# Environmental variability, reliability of information and the timing of migration

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**Running head**: information and migration

**Author contributions**

SB, JMM and ZB conceived the idea, JMM developed the model, ZB developed the programming code, SB ran and analysed scenarios. SB wrote the manuscript with input from the co-authors.

**Keywords**

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## Abstract

20  The timing of migration and migratory steps is highly relevant for fitness. Since environmental

21  conditions vary between years, the optimal time for migration varies accordingly. Therefore, migratory

22  animals could clearly benefit from acquiring information as to when it is the best time to migrate in a

23  specific year. Thus, environmental predictability and variability are fundamental characteristics of

24  migration systems but their relation and consequence for migratory progression has remained

25  unexplored.

26  We develop a simple dynamic model to identify the optimal migration behaviour in environments that

27  differ in predictability, variability and the number of intermediate stopover sites. Our results indicate

28  that higher predictability along migration routes enables organisms to better time migration when

29  phenology deviates from its long-term average and thus, increases fitness. Information is particularly

30  valuable in highly variable environments and in the final migration-step, i.e. before the destination.

31  Furthermore, we show that a general strategy for obtaining information in relatively uninformative but

32  variable environments is using intermediate stopover sites that enable migrants to better predict

33  conditions ahead.

34  Our study contributes to a better understanding of the relation between animal movement and

35  environmental predictability - an important, yet underappreciated factor that strongly influences

36  migratory progression.

## Introduction

38  Migration is an adaptation to conditions that vary seasonally or periodically between favourable,

39  resource-rich and unfavourable, or hostile [1]. Typically, there is an optimal time for migration, i.e.

40  success/ reward is highest when executed at this time [2]. Missing the optimal time incurs costs that

41  may range from reduced reproductive success to reduced survival, e.g. [3], and this applies not only

42  for departure from a starting site and arrival at a destination (breeding) site but also for intermediate

43 steps on stopover sites. In stable seasonal environments, in which the optimal time occurs invariantly

44 at the same time of the year, natural selection would push organisms to time migration at exactly this

45 best time [4]. In this case, a photoperiodic cue to time migration would be fully sufficient. Typically,

46 however, there is environmental variability between years, and the optimal time cannot be predicted

47 on the basis of photoperiod alone but requires additional (external) information [5]. If environmental

48 variables are correlated in space or time, individuals could obtain information about environmental

49 conditions at distant places or in the future whereas weak correlation means a low level of information

50 only [6]. Specifically, if phenologies of successive sites are correlated, this means they may have

51 different long-term averages for, e.g., the onset of spring, but they *deviate* similarly from this average

52 in a given year: Under strong correlation, for instance, an early onset of spring at one site means spring

53 is also earlier-than-average on the subsequent site (Fig. 1) while under weak correlation, the onset of

54 spring at one site can hardly predict the onset of spring at another.

55 Thus, migration systems can differ in two fundamental aspects – how variable they are between years

56 and in how far conditions at distant sites can be predicted from the current location, i.e. environmental

57 variability and predictability, respectively [7]. Many migrants have been shown to follow the temporal

58 availability of resources across heterogeneous landscapes [8], e.g. green wave of spring green up

59 [9,10], which suggests that migrants indeed have, or can acquire, knowledge on environmental

60 conditions at distant places. However, although it is generally acknowledged that information plays an

61 important role for animal behaviour [11,12], the link between spatial environmental predictability and

62 the timing of animal movements has not been systematically explored [13]. Consequently, we lack a

63 detailed understanding of how animals should schedule migrations under different levels of

64 information about optimal timing, how the best migration strategy would change in environments

65 differing in variability and which role intermediate stop-over sites could play in modifying these

66 relations. We address these questions with a simple model that calculates the optimal migration

67 behaviour from a starting ('wintering') to a destination ('breeding') site.

## Model description and scenarios

69  The migration route consists of $K$ locations, labelled as $k = 1, 2, ..., K,$ where $k=1$ marks the wintering

70  and $K$ the breeding site (Fig. 1a). Thus, $K=2$ represents a non-stop migration between wintering and

71  breeding site, and $K>2$ refers to migration with one or more intermediate (stopover) sites.

72  We describe phenology on sites with the 'onset of spring', i.e. the time when conditions become

73  favourable and mortality decreases (Fig. 1b-c). The long-term average for the onset of spring at site $k$

74  is $\tau(k)$ but the actual onset of spring in a given year may deviate from this average by $Y(k)$, which is a

75  random variable with zero mean and variance $\sigma^2(k)$, i.e. $E\{Y(k)\} = 0$ and $\text{Var}\{Y(k)\} = \sigma^2(k)$. Thus,

76  in a given year, the actual onset of spring is at time $\tau(k) - Y(k)$.

