The effect of environmental change on plastic sex-ratio strategies

Mirjam J. Borger[1,2], Jan Komdeur[1], David S. Richardson[3, 4], Magdalena Kozielska[1]

[1]Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

[2]Department of Evolutionary Biology, Bielefeld University, Germany

[3]Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich Research Park, NR4 7TJ Norwich, UK

[4] Nature Seychelles, P.O. Box 1310, Roche Caiman, Mahe, Republic of Seychelles

Corresponding author: Mirjam Borger, m.j.borger@rug.nl

Abstract

Offspring sex ratio manipulation has been widely studied, with numerous adaptive explanations proposed for biased sex ratios. While sex-ratio trends have been observed in many species, such patterns often disappear over time within populations or differ across populations. Environmental change is frequently proposed as underlying these inconsistencies, particularly for strategies relying on environmental cues. A textbook example comes from the Seychelles warbler (*Acrocephalus seychellensis*) study, where an initially reported environment-dependent sex-ratio trend could not be found in later years, possibly due to environmental change. Using an individual-based simulation inspired by the Seychelles warbler system, we tested how environmental change affects environmentally determined sex-ratio strategies. Our results indicate that such strategies are unlikely to disappear but instead shift to fit new environmental conditions. When strategies rely on multiple cues, strategies may remain constant, yet the relative importance of the cues may change. Moreover, in some cases, environmental improvement can, paradoxically, lead to population extinction, if the population sex ratio becomes extremely biased. More generally, plastic strategies have evolved to be adaptive within the environmental range they have been exposed to and are therefore not always adaptive in new environments outside this range, which, in extreme cases, can lead to population extinction.

Keywords: agent-based simulation, maladaptive plasticity, local resource competition, local resource enhancement, cooperative breeding, offspring sex ratio.

Introduction

In many species, the sex ratio at birth is around parity, a phenomenon that already intrigued Darwin (Darwin, 1871), as populations without paternal care only require a few males to fertilise all females. Düsing (1883), Cobb (1914) and Fisher (1930) provided an adaptive explanation (commonly referred to as Fisher's principle) stating that frequency-dependent selection favours an equal investment in male and female offspring. Even so, adaptive explanations for biases in offspring sex ratios have also been put forward. For instance, when one sex has a higher dispersal probability, it should be overproduced, as this reduces kin competition (Hamilton, 1967). Moreover, it has been hypothesised that parental individuals should plastically skew their offspring sex ratio based on the situation these individuals face. For example, optimal offspring sex ratios were hypothesised to depend on the condition of the mother (Trivers & Willard, 1973), the attractiveness of the father (Burley, 1981), the timing of reproduction within a season (Daan *et al.*, 1996), or the local environment of the parents (Komdeur, 1996).

In a great deal of vertebrate species, sex-ratio trends (correlations between the offspring sex ratio and another variable) have been found (e.g. see Griffin *et al.*, 2005 for some examples), and were often hypothesised to be caused by one of the above-mentioned adaptive processes. Yet many of the reported sex-ratio trends varied across years and/or populations, or disappeared when the same population was sampled again in a later period. For example, in red deer (*Cervus elaphus*), a trend was found where more sons were produced by dominant mothers (with good body condition), and more daughters by subordinate (bad body condition) mothers (Clutton-Brock *et al.*, 1986). However, a later study on the same population, could not find this trend (Kruuk *et al.*, 1999), which was suggested to be caused by a change in the environment and consequently the population density. In a laboratory population of zebra finches (*Taeniopygia guttata*), a trend was found where primarily sons were produced when mothers were mated with attractive males, and more daughters when mothers were mated with unattractive males (Burley, 1981). A similar study trying to repeat the experiment did not find this trend (von Engelhardt, 2004; Wang *et al.*, 2018). In a blue tit (*Cyanistes caeruleus*) population, a similar pattern was found where mothers overproduced sons when mated with attractive males, and daughters when mated with unattractive mates (Sheldon *et al.*, 1999). However In a different blue tit population, other trends were found (Korsten *et al.*, 2006). In the latter population sex-ratio trends were found to vary from year to year (in strength and direction), and it was suggested that environmental differences could cause this. These results, from different species, show that it can be difficult to conclude whether sex-ratio trends changed or disappeared because of a change in conditions, or whether the original studies reported extraordinary findings.

One textbook example of a vertebrate species exhibiting an offspring sex-ratio trend is the Seychelles warbler (*Acrocephalus sechellensis*). This species is a facultatively cooperative breeding birds, whereby some breeding pairs are assisted by helpers. Helpers are not a necessity for offspring survival, but they can increase the survival of offspring (Komdeur, 1994; Brouwer *et al.*, 2012) and parents (Hammers *et al.*, 2019). In this species, most helpers are female (Borger *et al.*, 2023), which also help more efficiently than male helpers (Richardson *et al.*, 2003). Yet, having helpers is not only beneficial, as group size also had a negative effect on survival (Brouwer *et al.*, 2006), likely due to resource competition. Moreover, it was initially found that sons had a higher natal dispersal probability than daughters (Komdeur, 1992), but this difference seemed to have disappeared over time (Eikenaar *et al.*, 2010; Speelman *et al.*, 2024; Borger *et al.*, 2025). Komdeur *et al.* (1997) found that Seychelles warblers produced mainly daughters in high-quality territories, and sons in low-quality territories. For one year, they also tested and found that sons were produced in territories that already had two or more helpers, independent of territory quality. The authors suggested an explanation for this trend based on local resource enhancement and local resource competition. In high-quality territories, there is little competition over resources, and obtaining helpers (often daughters from a previous breeding season) can thus increase the survival of newly produced offspring (local resource enhancement). Hence, producing daughters would be beneficial. Conversely, when competition over resources is high - in low-quality territories and in territories where multiple helpers are already present - producing the dispersive sex (sons) would increase the survival of newly produced offspring (local resource competition). In other words, producing sons would be beneficial. In a recent theoretical study, it was shown that a strategy producing this sex-ratio trend can indeed readily evolve (Borger *et al.*, 2026).

