University of Groningen

The limits of modifying migration speed to adjust to climate change

Schmaljohann, Heiko; Both, Christiaan

Document Version
Final author's version (accepted by publisher, after peer review)

[Link to publication in University of Groningen/UMCG research database](#)

University of Groningen

The limits of modifying migration speed to adjust to climate change

Schmaljohann, Heiko; Both, C

Document Version
Final author's version (accepted by publisher, after peer review)

[Link to publication in University of Groningen/UMCG research database](#)

1   **The limits of modifying migration speed to adjust to climate change**

2

3   Heiko Schmaljohann[1†], Christiaan Both[2]

4

5   **Affiliations:**

6   [1]Institute of Avian Research "Vogelwarte Helgoland", An der Vogelwarte 21, Wilhelmshaven

7   26836, Germany.

8   [2]Conservation Ecology Group, Groningen Institute of Evolutionary Lifesciences (GELIFES),

9   University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands.

10

11   [†]Correspondence to: heiko.schmaljohann@ifv-vogelwarte.de

12

13   **One Sentence Summary:** Modifying migration speed does not allow sufficient adjustment of

14   spring arrival in response to climate change in migratory birds.

Introductory paragraph

Predicting the range of variation over which organisms can adjust to environmental change is a major challenge in ecology[1,2]. This is exemplified in migratory birds which experience changes in different habitats throughout the annual cycle[3]. Earlier studies showed European population trends declining strongest in migrant species with least adjustment in spring arrival time[4,5]. Thus, the increasing mismatches with other trophic levels in seasonal breeding areas[6,7] likely contribute to their large-scale decline. Here we quantify the potential range of adjusting spring arrival dates through modifying migration speeds by reviewing 49 tracking studies. Among individual variation in migration speed was mainly determined by the relatively short stop-over duration. Assuming this population response reflects individual phenotypic plasticity, we calculated the potential for phenotypic plasticity to speed-up migration by reducing stop-over duration. Even a 50% reduction would lead to a mere two day advance in arrival, considering adjustments on the final 2,000 km of the spring journey. Hence, in contrast to previous studies[8-10], flexibility in the major determinant of migration duration seems insufficient to adjust to ongoing climate change, and is unlikely to explain some of the observed arrival advancements in long-distance migrants.

Main Text: Human induced environmental change affects populations of most organisms on the globe[1]. Some species cope well with these changes, but many have struggled to adjust, resulting in rapid population declines[11,12]. It has seldom been demonstrated over which range of environmental change a species group can flexibly adjust, and the different mechanisms of adjustment (such as phenotypic plasticity and evolutionary change) involved usually remain obscure. An assessment of adjustment range is important, because it defines the operating space of environmental change without biodiversity loss. Here we aim to define the potential range of phenotypic adjustment in migration speed of long-distance migrant birds in response to climate change.

Each spring, billions of birds migrate from (sub-)tropical wintering grounds to their breeding areas. At their wintering grounds birds have little information on the progress of spring at their distant breeding areas, but arriving too early or too late is costly[13]. Evolution has equipped migratory birds with endogenous timing mechanisms enabling them to arrive at their migratory destinations on average at the optimal time[14]. Climate change alters this optimal time via the advance of spring. Migrant birds have partly responded by arriving at their breeding sites significantly earlier[1,5,15], but responses have typically been insufficient, resulting in a phenological mismatch with the primary food source at the breeding area[7]. Whether a mismatch affects population trends depends on the seasonality of habitats used, and evidence shows that a phenological mismatch (caused by insufficient advancement of breeding area arrival, and/or failure to reduce the interval between arrival and laying) can contribute (among other causes) to large-scale population declines[4,5,7,11,12], especially in long-distance migratory birds. Most evidence strongly suggests that individual migrants advance their spring arrival by a phenotypic response in the duration of migration, with mean population arrival being earlier when conditions are beneficial at the wintering grounds or along the migration route[8-10]. The central question in this paper is whether we can predict to what degree a reduction in migration time allows adjustment of breeding area arrival in

57   response to ongoing climate change, and when further advancement in spring arrival would

58   need other mechanisms, such as evolutionary change[15].

59   Each migratory journey is characterized by a sequence of fuel storage at the departure

60   or stop-over sites, and migratory flights to the next stop-over or destination site[16]. The total

61   speed of migration is the distance travelled divided by the flight plus stop-over duration, and

62   shows a wide phenotypic plasticity, varying between and within species[13]. As the rate of

63   accumulating energy at stop-over is lower than the rate of energy expenditure in flight[16], the

64   time required to complete migration is mainly determined by stop-over duration and less by

65   travel speed[17]. Optimal migration theory is based on this premise[16], but how total stop-over

66   duration quantitatively affects total speed of migration has never been generally assessed

67   across multiple study systems. This is an essential step to assess the role of phenotypic

68   flexibility in adjustment to spatio-temporal changes in the environment. Recent advances in

69   miniaturized tracking devices, which precisely record bird movements, now allow assessment

70   of the dependency of the speed of migration on total stop-over duration. Inferences about

71   phenotypic plasticity ideally would be drawn from tracking individuals over multiple years.

72   However, the paucity of these data[18] and the knowledge that stop-over duration of individuals

73   depends on environments encountered[19] makes between-individual comparisons the most

74   suitable approach for estimating the potential degree of plasticity. We envision this potential

75   plasticity in energy accumulation rates in response to food availability, leading to shorter

76   stop-over duration to replenish reserves for the next flight bout, if food is more abundant. As

77   food availability in temperate and arctic regions often is positively related to temperature, we

78   expect climate change to result in shorter stop-over periods. This approach enabled us to

79   model how much individual birds could potentially advance spring arrival date by shortening

80   their stop-overs.