77  We assume that conditions at neighbouring sites (e.g. $k$ and $k+1$, $k < K$) are correlated, i.e. the joint

78  distribution of $Y(k)$ and $Y(k+1)$ is a bivariate normal distribution with correlation coefficient $\rho(k)$. This

79  correlation coefficient shows to what extent the onset of spring on site $k$ predicts the onset of spring on

80  site $k+1$. Given the value of $Y(k)$ we assume that values at later sites are conditionally independent of

81  the values at previous sites (the Markov property). With this assumption, the product of all $\rho(k)$ (i.e.

82  $\rho = \prod_{k=1}^{K-1} \rho(k)$) is the correlation between $Y(1)$ and $Y(K)$ and hence indicates the expected

83  predictability across the entire migration landscape, i.e. the predictability of conditions at the breeding

84  site from conditions at the wintering site.

85

## Decision making on the migratory journey

87  Individuals start migration at the wintering site ($k=1$), subsequently move to following sites and if

88  surviving the journey, finally arrive at the breeding site $K$. We allow no skipping of sites but assume

89  that travel time between sites is negligible compared to time spent on sites. On arrival at site $k$, an

90  animal immediately observes its phenological stage, i.e. by how much the actual onset of spring

91  deviates from its long-term average. More formally, the animal observes $y$, i.e. the actual value of $Y(k)$

92  for that year. It then decides when to leave this site and move on to the next site $k+1$. The migration

93  strategy of an animal is specified by a function $L$ of two variables, where $L(y,k)$ is the target time at

94  which to leave site $k$ when the deviation from the average onset of spring at this location is $y$. The

95  animal leaves the site immediately if it arrives after this target time, otherwise remaining there until

96  the target time is reached. Thus, if the animal arrives at site $k$ at time $t$ and the deviation in the onset of

97  spring at this site is $y$, the animal leaves the site at time $\max\{t, L(y, k)\}$.

98

## The optimisation criterion

100  We describe the consequences of arriving at site $k$ at a specific time by assuming that site $k$ is

101  characterised by a mortality rate, which depends on time of year and the advancement of spring at that

102  site. Specifically, if the onset of spring on a site deviates by $Y(k) = y$ then the mortality rate at location

103  $k$ at time of year $t$ is $M(t + y, k)$ (for $k = 1,2, \dots K$) for which we use the following function:

104  $$M(t + y, k) = m_{min} + \frac{m_{max}}{1+e^{-0.05\left(-(t+y-\tau(k))\right)}}$$

105  i.e. mortality decreases sigmoidally from a maximum value ($m_{max} + m_{min}$) to the minimum value of

106  $m_{min}$, except for the starting site, where we kept mortality at $m_{min}$ throughout; we used $m_{max}$=0.005 and

107  $m_{min}$= 0.0001. The inflection point of the mortality function is at $t = \tau(k) - y$, which characterises when

108  mortality decreases at the fastest pace, i.e. when spring starts (Fig. 1b-c).

109  Let $S(k) = 1 - M(t + y, k)$ denote the probability that an individual survives while at location $k$. We

110  do not consider mortality during movement between sites, assuming that mortality during movement is

111  low compared to mortality on sites and constant for all movement episodes. Thus, $s =$

112  $S(1)S(2) \cdots S(K - 1)$ is the probability that an animal survives the entire journey. If the animal

113  survives the journey to the breeding site $K$, it starts (preparations for) reproduction immediately after

114  arrival. Its terminal reward there is then given by a function of the onset of spring at this site and the

115  time of arrival $t$ at the site $R(y,t)$. We assume that $R(y,t) = F(t + y, \tau(K), R_{wide}) + R_{future} \prod_{n=t}^{Q}(1 -$

116  $M(n + y, K))$, where $F(t + y, \tau(K), R_{wide})$ is a bell-shaped function of $t + y$ centred at $\tau(K)$ with a

117  spread of $R_{wide}$, which gives the value of an offspring born at time $t$ in a year when spring is advanced

5

118  by $y$. The second part $\prod_{n=t}^{Q}\left(1 - M(n + y, K)\right)$ gives the probability of survival until the end of season,

119  $Q$ ($Q$= day 100) weighed by the expected future reproductive success, $R_{future}$. We used $R_{future}$=1

120  and $R_{wide} = 30$.

121  The payoff (reproductive value) for the strategy $L$ is then

122  $$E_L\{sR\left(Y(K), T(K)\right)\},$$

123  where the random variable $Y(K)$ is the deviation of spring at site $K$ (see above) and the random

124  variable $T(K)$ is the time of arrival at the site, and $E_L\{\cdot\}$ denotes the expectation given strategy $L$. An

125  optimal strategy maximises this payoff.

126  For model details and dynamic programming equations, see Supplementary Material S1; the R-code of

127  the model can be found under https://github.com/silkebauer/PredictionMigration.