Recently, the results of Komdeur *et al.*, (1997; spanning the period 1993-1995) were re-analysed with newer data (spanning the period 1996-2018) from the same population (Borger *et al.*, 2025). The effects of territory quality and number of helpers on the offspring sex ratio could not be found. Again, it was hypothesised that the trend in the sex ratio had disappeared due to environmental change, because the sex-ratio strategy was no longer adaptive under the current environmental conditions. Cousin Island (where the main study population of the Seychelles warbler resides) was restored from a coconut planation to a nature reserve in 1968 (Penny, 1967)*;* ever since, the natural vegetation has been able to grow back and increase. Therefore, territory quality has improved over the years, and the variation in territory quality might have decreased. These factors were hypothesised to have led to a weakening, and eventual disappearance, of the originally strong sex-ratio trend. However, to understand the effects of environmental change on sex-ratio strategies, a theoretical model is required, as verbal reasoning can fall short in disentangling the complex interplay of eco-evolutionary factors involved.

Here, we extended the individual-based model from Borger *et al.*, (2026) to study the effects of a changing environment on environment-dependent sex-ratio strategies. We used the Seychelles warbler life history as a case study to keep the model concrete, but we also examine more cases (especially a range of environmental change) to get a broad overview of the interplay between environmental change and plastic sex-ratio strategies.

Methods

As our point of departure, we use the individual-based model of Borger *et al.*, (2026), which was designed to study the evolution of plastic sex-ratio strategies, and was inspired by the Seychelles warbler study system. There, the environment was variable in space, but constant over time. That model also considered the evolution of dispersal strategies, but, for simplicity, here we consider only fixed, sex-specific dispersal parameters. Here, we study cases where the environment is variable over space and time, so that territory quality changes over the course of the simulation runs.

Model overview

The simulations run over multiple discrete time steps, with each time step representing a breeding season. Within seasons, multiple behaviours are exhibited, some based on heritable strategies. Across seasons, the frequency distribution of these heritable strategies can change due to a combination of natural selection, mutation and genetic drift. Generations overlap, as individuals can survive for multiple breeding seasons.

In the model, a fixed number of territories exists (1000 for the results below). Territories can contain multiple individuals, including a breeding male and female, helpers (both male and female; yet females are more efficient helpers and stay more often) which were offspring that remained philopatric in previous seasons, and newly born offspring. Some individuals do not live in a territory and are called "floaters". Territories can differ in quality, reflecting the resources available in each territory at the start of a breeding season. In the simulations for this study, territory quality is first set as temporally stable over a long time, to assure that a sex ratio strategy can evolve, after which territory quality changes over time to answer our question. We monitored for 1000 breeding seasons if and how the sex-ratio strategies would change. During a season, first reproduction takes place, after which resources are divided between group members. Next, survival is checked, and lastly status changes happen, after which a new season starts.

Sex-ratio strategies. Individuals have a heritable sex-ratio strategy, to allow for the evolution of territory quality-dependent sex-ratio strategies. The offspring sex is based on the sex-ratio strategy of the mother. In the baseline version of the model, this is a function M(Q) that, for each territory quality (Q), describes the probability that an offspring is a son. M(Q) is given by a logistic function, as this is how empirical sex ratio data is commonly analysed:

$$M(Q) = \frac{1}{1+ e^{-\beta*(Q-\alpha)}}. \quad (1)$$

α and β are 'loci' of individuals, which are heritable, and hence the sex-ratio strategy is an evolvable trait. The value of α is equal to the territory quality where an even sex ratio (M(Q) = 0.5) is produced (the inflection point). The value of β corresponds to the slope of M(Q), which is usually an S-shaped curve. Other shapes of the sex ratio function can also evolve if α evolves to a value outside the interval of Q-values.

We also consider an extension of the model where the sex-ratio strategy depends on both territory quality and the number of helpers on the territory (as was tested and found for one year in the Seychelles warbler system; Komdeur *et al.*, 1997). In this case, three logistic functions evolve. $M_0(Q)$ represents the territory quality-dependent sex-ratio strategy in territories without helpers, $M_1(Q)$ represent the sex-ratio strategy in territories with one helper, and $M_2(Q)$ represents the sex-ratio strategy in territories with two or more helpers. All these functions are defined as:

$$M_i(Q) = \frac{1}{1+ e^{-\beta_i*(Q-\alpha_i)}}. \quad (2)$$

Environmental change. Territory quality is proportionally related to the number of resources available for adults and chicks to feed on (see Supplement 1 for more details on this), but was normalised around 0 for generality. For the first five million breeding seasons, territory quality is constant to ensure more than sufficient time for a sex-ratio strategy to evolve (see Borger *et al.* 2026). Afterwards, the territory quality changes, either over 50 breeding seasons (rapid environmental change) or over 500 breeding seasons (slower environmental change). First, we studied a case like the Seychelles warbler, where the territory quality improves and the variance in territory quality decreases. We picked a change in territory quality range from [-1;1] to [0;1] to reflect this. Each breeding season, the quality of a territory improves with a certain fixed change, until after 50 or 500 breeding seasons the new range is reached. The relative order of territory qualities stayed the same over time, and hence in this case, low-quality territories improved more than high-quality territories.