81   Based on 49 tracking studies of 46 bird species including 320 individuals on spring

82   migration (Supplementary Tables S1, S2), we show that 66% of variation in total migration

4

83   speed was explained by total stop-over duration and bird group (linear mixed effect model of

84   total speed of migration, with explanatory variables: total stop-over duration, bird group, their

85   two-way interaction, and field study as a random factor in a Bayesian approach, Methods,

86   Supplementary Tables S3). We considered a stop-over as a more than one day stay at the

87   same location. Note that tracks without stop-over days (Fig. 1a) do not necessarily mean non-

88   stop migration, but rather continuous migration (e.g. nocturnal migration and diurnal

89   resting/foraging). For these studies, average migration distance was 6,128 km (25th quantile:

90   3,0954 km; 75th quantile: 7,578 km), and species were pooled into seven taxonomic bird

91   groups, i.e., geese ($n_{individuals}$=57), storks ($n_{individuals}$ =12), raptors ($n_{individuals}$ =21), waders

92   ($n_{individuals}$ =69), gulls ($n_{individuals}$ =30), swifts ($n_{individuals}$ =17), and songbirds ($n_{individuals}$ =114;

93   Supplementary Table S1).

94   As long predicted by optimal migration theory[16], we quantify here its major

95   assumption: Total speed of migration was mostly affected by total stop-over duration, with a

96   negative slope (Fig. 1a,c). The slopes describing the effect of stop-over duration on migration

97   speed were of similar magnitude across six taxonomic bird groups (Fig. 1c), except in geese,

98   where the effect was stronger. The generality of the pattern among diverse taxonomic groups

99   suggests that the general biological mechanism of regulating total speed of migration is by

100 variation in stop-over duration.

101   That flexibility in arrival dates at the breeding area results from variation in total stop-

102 over duration is well illustrated for two migratory songbirds during an exceptionally late

103 spring arrival in 2011; as a consequence of a drought at their eastern African stop-over site,

104 they doubled their total stop-over duration in comparison to the population mean to 18 days[19].

105 According to our general pattern (Fig. 1) their total speed of migration decreased from 240

106 km/day (95% CrI: 196 – 296 km/d) to 183 km/day (95% CrI: 153 – 219 km/d) predicting a

107 delayed arrival at the 8,700 km distant breeding areas of 11d (95% CrI: 8 – 15 d) tightly

108 matching the field observations (7 – 16 d)[19].

109   Given that variation in total speed of migration is mostly determined by variation in

110   total stop-over duration, we predict the range of advancement in spring arrival date by this

111   mechanism specifically for songbirds. For this modelling we assumed that individual

112   departure dates are rather inflexible[18,20] and ignored that they can be modulated by

113   environmental conditions[21]. A 20% reduction in total stop-over duration would result in a two

114   day advance in breeding area arrival for migration distances of 5,000 km, and seven days for

115   10,000 km (Fig. 2a; Supplementary Figure S1). To place these potential advances into an

116   ecological context, consider that climate change has the largest advancing effect on primary

117   consumers[22] and that time-series of caterpillar peak dates in European temperate forests

118   (primary prey for nestlings of many songbird species) advanced by 20 d (UK, 1980-2008[23]),

119   15 d (Netherlands, 1985-2005[24]) and 9 d (Czech Republic, 1961-2007[25]). As most of the

120   central and western European long-distance songbird migrants travel about 5,000-7,000 km, a

121   10 d advance would require a 50% reduction in total stop-over duration, and a 20 d advance

122   would be unfeasible (Fig. 2a) through the predicted effect of total stop-over duration on total

123   speed of migration (Fig. 1). Although these estimates demonstrate that individuals are highly

124   unlikely to advance sufficiently by modifying migration speed alone, in reality it is even more

125   difficult, because individuals can only anticipate environmental conditions when approaching

126   their breeding grounds. Within the Palearctic-African migration system, this likely happens

127   after crossing the Mediterranean Sea, i.e., on the final 1,000-3,000 km of their journey.

128   According to our data, songbirds would migrate 3 d, 7 d, and 13 d for the last 1,000 km, 2,000

129   km, and 3,000 km, respectively. Reducing total stop-over duration by 50% only results in a

130   0.6 d, 1.8 d, and 3.1 d advance, respectively (Methods). Our analysis clearly demonstrates that

131   the predicted phenotypic plasticity in the major component of migration speed, as estimated in

132   the among-individual approach, is insufficient to keep up with the advancing spring of major

133   breeding habitats.

134   Our predicted potential for adjusting arrival date can serve as a quantitative

135   comparison for interpreting observed rates of advancement on the population level. In a

136   dataset on arrival dates of the annual first 3-10 arriving males of ten trans-Saharan migrant

137   species for 36-years (1981-2016) from Drenthe (NL, 52° 52 N, 6° 16' E)[3], arrival date trend

138   varied between a delay of +2.6 d (95% CrI: -4.6 – +9.9 d) for spotted flycatchers (*Muscipata*

139   *striata*), to an advance of –15.9 d (95% CrI: -21.1 – -10.7 d) in pied flycatchers (*Ficedula*

140   *hypoleuca*) (Fig. 2b). These values were generally in the same order of magnitude as long-

141   term changes in the migration phenology of UK breeding birds[5]. The most extreme observed

142   advances in arrival (Fig. 2b) cannot be simply explained by a reduction in total stop-over

143   duration and hence by maximizing total speed of migration due to favourable conditions en

144   route (Fig. 2a). Alternatively, our among-individual comparison might not sufficiently well

145   capture the true but unknown within-individual phenotypic plasticity. It seems, however,

146   unlikely that the within-individual effect of reducing stop-over time on advancing arrival

147   timing would be much stronger than predicted by our approach, because environmental

148   conditions significantly affect stop-over duration[26]. The most likely candidate mechanism

149   causing these earlier arrivals at the breeding areas is therefore a progressive advance in

150   departure date from the wintering grounds[8]. This is supported by observations of pied

151   flycatchers that have advanced spring passage through North-Africa by ca. 8d between 1970-

152   2000[3] clearly demonstrating that advances have not solely been caused by speeding up

153   migration at their final part of migration[27].

