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

2
3 Heiko Schmaljohann^{1†}, Christiaan Both²

4
5 **Affiliations:**

6 ¹Institute of Avian Research “Vogelwarte Helgoland”, An der Vogelwarte 21, Wilhelmshaven
7 26836, Germany.

8 ²Conservation 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.

15 **Introductory paragraph**

16 Predicting the range of variation over which organisms can adjust to environmental change is
17 a major challenge in ecology^{1,2}. This is exemplified in migratory birds which experience
18 changes in different habitats throughout the annual cycle³. Earlier studies showed European
19 population trends declining strongest in migrant species with least adjustment in spring arrival
20 time^{4,5}. Thus, the increasing mismatches with other trophic levels in seasonal breeding areas^{6,7}
21 likely contribute to their large-scale decline. Here we quantify the potential range of adjusting
22 spring arrival dates through modifying migration speeds by reviewing 49 tracking studies.
23 Among individual variation in migration speed was mainly determined by the relatively short
24 stop-over duration. Assuming this population response reflects individual phenotypic
25 plasticity, we calculated the potential for phenotypic plasticity to speed-up migration by
26 reducing stop-over duration. Even a 50% reduction would lead to a mere two day advance in
27 arrival, considering adjustments on the final 2,000 km of the spring journey. Hence, in
28 contrast to previous studies⁸⁻¹⁰, flexibility in the major determinant of migration duration
29 seems insufficient to adjust to ongoing climate change, and is unlikely to explain some of the
30 observed arrival advancements in long-distance migrants.

31 **Main Text:** Human induced environmental change affects populations of most organisms on
32 the globe¹. Some species cope well with these changes, but many have struggled to adjust,
33 resulting in rapid population declines^{11,12}. It has seldom been demonstrated over which range
34 of environmental change a species group can flexibly adjust, and the different mechanisms of
35 adjustment (such as phenotypic plasticity and evolutionary change) involved usually remain
36 obscure. An assessment of adjustment range is important, because it defines the operating
37 space of environmental change without biodiversity loss. Here we aim to define the potential
38 range of phenotypic adjustment in migration speed of long-distance migrant birds in response
39 to climate change.

40 Each spring, billions of birds migrate from (sub-)tropical wintering grounds to their
41 breeding areas. At their wintering grounds birds have little information on the progress of
42 spring at their distant breeding areas, but arriving too early or too late is costly¹³. Evolution
43 has equipped migratory birds with endogenous timing mechanisms enabling them to arrive at
44 their migratory destinations on average at the optimal time¹⁴. Climate change alters this
45 optimal time via the advance of spring. Migrant birds have partly responded by arriving at
46 their breeding sites significantly earlier^{1,5,15}, but responses have typically been insufficient,
47 resulting in a phenological mismatch with the primary food source at the breeding area⁷.
48 Whether a mismatch affects population trends depends on the seasonality of habitats used,
49 and evidence shows that a phenological mismatch (caused by insufficient advancement of
50 breeding area arrival, and/or failure to reduce the interval between arrival and laying) can
51 contribute (among other causes) to large-scale population declines^{4,5,7,11,12}, especially in long-
52 distance migratory birds. Most evidence strongly suggests that individual migrants advance
53 their spring arrival by a phenotypic response in the duration of migration, with mean
54 population arrival being earlier when conditions are beneficial at the wintering grounds or
55 along the migration route⁸⁻¹⁰. The central question in this paper is whether we can predict to
56 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 change¹⁵.

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 site¹⁶. 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 species¹³. As the rate of
63 accumulating energy at stop-over is lower than the rate of energy expenditure in flight¹⁶, the
64 time required to complete migration is mainly determined by stop-over duration and less by
65 travel speed¹⁷. Optimal migration theory is based on this premise¹⁶, 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 data¹⁸ and the knowledge that stop-over duration of individuals
73 depends on environments encountered¹⁹ 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

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 ($n_{\text{individuals}}=57$), storks ($n_{\text{individuals}}=12$), raptors ($n_{\text{individuals}}=21$), waders
92 ($n_{\text{individuals}}=69$), gulls ($n_{\text{individuals}}=30$), swifts ($n_{\text{individuals}}=17$), and songbirds ($n_{\text{individuals}}=114$;
93 Supplementary Table S1).