Second, we studied additional cases of environmental change to examine if there are general patterns in the effects of environmental change on plastic sex-ratio strategies, to examine the effects of

environmental deterioration versus improvement, and to separate the effects of changes in values of territory quality and variance of territory quality. In all cases, territory quality range is [-1;1] for the first five million breeding seasons and after that, changes either over 50 breeding seasons or 500 breeding seasons towards a new range of [-2;-1], [-2;0], [-2;1], [-2;2], [-1;0], [-1;2], [0;2] or [1;2] respectively.

For a more detailed explanation of the model, see Supplement 1, the methods of Borger *et al.*, (2026), and for biological justifications of all parameters, see their Supplement 1.

Technical note

Simulations were conducted using C++ in Visual Studio (Visual Studio Community, 2022, version 17.4.4). Figures were produced using R version 4.2.2 (R Core Team, 2022), and the packages *ggplot* (Wickham, 2016) and *cowplot* (Wilke, 2020).

Results

Seychelles warbler case study M(Q)

Figure 1 shows the simulation results for the situation in which the sex-ratio strategy *M* only depends on territory quality. For both the fast (50 breeding seasons) and slow (500 breeding seasons) environmental change, the sex-ratio strategy does not change much for the first 100 breeding seasons, while after that the sex-ratio strategy starts to shift to the right, to better fit the new environment. This shift is more gradual for the slow environmental change. The change in the sex-ratio strategy is mostly caused by selective disappearance (individuals with a low value for inflection point α become less prevalent), and to a lesser extent by the appearance of new, higher, values for α, both for fast and slow environmental change. As the environment improves, more resources become available and hence the total population size grows. However, due to a mismatch between the plastic sex-ratio strategy and the new environment, mostly daughters are produced, while the number of sons at first decreases. Only after some time, the number of sons starts to increase again, but the sex ratio (of both the entire population and the offspring) remains more female-biased for the 1000 seasons. In some cases (1/50 replicate simulations for this parameter combination), the population is going extinct even though the number of resources available increases. While the population size increases, the number of males decreases and sometimes this becomes so extreme that only females are left, and hence reproduction cannot take place anymore. The risk of extinction is low for large populations, but small populations (with potentially more realistic population sizes) are more prone to extinction, as is the case for the Seychelles warbler on Cousin Island which inhabits around 100 territories (for simulations with 100 territories, 7/50 replicates went extinct for fast environmental change and 8 /50 for slow environmental change).