154   Climate change likely will continue to change phenologies at different rates[22], and here

155   we have shown that long-distance migrant birds, with their relatively complex annual cycles,

156   have limited capacities to flexibly adjust their migration phenology through modifying

157   migration speed. This result could suggest that the observed strong advances in breeding area

158   arrival in some species (Fig. 2b)[5] are caused by improving conditions prior to departure at the

159   wintering grounds[21] resulting in an earlier spring departure timing through flexibility in

160   departure timing. Although we cannot rule out this mechanism, it is generally considered that

161   departure in long-distance migrants is triggered by photoperiod and hence not very

162   flexible[14,18,20]. Furthermore, conditions at wintering grounds often do not predict when

163   breeding grounds become profitable for arrival[3]. Alternatively, strong advances in breeding

164   area arrival are caused by an evolutionary response in spring departure timing[15]. In North

165   America, advances in spring arrival date across different species showed little plasticity

166   within individuals, and could not explain the population advance over the years, suggesting

167   ongoing evolutionary change although knowledge on heritability of arrival date was lacking[28].

168   Diurnal migrants that forage on the wing, e.g. swifts and swallows, have advanced their

169   arrival time stronger than nocturnal migrants in Britain[5]. This might not be caused by a

170   different evolutionary response, but possibly by a stronger phenotypic response to improving

171   foraging conditions en route yielding a stronger increase in rates of accumulating energy than

172   in nocturnal migrants. Evolution requires a genetic basis for variation in departure/arrival

173   dates and directional selection for an earlier arrival. The only system providing data on both

174   significant heritability and directional selection on arrival date concluded that the advance of

175   6 d in arrival over 20 years in great reed warbler (*Acrocephalus arundinaceus*) resulted from

176   phenotypic plasticity[9]. There are no other bird systems in which these mechanisms have

177   unequivocally been shown[10], let alone whether species differ in having e.g. enough genetic

178   variation in spring departure present in populations for evolution to operate. Our ability to

179   forecast the adaptive capacity of long-distance migrants to continuing global change requires

180   a much better understanding of why individuals within species differ in their annual timing,

181   but also why the responses to a changing environment differ considerably among-species

182   (Fig. 2b). To achieve this we need to better understand the (phenology of) trophic links during

183   breeding and especially including the conditions encountered at the wintering grounds.

184   Migrants are currently experiencing drastic environmental changes at their wintering grounds

185 that impact their survival[29], and these conditions likely have knock-on effects on later annual

186 cycle stages[30] and hence these birds are in double jeopardy.

187

Methods

188 **Methods**

189 Methods, including statements of data availability and any associated accession codes and

190 references, are available in the online version of this paper.

191

References

192 **References**

193   1. Walther, G.-R. *et al.* Ecological responses to recent climate change. *Nature* **416,** 389-395 (2002).
194   2. Visser, M. E. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc.*
195   *R. Soc. Lond. B* **275**, 649-659 (2008).
196   3. Both, C. Flexibility of timing of avian migration to climate change masked by environmental constraints en
197   route. *Curr. Biol.* **20,** 1-6 (2010).
198   4. Møller, A. P., Rubolini, D. & Lehikoinen, E. Populations of migratory bird species that did not show a
199   phenological response to climate change are declining. *P. Natl. Acad. Sci. USA* **105,** 16195-16200 (2008).
200   5. Newson, S. E. *et al.* Long-term changes in the migration phenology of UK breeding birds detected by
201   large-scale citizen science recording schemes. *Ibis* **158,** 481-495 (2016).
202   6. Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. Climate change and population declines in a long-
203   distance migratory bird. *Nature* **441,** 81-83 (2006).
204   7. Both, C. *et al.* Avian population consequences of climate change are most severe for long-distance migrants
205   in seasonal habitats. *Proc. R. Soc. Lond. B* **277,** 1259-1266 (2010).
206   8. Knudsen, E. *et al.* Challenging claims in the study of migratory birds and climate change. *Biol. Rev.* **86,**
207   928-946 (2011).
208   9. Tarka, M., Hansson, B. & Hasselquist, D. Selection and evolutionary potential of spring arrival phenology
209   in males and females of a migratory songbird. *J. Evol. Biol.* **28,** 1024-1038 (2015).
210   10. Charmantier, A. & Gienapp, P. Climate change and timing of avian breeding and migration: evolutionary
211   versus plastic changes. *Evol. Appl.* **7,** 15-28 (2014).
212   11. Stephens, P. A. *et al.* Consistent response of bird populations to climate change on two continents. *Science*
213   **352,** 84-87 (2016).
214   12. Saino, N. *et al.* Climate warming, ecological mismatch at arrival and population decline in migratory birds.
215   *Proc. R. Soc. Lond. B: Biological Sciences* **278,** 835-842 (2011).
216   13. Sergio, F. *et al.* Individual improvements and selective mortality shape lifelong migratory performance.
217   *Nature* **515,** 410-413 (2014).
218   14. Gwinner, E. Circadian and circannual programmes in avian migration. *J. Exp. Biol.* **199,** 39-48 (1996).
219   15. Jonzén, N. *et al.* Rapid advance of spring arrival dates in long-distance migratory birds. *Science* **312,** 1959-
220   1961 (2006).
221   16. Alerstam, T. & Lindström, Å. in *Bird Migration: Physiology and Ecophysiology* (ed E. Gwinner) 331-351
222   (Springer, 1990).
223   17. Nilsson, C., Klaassen, R. H. G. & Alerstam, T. Differences in speed and duration of bird migration between
224   spring and autumn. *Am. Nat.* **181,** 837-845 (2013).
225   18. Stanley, C. Q., MacPherson, M., Fraser, K. C., McKinnon, E. A. & Stutchbury, B. J. M. Repeat tracking of
226   individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE* **7,** e40688
227   (2012).
228   19. Tøttrup, A. P. *et al.* Drought in Africa caused delayed arrival of European songbirds. *Science* **338,** 1307
229   (2012).
230   20. Conklin, J. R., Battley, P. F. & Potter, M. A. Absolute consistency: Individual versus population variation
231   in annual-cycle schedules of a long-distance migrant bird. *PLoS ONE* **8,** e54535 (2013).
232   21. Studds, C. E. & Marra, P. P. Rainfall-induced changes in food availability modify the spring departure
233   programme of a migratory bird. *Proc. R. Soc. Lond. B* **278,** 3437-3443 (2011).