94 As long predicted by optimal migration theory¹⁶, 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 days¹⁹.
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 conditions²¹. 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 consumers²² 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, 1980-2008²³),
119 15 d (Netherlands, 1985-2005²⁴) and 9 d (Czech Republic, 1961-2007²⁵). 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 birds⁵. 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 duration²⁶. 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 grounds⁸. This is supported by observations of pied
151 flycatchers that have advanced spring passage through North-Africa by ca. 8d between 1970-
152 2000³ clearly demonstrating that advances have not solely been caused by speeding up
153 migration at their final part of migration²⁷.

154 Climate change likely will continue to change phenologies at different rates²², 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 grounds²¹ 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 arrival³. Alternatively, strong advances in breeding
164 area arrival are caused by an evolutionary response in spring departure timing¹⁵. 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 lacking²⁸.
168 Diurnal migrants that forage on the wing, e.g. swifts and swallows, have advanced their
169 arrival time stronger than nocturnal migrants in Britain⁵. 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 plasticity⁹. There are no other bird systems in which these mechanisms have
177 unequivocally been shown¹⁰, 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 survival²⁹, and these conditions likely have knock-on effects on later annual
186 cycle stages³⁰ and hence these birds are in double jeopardy.

187

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

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- 253

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258 **Author contribution**

259 H.S. designed the study. H.S. analysed the tracking data and modelled the phenotypic
260 response. C.B. analysed the phenology data. H.S. and C.B. wrote the paper.

261 **Additional Information**

262 Supplementary information is available in the online version of the paper. Reprints and
263 permissions information is available online at www.nature.com/reprints. Publisher's note:
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265 institutional affiliations. Correspondence and requests for materials should be addressed to
266 H.S.

267 **Competing financial interests**

268 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.

293 **Methods**

294 **Total speed of migration and total stop-over duration.** We considered individual tracking
295 data of 49 migration studies (Supplementary Tables S1, S2). Detailed information about total
296 migration distance, total duration of migration, and total stop-over duration for spring
297 migration were given on individual level for 320 birds (Supplementary Tables S1, S2). Total
298 speed of migration was individually estimated as the individual total duration of migration
299 divided by the corresponding total migration distance. All values were considered as provided
300 in the original publications. There are obviously differences in how stop-overs were defined
301 and in how accurate total migration distances were estimated, e.g. global positioning system
302 data vs. light-level geolocation data³¹ and accurately determined migration distance vs. great
303 circle distance between wintering ground and breeding area. We did not correct for these
304 general differences in data quality. As still a high proportion of the variation (66%) in total
305 speed of migration was explained by total stop-over duration and bird group (Fig. 1), we are
306 convinced that if data quality were less variable, the dependence of total speed of migration
307 on total stop-over duration and bird group would be even stronger.

308 Statistics were calculated using the statistical software R 3.2.1³². We applied a Bayesian
309 approach to analyse the data³³. Variation in total speed of migration was modelled using a
310 linear mixed effect model. Total stop-over duration and bird group were used as explanatory
311 variables. Their two-way interaction was considered to estimate bird group-specific
312 regressions. Total number of stop-over days and total speed of migration were both log10-
313 transformed to obtain a linear relationship between these parameters. As a few individual
314 birds did not perform a single stop-over day during their migration, i.e., their total stop-over
315 duration was zero, we added the 6th quantile of all individual total stop-over durations which
316 is 1.14 (days) to that value before transformation. Field study was included as a random factor
317 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 factors³⁵. 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

$$333 \quad \text{Total speed of migration}_i = 10^{(\beta_{0,i} + \beta_{1,i} * \log_{10}(\text{total stopover duration}_i))} \text{ eqn. (1).}$$

