions (e.g. windspeeds or directions) could alter the proportions of
27 262 recruits migrating at different time or taking different routes. However, while wind
28 263 conditions can have important effects on migrating birds [42], individual consistency in
29 264 migratory destinations and timings would mean that such effects could only operate in early
30 265 life (ie during settlement/recruitment).
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34 267 *3. Demographic effects on generational shifts*

35 268 Disproportionate changes in survival rates of recruits that differ in distribution or timing
36 269 could lead to generational shifts. For example, while the numbers of individuals recruiting
37 270 into more northerly winter locations or arriving early on the breeding grounds may not be
38 271 changing, those individuals could be increasingly likely to survive, for example as a
39 272 consequence of ameliorating weather conditions in northerly areas or on arrival in the
40 273 breeding areas. Changing patterns of survival may be particularly relevant in systems with
41 274 range expansion into areas in which weather conditions are changing as a consequence of
42 275 climatic change [43], and these effects could operate alongside developmental or
43 276 environmental effects.
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49 278 *Drivers of generational shifts in Icelandic godwits*

50 279 In Icelandic black-tailed godwits, rapid warming has occurred on the breeding grounds in
51 280 recent decades, and nesting dates are earlier [6] and productivity is higher [26] in warmer
52 281 years. This warming-driven increase in productivity is likely to have fuelled the colonisation
53 282 of colder breeding areas in the north, where nest-laying and hatching dates are, on average,
54 283 later than in more southerly breeding areas [6]. Individuals from these colder and more
55 284 recently colonised breeding areas are more likely to also winter in the more recently
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58 285 colonised non-breeding areas [31], and these seasonal links could thus result from regional-
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3 286 scale differences in timing of fledging and subsequent social cues available to juveniles
4 287 undertaking their first migration.

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6 289 Warming-driven advances in nesting dates could also have driven the advancing spring
7 290 arrival of godwits in Iceland, as previous analyses have shown that (a) individuals wintering
8 291 in more southerly areas of Europe [29] and breeding in the warmer areas of south and west
9 292 Iceland [32] arrive first, and (b) more recently hatched individuals tend to have earlier spring
10 293 arrival dates than individuals hatched in the 1990s [13]. This suggests that the generational
11 294 shifts driving the phenological advance in this system (Fig. 2) could potentially result from
12 295 increased numbers of early-hatched individuals from the traditionally occupied areas of
13 296 Iceland that, because of their early fledging, are also more likely to have the time, condition
14 297 and social cues to both locate traditionally occupied winter areas and return early in spring.
15 298 Increased survival rates of early-arrivers and northerly winterers could also be contributing
16 299 to these changes in space and time.

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18 301 *Climate change and generational shifts in space and time*

19 302 If climate-driven shifts in breeding phenology can alter the frequency of juveniles
20 303 undertaking different migratory routes, destinations and timings, this could be an important
21 304 route through which climate-associated shifts in range and phenology are manifest. A
22 305 common pattern among migratory species at present is those migrating longer distances are
23 306 less likely to show shifts in migration phenology [44,45]. As longer-distance migrants
24 307 typically arrive later on the breeding grounds and have a smaller gap between arrival and
25 308 laying than shorter-distance migrants [13], they may have a more limited capacity to alter
26 309 breeding phenology (and thus generational shifts resulting from shifts in breeding
27 310 phenology are less likely to occur). The effects of climate warming on breeding phenology
28 311 can thus have potentially far-reaching consequences for migratory populations.