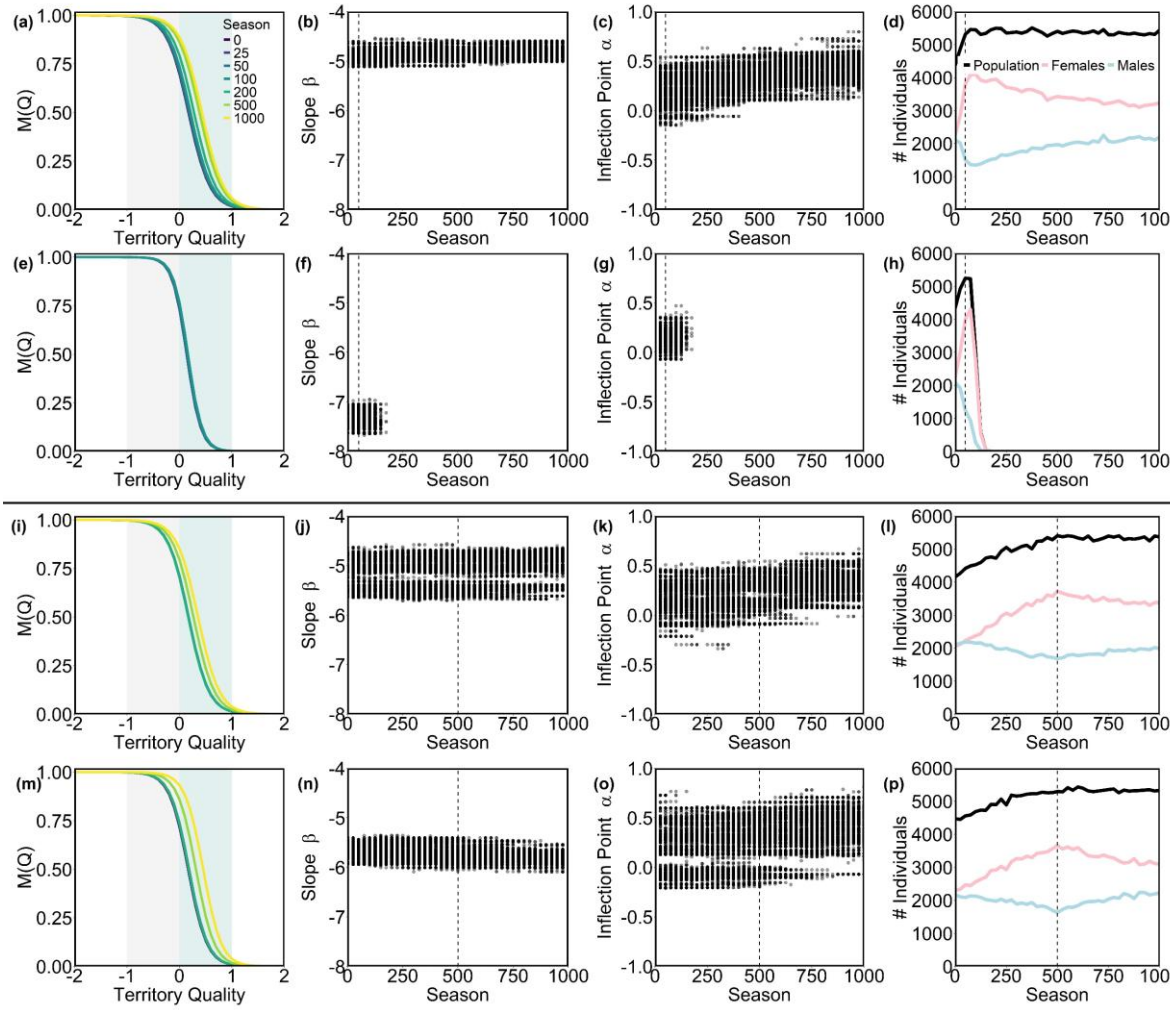

Figure 1: Change in offspring sex-ratio strategies over time after environmental change. Each row shows a replicate simulation, the two top rows for fast environmental change, and the two bottom rows for slow environmental change. The panels in the left column (a, e, i, m) illustrate the change in the population average sex-ratio strategy in the period after the initiation of environmental change (for 1,000 seasons). The grey shading indicates the territory quality range before environmental change [-1;1] and the azure shading indicates the territory quality range after change (here [0;1]). The panels in the second column (b, f, j, n) show the values of β (the slope of the sex-ratio strategy) over time, where each dot represents the value of one breeding female. The panels in the third column (c, g, k, o) show the values of α (the inflection point of the sex-ratio strategy) over time, again where each dot represents the value of one breeding female. The panels in the right column (d, h, l, p) show the number of individuals in the population over time, for the total population and for females and males separately. The environmental change starts at season 0 and is finished after either 50 or 500 seasons, indicated by the vertical dashed line in all panels but the ones in the left column. The population of the replicate in the second row went extinct after about 200 seasons.

206

207 *Seychelles warbler case study $M_i(Q)$*

208 Figure 2 shows one representative replicate simulation for the situation in which the sex-ratio strategy

209 *M* depends both on territory quality and the number of helpers. Figure 2 only shows a case for fast

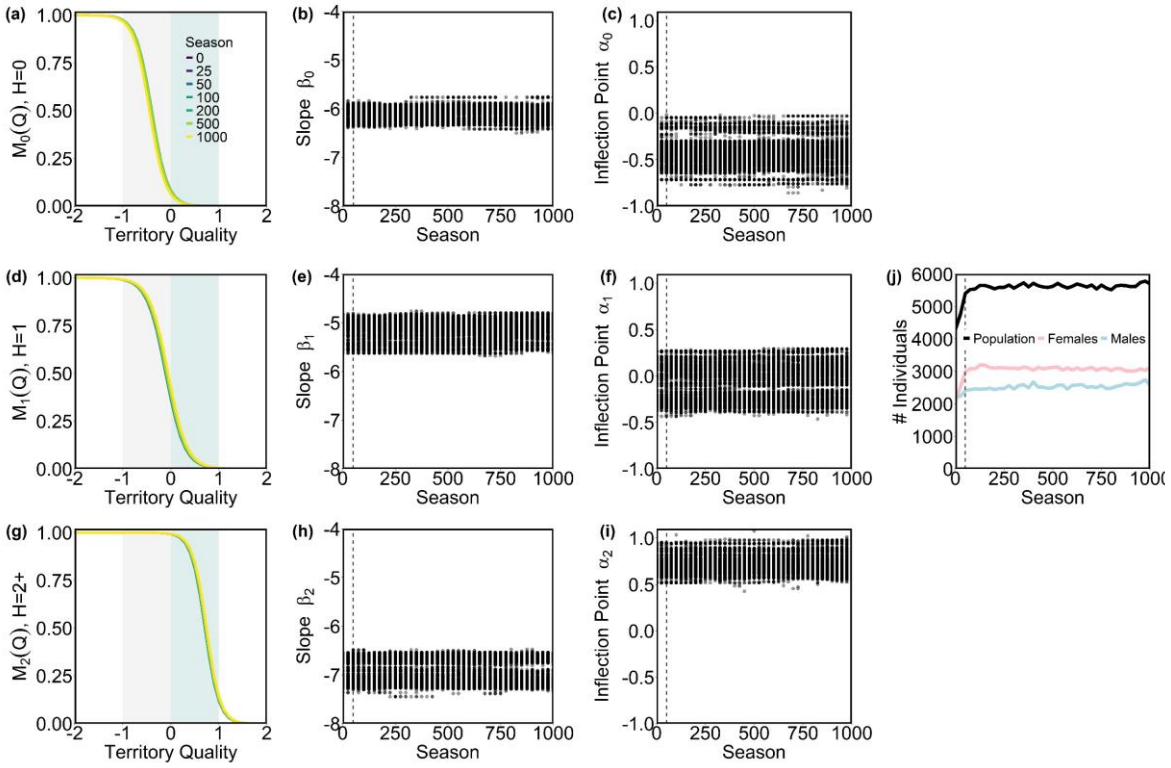

Figure 2: Change in offspring sex-ratio strategies based on territory quality and number of helpers after environmental change. One representative replicate of a simulation with fast environmental change. Here, the top row (panels a, b, c) shows the sex-ratio reaction norm when helpers are absent, the middle row (panels d, e, f) shows the sex-ratio reaction norm when one helper is present and the bottom row shows the sex-ratio reaction norm when two or more helpers are present. The panels in the left column (a, d, g) show the change in the population average reaction norm. The grey shading indicates the territory quality range before environmental change [-1;1], and the azure shading indicates the territory quality range after change (here [0;1]). The panels in the second column (b, e, h) show the values of β (the slopes of the sex-ratio strategy) over time, where each dot represents the value of one breeding female. The panels in the third column (c, f, i) show the values of α (the inflection point of the sex-ratio strategy) over time, again where each dot represents the value of one breeding female. (j) shows the number of individuals in the population over time, for the total population as well as for females and males separately. The environmental change in this replicate finished after 50 seasons, indicated by the vertical dashed line in all plots except those in the left column.