128

## Scenarios

130  To explore the interplay between predictability, environmental variability and the timing of migration,

131  we systematically varied the correlation (landscape $\rho$) across the entire migration landscape, the

132  number of intermediate sites ($K$), and environmental (year-to-year) variability ($\sigma^2$) and analysed their

133  effects on migration times, i.e. departure and arrival dates, spread of arrival dates and fitness, i.e.

134  reproductive values.

135  We varied the correlation across the entire migration landscape $\rho$ between $\rho = 0.0$ to $\rho = 1$, i.e. from

136  completely unpredictable to perfectly predictable. Unless stated otherwise, we set $\rho(k) = \rho_0$ for all $k$,

137  i.e. the same $\rho(k)$ for all sites, such that the landscape $\rho$ is given by $\rho = \rho_0^{K-1}$. We varied the number of

138  sites, $K$, to include from zero to nine intermediate sites (i.e. $K = 2, \ldots, 11$) while keeping the landscape

139  $\rho$ constant. Please note that the latter required changes in $\rho_0$ such that for a given landscape $\rho$, sites in

140  landscapes with more intermediate sites are more 'informative' (i.e. they have a higher $\rho_0$) than

141  landscapes with fewer sites. Alternatively, we could have kept $\rho_0$ constant when adding sites but this

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142 would have changed the landscape $\rho$, making it less straightforward to compare landscapes with

143 different numbers of intermediate sites. For the relation between landscape $\rho$ and $\rho_0$, see Fig. S1.

144 We also varied environmental year-to-year variability $\sigma^2(k)$, between 1 and 10, i.e. from a nearly

145 invariable environment in which spring starts at almost the same day every year to highly variable

146 environments with great variation in the onset of spring; again, we used $\sigma(k)= \sigma(k+1)$ for all $k$.

147 Finally, for identifying the importance of information at specific places, we lowered $\rho(k)$ on one

148 specific site in a five-site migration landscape while using the same $\rho(k)$ on all other sites. This lower

149 correlation at one place could be interpreted as an 'information barrier', and we varied the specific

150 location of this barrier.


# Results

## Value of information under varying degrees of environmental variability in non-stop migrations

154 The correlation between sites, and thus, the level of predictability, clearly influenced migration timing

155 but this strongly depended on the overall variability of environment and the deviation in the onset of

156 spring from its long-term average at the starting site (Fig. 2). For high landscape $\rho$, migrants responded

157 to deviations in the onset of spring directly and proportionally, i.e., they could accurately predict when

158 spring starts at the destination site and departed from the starting site accordingly. For instance, if

159 spring started 10 days earlier than the long-term average, then migrants also departed 10 days earlier

160 (day 60), so as to arrive at the breeding site at the start of spring that year (day 70, Fig. 2a).

161 However, a lower correlation between sites makes it harder for migrants to predict conditions at the

162 breeding site from conditions at the starting site. For instance, if individuals experience an extreme

163 deviation from the average onset of spring at the wintering site, they have no reliable information as to

164 whether this is also the case at the breeding site. Consequently, departure from the starting site

165 becomes more and more independent of the onset of spring, even if the actual onset of spring strongly

166  deviates from its long-term average, and in the extreme case of no predictability (landscape $\rho \approx 0.0$),

167  migrants depart on a fixed day (Fig. 2a).

168  Increasing environmental variability modified this relation between predictability and timing of

169  migration (Fig. 2a-c): In relatively constant environments (Fig. 2a), large deviations from the average

170  onset of spring are unlikely but such deviations are no exception anymore under high environmental

171  variability (Fig. 2c). Consequently, arrivals become increasingly later already at intermediate

172  landscape $\rho$ and indicate that migrants avoid arriving at the breeding site before spring has started,

173  which would increase mortality. Thus, migrants jeopardize reproductive success but play it safe when

174  it comes to survival - an intuitively reasonable strategy in highly variable environments with low

175  predictability in which it is nearly impossible to predict the period suitable for reproduction.

176  This pattern is also reflected in reproductive values (Fig. 3a), where the highest reproductive values

177  are reached under high predictability (high landscape $\rho$) or low environmental variability (low $\sigma$) while

178  reproductive values are low for highly variable environments or those with low predictability.

179

## From non-stop migration to many intermediate steps

181  Adding intermediate sites between starting site and destination changed migration from non-stop

182  ('skip') to 'jump' and 'hop' migrations. As we kept the correlation across the migration landscape the

183  same, adding intermediate sites changed the pairwise correlation between sites, $\rho_0$ (see 'Scenarios').

184  The $\rho_0$ differ little from landscape $\rho$ for very low or very high landscape $\rho$ (Fig. S1) but $\rho_0$ is

185  significantly larger than landscape $\rho$ at low to intermediate landscape $\rho$, and when there are many

186  intermediate sites, suggesting that intermediate sites can be valuable when predictability is

187  intermediate.