234   22. Thackeray, S. J. *et al.* Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535,** 241-
235   245 (2016).
236   23. Charmantier, A. *et al.* Adaptive phenotypic plasticity in response to climate change in a wild bird
237   population. *Science* **320,** 800-803 (2008).
238   24. Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B. & Visser, M. E. Climate change and unequal
239   phenological changes across four trophic levels: constraints or adaptations? *J Anim. Ecol.* **78**, 73 - 83
240   (2009).
241   25. Bauer, Z. *et al.* Changing climate and the phenological response of great tit and collared flycatcher
242   populations in floodplain forest ecosystems in Central Europe. *Int. J. Biometeorol.* **54,** 99-111 (2010).
243   26. Deppe, J. L. *et al.* Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it
244   takes to cross the Gulf of Mexico. *P. Natl. Acad. Sci. USA* **112,** E6331-E6338 (2015).
245   27. Jonzén, N., Hedenström, A. & Lundberg, P. Climate change and the optimal arrival of migratory birds.
246   *Proc. R. Soc. Lond. B* **274,** 269-274 (2007).
247   28. Van Buskirk, J., Mulvihill, R. S. & Leberman, R. C. Phenotypic plasticity alone cannot explain climate-
248   induced change in avian migration timing. *Ecol. Evol.* **2**, 2430-2437 (2012).
249   29. Zwarts, L., Bijlsma, R. G., van der Kamp, J. & Wymenga, E. *Living on the edge: Wetlands and birds in a*
250   *changing Sahel*. (KNNV Uitgeverij, 2009).
251   30. Harrison, X. A., Blount, A. D., Inger, R., Norris, D. R. & Bearhop, S. Carry-over effects as drivers of
252   fitness differences in animals. *J. Anim. Ecol.* **80**, 4-18 (2011).
253

Acknowledgments

Author contribution

H.S. designed the study. H.S. analysed the tracking data and modelled the phenotypic

response. C.B. analysed the phenology data. H.S. and C.B. wrote the paper.

Additional Information

Supplementary information is available in the online version of the paper. Reprints and

permissions information is available online at www.nature.com/reprints. Publisher's note:

Springer Nature remains neutral with regard to jurisdictional claims in published maps and

institutional affiliations. Correspondence and requests for materials should be addressed to

H.S.

Competing financial interests

The authors declare no competing financial interests.

269 **Figure 1 | Total stop-over duration explains variation in total speed of migration in**

270 **seven taxonomic bird groups. a**, Individual total speed of migration plotted against

271 individual total stop-over duration for seven taxonomic bird groups in spring (geese: dark

272 blue, storks: grey, raptors: orange, waders: light blue, gulls: green, swifts: yellow, and

273 songbirds: purple). Total stop-over duration and bird group explained 66% of variation in

274 total migration speed (Methods). **b**, 95% credible intervals (CrI) of the estimated intercept, β_0,

275 and **c**,) of the slope, β_1, for the bird group-specific regressions. **d**, 95% CrI of total number of

276 stop-over days for a 1,000 km long migratory journey. Sample size per bird group is given in

277 **b**.

278

279 **Figure 2 | Change in (a) predicted total duration of migration as a function of a change**

280 **in total stop-over duration in migratory songbirds, (b) arrival dates of ten migratory**

281 **birds between 1982-2016 (NL). a**, The average total duration of migration was estimated for

282 different migration distances based on the songbird-specific total number of stop-over days

283 with 3.2 days per 1,000 km (Fig. 1d). Predicted changes in total migration duration were

284 calculated based on the mechanism of how a change in total stop-over duration affects total

285 speed of migration. Contour lines clarified these changes in steps of 5 d intervals. Numbers

286 given in the middle of the figure indicate total duration of migration in days for a given

287 migration distance, e.g. arrows point out total duration of migration for 14,000 km. **b**, Each

288 year between 1981-2016 arrival of the first 10 males (filled circle) or the first 3 males (open

289 circles) were scored by the same observer in a restricted area in Drenthe (NL). Species

290 specific estimates are the linear slopes of the annual mean against year, multiplied by 35 years

291 and ordered from strongest advancements towards delays. Mean slopes, corresponding 95%

292 credible intervals, and number of considered years are given.