environmental change, but results are similar for slow environmental change. Here, the sex-ratio strategy does not change considerably over time, and indeed there are no clear changes in the values of the inflection points and slopes. The population size does increase. More females are produced than before, but also the number of males increases a little. Hence, the sex ratio is more female biased after the environmental change than before, but not as strong as in the case where *M* only depends on territory quality, and no extinctions happen. In other words, in this case, where *M* depends both on territory quality and on the number of helpers, the relative importance of both cues changes as well as the way they interact. While before the environmental change territory quality had a large influence on the sex of the offspring and only part of the population had helpers (mostly M_0 and M_1 were

219 expressed), this changes after the environmental change. After environmental change, territories first
220 produce daughters with a high probability, which results in a high probability of obtaining helpers.
221 When two or more helpers are present, territory quality becomes more important again, and high-
222 quality territories produce mostly daughters, while the new 'low-quality' territories produce mostly
223 sons. As the quality of the environment has improved, there is less resource competition and hence
224 more territories have the capacity for helpers (hence M_2 is expressed more than before), and daughters
225 are produced when helpers are not there (M_0, or when there is only one helper M_1), while sons are
226 produced when helpers are present (M_2).
227
228 *Other cases of environmental change*
229 Next, we consider other cases of environmental change to further study the effect of environmental
230 change on sex-ratio strategies and the consequential population dynamics, like extinction. To separate
231 the effect of variance of territory qualities between territories and the values of territory quality
232 (changes to higher qualities or lower qualities), we study eight more environmental change cases, all
233 starting with a range of [-1;1] and over 50 or 500 breeding seasons a change to [-2;-1], [-2;0], [-2;1], [-
234 2;2], [-1;0], [-1;2], [0;2] or [1;2] respectively, see Figure 3 for five of these cases.
235
236 We see that an increase in variance of territory quality causes some change. When the range of
237 territory quality increases to [-2;2], the sex-ratio strategy shifts to the right. The population size
238 decreases a little, most likely because territories with extremely low qualities cannot produce any
239 offspring anymore, as all resources are consumed by the adults and nothing is left for offspring. The
240 sex ratio becomes slightly more female biased, as high-quality territories are the most productive ones.
241
242 Similarly, when the environmental change is not too extreme (to [-2;1], [-1;0], or [-1;2]), the sex-ratio
243 strategy changes somewhat to better fit the new range. However, the strategy already fits the new
244 range quite well and therefore a strong change in the sex-ratio strategy is not necessary. When the
245 overall quality decreases, the total population size decreases and the sex ratio becomes slightly more
246 skewed towards males. See Supplement 2 for a figure on these cases.
247
248 Most important for population dynamics however, are big changes in territory quality. Population
249 dynamics change considerably both when the territory quality improves and when it deteriorates.
250 When the environment deteriorates, less resources are available. In the most extreme change, to [-2;-
251 1], the new environment is of such poor quality that the population goes extinct (in 50/50 replicates
252 for both fast and slow environmental change; and for both $M(Q)$ and $M_i(Q)$). Here, the biggest problem
253 is the productivity of the population, although the sex ratio also becomes more skewed, in this case