29 312

30 313 *Future research*

31 314 Identifying the contribution of developmental, environmental and demographic change to
32 315 generational shifts, and the conditions in which each might be most relevant, will require
33 316 studies in which the effects of natal conditions, environmental conditions experienced by
34 317 juvenile individuals undertaking different migratory routes and timings, and the
35 318 demographic consequences of conditions experienced at destinations can be measured.
36 319 Tracking individuals from fledging to recruitment into adulthood is difficult because survival
37 320 rates at this life stage are typically low, and retrieval of tags can be challenging because the
38 321 subsequent breeding locations of these individuals is typically unknown, but technological
39 322 advances will hopefully make these issues more tractable in the near future. Long-term
40 323 studies of seasonal patterns of nest loss, timing of replacement clutches and juvenile
41 324 fledging will also be particularly valuable in identifying the potential role of breeding
42 325 phenology in driving change in migratory systems. Quantifying the developmental,
43 326 environmental and demographic processes that influence individual migratory routes,
44 327 destinations and timings will be key to understanding future rates and directions of spatial
45 328 and phenological change in migratory species, and the associated implications for designing
46 329 effective protected area networks and conservation actions for these species.
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16 338 **Competing interests**

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18 339 We have no competing interests

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20 340 **Ethics**

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22 341 All required approval and licenses were obtained

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24 342 **Author contributions**

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26 343 All three authors conceived and designed the study and generated the data. JAG conducted
27 344 the analyses and all three authors contributed to the writing of the manuscript.

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31 346 **References**

- 32
33 347 1. Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Škorpilová, J. & Gregory,
34 348 R. D. (2014) The decline of Afro-Palaeartic migrants and an assessment of potential
35 349 causes. *Ibis*, 156, 1-22.
36 350
37 351 2. Gilroy, J. J., Gill, J. A., Butchart, S. H., Jones, V. R. & Franco, A. M. (2016) Migratory
38 352 diversity predicts population declines in birds. *Ecology letters*, 19, 308-317.
39 353
40 354 3. Studds, C. E., Kendall, B. E., Murray, N. J., Wilson, H. B., Rogers, D. I., Clemens, R. S.,
41 355 Gosbell, K., Hassell, C. J., Jessop, R., Melville, D. S. & Milton, D. A. (2017) Rapid
42 356 population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as
43 357 stopover sites. *Nature Communications*, 8, 14895.
44 358
45 359 4. Runge, C. A., Watson, J. E., Butchart, S. H., Hanson, J. O., Possingham, H. P. & Fuller, R.
46 360 A. (2015) Protected areas and global conservation of migratory birds. *Science*, 350,
47 361 1255-1258.
48 362
49 363 5. Méndez, V., Gill, J. A., Alves, J. A., Burton, N. H. & Davies, R. G. (2018) Consequences of
50 364 population change for local abundance and site occupancy of wintering waterbirds.
51 365 *Diversity and Distributions*, 24, 24-35.
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42
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60

- 367 6. Alves, J.A., Gunnarsson, T.G., Sutherland, W.J., Potts, P.M. & Gill, J.A. (2019) Linking
368 warming effects on phenology and demography with range expansion in a migratory
369 bird population. *Ecology and Evolution*.
- 370
- 371 7. Møller, A. P., Rubolini, D. & Lehikoinen, E. (2008) Populations of migratory bird species
372 that did not show a phenological response to climate change are declining.
373 *Proceedings of the National Academy of Sciences*. 105, 16195–16200.
- 374
- 375 8. Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. & Post, E. (2010) The effects of
376 phenological mismatches on demography. *Philosophical Transactions of the Royal
377 Society of London B: Biological Sciences*, 365, 3177-3186.
- 378
- 379 9. Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W.J.,
380 Bach, L.A., Coppack, T., Ergon, T., Gienapp, P., Gill, J.A., Gordo, O., Hedenström, A.,
381 Lehikoinen, E., Marra, P.P., Møller, A.P., Nilsson, A.L.K., Péron, G., Ranta, E., Rubolini,
382 D., Sparks, T.H., Spina, F., Studds, C.E., Sæther, S.A., Tryjanowski, P. & Stenseth, N.C.
383 (2011) Challenging claims in the study of migratory birds and climate change.
384 *Biological Reviews*, 86, 928-946
- 385
- 386 10. La Sorte, F. A. & Thompson, F. R. (2007) Poleward shifts in winter ranges of North
387 American birds. *Ecology*, 88, 1803-1812.
- 388
- 389 11. Virkkala, R. & Lehikoinen, A. (2014) Patterns of climate-induced density shifts of
390 species: poleward shifts faster in northern boreal birds than in southern birds. *Global
391 Change Biology*, 20, 2995-3003.
- 392
- 393 12. Sanderson, F. J., Pople, R. G., Ieronymidou, C., Burfield, I. J., Gregory, R. D., Willis, S. G.,
394 Howard, C., Stephens, P. A., Beresford, A. E & Donald, P. F. (2016) Assessing the
395 performance of EU nature legislation in protecting target bird species in an era of
396 climate change. *Conservation Letters*, 9, 172-180.
- 397
- 398 13. Gill, J. A., Alves, J. A., Sutherland, W. J., Appleton, G. F., Potts, P. M. & Gunnarsson, T.
399 G. (2014) Why is timing of bird migration advancing when individuals are not?
400 *Proceedings of the Royal Society of London B: Biological Sciences*, 281, 20132161.
- 401
- 402 14. Vardanis, Y., Klaassen, R. H., Strandberg, R. & Alerstam, T. (2011) Individuality in bird
403 migration: routes and timing. *Biology Letters*, rsbl20101180.
- 404
- 405 15. Stanley, C. Q., MacPherson, M., Fraser, K. C., McKinnon, E. A. & Stutchbury, B. J. (2012)
406 Repeat tracking of individual songbirds reveals consistent migration timing but
407 flexibility in route. *PloS one*, 7, e40688.
- 408
- 409 16. Conklin, J. R., Battley, P. F. & Potter, M. A. (2013) Absolute consistency: individual
410 versus population variation in annual-cycle schedules of a long-distance migrant bird.
411 *PLoS One*, 8, e54535.

