The evolution of sex ratio strategies in cooperative breeders

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Abstract

1. The offspring sex ratio is often biased in cooperative breeders. Two hypotheses explain why this could be adaptive: 1) the local resource enhancement hypothesis, and 2) the local resource competition hypothesis. The first poses that offspring of the helping sex should be overproduced, as helpers provide fitness benefits to parents and future siblings. The second poses that offspring of the (non-helping) dispersing sex should be overproduced, as a reduction in local competition over resources increases the parents' fitness.

2. Here, we study the evolution of sex ratio strategies using evolutionary individual-based simulations to understand the relative importance of both hypotheses. We use the cooperatively breeding Seychelles warblers as inspiration, but our results can be interpreted more widely. Seychelles warblers were hypothesised to adapt their offspring sex ratio to the quality of the territory they reside in, as competition over resources is strong in low-quality territories, while the presence of helpers is beneficial in high-quality territories.

3. We found that an offspring sex ratio strategy based on territory quality evolves readily; as in Seychelles warblers, daughters (the helping sex) are overproduced in high-quality territories, while sons (the non-helping sex) are overproduced in low-quality territories. However, very similar sex ratio trends evolved when we switched off the sex difference in helping tendency or the sex difference in dispersal. When we removed all sex differences, territory-quality-based sex ratio trends (varying in steepness and direction) still readily evolved, which can be explained by the fact that many alternative trends are neutrally evolutionarily stable.

4. We conclude that in the Seychelles warbler, it is not possible to disentangle the effects of local resource enhancement and local resource competition based on the observed sex ratio trend. More generally, our study suggests that the sex ratio patterns found in nature will often have different explanations, making it difficult to pinpoint the causal determinant of a pattern.

Keywords (max 8): Offspring sex ratio, helpers at the nest, agent-based simulation, primary sex ratio, local kin competition, cooperative breeding,

Introduction

The offspring sex ratio in cooperatively breeding species is often strongly biased (Griffin et al., 2005), but whether and to what extent this bias is adaptive is generally unclear. In cooperatively breeding species, it is common that offspring of one sex are philopatric and become a helper in the next breeding season, while offspring of the other sex tend to disperse (in birds, for example, female helpers are found in: white-throated magpie-jays, Berg 2004; Seychelles warblers, Komdeur et al., 1997; and male helpers in: superb fairy-wrens, Cockburn & Double 2008; greater anis, Hendrix & Riehl 2023; acorn woodpeckers, Koenig et al., 2001). Because of this sex-specific behaviour, the sex ratio patterns found might be adaptive. Two contrasting hypotheses have been proposed to explain these patterns: local resource enhancement (Gowaty & Lennartz, 1985) and local resource competition (Clark, 1978).

The local resource enhancement hypothesis poses that offspring of the helping sex should be overproduced, as these provide fitness benefits to the parents and future siblings (usually by enhancing the resource availability or by decreasing the energy expenditure for their parents and/or siblings). Conversely, the local resource competition hypothesis poses that offspring of the non-helping, dispersing sex should be overproduced, as these offspring leave and therefore do not compete with their parents and future siblings for resources in their local, natal environment.

Local resource enhancement and local resource competition will often act simultaneously, and their relative strengths are likely situation dependent. For example, producing the helping sex might be beneficial when no or few helpers are present, while producing the dispersing sex may be the selectively favoured option when helpers are already present (Ligon & Ligon, 1990). Moreover, in a heterogeneous environment, the relative strength of these selective forces may vary in space and/or time. For instance, in high-quality territories with abundant resources, competition between (current) offspring and (older sibling) helpers over resources might be low, and hence helpers could enhance the survival of current offspring by feeding them extra, more than only the parents could. In such a case, local resource enhancement might be stronger than local resource competition, leading to an overproduction of the helping sex. On the contrary, in low-quality territories with only a few resources, local resource competition between current offspring and older siblings might be strong, as there are not enough resources to feed both the new offspring and the older siblings. In such a case, local resource competition may be stronger than local resource enhancement, and hence an overproduction of the dispersing sex might be expected.