Methods

Total speed of migration and total stop-over duration. We considered individual tracking

data of 49 migration studies (Supplementary Tables S1, S2). Detailed information about total

migration distance, total duration of migration, and total stop-over duration for spring

migration were given on individual level for 320 birds (Supplementary Tables S1, S2). Total

speed of migration was individually estimated as the individual total duration of migration

divided by the corresponding total migration distance. All values were considered as provided

in the original publications. There are obviously differences in how stop-overs were defined

and in how accurate total migration distances were estimated, e.g. global positioning system

data vs. light-level geolocation data[31] and accurately determined migration distance vs. great

circle distance between wintering ground and breeding area. We did not correct for these

general differences in data quality. As still a high proportion of the variation (66%) in total

speed of migration was explained by total stop-over duration and bird group (Fig. 1), we are

convinced that if data quality were less variable, the dependence of total speed of migration

on total stop-over duration and bird group would be even stronger.

Statistics were calculated using the statistical software R 3.2.1[32]. We applied a Bayesian

approach to analyse the data[33]. Variation in total speed of migration was modelled using a

linear mixed effect model. Total stop-over duration and bird group were used as explanatory

variables. Their two-way interaction was considered to estimate bird group-specific

regressions. Total number of stop-over days and total speed of migration were both log10-

transformed to obtain a linear relationship between these parameters. As a few individual

birds did not perform a single stop-over day during their migration, i.e., their total stop-over

duration was zero, we added the 6th quantile of all individual total stop-over durations which

is 1.14 (days) to that value before transformation. Field study was included as a random factor

to account for repeated measures of the same species within the same study. We allowed for

318   both random intercepts and random slopes in the linear mixed effect model, i.e., an own

319   intercept and slope were permitted for each field study. Diagnostic residual and random effect

320   plots did not show deviation from the model assumptions. We used improper prior

321   distributions, namely $p(\beta) \sim 1$ for the coefficients, and $p(\beta) \sim 1/\sigma$ for the variance parameters.

322   To obtain the posterior distribution we directly simulated 2,000 values from the joint posterior

323   distribution of the model parameters using the function sim of the package "arm"[34]. The

324   medians of the simulated values from the joint posterior distributions of the model parameters

325   were used as estimates, and the 2.5% and 97.5% quantiles as lower and upper limits of the

326   95% credible intervals (CrI). The corresponding values are given in Figure 1 and

327   Supplementary Table S3. 66% of variance was explained by the fixed factors total stop-over

328   duration and bird group. 93% of variance was explained by the entire model, i.e., by both

329   fixed and random factors[35]. Considering the variation of the specific $\beta_{0,i}$- and $\beta_{1,i}$-values (Fig.

330   1b,c), there is a bird group-specific[i] mechanism of how total stop-over duration affects total

331   speed of migration:

332

333    $$Total\ speed\ of\ migration_i = 10^{(\beta_{0,i} + \beta_{1,i} * log10(total\ stopover\ duration_i))}$$ eqn. (1).

334

335   **Number of stop-over days per migration distance.** The number of total stop-over days per

336   1,000 km of migration was calculated as the log10-transformed total stop-over duration

337   divided by total migration distance and multiplied by 1,000. Variation in number of total stop-

338   over days per 1,000 km was modelled using a linear mixed effect model. Bird group was used

339   as an explanatory variable. Field study was included as a random factor. Here we could allow

340   only for random intercepts in the linear mixed effect model, but not for random slopes.

341   Diagnostic residual and random effect plots did not show deviation from the model

342   assumptions. Estimates and 95% CrI were calculated as described above.

343

Change in predicted total duration of migration as a function of a change in total stop-over duration for songbird migrants. Based on the data provided by the tracking studies of songbirds and our calculations, songbirds perform 3.2 d (95% CrI: 2.3 – 4.8 d) of stop-over per 1,000 km (Fig. 1d). First, we calculated the total number of stop-over days for a migration range of 5,000 km assuming 3.2 stop-over days per 1,000 km of migration, i.e. 16 d. For this 5,000 km migration range we let then vary the total stop-over duration from -50% to +50% in steps of 1%. We incorporated these 101 different estimates of total stop-over durations into eqn. 1 with the songbird-specific estimates for the intercept and the slope (Fig. 1b,c and eqn. 1) to model the corresponding 101 different total speeds of migration. By dividing the migration range of 5,000 km by these values we received 101 different estimates of total duration of migration based in the 101 different total speeds of migration. Finally, these 101 estimates of total duration of migration were related to the original (not changed) estimate of total duration of migration, i.e. the 51st value. Thus, decreasing the total stop-over duration resulted in a shorter total duration of migration and increasing the total stop-over duration resulted in a longer total duration of migration (Fig. 2a). This procedure was repeated for different migration ranges increasing in steps of 100 km to the maximum migration range of 15,000 km considered here. The graphical solution of this modelling is given in Figure 2a and Supplementary Figure S1. We modelled the effect of a change in total stop-over duration in the same way also for the lower (Supplementary Figure S1a) and the upper limit of the 95% CrI (Supplementary Figure S1c) for the estimated average number of stop-over days per 1,000 km (Fig. 1d). The graphical solutions of these modelling are given in Supplementary Figure S1.

Arrival dates of 10 migratory birds between 1982 – 2016. Every year between 1981 – 2016 the first arriving three to ten males were recorded by the same observer, Rob G. Bijlsma, of all migrant species that do not winter in the area, and breed in the forests of Drenthe (northern

14

370   Netherlands, 6° 17' E, 52° 52' N)[7]. The area was visited on a daily basis during spring and

371   summer (from late February onwards). Individuals that were recorded once were not counted

372   as new arrivals the next day, so data are from separate individuals within a year. The study

373   area is forested with conifers and interspersed with heaths and deciduous woodland. Arrival

374   dates of males was monitored by observing singing birds, and given the intensity of the

375   observer's presence, are probably accurate[7]. For instance, when birds were seen before any

376   song was heard, singing was almost always recorded later the same day. Sample size

377   differences between species in number of individuals per year depend on their general

378   abundance. From the abundant species the first ten individuals were recorded, whereas from

379   other species the first three individuals were recorded as indicated in Figure 2b. Variation in

380   arrival date was modelled for each species separately by a simple linear regression. Julian day

381   of the tenth or third recorded individual was used as the explanatory variable. Diagnostic

382   residual plots did not show deviation from the model assumptions. The species-specific

383   median of the simulated values from the joint posterior distribution of the model parameter

384   was used as the estimated slope, and the 2.5% and 97.5% quantiles as lower and upper limits

385   of the 95% credible intervals (CrI).