188  The value of intermediate sites is reflected in fitness-consequences: The lowest reproductive values

189  result in landscapes with no predictability (landscape $\rho \sim 0.0$) but also when there are no intermediate

190  sites ($K = 2$) (Fig. 3b). For a specific landscape $\rho$, the addition of intermediate sites increases

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191  reproductive values, and this effect is more pronounced at intermediate $\rho$. However, there is also a

192  saturation effect – adding a few sites increases reproductive values much more under low $K$ but less so

193  when there are already some intermediate sites. The effect of additional sites increasing reproductive

194  values depends on environmental variability. In less variable environments (low sigma), adding

195  intermediate sites has hardly any effect since the onsets of spring occur at their long-term averages;

196  yet, the more variable an environment is, the more helpful are intermediate sites in predicting

197  conditions ahead (Fig. S2).

198  The number of intermediate sites has consequences for the timing of departure from first, staging at

199  intermediate sites and arrival times at the breeding site (Fig. 4). At low to intermediate landscape $\rho$,

200  migrants depart increasingly earlier from the starting site when there are more intermediate sites and

201  stay increasingly longer on intermediate sites as they successively obtain information on sites ahead

202  and, if required, wait for the onset of spring on the successive site. Ultimately, this leads to a larger

203  spread in arrivals between years with more sites at intermediate landscape $\rho$. In contrast, for non-stop

204  migrations, for very low or very high landscape $\rho$, arrivals at the breeding site occur within a very

205  confined period.

206

207  ## Importance of predictability on specific places

208  Introducing an 'information barrier' – a much lower predictability between two sites than between the

209  others – showed that information is not equally valuable at all sites: $\rho(k)$ on sites close to the

210  destination was generally more important than $\rho(k)$ at earlier sites (Fig. 5). Particularly, a barrier on the

211  penultimate site were highly influential for departure and arrival times – it delayed departure from first

212  site and advanced arrival at the last site – and was clearly detrimental for fitness (reduced reproductive

213  values) while no such effects appeared when a barrier was inserted between any of the earlier sites.

9

## Discussion

Our model has important implications for understanding the timing of migration in environments that differ in variability and predictability. Generally, we predict that information on distant conditions is particularly important in variable environments and before the 'final' stages (i.e. those with the strongest fitness-consequences). Furthermore, we suggest that using intermediate sites is a strategy for obtaining information in variable environments or in those that are relatively uninformative. These predictions have implications that particularly concern environmental predictability along major migration routes and their consequences for the timing of migration, the capacity of migrants to respond to changes in phenology and the use of intermediate sites as source of information. Although some of these predictions and implications remain to be fully scrutinized in future investigations, several are already supported by earlier studies (see below).

Our model makes a few important assumptions: First, if the onset of spring in one site is predictive of that on the next site, then the relationship between the onsets of spring on the sites is specified by the joint probability distribution. For simplicity, we assumed that this joint distribution is bivariate normal and thus, specified by the mean, variances and correlation [4] but, of course, other joint distributions are possible.

Second, we assume that mortality decreases in spring and thus, that arrival before the onset of spring poses a significant mortality risk. A lower survival has indeed been found for early-arriving individuals in long-distance migrant birds [14] but the relation between the timing of arrival (in the breeding grounds) and survival has only been investigated in a few studies and even less for the timing of stopover site use. We think that this relation will certainly apply to temperate or Arctic regions, i.e. regions with a strong seasonality [7], where resources only become available in the course of the season but perhaps less pronounced in tropical or subtropical regions.

Thus, although we think that these assumptions are generally justified, deviations in specific empirical migration systems might exist and could be incorporated in an adjusted model.

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## Predictability in real environments

240

241 Environmental variables are often spatially and temporally correlated and thus, conditions at distant

242 places can, in principle, be predicted from afar. The strength of correlations typically decreases with

243 distance, i.e. the closer two sites are, the better can conditions be predicted [6]. Applied to migrations,

244 this means that for short-distance migrants, correlations between wintering and breeding sites are

245 expected to be stronger than for long-distance migrants [15]. Consequently, short-distance migrants

246 are better able to predict phenology on breeding sites from their wintering sites and thus, have a higher

247 capacity for 'correctly' timing migrations under phenological deviations from long-term average [16].

248 In contrast, wintering and breeding grounds of long-distance migrants are much farther apart and

249 typically far less or not correlated. In such cases and in support of our predictions for no-correlation,

250 long-distance migrants depart on a fixed day irrespective of the deviations from the average onset of

251 spring in the wintering site, e.g. [17], and often fail to adequately respond to phenological changes

252 [16,18,19]. However, when long-distance migrants approach their breeding sites, they should be

253 increasingly better able to predict the advancement of spring and adjust migratory progression as

254 correlations become stronger with the remaining shorter distance. Indeed, such behaviour has been

255 found in Palaearctic-African migratory birds that adjust migration speed or migratory progression in

256 the Mediterranean in response to the advancement of spring in Europe [20,21].