- 1
2
3 412
- 4 413 17. López-López, P., García-Ripollés, C. & Urios, V. (2014) Individual repeatability in timing
5 414 and spatial flexibility of migration routes of trans-Saharan migratory raptors. *Current*
6 415 *Zoology*, 60, 642-652.
7 416
- 8 417 18. Lourenço, P.M., Alves, J.A., Reneerkens, J., Loonstra, J., Potts, P.M., Granadeiro, J.P. &
9 418 Catry, T. (2016) Influence of age and sex on winter site fidelity of sanderlings *Calidris*
10 419 *alba*. *PeerJ*, 4:e2517.
11 420
- 12 421 19. Hasselquist, D., Montràs-Janer, T., Tarka, M. & Hansson, B. (2017) Individual
13 422 consistency of long-distance migration in a songbird: significant repeatability of
14 423 autumn route, stopovers and wintering sites but not in timing of migration. *Journal of*
15 424 *Avian Biology*, 48, 91-102.
16 425
- 17 426 20. Pedersen, L., Jackson, K., Thorup, K. & Tøttrup, A. P. (2018) Full-year tracking suggests
18 427 endogenous control of migration timing in a long-distance migratory songbird.
19 428 *Behavioral Ecology and Sociobiology*, 72, 139.
20 429
- 21 430 21. Gill, J. A., Norris, K., Potts, P. M., Gunnarsson, T. G., Atkinson, P. W. & Sutherland, W. J.
22 431 (2001) The buffer effect and large-scale population regulation in migratory birds.
23 432 *Nature*, 412, 436.
24 433
- 25 434 22. Gunnarsson, T. G., Gill, J. A., Sigurbjörnsson, T. & Sutherland, W. J. (2004) Pair bonds:
26 435 arrival synchrony in migratory birds. *Nature*, 431, 646.
27 436
- 28 437 23. Alves, J. A., Gunnarsson, T. G., Hayhow, D. B., Appleton, G. F., Potts, P. M., Sutherland,
29 438 W. J. & Gill, J. A. (2013) Costs, benefits, and fitness consequences of different
30 439 migratory strategies. *Ecology*, 94, 11-17.
31 440
- 32 441 24. Gunnarsson, T. G. & Tómasson, G. (2011) Flexibility in spring arrival of migratory birds
33 442 at northern latitudes under rapid temperature changes. *Bird Study*, 58, 1-12.
34 443
- 35 444 25. Gunnarsson, T. G., Gill, J. A., Appleton, G. F., Gíslason, H., Gardarsson, A., Watkinson,
36 445 A. R. & Sutherland, W. J. (2006a) Large-scale habitat associations of birds in lowland
37 446 Iceland: implications for conservation. *Biological Conservation*, 128, 265-275.
38 447
- 39 448 26. Gunnarsson, T. G., Jóhannesdóttir, L., Alves, J. A., Þórisson, B. & Gill, J. A. (2017) Effects
40 449 of spring temperature and volcanic eruptions on wader productivity. *Ibis*, 159, 467-
41 450 471.
42 451
- 43 452 27. Gunnarsson, T. G., Gill, J. A., Petersen, A., Appleton, G. F. & Sutherland, W. J. (2005b) A
44 453 double buffer effect in a migratory shorebird population. *Journal of Animal Ecology*,
45 454 74, 965-971.
46 455
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46
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58
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60