386   Trends in first arrival dates can be affected by population trends, because as in

387   declining populations fewer individuals will be in the early tail, whereas in growing

388   populations more individuals will be in the early tail. We checked for this possible artefact by

389   considering population trends as observed in a forest area (Dwingelderveld, 6° 24' E, 52° 48'

390   N) of similar habitat ca. 10 km south-east of the area from where the phenological

391   observations were made (Fig. 2b). Each year, Joop Kleine counted breeding birds by territory

392   mapping in Dwindelderveld. Here we considered his data from 1987-2016 for the same set of

393   species as incorporated in our phenological observations (Fig. 2b). For each of the ten species,

394   we calculated the population trend as the slope of log10-transformed population size to year.

395   Four species showed a significant population decline, three a significant increase, and three no

396 significant change over the years. We found no correlation between local population trend

397 (1991-2011) and the trend in phenology (1982-2016, Fig. 2b; Pearson correlation: r = -0.12, N

398 = 10, p = 0.74). The strongest advancements in arrival were observed in a species with

399 declining population size (common cuckoo), a species without a trend (wood warbler) and an

400 increasing species (pied flycatcher). Therefore, we feel rather confident that the variation in

401 arrival trend, as observed between species in Figure 2b, is not a matter of changes in their
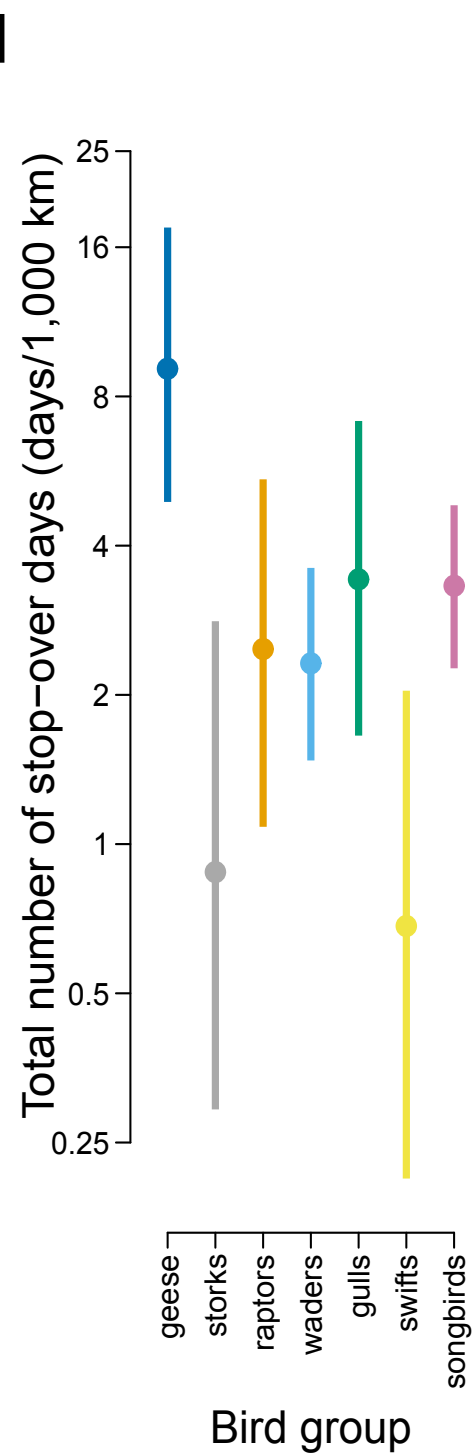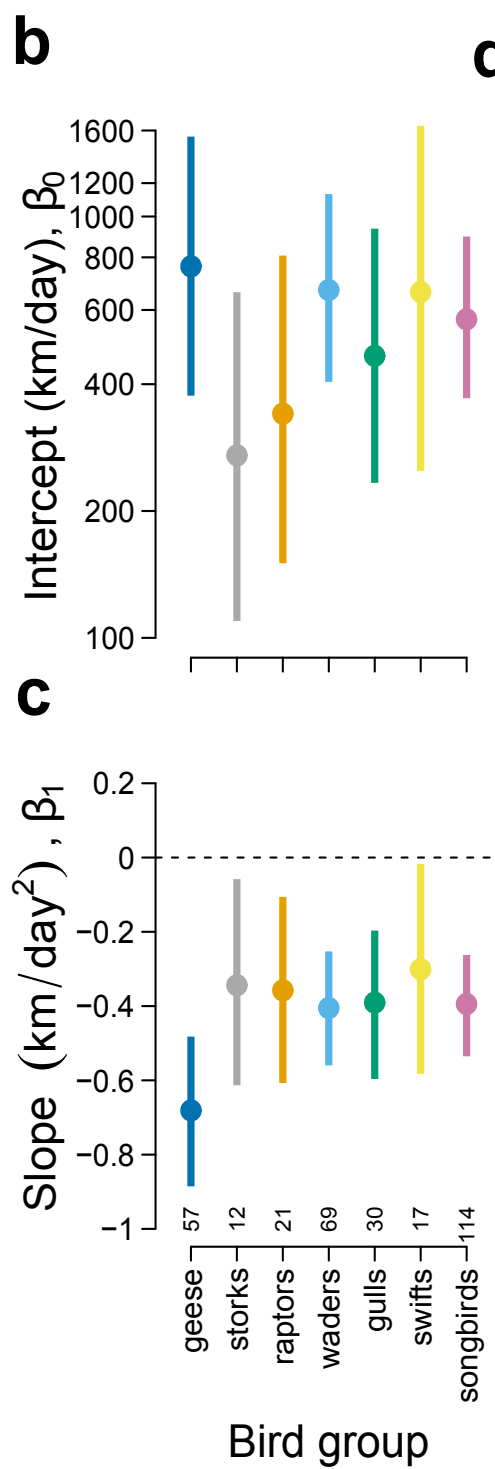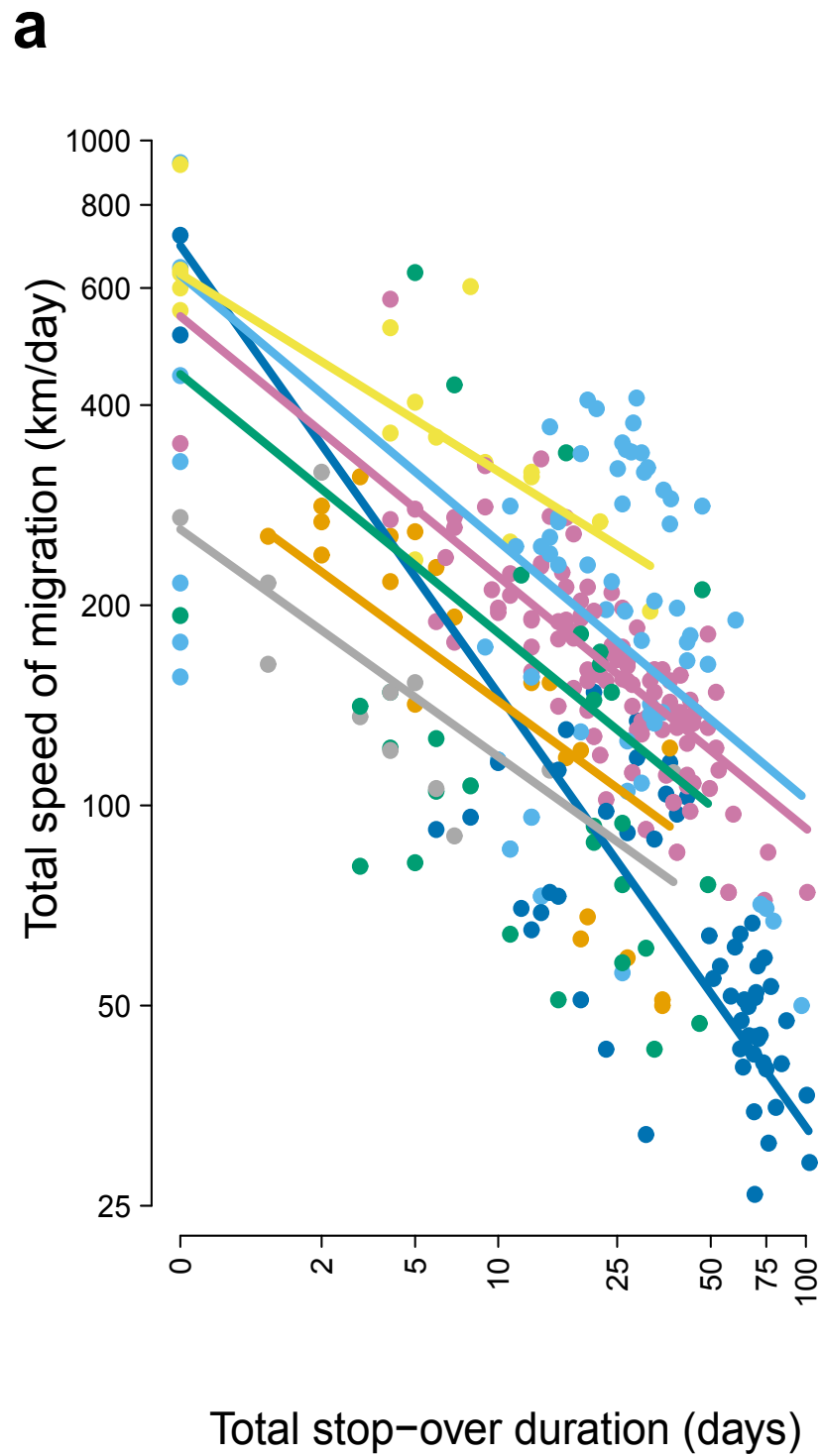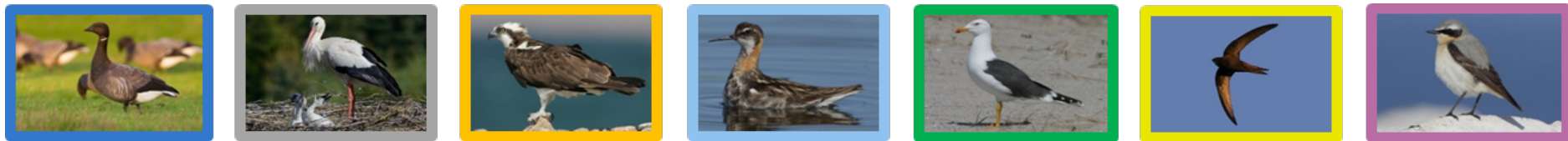
402 abundance.

403

404 **Data availability:** The authors declare that the data supporting the findings of the total speed

405 of migration and total stop-over duration analysis are available within the article's

406 supplementary information files. The data that support the findings of the arrival date analysis

407 are available from C.B. upon request.