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

344 **Change in predicted total duration of migration as a function of a change in total stop-**
345 **over duration for songbird migrants.** Based on the data provided by the tracking studies of
346 songbirds and our calculations, songbirds perform 3.2 d (95% CrI: 2.3 – 4.8 d) of stop-over
347 per 1,000 km (Fig. 1d). First, we calculated the total number of stop-over days for a migration
348 range of 5,000 km assuming 3.2 stop-over days per 1,000 km of migration, i.e. 16 d. For this
349 5,000 km migration range we let then vary the total stop-over duration from -50% to +50% in
350 steps of 1%. We incorporated these 101 different estimates of total stop-over durations into
351 eqn. 1 with the songbird-specific estimates for the intercept and the slope (Fig. 1b,c and eqn.
352 1) to model the corresponding 101 different total speeds of migration. By dividing the
353 migration range of 5,000 km by these values we received 101 different estimates of total
354 duration of migration based in the 101 different total speeds of migration. Finally, these 101
355 estimates of total duration of migration were related to the original (not changed) estimate of
356 total duration of migration, i.e. the 51st value. Thus, decreasing the total stop-over duration
357 resulted in a shorter total duration of migration and increasing the total stop-over duration
358 resulted in a longer total duration of migration (Fig. 2a). This procedure was repeated for
359 different migration ranges increasing in steps of 100 km to the maximum migration range of
360 15,000 km considered here. The graphical solution of this modelling is given in Figure 2a and
361 Supplementary Figure S1. We modelled the effect of a change in total stop-over duration in
362 the same way also for the lower (Supplementary Figure S1a) and the upper limit of the 95%
363 CrI (Supplementary Figure S1c) for the estimated average number of stop-over days per 1,000
364 km (Fig. 1d). The graphical solutions of these modelling are given in Supplementary Figure
365 S1.

366

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

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 accurate⁷. 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