- 456 28. Prater, A. J. (1975) The wintering population of the Black-tailed Godwit. *Bird Study*, 22,
457 169-176.
- 458
459 29. Alves, J. A., Gunnarsson, T. G., Potts, P. M., Gélinaud, G., Sutherland, W. J. & Gill, J. A.
460 (2012) Overtaking on migration: does longer distance migration always incur a
461 penalty? *Oikos*, 121, 464-470.
- 462
463 30. Gunnarsson, T.G., Gill, J.A., Potts, P.M., Atkinson, P.W., Croger, R.E., Gélinaud, G.,
464 Gardarsson, A. & Sutherland, W.J. (2005c) Estimating population size in black-tailed
465 godwits *Limosa limosa islandica* by colour-marking. *Bird Study*, 52, 153-158.
- 466
467 31. Gunnarsson, T. G., Gill, J. A., Newton, J., Potts, P. M. & Sutherland, W. J. (2005a)
468 Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the*
469 *Royal Society of London B: Biological Sciences*, 272, 2319-2323.
- 470
471 32. Gunnarsson, T.G., Gill, J.A., Atkinson, P.W., Gélinaud, G., Potts, P.M., Croger, R.E.,
472 Gudmundsson, G.A., Appleton, G.F. & Sutherland, W.J. (2006b) Population-scale
473 drivers of individual arrival times in migratory birds. *Journal of Animal Ecology*, 75,
474 1119-1127.
- 475
476 33. Verhoeven, M. A., Loonstra, A. J., Hooijmeijer, J. C., Masero, J. A., Piersma, T. &
477 Senner, N. R. (2018) Generational shift in spring staging site use by a long-distance
478 migratory bird. *Biology letters*, 14, 20170663.
- 479
480 34. Kokko, H. & Sutherland, W. J. (2001) Ecological traps in changing environments:
481 ecological and evolutionary consequences of a behaviourally mediated Allee effect.
482 *Evolutionary Ecology Research*, 3, 603-610.
- 483
484 35. Winger, B. M., Auteri, G. G., Pegan, T. M. & Weeks, B. C. (2018). A long winter for the
485 Red Queen: rethinking the evolution of seasonal migration. *Biological Reviews*.
486 doi: 10.1111/brv.12476
- 487
488 36. Dunn, P. O. & Møller, A. P. (2014) Changes in breeding phenology and population size
489 of birds. *Journal of Animal Ecology*, 83, 729-739.
- 490
491 37. Visser, M. E., te Marvelde, L. & Lof, M. E. (2012) Adaptive phenological mismatches of
492 birds and their food in a warming world. *Journal of Ornithology*, 153, 75-84.
- 493
494 38. Charmantier, A. & Gienapp, P. (2014) Climate change and timing of avian breeding and
495 migration: evolutionary versus plastic changes. *Evolutionary Applications*, 7, 15-28.
- 496
497 39. Townsend, A. K., Sillett, T. S., Lany, N. K., Kaiser, S. A., Rodenhouse, N. L., Webster, M.
498 S. & Holmes, R. T. (2013) Warm springs, early lay dates, and double brooding in a