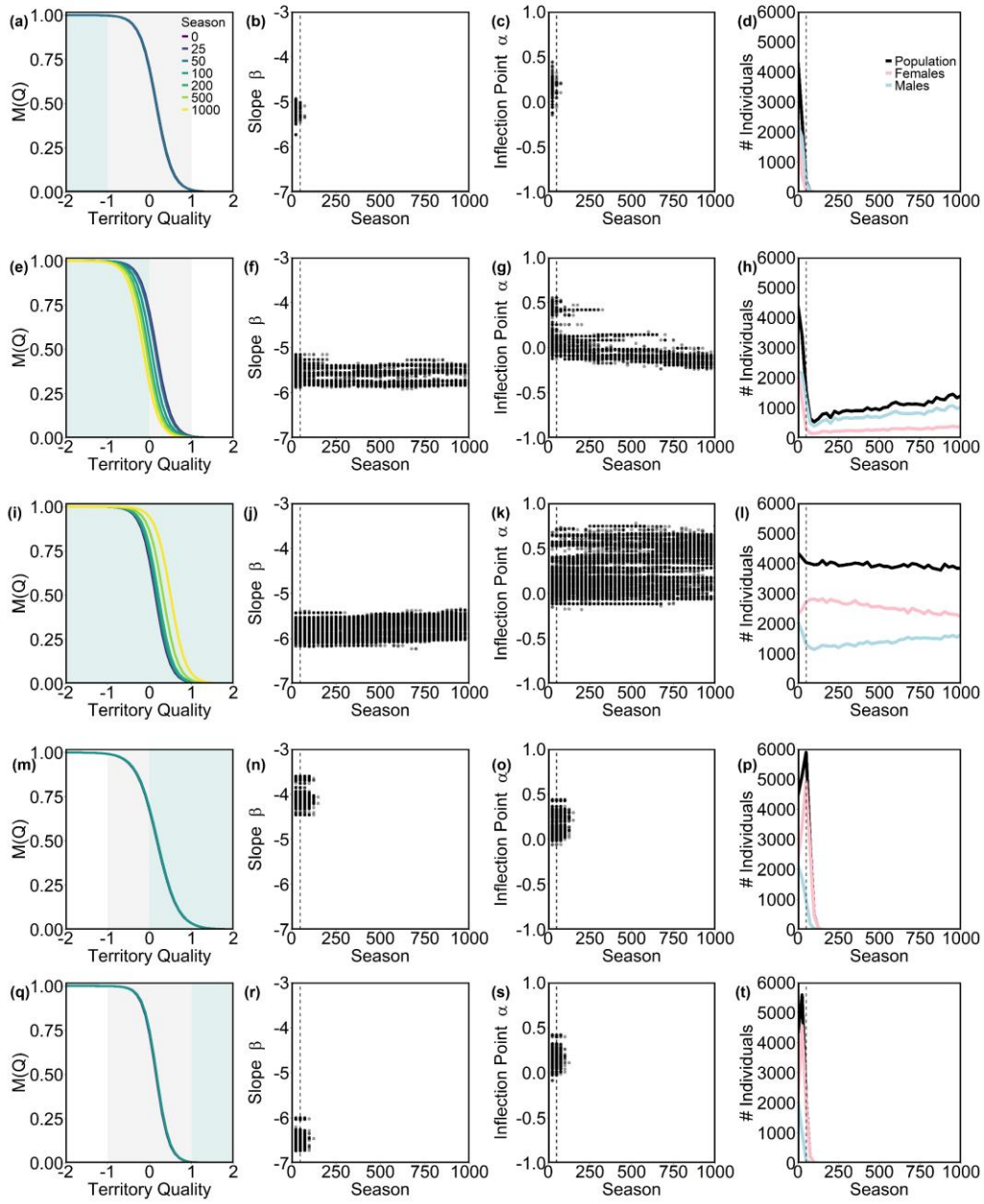

Figure 3: Change in offspring sex-ratio strategies over time after different types of environmental change. Each row consists of one representative replicate simulation per type of environmental change, for cases where the sex-ratio strategy only depends on territory quality. All environments have a territory quality range of [-1;1] before environmental change and a territory quality range of [-2;-1] (top row), [-2;0] (second row), [-2;2] (middle row), [0;2] (fourth row), or [1;2] (bottom row) after environmental change. The grey and azure shading indicate the territory quality before and after environmental change, respectively. The panels in the first column (a, e, i, m, q) show the change in the population average sex-ratio strategy over time. The panels in the second column (b, f, j, n, r) show the values of β (the slopes of the sex-ratio strategy) over time, where each dot represents the value of one breeding female. The panels in the third column (c, g, k, o, s) show the values of α (the inflection point of the sex-ratio strategy) over time, again with each dot representing the value of one breeding female. The panels in the fourth column (d, h, l, p, t) show the number of individuals in the population over time, for the total population as well as for females and males separately. The environmental change in this replicate finished after 50 seasons, indicated by the vertical dashed line in all plots except those in the left column.

towards a male bias. When environment deterioration is less extreme (to [-2;0]), the population sometimes goes extinct (8/50 replicates for fast environmental change when *M* depends only on territory quality, and no extinctions in the other cases), or more often survives but with a much smaller population size and a male-biased sex ratio.

When territory quality improvement is more extreme than in our Seychelles warbler case study, the population also changes considerably. In the most extreme case, an improvement to [1;2], causes population extinction in most cases (50/50 replicates for both fast and slow environmental change when *M* is only dependent on *Q*; and when *M* depends on *Q* and number of helpers, extinction occurs in 40/50 replicates for fast, and 34/50 for slow environmental change). When territory qualities improve to [0;2], the extinction rate is high when *M* depends only on territory quality (50/50 replicates for fast environmental change and 47/50 for slow environmental change), while no populations are going extinct when the sex-ratio strategy depends on both territory quality and the number of helpers. In other words, the sex-ratio strategy depends on two cues here, and while one cue becomes less adaptive, the other cue can become more helpful and can save a population from extinction.

Discussion

We found that environmental change can impact sex-ratio strategies, and population persistence, depending on the strength of environmental change. When environmental change is limited (as in our Seychelles warbler case study), the sex-ratio strategy slowly evolves to better fit the new environmental range. This might cause changes in the population sex ratio and size (an increase in size when the environment improves, a decrease when the environment deteriorates). Sometimes however, the change in population sex ratio is so strong that one of the sexes is not being produced anymore and the population goes extinct. This risk is higher in smaller populations, and also when environmental change is more extreme. When the environment deteriorates substantially, not enough resources are left to sustain a population, leading to population extinction or, in a less extreme cases, to reductions in population size. When the environment improves substantially, populations grow in size, but because of the sex-ratio strategy one sex is greatly overproduced, which can also lead to population extinction. When the sex-ratio strategy is dependent on more cues than just the environmental one, it can buffer populations from going extinct by becoming more reliant on the second cue, but this effect weakens when the environmental change becomes more extreme.

The change in sex-ratio strategies over time in our model is mostly caused by selective disappearance, rather than by the appearance of new, more adaptive alleles. This can limit the ability of a population to evolve, and could cause the extinction of populations, ironically especially when the environment

improves. This result is logical given the 'short' (in evolutionary terms) timescale we follow populations after environmental change, although we used a relatively high mutation rate. To check the effect of the mutation rate on population extinction, we ran more simulations with a mutation step size double of what we used before (σ=0.1, i.e. extremely high). Still, we reached similar conclusions as with the normal mutation step size (see Supplement 3), where almost all populations are going extinct when the environmental improvement is most extreme (to [1;2]), and when the sex-ratio strategy depends only on territory quality and the environment improves to [0;2]. Mutations have a random direction and are not always adaptive, therefore more mutations (and more time to obtain those mutations) are necessary for populations to adapt to extreme environmental change, which is not always available, leading to population extinction, even when a strategy is plastic.