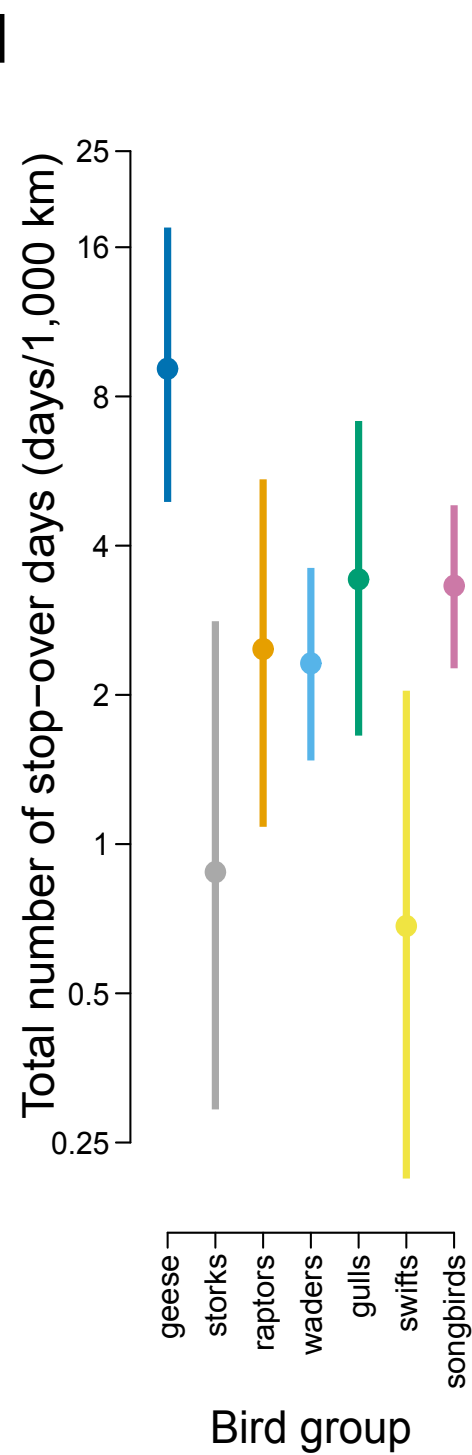
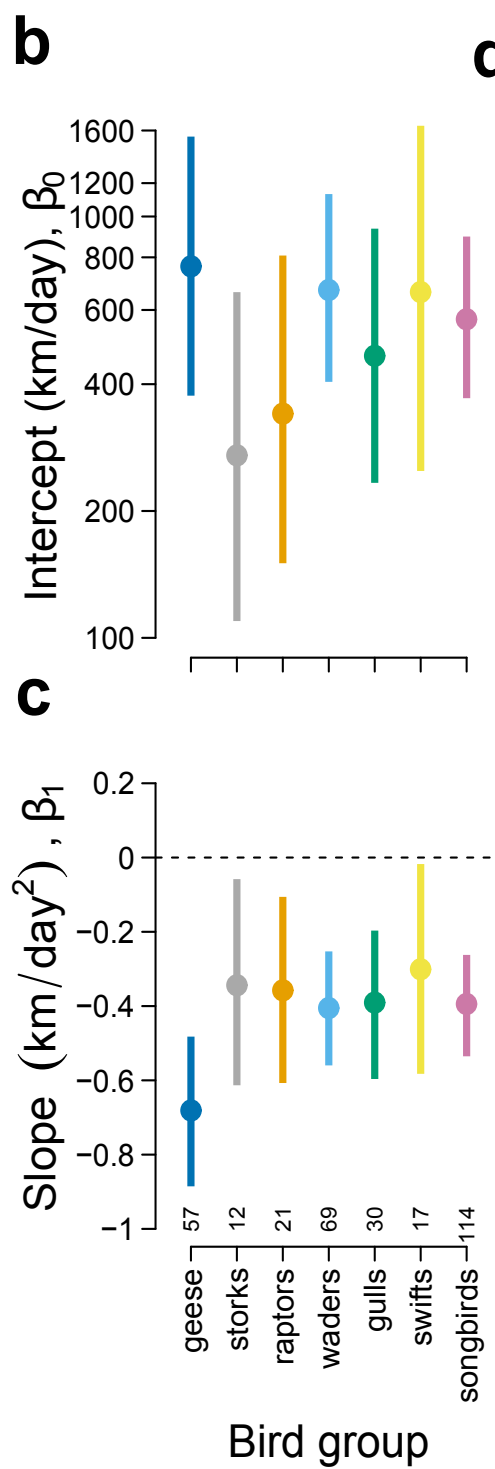
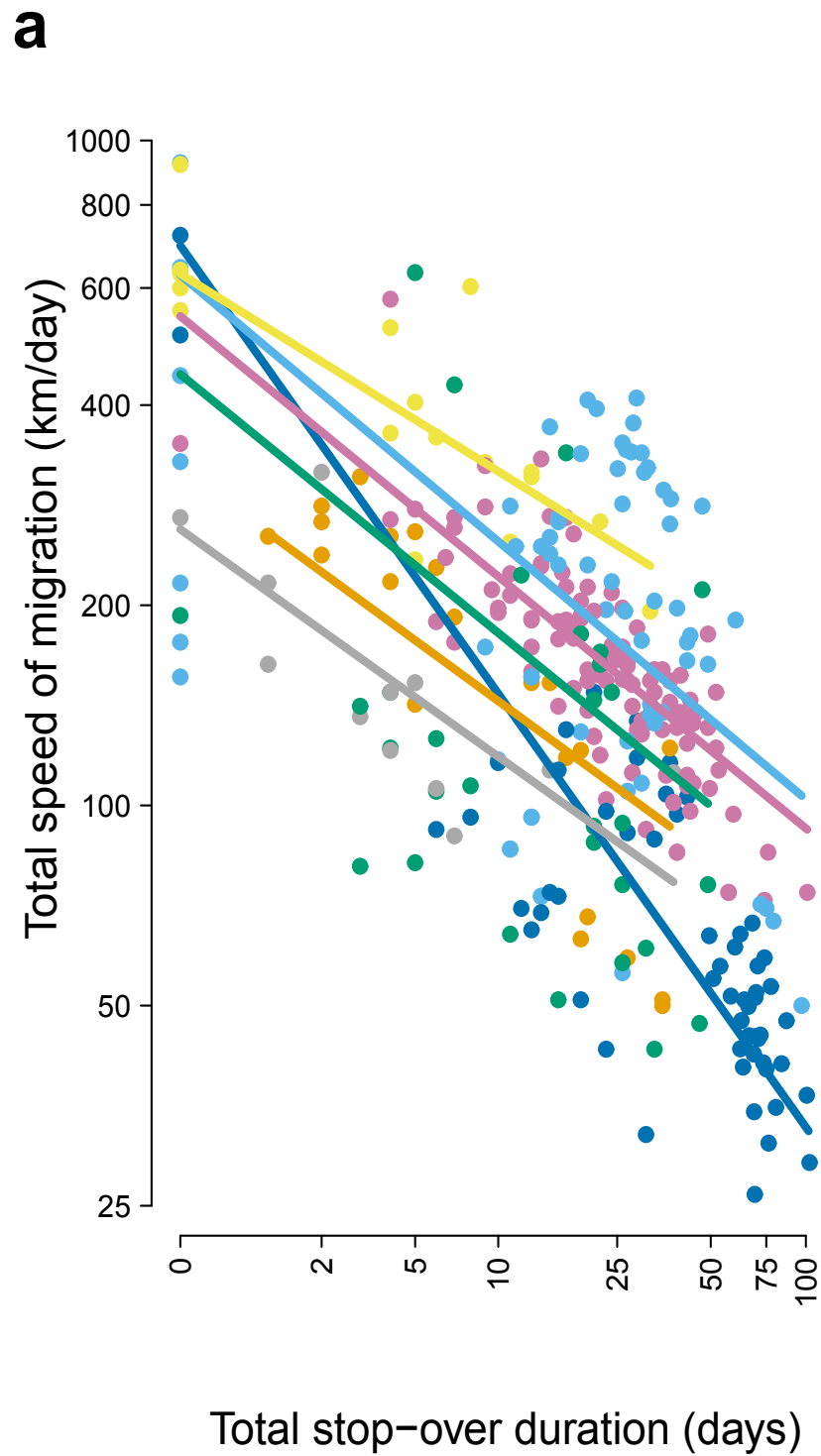
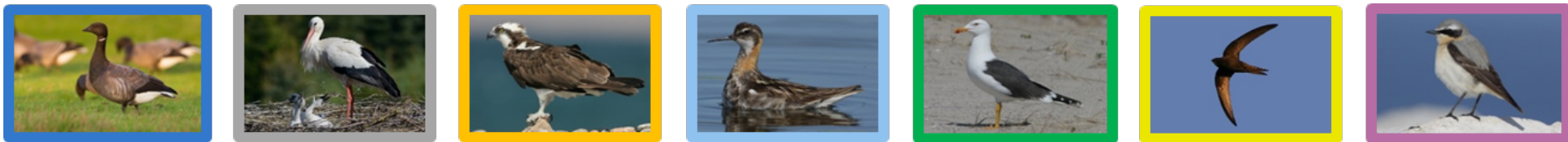
404 **Data availability:** The authors declare that the data supporting the findings of the total speed
405 of migration and total stop-over duration analysis are available within the article's
406 supplementary information files. The data that support the findings of the arrival date analysis
407 are 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).