257 However, correlations are rarely only distance-dependent but vary between habitats [22], ecosystems

258 and topographies. Locations within one climatic zone or regions that are under the influence of large-

259 scale climatic phenomena, e.g. Southern Oscillation (SO), North-Atlantic Oscillation (NAO) [23], are

260 probably more similar and thus, more predictable, than landscapes that are separated by physical

261 barriers like mountain ranges, deserts or stretches of sea that interrupt existing correlations [23].

262 Migrants often avoid crossing barriers and use detours instead, i.e. they deliberately fly, walk or swim

263 longer distances than the shortest possible route [24]. Although reasons for taking such detours have

264 been brought forward [25], another reason could be that making detours (or using additional stop-

265   overs, see below) can be beneficial if such longer route provides more information than a shorter one

266   and yields clear fitness-benefits by syncing the timing of arrival with local phenology. However, if

267   barriers cannot be avoided, e.g. for birds migrating from sub-Saharan non-breeding to European

268   breeding grounds, and migrants cannot predict conditions 'behind' the barrier, they migrate on a fixed

269   day, using an invariable cue such as photoperiod [5]. Once behind the barrier, information may

270   become available and migrants may wait out the progress of the season and adjust arrival to local

271   phenology [26].

272   Although most studies that investigate the consequences of climatic/phenological changes on migrants

273   implicitly assume a relation between migration distance and predictability, a formal quantification of

274   climatic connectivity and thus, predictability, across major migration routes (similar to [27]) is still

275   lacking. Calculating predictability across the world would allow us to compare major migration

276   systems with regard to their environmental information content and the possibility for migrants to

277   predict phenology on distant sites [13]. Repeating such analyses over the past decades could identify

278   whether uneven climate changes have altered existing correlations and whether these changed

279   correlations could be one causative factor in the population trends of migrants [28]. Furthermore, such

280   analyses could also identify environments in which memory of resource phenology would be expected

281   to be a successful strategy [29,30].

282

## 283 Intermediate sites as information source

284   Similar to making detours, using intermediate sites can be important for obtaining information on

285   conditions ahead. Indeed, many migrants use intermediate staging sites even if it was energetically

286   possible to migrate non-stop (e.g. in ungulates [31] or birds [32–34]). According to our results, we

287   predict that migrants with at least a few stop-over sites should be less affected by changes in

288   phenology than those migrating non-stop [35]. This seems to be empirically supported in, e.g., Arctic-

289   breeding geese, of which many populations and species cope with climate change very well [36]; yet,

290   non-stop migrating Brent geese (*Branta bernicla hrota*) arrive at their Arctic breeding sites out of sync

291 with local phenology (phenological mismatch), and consequently, are one of the few goose species

292 with currently declining populations [37]. Of course, how many stop-over sites are ultimately used

293 will be governed by refuelling needs but also by a trade-off between the benefit of obtaining

294 information and the costs of staging, e.g., a higher predation risk because of unfamiliarity in a novel

295 environment [38] or the morphological adjustments from locomotion to digestion [39].

296 If – as we predict – stop-over sites are also used for obtaining information, they might be 'strategically

297 chosen' and located at places where information is advantageous or where they increase predictability.

298 For instance, although purely speculative at this point, shorebirds show a variety of skip, jump or hop

299 migration patterns [34,40,41] that differ between populations at different geographic places and may

300 be shaped by the need for acquiring information.

301 However, we also found that information is not equally important across all sites – information

302 becomes particularly valuable close to the destination. Thus, we expect migrants to use stop-over sites

303 close to breeding locations to assess the progress of spring at their breeding sites. Such pattern has

304 indeed been found in birds migrating from African non-breeding to European breeding sites and

305 stopping over in the Mediterranean. For instance, semi-collared flycatchers (*Ficedula semitorquata*)

306 stayed three times longer (15 days instead of 5) in the Mediterranean basin in a year with a cold spell

307 in Europe before proceeding to Eastern Bulgarian breeding sites [21].

308

309 Our results contribute to a better understanding of the relation between environmental predictability

310 and the timing of movements [13], showing how different levels of information shape migration

311 strategies and how environments differing in variability and number of stop-over sites modify these.

312 Such a better understanding of the relationship between information and movement is important for

313 assessing the consequences of large-scale climatic changes that may shift phenologies [35], change

314 environmental variability and disrupt existing correlations [4], including changes in correlations from

315 human structures and activities, e.g. supplemental feeding or sensory pollution through anthropogenic

316 light and noise [48,49].