When comparing our results to the Seychelles warbler population (Komdeur *et al.*, 1997; Borger *et al.*, 2025), it seems improbable that a change in the environmental cue (territory quality) can have caused the sex-ratio strategy to flatten, and therefore for the sex-ratio trend to disappear. Also, in all our other cases of environmental change where the population persists, the sex-ratio strategy never flattens but instead shifts to fit its new range. Thus, it seems unlikely that environmental change can cause the environment-dependent sex-ratio strategies to flatten in the warbler. Hence, the disappearance of sex-ratio trends over time in the same population of the Seychelles warbler needs a different explanation. Moreover, our model does not explain differences between populations, as different selective pressures in different environments can lead to different adaptive plastic strategies. Hence, to understand the adaptive nature of the sex-ratio trends that have been found, it might be better to retest the same population later, with more data, than to compare between populations.

An important assumption in our model is that a logistic function with a linear exponential is used to represent the sex-ratio strategy. This is chosen purposefully, as this is how empirical sex ratio data is generally treated in statistical models. However, one could argue that this limits how the sex-ratio strategy could adapt to the environmental change. While in the long run many strategies can in principle evolve in this model (see the supplementary materials of Borger *et al.*, 2026), it could be possible that in the short term this assumption limits our results. To test if, with enough time, a different sex-ratio strategy would evolve, we also ran simulations with a fixed territory quality range of [0;1] for five million seasons (starting with all parameter values at 0, so that the sex-ratio strategy starts independent of territory quality at 0.5 for all individuals). Here, once again a sex-ratio strategy evolved as in Figure 1a (daughters are produced in the highest territory quality, sons in lower quality territories), see Supplement 4. This indicates that our findings are not solely caused by constraints in the model. Instead, a territory-quality dependent sex-ratio strategy as in Figure 1a also evolves when starting with

a flat (territory-quality independent) sex-ratio strategy. This suggests that even when the environment has a narrow range and overall is good, an environment-dependent sex-ratio strategy is more adaptive than a flat, territory-quality independent sex-ratio strategy.

In this study, we examined the evolution of plastic reaction norms under environmental change, a relevant topic (Fox *et al.*, 2019), that is difficult to study empirically. We show examples where plastic strategies can evolve adaptively, but become maladaptive after environmental change, something more commonly referred to as environmental stress (Ghalambor *et al.*, 2007). In other words, plastic strategies can only be selected on the parts that are being expressed, that is, selection acts on the phenotype in the environments that are being experienced. On the phenotype outside of the range that was expressed, selection cannot act and hence cannot produce an adaptive plastic strategy in those environments. This can cause maladaptive phenotypes and in extreme cases, population extinction, when there is extreme environmental change. Potentially, plastic responses based on multiple cues can aid in adapting to new environments, as found in our work here. However, while it has been hypothesised (e.g. Bonamour *et al.*, 2019) and found (e.g. Schoeppner & Relyea, 2009), that plastic strategies can depend on multiple cues, it is unknown how common this is. Moreover, while in our model it is impossible, it could be adaptive to switch off plastic responses and instead change to a fixed or less plastic strategy when the environmental change is extreme, as was for example found in a study by Campbell-Staton *et al.*, (2021). They showed that forest crested anoles (*Anolis cristatellus*) were plastically changing their gene expression depending on temperature, while urban crested anoles living in urban heat islands displayed reduced gene expression plasticity.

In conclusion, a change in the environment can cause environment-dependent sex-ratio strategies to change to some extent, and selective disappearance can play an important role in this (at least in the short term). Sometimes an improvement in the environment can cause populations to go extinct, as adaptive plastic strategies can become maladaptive outside of the range they have evolved in. If the sex-ratio strategy is based on multiple cues (the environment that is changing and another cue), this can sometimes protect the population from extinction. In such cases, the relative importance of both cues and the way they interact changes, even when the overall sex-ratio strategy does not quantitatively change after environmental change. Potentially, making plastic strategies depend on multiple cues is a way to increase the robustness of the strategy and increase its effectiveness in changing or unpredictable environments.

Acknowledgements

We thank H. Hildenbrandt for his help in extending the model to include environmental change. Moreover, we thank F.J. Weissing for his thoughts and comments on this research project.

Funding

MJB was funded by the German Research Foundation (DFG Project no. 316099922) as part of the CRC NC³ (SFB TRR 212), and by ALW-NWO Grant No. ALWOP.531 awarded to JK and DSR. M.K. was supported by the European Research Council (ERC Advanced Grant No. 789240 awarded to F.J. Weissing).

Data

The data will be made publicly available once the manuscript is published.

References

Bonamour, S., Chevin, L.-M., Charmantier, A. & Teplitsky, C. 2019. Phenotypic plasticity in response to climate change: the importance of cue variation. *Phil. Trans. R. Soc. B* **374**: 20180178.

Borger, M.J., Lee, K.G.L., Weissing, F.J., Richardson, D.S., Dugdale, H.L., Burke, T., *et al.* 2025. A path analysis disentangling determinants of natal dispersal in a cooperatively breeding bird. *Journal of Evolutionary Biology* **voaf084**.

Borger, M.J., Richardson, D.S., Dugdale, H., Burke, T. & Komdeur, J. 2023. Testing the environmental buffering hypothesis of cooperative breeding in the Seychelles warbler. *acta ethol* **26**: 211–224.

Borger, M.J., Weissing, F.J., Hildenbrandt, H. & Kozielska, M. 2026. The evolution of plastic sex ratio strategies in cooperative breeders. EcoEvoRxiv.