Empirical studies testing these verbal hypotheses on sex ratio strategies in cooperatively breeding species found mixed results, finding no deviation from an even sex ratio (Berg, 2004; Gressler et al., 2014; Hendrix & Riehl, 2023; Kingma et al., 2011; Koenig et al., 2001), a deviation that does not agree with either the local resource enhancement or the local resource competition hypothesis (Cockburn & Double, 2008), a deviation that agrees with the local resource enhancement hypothesis (Allainé et al., 2000; Creel et al., 1998; Gowaty & Lennartz, 1985) or deviations that agree with both hypotheses (Dickinson, 2004; Komdeur et al., 1997).

Formal models are needed to place these verbal arguments and empirical findings in context. So far, a few attempts have been made in this direction (Pen & Weissing, 2000; Stubblefield & Orzack, 2013; Wild, 2006; Wild & West, 2007). All of these studies used an inclusive fitness approach to determine the optimal population primary sex ratio in cooperative breeders, and all concluded that an overproduction of either sex can be expected depending on the life history of the species. Although fitness-based approaches provide considerable insights into the interplay of different determinants of selection, they have the drawback that they do not explicitly consider the dynamics of evolution. They tend to focus on evolutionarily stable equilibria, based on the implicit assumption that the evolutionary dynamics follows the fitness gradient. When different selective processes are acting in concert (Fawcett et al., 2007, 2011), the evolving strategies are condition dependent (Weissing, 1996), and/or the evolving populations are polymorphic (Long & Weissing, 2023), this may not be justified. Therefore, we studied the evolution of sex ratio strategies using evolutionary individual-based simulations. These simulations moreover have the advantage that stochasticity is included, and that therefore a more realistic representation of evolution can be reached.

In our study, we are mainly striving for conceptual insights, but to be concrete (and realistic), we used the Seychelles warbler study system as an inspiration for our model. Seychelles warblers are facultative cooperative breeders, meaning that it is not a necessity for raising offspring to have helpers, but that some breeding pairs are assisted by helpers and that helpers do increase the survival of offspring. Helpers are predominantly female (Borger et al., 2023), and female helpers help more efficiently than male helpers (Richardson et al., 2003). Initially, it was found that sons had a higher dispersal probability than daughters (Komdeur, 1992). Komdeur et al., (1997) found that Seychelles warblers produced mainly daughters in high-quality territories and mostly sons in low-quality territories. However, sons were overproduced in high-quality territories that had two or more helpers. Based on these findings, Komdeur and colleagues hypothesised that the sex ratio trend is adaptive, as daughters are produced when it seems beneficial to have additional helpers, whereas sons are produced when it seems more beneficial to have dispersing offspring.

Here, we scrutinise this verbal hypothesis and investigate the relative importance of both local resource enhancement and local resource competition for the evolution of a territory-quality-dependent sex ratio strategy. Moreover, we study the co-evolution of offspring sex ratio strategies and offspring dispersal strategies, as sex ratios and sex-dependent dispersal are mutually dependent regarding their fitness implications.

Materials and Methods

Model overview

Our individual-based model investigates how territory quality, group size and composition, and sex- and status-related differences in philopatry and helping efficiency influence the evolution of situation-dependent sex ratio strategies. While the model is intended to be conceptual and aiming at general conclusions, model setup and parameter choices were inspired by the Seychelles warbler system to keep the model realistic. Simulations progress in discrete time steps, each representing a breeding season. Within each season, reproduction occurs and various behavioural decisions are made, some guided by heritable strategies. Across seasons, the frequency distribution of these strategies changes due to a combination of natural selection, mutation and genetic drift. Individuals can survive for multiple seasons; hence generations overlap.