## Beyond migration: Information and the timing of life-history transitions

A variety of life-history transitions exist that are conceptually similar to migration in that they are escapes from seasonally or periodically varying conditions and that their success also highly depends on timing, e.g. timing of flowering in plants determines expected fruit set [42,43], emergence-time from hibernation determines reproductive success in bats [44], and timing of diapause stages in killifish influences survival [45]. Similar to the predictions that we derived for the timing and success of migrations, we predict several general patterns for the timing of other transitions. First, in more variable environments, we expect "safe" strategies, i.e. strategies that enhance long-term fitness, even at the expense of short-term fitness benefits, particularly in longer-lived organisms with more than one reproductive bout. Such safe strategies might include to react only to very strong, reliable cues – those with high predictability. For instance, the different levels of spring predictability across North America, Europe and East Asia explained the differences in leaf-unfolding strategies in their woody floras: In regions with high variability, woody species have higher winter chilling requirements and need longer periods above a certain temperature threshold to start to leaf-out compared to species in regions with lower variability [46].

Second, in more variable environments, we expect transitions with more intermediate stages – which provide flexibility in the timing of life-history stages [47]. An interesting example is the diversity of annual cycles and the number of intermediate stages in killifish (Cyprinodontiformes), which live in ephemeral aquatic habitats that range from stable and predictable to stochastic and unpredictable [45]. Depending on the predictability and uncertainty of their specific environment, killifish can enter up to three diapause stages before hatching and thereby, halt development at multiple points, which favours hatching at an appropriate time and complete development as false-starts are largely avoided.

Thus, the role of information in the timing of transitions under environmental variability seems to be an over-arching phenomenon across species and taxa. Naturally, various strategies exist for obtaining and using information depending on specific environments and species. Yet, using intermediate stages

343 is such a general strategy as well as the use of strong, reliable environmental signals before the

344 transition that bears the strongest fitness consequences.

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490 **Fig. 1**. Migration between a non-breeding and breeding site often involves several intermittent stop-

491 over sites (a). We incorporated phenology on all sites as changes in mortality over time (b-c) and the

492 onset of spring is the time when mortality decreases at its highest rate. Phenology has a long-term

493 average (thick white line) from which it may deviate in a given year (as indicated by the arrows). If

494 phenologies of successive sites are correlated (high $\rho$), these deviations from the long-term averages

495 are similar at site $k$ and site $k+1$ (red arrows) while for low correlation (low $\rho$, orange arrows), they can

496 be highly dissimilar and thus, not predicted from a present site. The long-term average of onset of

497 spring is at $\tau(k)$.

498 **Fig. 2**. Arrival at the destination site (days, colour shades) changes with landscape $\rho$ (x-axis), with

499 how much the onset of spring deviated from its long-term average at the wintering site (y-axis), and

500 with environmental variability (increasing $\sigma$ in a-c) in a migration landscape with no intermediate

501 decision points ($K=2$): With high landscape $\rho$, migrants adjust departure from starting site (and arrival

502 at destination) to deviations from the average onset of spring, i.e. they depart as many days earlier

503 (green shades) as spring is advanced or as many days later (blue shades) as spring is delayed.

504 However, under lower landscape $\rho$ migrants cannot predict when spring starts at the destination site

505 and therefore, their best choice is to depart at the time when spring starts on average at the destination

506 site (white areas, day 70).

507 Increasing environmental variability (b-c) modifies this pattern. In variable environments, the actual

508 onset of spring can deviate greatly from its long-term average. Since arriving at a site before spring

509 has started poses a significant mortality risk, the best migrants can do in environments that are highly

510 variable AND hardly predictable is to migrate late (large blue areas in c) and so ensure survival but

511 possibly miss out on this year's reproduction.

512 **Fig. 3**. Reproductive values as dependent on landscape $\rho$ and (a) environmental variability (using $K=2$,

513 for other values of K, see Supplementary Fig. S2) and (b) number of sites, $K$ (using $\sigma^2=10$, for

514 comparison to other values of $\sigma^2$, see Supplementary Fig. S2).

515  **Fig. 4**. Temporal spread of arrival dates at the destination site as dependent on landscape $\rho$ and the

516  number of sites. Intensity of colours indicates the length of periods (days) over which around 80% of

517  arrivals occur, i.e. lighter colours show a more confined arrival period and darker colours spread-out

518  arrivals. Arrivals are almost invariably at the same day at extreme values for landscape $\rho$ (e.g. $\rho = 0$ or

519  $\rho = 1$) and for non-stop migrations ($K=2$), and for these, increasing $\rho$ or $K$ has no effect. In contrast, for