Brouwer, L., Richardson, D.S., Eikenaar, C. & Komdeur, J. 2006. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. *Journal of Animal Ecology* **75**: 1321–1329.

Brouwer, L., Richardson, D.S. & Komdeur, J. 2012. Helpers at the Nest Improve Late-Life Offspring Performance: Evidence from a Long-Term Study and a Cross-Foster Experiment. *PLoS ONE* **7**: e33167.

Burley, N. 1981. Sex ratio manipulation and selection for attractiveness. *Science* **211**: 721–722.

Campbell-Staton, S.C., Velotta, J.P. & Winchell, K.M. 2021. Selection on adaptive and maladaptive gene expression plasticity during thermal adaptation to urban heat islands. *Nat Commun* **12**: 6195.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. 1986. Great expectations: dominance, breeding success and offspring sex ratios in red deer. *Animal Behaviour* **34**: 460–471.

Cobb, J.A. 1914. The problem of the sex-ratio. *Eugenics Review* **6**: 157–163.

Daan, S., Dijkstra, C. & Weissing, F.J. 1996. An evolutionary explanation for seasonal trends in avian sex ratios. *Behavioral Ecology* **7**: 426–430.

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. Princeton University Press.

Düsing, C. 1883. Die factoren welchen die sexualität enscheiden. *Jenaische Zeitschrift für Naturwissenschaft* **16**: 428–464.

Eikenaar, C., Brouwer, L., Richardson, D. & Komdeur, J. 2010. Sex biased natal dispersal is not a fixed trait in a stable population of Seychelles warblers. *Behav* **147**: 1577–1590.

Fisher, R. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford, UK.

Fox, R.J., Donelson, J.M., Schunter, C., Ravasi, T. & Gaitán-Espitia, J.D. 2019. Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Phil. Trans. R. Soc. B* **374**: 20180174.

409 Ghalambor, C.K., McKAY, J.K., Carroll, S.P. & Reznick, D.N. 2007. Adaptive versus non-adaptive
410 phenotypic plasticity and the potential for contemporary adaptation in new
411 environments. *Functional Ecology* **21**: 394–407.

412 Griffin, A.S., Sheldon, B.C. & West, S.A. 2005. Cooperative breeders adjust offspring sex ratios to
413 produce helpful helpers. *The American Naturalist* **166**: 628–632.

414 Hamilton, W.D. 1967. Extraordinary Sex Ratios: A sex-ratio theory for sex linkage and inbreeding
415 has new implications in cytogenetics and entomology. *Science* **156**: 477–488.

416 Hammers, M., Kingma, S.A., Spurgin, L.G., Bebbington, K., Dugdale, H.L., Burke, T., *et al*. 2019.
417 Breeders that receive help age more slowly in a cooperatively breeding bird. *Nat*
418 *Commun* **10**: 1301.

419 Komdeur, J. 1994. Experimental evidence for helping and hindering by previous offspring in the
420 cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behavioral Ecology*
421 *and Sociobiology* **34**: 175–186.

422 Komdeur, J. 1996. Facultative sex ratio bias in the offspring of Seychelles warblers. *Proc. R. Soc.*
423 *B.* **263**: 661–666.

424 Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of
425 cooperative breeding in the Seychelles warbler. *Nature* **358**: 493–495.

426 Komdeur, J., Daan, S., Tinbergen, J. & Mateman, C. 1997. Extreme adaptive modification in sex
427 ratio of the Seychelles warbler's eggs. *Nature* **385**: 522–525.

428 Korsten, P., Lessells, C.M., Mateman, A.C., Van Der Velde, M. & Komdeur, J. 2006. Primary sex
429 ratio adjustment to experimentally reduced male UV attractiveness in blue tits.
430 *Behavioral Ecology* **17**: 539–546.

431 Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guinness, F.E. 1999.
432 Population density affects sex ratio variation in red deer. *Nature* **399**: 459–461.

433 Penny, M. 1967. A New Sanctuary in the Seychelles. *Oryx* **9**: 214–216.

434 R Core Team. 2022. R: A language and environment for statistical computing.

435 Richardson, D.S., Burke, T. & Komdeur, J. 2003. Sex-specific associative learning cues and
436 inclusive fitness benefits in the Seychelles warbler. *Journal of Evolutionary Biology* **16**:
437 854–861.

438 Schoeppner, N.M. & Relyea, R.A. 2009. Phenotypic plasticity in response to fine-grained
439 environmental variation in predation. *Functional Ecology* **23**: 587–594.

440 Sheldon, B.C., Andersson, S., Griffith, S.C., Örnborg, J. & Sendecka, J. 1999. Ultraviolet colour
441 variation influences blue tit sex ratios. *Nature* **402**: 874–877.

442 Speelman, F.J.D., Borger, M.J., Hammers, M., Van Eerden, A.O.K., Richardson, D.S., Burke, T., *et*
443 *al*. 2024. Implications of adult sex ratios for natal dispersal in a cooperative breeder.
444 *Animal Behaviour* **208**: 19–29.

445 Trivers, R.L. & Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of
446 offspring. *Science* **179**: 90–92.

447 von Engelhardt, N.B. 2004. Proximate control of avian sex allocation. University of Groningen,
448 Groningen, The Netherlands.

449 Wang, D., Forstmeier, W., Ihle, M., Khadraoui, M., Jerónimo, S., Martin, K., *et al*. 2018.
450 Irreproducible text-book "knowledge": The effects of color bands on zebra finch fitness.
451 *Evolution* **72**: 961–976.

452 Wickham, H. 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York.

453 Wilke, C.O. 2020. cowplot: streamlined plot theme and plot annotations for 'ggplot2.'

454