408 **Code availability:** R code for modelling will be shared upon request, please address H.S.

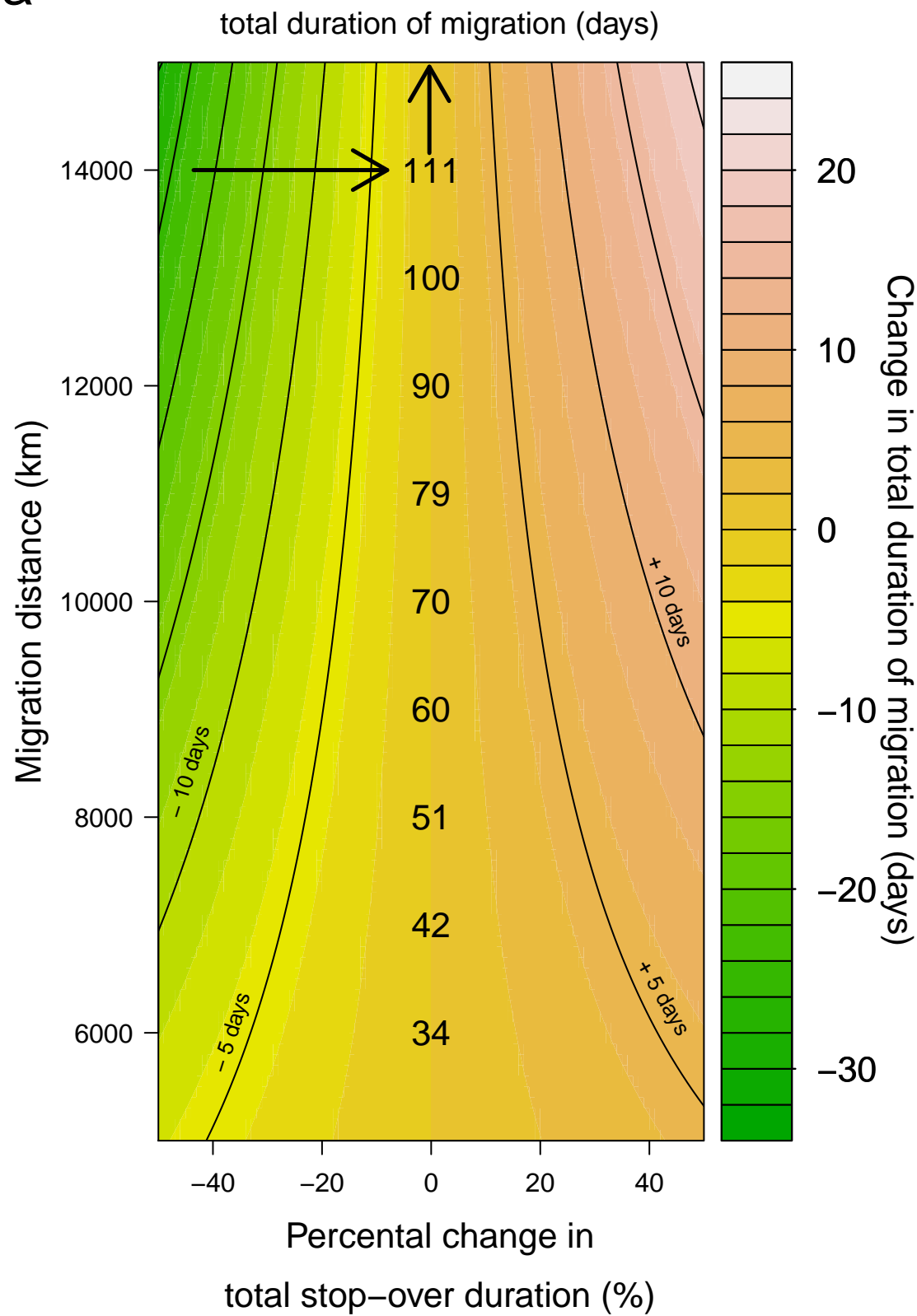409 (heiko.schmaljohann@ifv-vogelwarte.de).

410

References

412 31. Rakhimberdiev, E. *et al.* Comparing inferences of solar geolocation data against high-precision GPS data:
413   annual movements of a double-tagged black-tailed godwit. *J. Avian Biol.* **47,** 589-596 (2016).
414 32. R Core Team. R: A language and environment for statistical computing. (2015).
415 33. Korner-Nievergelt, F. *et al. Bayesian data analysis in ecology using linear models with R, BUGS, and Stan.*
416   (Elsevier, 2015).
417 34. Gelman, A. & Hill, J. *Data analysis using regression and multilevel/hierarchical models.* (Cambridge
418   University Press, 2007).
419 35. Johnson, P. C. D. Extension Nakagawa & Schielzeth's R^{2GLMM} to random slopes models. *Method. Ecol.*
420   *Evol.* **5,** 944-946 (2014).

a

b

c

d

a

total duration of migration (days)

Migration distance (km)

Percental change in
total stop-over duration (%)

Change in total duration of migration (days)

b

pied flycatcher	(36 yrs)
Ficedula hypoleuca	
wood warbler	(35 yrs)
Phylloscopus sibilatrix	
common cuckoo	(36 yrs)
Cuculus canorus	
common redstart	(28 yrs)
Phoenicurus phoenicurus	
common whitethroat	(34 yrs)
Sylvia communis	
garden warbler	(34 yrs)
Sylvia borin	
tree pipit	(35 yrs)
Anthus trivialis	
barn swallow	(35 yrs)
Hirundo rustica	
willow warbler	(35 yrs)
Phylloscopus trochilus	
spotted flycatcher	(32 yrs)
Muscicapa striata	

Change in arrival date

(days/35 years)