520  values of landscape $\rho$ between these extremes, increasing the number of sites leads to a more spread-
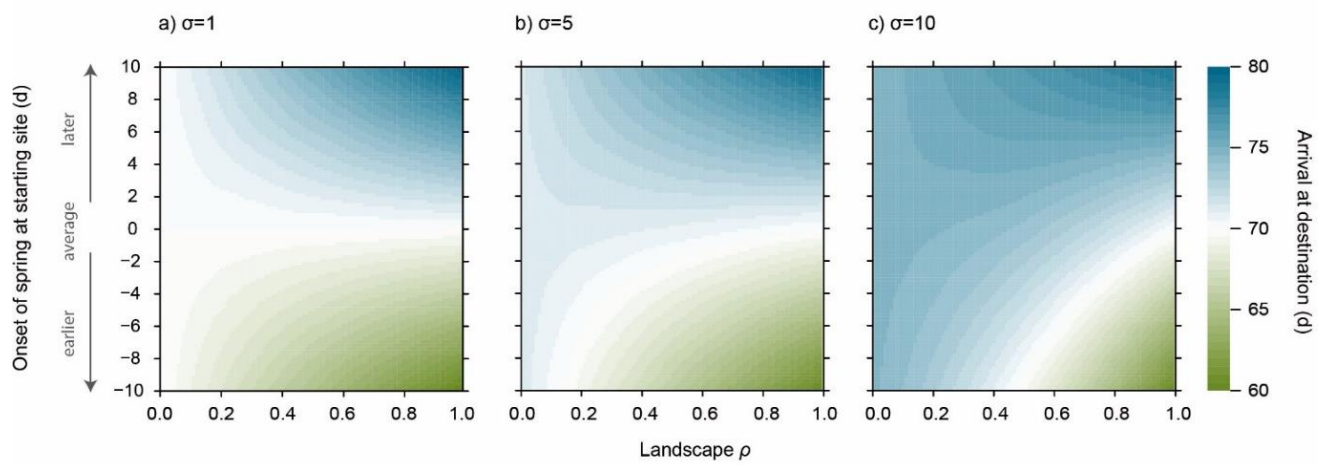
521  out arrival (for $K>2$).

522  **Fig. 5**. If there are gaps in predictability, i.e. the correlation between two specific sites is lower than

523  the correlation between other sites, the position of such barriers appears to be crucial for departure

524  from first site (grey lines) and arrival at destination (black lines) as well as for reproductive values

525  (coral-red dots and lines): While barriers hardly matter early in migration, they can substantially

526  reduce reproductive values when they occur close to the destination. Line colours from light to dark

527  coral-red depict barriers with a $\rho(k)$ of 0.7, 0.5, 0.3 and 0.1, respectively, compared to $\rho$ between all
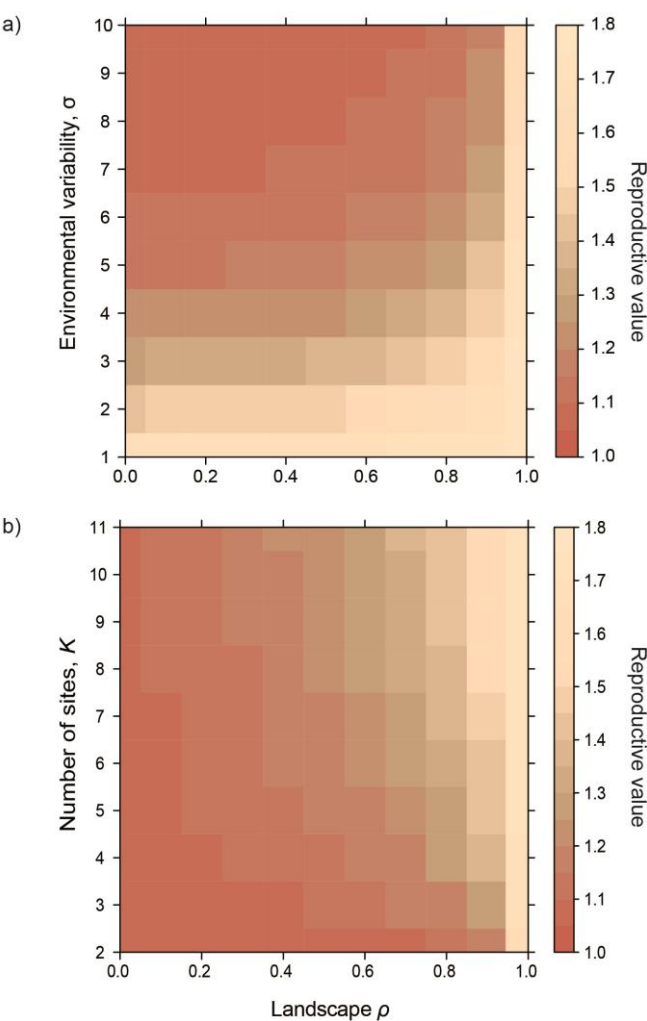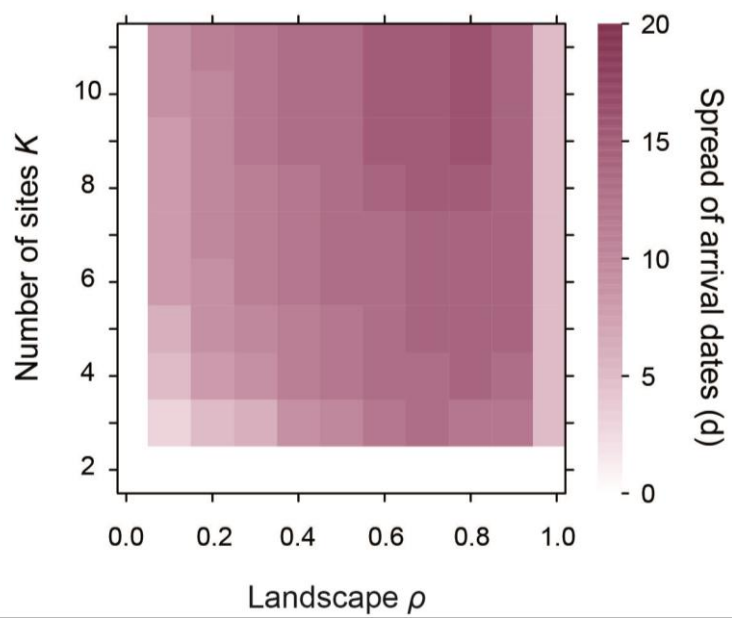
528  other sites of 0.9.