- 1
2
3 499 North American migratory songbird, the black-throated blue warbler. *PLoS One*, 8,
4 500 e59467.
5 501
6 502
7 40. Visser, M. E., Gienapp, P., Husby, A., Morrissey, M., de la Hera, I., Pulido, F. & Both, C.
8 503 (2015) Effects of spring temperatures on the strength of selection on timing of
9 504 reproduction in a long-distance migratory bird. *PLoS Biology*, 13, e1002120.
10 505
11 506
12 41. Meyburg, B. U., Bergmanis, U., Langgemach, T., Graszynski, K., Hinz, A., Börner, I.,
13 507 Meyburg, C. & Vansteelant, W. M. (2017) Orientation of native versus translocated
14 508 juvenile lesser spotted eagles (*Clanga pomarina*) on the first autumn migration.
15 509 *Journal of Experimental Biology*, 220, 2765-2776.
16 510
17 511
18 42. Shamoun-Baranes, J., Leyrer, J., van Loon, E., Bocher, P., Robin, F., Meunier, F. &
19 512 Piersma, T. (2010) Stochastic atmospheric assistance and the use of emergency
20 513 staging sites by migrants. *Proceedings of the Royal Society of London B: Biological*
21 514 *Sciences*, rspb20092112.
22 515
23 516
24 43. McKechnie, A. E. & Wolf, B. O. (2010) Climate change increases the likelihood of
25 517 catastrophic avian mortality events during extreme heat waves. *Biology Letters*, 6,
26 518 253-256.
27 519
28 520
29 44. Butler C. J. (2003) The disproportionate effect of global warming on the arrival dates
30 521 of short-distance migratory birds in North America. *Ibis*, 145, 484–495.
31 522
32 523
33 45. Rubolini, D, Møller, A. P., Rainio, K. & Lehikoinen, E. (2007) Intraspecific consistency
34 524 and geographic variability in temporal trends of spring migration phenology among
35 525 European bird species. *Climate Research*, 35, 135–146.
36 526
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529 Table 1. The 121 winter locations across 26 regions and nine countries used by the
 530 individual godwits shown in Figure 3. Regions in bold are colonised since the 1960s.

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Country	Region	Lat-Long	No. of locations
N Ireland	East	54°N, 05°W	1
Ireland	West	53°N, 08°W	1
	Central	52°N, 08°W	2
	East	53°N, 06°W	6
	South	51°N, 08°W	11
Wales	North	53°N, 03°W	2
	West	52°N, 04°W	1
England	North-west	53°N, 03°W	9
	Central	52°N, 01°W	2
	East	52°N, 01°E	27
	South	50°N, 01°W	10
	South-east	51°N, 01°E	3
	South-west	50°N, 03°W	7
	Netherlands	North	53°N, 06°E
Central		52°N, 06°E	2
West		52°N, 04°E	3
France	North	48°N, 01°W	3
	North-west	47°N, 02°W	7
	West	46°N, 01°W	10
Portugal	South	37°N, 08°W	4
	West	38°N, 09°W	3
Spain	North	43°N, 03°W	1
	North-west	42°N, 08°W	1
	West	38°N, 06°W	1
	South	37°N, 06°W	2
Morocco	West	30°N, 09°W	1

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533 Table 2. Results of GLMs of (a) annual and individual variation in arrival dates of 85 godwits
 534 (3-12 years between 1999 and 2018) and variation in (b) annual trends in arrival dates and
 535 (c) mean arrival dates, in relation to the year in which those 85 individuals were first
 536 observed on arrival in Iceland.

	d.f.	<i>F</i>	<i>p</i>	Slope (\pm SE)
(a)				
Year	1	0.99	0.32	0.062 \pm 0.06
Individual	84	2.06	0.001	
Error	300			
(b)				
First observation year	1	0.02	0.89	0.004 \pm 0.03
Error	83			
(c)				
First observation year	1	8.83	0.004	-0.21 \pm 0.07
Error	83			

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544 Table 3. Results of binomial models of variation through consecutive time intervals in the
 545 frequency of individually-marked godwits recorded in winter locations (a) occupied since
 546 the 1960s (old, 0) or colonised since then (new, 1), and (b) north (0) and south (1) of 52°N.