Our model contains a fixed number of territories. Each territory can harbour a breeding female, a breeding male, several male and/or female helpers (previous offspring that remained philopatric), and newly born offspring. Some individuals are not affiliated with specific territories and are called "floaters". Territories differ in quality, corresponding to the amount of resources available at the start of a breeding season, and we assume that quality stays constant across seasons. The adult members of the group consume part of the resources. Hence, a larger group size implies that fewer resources are left over for the offspring, especially on low-quality territories. Conversely, the adult members contribute to provisioning the offspring with resources. Hence, a larger number of helpers can be beneficial for offspring survival, especially on high-quality territories. If the provisioning efficiency of helpers is sex-dependent (as in the Seychelles warbler), it may be advantageous to recruit only helpers of the more efficient sex, as the same provisioning efficiency can be achieved with fewer helpers. In our model, this can be achieved by biasing the offspring sex ratio and/or the "philopatry" of chicks (the tendency to stay on the natal territory and help the breeding pair raise offspring in subsequent breeding seasons) towards the more efficient sex.

The breeding season starts with a round of reproduction. Similarly to the Seychelles warblers, a single offspring is produced in all territories where a breeding pair is present. Offspring are provisioned with resources, depending on the amount of resources initially present on their territory, the resources consumed by the adult members of the breeding group, and the provisioning efficiency of the group. Offspring are assigned a sex, depending on the sex ratio strategy of their mother. They inherit the genes underlying the heritable strategies from their parents in a Mendelian fashion. Offspring survival is positively related to the resources received, while adult individuals have a fixed probability to survive to the following breeding season. Territory and status changes can occur in the final stage of a breeding season. At this stage, "empty" breeder positions are filled by helpers, floaters, or newly produced offspring of the corresponding sex. Individuals are assigned to empty breeding positions via a weighted lottery, where the success probability of a given individual depends on whether the individual is a helper, a floater, or a newly produced offspring. After as many empty breeding positions as possible have been filled, the remaining newly produced offspring decide whether to stay on their natal territory or to become a floater. This "philopatry decision" may depend on a heritable strategy. Once the status updates are completed, the next breeding season begins.

Model details

<u>Resources and territory quality.</u> The simulations reported below are based on a system of 1000 territories, resulting in an equilibrium population size of approximately 4000 individuals, which ensures that natural selection dominates genetic drift. The territories differ in the amount R of resources available at the start of the breeding season. At the start of the simulation, a resource level is associated with each territory, where R is drawn from a uniform distribution on the interval $[R_{\mathrm{min}}, R_{\mathrm{max}}]$. As motivated below, our default setting was $R_{min} = 50$ and $R_{max} = 150$, but to have a measure of territory quality that does not depend on such modelling detail, we define territory quality as follows:

$$Q(R) = 2 * \frac{R-\bar{R}}{R_{max} - R_{min}}, where\ \bar{R} = \frac{1}{2} * (R_{max} + R_{min}). \quad (1)$$

Hence, Q is linearly related to R and ranges from -1 (if $R = R_{min}$) to +1 (if $R = R_{max}$), with Q=0 corresponding to the average resource level $R = \bar{R}$.

Offspring provisioning and offspring survival. On a territory with initial resource availability R, the provisioning of offspring by the breeders and helpers proceeds in steps. First, a fixed amount n_a*C_a is deducted from R, which corresponds to the resources consumed by the breeders and helpers (n_a denotes the number of adult individuals on the territory and C_a the amount of resources consumed per adult). The remainder $\Delta = R - n_a * C_a$ can in principle be provisioned to the offspring. However, provisioning is limited by the fact that each breeder, each female helper, and each male helper has a limited provisioning efficiency E_b, E_f, and E_m, respectively. The actual amount of resources provisioned to the offspring, R_a, is the minimum of either the resources available for provisioning (Δ) or the sum of the provisioning efficiencies of all adult members of the breeding group. We assume that the survival probability of the offspring is increasing in an S-shaped manner with R_a:

$$S(R_a) = \frac{{R_a}^2}{{R_a}^2 + K^2}, \quad (2)$$

where the parameter K corresponds to the value of R_a at which the survival probability is equal to 50%. As motivated below, we chose K = 18 for the current study.