**Figure 1**

a)  b)  c)
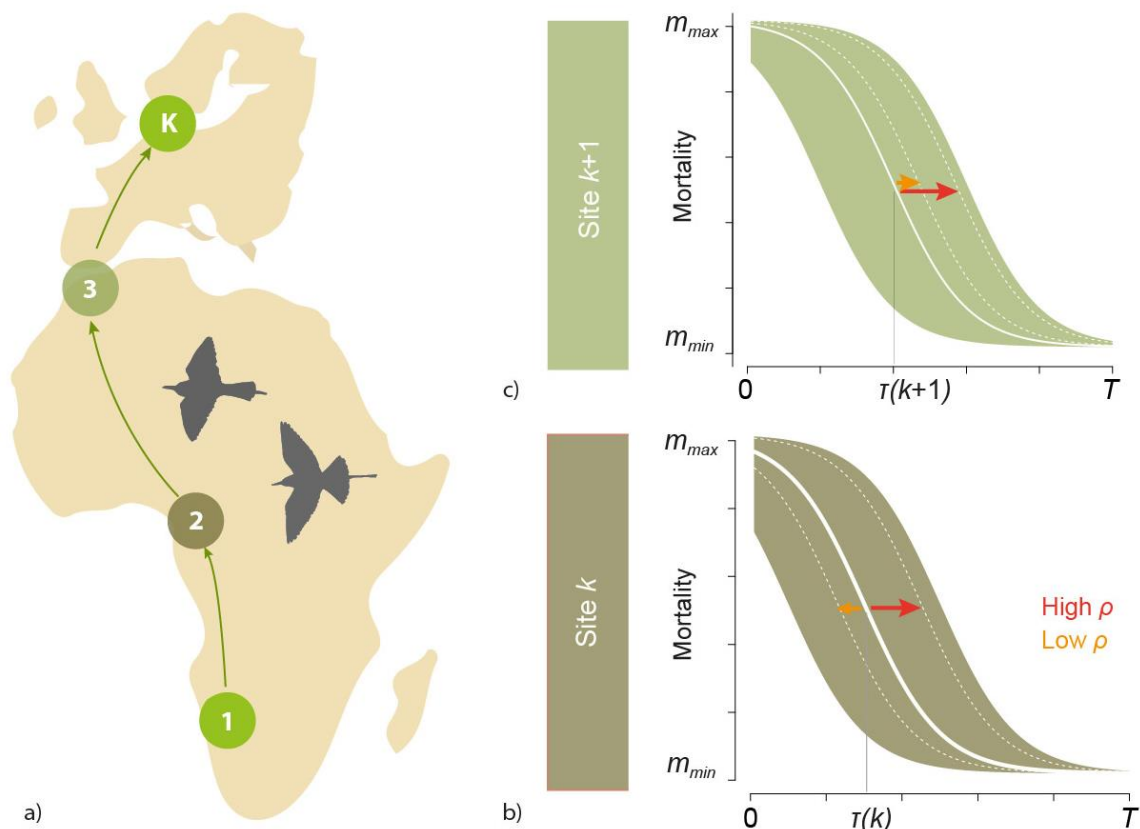
532 **Figure 2**



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535 Figure 3

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**Figure 4**

541 **Figure 5**

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