	Estimate	SE	<i>p</i>	Odds ratio
(a)				
Intercept	0.4	0.25		
Year	-0.77	0.13	0.001	0.46
(b)				
Intercept	-0.008	0.23		
Year	-0.29	0.11	0.006	0.74

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3 552 **Figure Legends**

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7 554 Figure 1. Number of years on which 85 individually-marked Icelandic godwits have been
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9 555 recorded on spring arrival in Iceland, between 1999 and 2018.

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13 557 Figure 2. Changes in the mean (a) annual change in arrival date and (b) arrival date (days
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15 558 since 1 April) in Iceland of 85 individual godwits with the year in which they were first
16 559 observed on arrival in Iceland (see Table 2c for model details).

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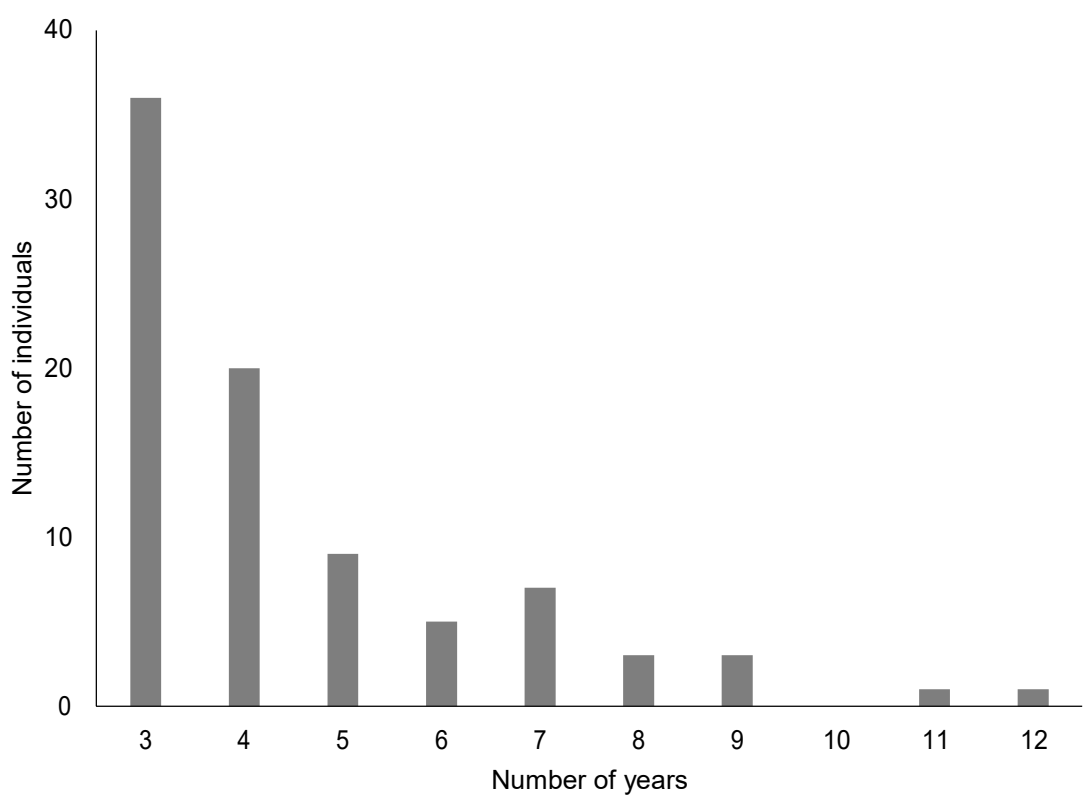
19 561 Figure 3. The total number of (a) countries, (b) regions and (c) locations on which individual
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21 562 godwits have ever been recorded in the total number of years over which each has been
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23 563 tracked. The number of individuals tracked for each total number of years is shown above
24 564 the bars in (a), see Table 1 for numbers of locations, regions and countries.