Sex ratio strategies. To allow for the evolution of a quality-dependent sex ratio trend, we endowed our individuals with a heritable (and, hence, evolvable) sex ratio strategy. In the baseline version of our model, this is a function *M(Q)* that for each territory quality Q determines the probability that a newly produced offspring is a son. We make the standard assumption for birds (Hardy, 2002) that the offspring sex ratio is determined by the mother. In empirical studies, sex ratio trends are typically investigated with logistic regression methods (Hardy, 2002; Pen et al., 1999). Therefore, we assume that *M(Q)* is given by a logistic function:

$$M(Q) = \frac{1}{1+ e^{-\beta*(Q-\alpha)}}, \quad (3)$$

where α and β are heritable and, hence, evolvable traits (see below). The value of α corresponds to the territory quality at which an even offspring sex ratio is produced: *M(α)* = 0.5, and is also called the inflection point. Generally, *M(Q)* is an S-shaped function that is either monotonically increasing (if β > 0) or decreasing (if β < 0). Hence, if β (i.e. the slope) is positive, the proportion of sons increases with territory quality, while it decreases with territory quality if β is negative. If β = 0, *M(Q)* = 0.5, irrespective of territory quality. Other sex ratios that are relatively independent of territory quality can also be realised if *α* evolves to a value outside the interval of *Q*-values that are relevant to our model (-1 ≤ *Q* ≤ 1).

We also considered an extended version of the model where the sex ratio strategy not only depends on territory quality, but also on the number of helpers already present on a territory (as was found for one year in the Seychelles warbler system; Komdeur et al., 1997). Here, three logistic functions $M_0(Q)$, $M_1(Q)$, and $M_2(Q)$ could evolve that determine the *Q*-dependent offspring sex ratio in the absence of helpers, in the presence of one helper, and in the presence of two or more helpers, respectively. These functions are given by:

$$M_i(Q) = \frac{1}{1+ e^{-\beta_i*(Q-\alpha_i)}}. \quad (4)$$

Inheritance of sex ratio strategies. Individuals in the model are haploid (for simplicity; equivalent results would be obtained for a diploid population with additive gene interaction). Heritable strategies are implemented genetically by assigning one gene locus to each evolvable parameter. The alleles at each locus correspond to the possible values of the corresponding parameter. For example, the maternal sex ratio strategy *M(Q)* in equation (3) is determined by the allelic values α and β at the two loci corresponding to these parameters. Similarly, the sex ratio strategies in the extended model in equation (4) are determined by the allelic values α_0, β_0, α_1, β_1, α_2 and β_2 at the six loci corresponding to these parameters. At the start of a simulation, all these values were initialised at zero, implying that initially an even offspring sex ratio (i.e., $M = 0.5$) is produced irrespective of territory quality. Non-zero values of the alleles can then later arise through mutation (see below). Offspring inherit their alleles from their parents in a Mendelian fashion, where we assume that gene loci that together encode one strategy are genetically linked while all other loci can recombine freely. For the sex ratio strategy $M(Q)$ in equation (4) this means that the allele combinations (α_0, β_0), (α_1, β_1) and (α_2, β_2) are transmitted as a package, with free recombination across these combinations.