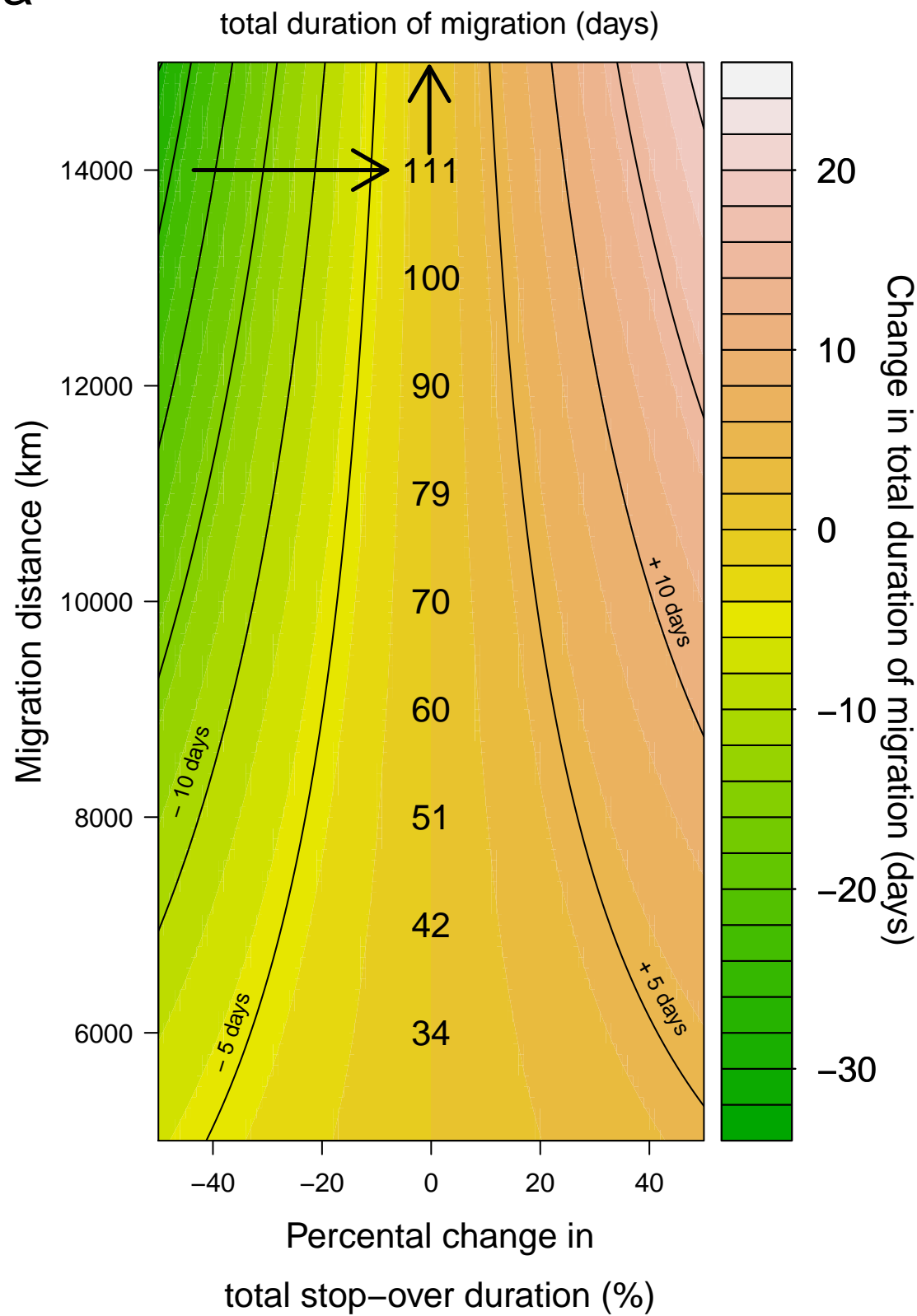
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a



b