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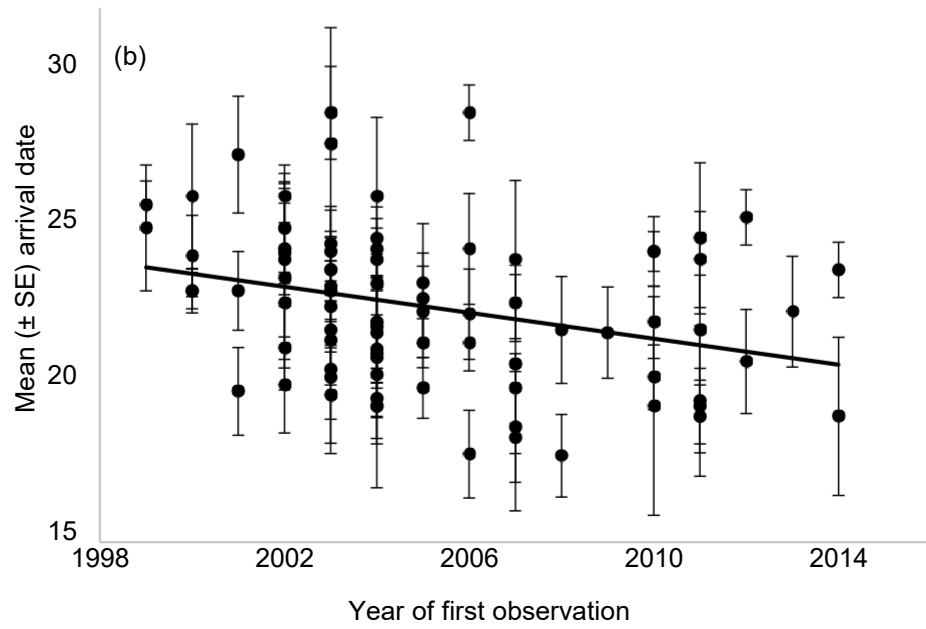
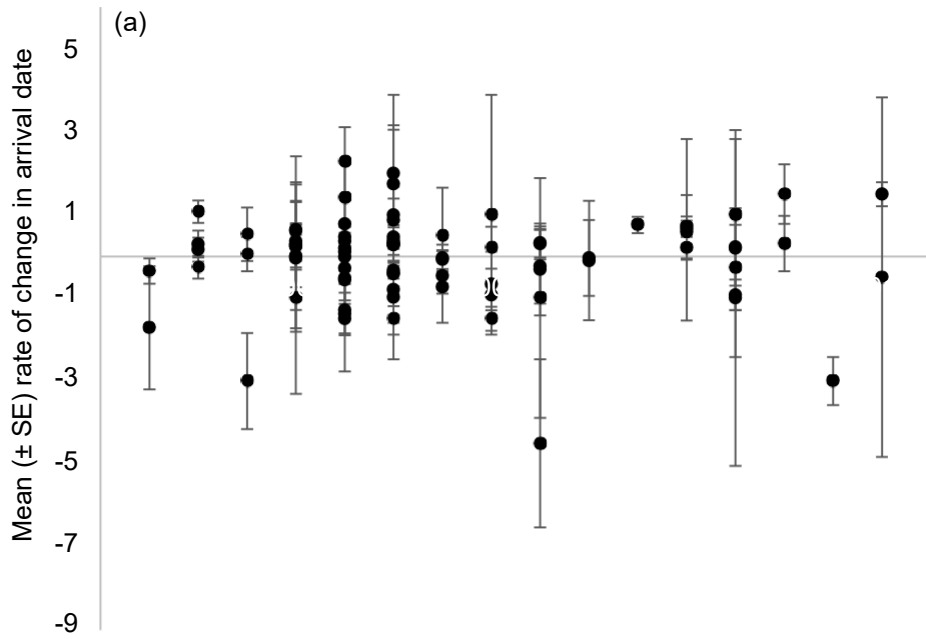
27 566 Figure 4. Changes through consecutive 5-year time intervals in the (a) proportion of
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29 567 individual godwits wintering in locations that have been occupied since the 1960s (old) or
30 568 colonised since then (new), and (b) latitude of those winter locations. Numbers observed in
31 569 each time period are shown in (a).