Sex-differential philopatry. In the baseline version of the model, female and male philopatry (the probability of staying as a helper in the natal territory) is given by two parameters P_f and P_m that are fixed throughout the simulations. However, we also considered a model variant where female and male philopatry could evolve. Here, female and male philopatry are heritable situation-dependent strategies that are implemented by logistic functions:

$$P_f(Q) = \frac{1}{1+ e^{-\delta_f *(Q- \gamma_f)}}, \text{and } P_m(Q) = \frac{1}{1+ e^{-\delta_m *(Q- \gamma_m)}}. \qquad (5)$$

In other words, female and male offspring can make their decision to stay in their natal territory dependent on the quality of their natal territory. $P_f(Q)$ and $P_m(Q)$ are expressed in a sex-specific manner, where both strategies are inherited, but only the strategy corresponding to the chicks' sex is expressed. As in the case of situation-dependent sex ratio strategies, the logistic parameters γ_f, δ_f, γ_m and δ_m are encoded by the alleles at four gene loci, and are linked within a strategy, but can recombine between strategies. Again, the logistic parameters were initialised at zero at the start of a simulation, implying that initially half of the offspring stay on their natal territory while the other half become floaters, independent of territory quality.

Mutation. Once an offspring has received its set of alleles from its parents, mutation occurs with probability μ at each locus. If a mutation occurs, a mutational step size is drawn from a normal distribution with mean zero and standard deviation σ. The step size is then added to the value inherited from the parents. Throughout, we chose $\mu = 0.01$ and $\sigma = 0.05$.

Parameter choices. The resource levels in our model are in arbitrary units. We assume that an adult individual consumes $C_a = 20$ resource units. This implies that a territory of lowest quality $R_{min} = 50$ can just support a pair of breeders (while being able to reproduce), while a territory of highest quality $R_{max} = 150$ can support a breeding pair and five helpers. In a high-quality territory with zero, one, or two helpers, sufficient resources are left for the offspring. In the Seychelles warbler, female helpers provision the offspring at a similar rate as the breeders ($E_f = E_b$), while the provisioning rate of male helpers is substantially lower ($E_m < E_b$). In fact, the provisioning ratio is approximately $E_b : E_f : E_m = 7 : 7 : 3$ (Richardson et al., 2003). We therefore set $E_f = E_b = 7$ and $E_m = 3$. In other words, if sufficient resources are available on a territory, a breeder and a female helper can each contribute 7 units of resource to the provisioning of the offspring, while a male helper can only contribute 3 units. When less resources are available (Δ) than the maximal feeding efficiency of the breeding group, all the remaining resources are fed to the offspring. Regarding offspring survival, we assumed the survival probability of an offspring to be smaller than 50% if it is only provisioned by the breeding pair (bringing in 14 units of resources) but larger than 50% in the presence of a female helper (bringing in an additional seven resource units; see Supplement 1 for further explanation). As offspring survival is 50% if K resource units are provided to the offspring (see equation 1), we chose $K = 18$, which is about midway between 14 and 21. If sufficient resources are available in the territory, offspring survival is 0.38 in the absence of female helpers, 0.58 in the presence of one female helper, and 0.71 in the presence of two female helpers. The survival probability of adults was set to 0.9, which is comparable to (but somewhat higher) than the annual survival probability of adult Seychelles warblers.

Status change. After survival, individuals can change their status. First, breeding positions that became vacant by the death of previous breeders become available to others. In the model, vacant breeding spots are filled in order of decreasing territory quality. All available helpers, floaters and offspring of the correct sex (of the available breeding position) participate in a weighted lottery, where the winner becomes the new breeder in the vacant spot under consideration. The weighing factor of chicks was always lower than that of helpers and floaters (in the results shown below, this weighing factor was 0.2). In the baseline scenario based on Seychelles warbler parameters, the weighing factor for helpers was higher (0.5) than that of floaters (0.3), to reflect potential benefits of philopatry (see Supplement 1 for details). We varied the philopatry probability of sons (P_m) and daughters (P_f), but as a default we set P_m=0.3 and P_f=0.7 (see Supplement 1 for details).

Technical note

Simulations were conducted using C++ in Visual Studio (Visual Studio Community, 2022, version 17.4.4). Figures were generated using R version 4.2.2 (R Core Team, 2021), utilising the ggplot2 (Wickham, 2016) and cowplot (Wilke, 2020) packages.