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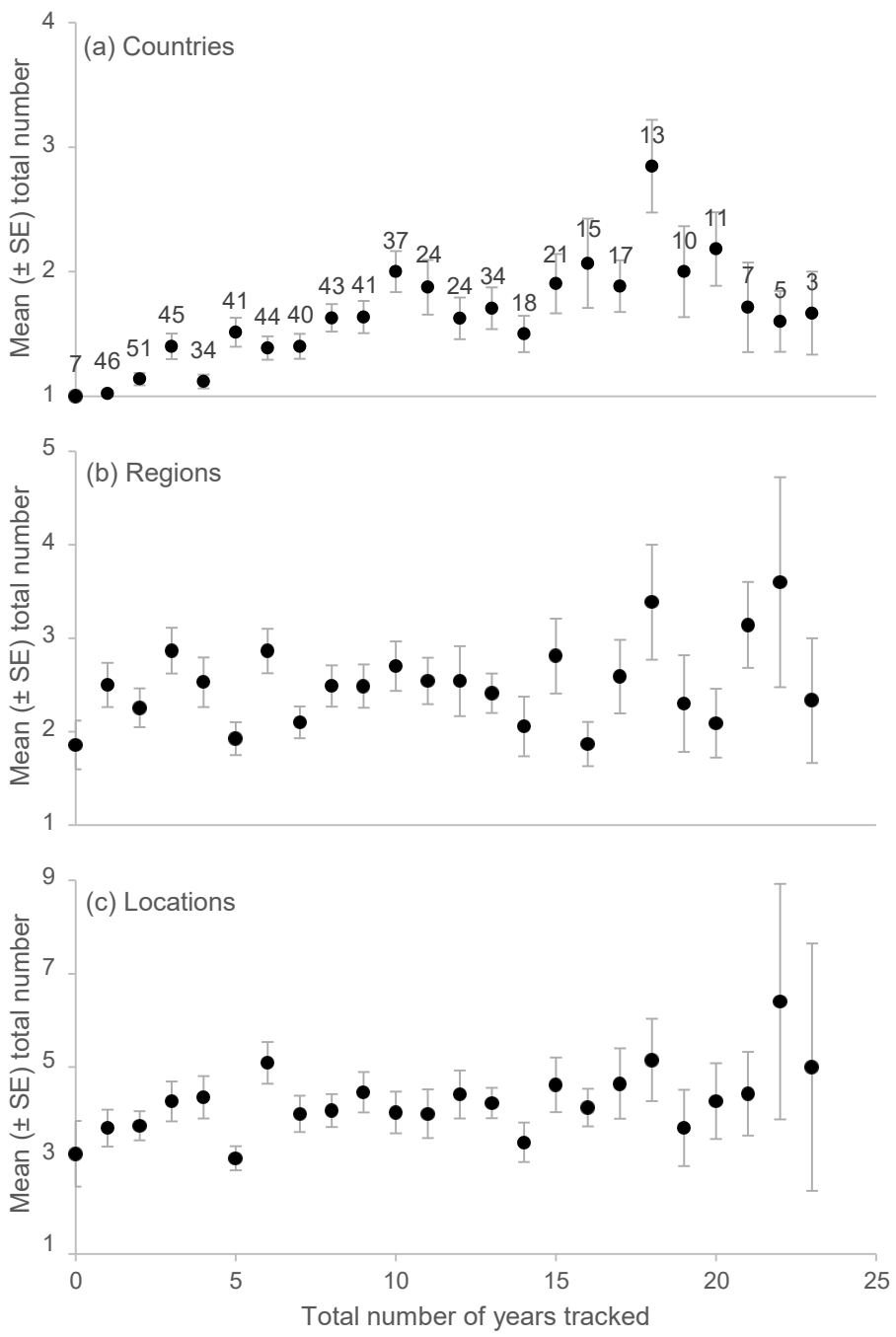
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