Results

Dependence of sex ratios on territory quality

Figure 1 shows the simulation results for the default parameter setting (based on Seychelles warbler data), with a sex ratio strategy depending on territory quality. In all simulations, a sex ratio strategy evolved where more females are produced in high-quality territories, and more males are produced in low-quality territories. Typically, a clear-cut sex ratio pattern evolved with some individual variation around the population average (e.g. Fig. 1a). In some cases, two distinct strategies coexisted for a limited number of seasons (as illustrated in Fig. 1b). Instead of converging to an intermediate value, the slope of the sex ratio trend (β) continues to decrease. However, the rate of decrease slows down: once β is strongly negative, any further decrease has a minute effect on the sex ratio strategy, and hence stochasticity can become stronger than selection. When we changed the parameters so that males had a higher staying probability and a higher helping efficiency than females (i.e. the opposite of the Seychelles warbler case), opposite curves evolved where more sons were produced in high-quality territories and more daughters in low-quality territories.

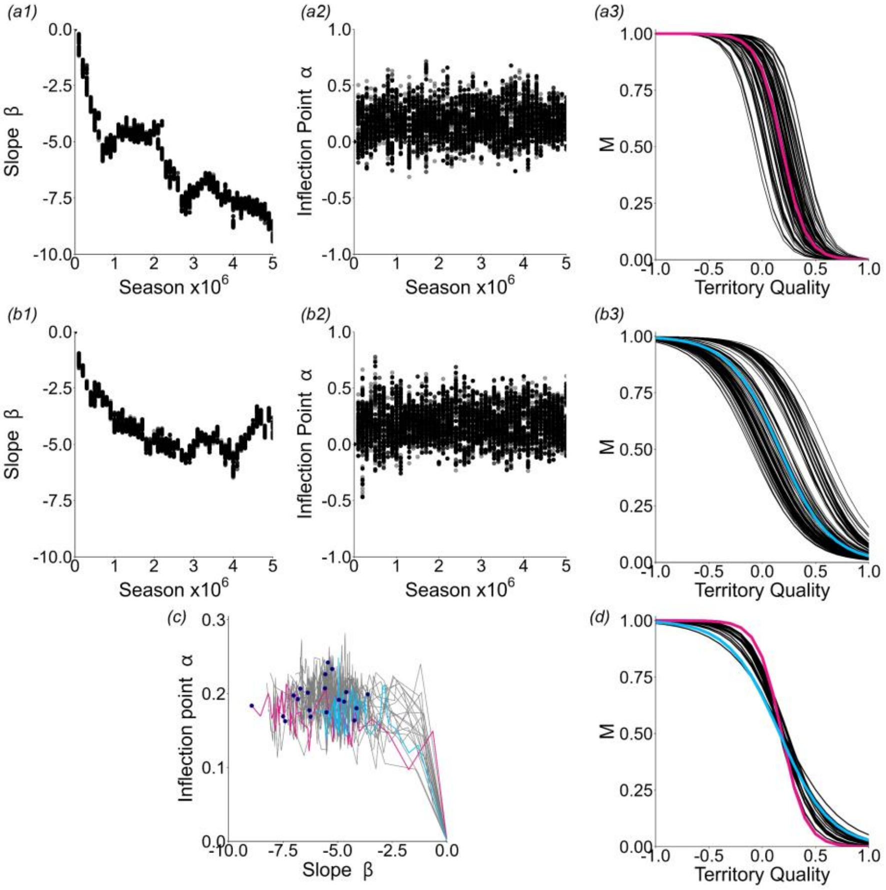

Figure 1: Evolution of a sex ratio strategy based on territory quality. (a) and (b) illustrate the individual variation in sex ratio strategies within two replicate simulations; (c) and (d) show the population averages of 20 replicate simulations. (a1) and (b1) represent the genetic values of the slope (β) of the reaction norms over time. Each dot represents the value of one breeding female. (a2) and (b2) represent the genetic values of the inflection point (α) of the reaction norms over time. Each dot represents the value of one breeding female individual. (a3) and (b3) represent the individual sex ratio strategies (M) of each breeding female at the end of the simulation. The pink and blue lines show the population average sex ratio strategy of the two replicates, respectively. (c) shows for 20 replicates how the population averages of slopes (β) and inflection points (α) changed over time. Each simulation started in (0,0) and ended in one of the dark blue dots. The replicates shown in (a) and (b) are represented by the same pink and blue as used in (a3) and (b3), respectively. (d) shows the population average genetic sex ratio reaction norms of these 20 replicates at the end of the simulation. The pink and blue lines represent the replicates shown in (a) and (b), respectively.

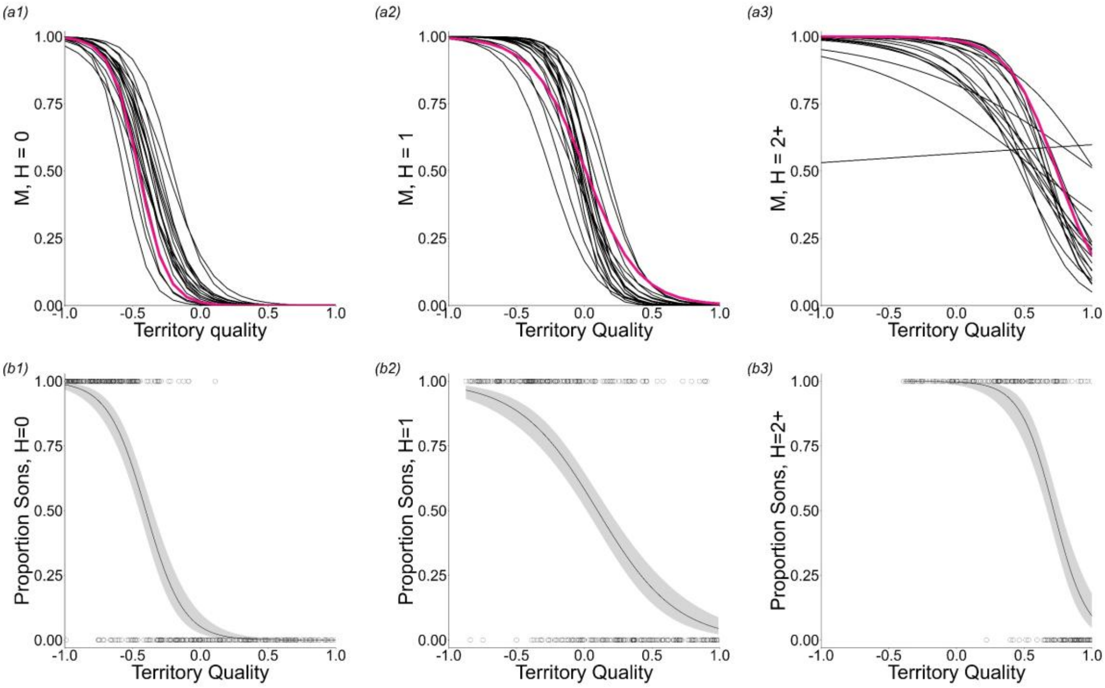

Figure 2: Evolution of a sex ratio strategy based on territory quality and the number of helpers already present. (a) Evolved sex ratio reaction norms, averaged over all individuals in the population, in 20 replicates at the end of the simulation, for the absence of helpers (a1), the presence of one helper (a2) and the presence of two or more helpers (a3). (b) The realised proportion of sons at birth in relation to territory quality and number of helpers in one representative replicate simulation (the pink replicate in a). Each dot represents a single offspring, and the lines plus confidence intervals show the best-fitting logistic curves through these points (as one would do with empirical data).

Dependence of sex ratios on territory quality and number of helpers

We also studied the evolution of a more complex sex ratio strategy that is not only based on territory quality but also on the number of helpers already present (Fig. 2). Also in this case, a strategy evolved where more daughters are produced in high-quality territories, while more sons are produced in territories of low quality. The number of helpers mainly affects the inflection points of the evolved curves: the inflection point α increases with the number of helpers already present. This implies that the range of territories where predominantly female offspring (i.e., additional helpers) are produced becomes smaller with the number of helpers present. The evolved curves for the situation of 2+ helpers varied considerably more across replicate simulations than the curves for 0 or 1 helpers. This is not surprising, because selection is weaker in the 2+ case, as there are fewer territories with 2+ helpers. Lastly, we found that deviations between genetic reaction norms and realised sex ratio strategies appeared. For example, territories with low quality often did not have enough resources to obtain 2+ helpers or to produce surviving offspring when 2+ helpers were present. Hence, this part of the genetic reaction norm for 2+ helpers was never under direct selective pressures.

Determinants of the evolved sex ratio patterns

In the Seychelles warbler, there are three key differences which might affect the selective pressures on sex ratio strategies. First, there is a difference in helping efficiency between male and female helpers. Second, there is a difference in philopatry between sons and daughters. Third, there is a difference in the probability of helpers and floaters obtaining a breeding position. As our default set of parameter values reflects the biology of Seychelles warblers, all three factors could have determined the sex ratio trends in Figs. 1 and 2. To study the separate effects of these factors, we removed some of the asymmetries or changed their direction. Figure 3 summarises the evolution of sex ratio strategies in five such scenarios. All scenarios in Figure 3 have in common that helpers and floaters have the same probability of obtaining a free breeder position; hence, there are no benefits of philopatry in terms of an enhanced probability of becoming a breeder.

<u>Scenario A: No differences between the sexes.</u> As a control, we set the staying probability for males and females to the same level (0.5) and the helping efficiency to 0 for both sexes. As there were no differences between the sexes, one might have expected that the initial state of the population (where all breeders produced a 1:1 sex ratio) would have remained constant throughout evolution. Figure 3A indicates that this was not the outcome of our simulations. At the population level (shown in Fig. 3A), a shallow territory-quality-dependent sex ratio strategy evolved in most replicates, where in some cases sons and in other cases daughters are

overproduced in high-quality territories. In some replicates, the evolved sex-ratio trend was as pronounced as in the Seychelles warbler simulations (Fig. 1d). Even in the cases of a flat sex-ratio trend at the population level, the sex ratio strategies were often dependent on territory quality: the flat population-level trend resulted from the "averaging out" of a diversity of individual-level sex-ratio strategies that varied with territory quality in different ways (see Supplement 2). Additionally, in some replicates, polymorphisms evolved where part of the population would always produce sons and the other part would always produce daughters, or a mix between such a polymorphism and a territory-quality-dependent sex ratio strategy. These outcomes can be explained by the fact that, in the absence of sex differences, selection is in the direction of an overall 1:1 sex ratio at the population level (Fisher's principle; Fisher, 1930). However, as first noticed by Kolman (1960), there are many ways to produce a 1:1 population sex ratio. For example, an even sex ratio could be achieved by a monomorphic population where all individuals produce equal numbers of sons and daughters, or by a dimorphic population where half of the population specialises in producing only sons while the other half specialises in producing only daughters. As our simulations demonstrate, there are even more options for achieving a 1:1 overall sex ratio if we allow for situation-dependent sex ratio strategies. For example, an individual strategy producing only one sex in low-quality territories and the other sex in high-quality territories will produce an overall even sex ratio if the total productivity of all low-quality territories is the same as that of all high-quality territories. In other words, there is a vast number of configurations that all yield a 1:1 population sex ratio, and none of these configurations is selectively superior to the other. In individual-based simulations (and natural situations), where genetic drift and other forms of stochasticity are relevant, the diversity of outcomes should therefore not come as a surprise.

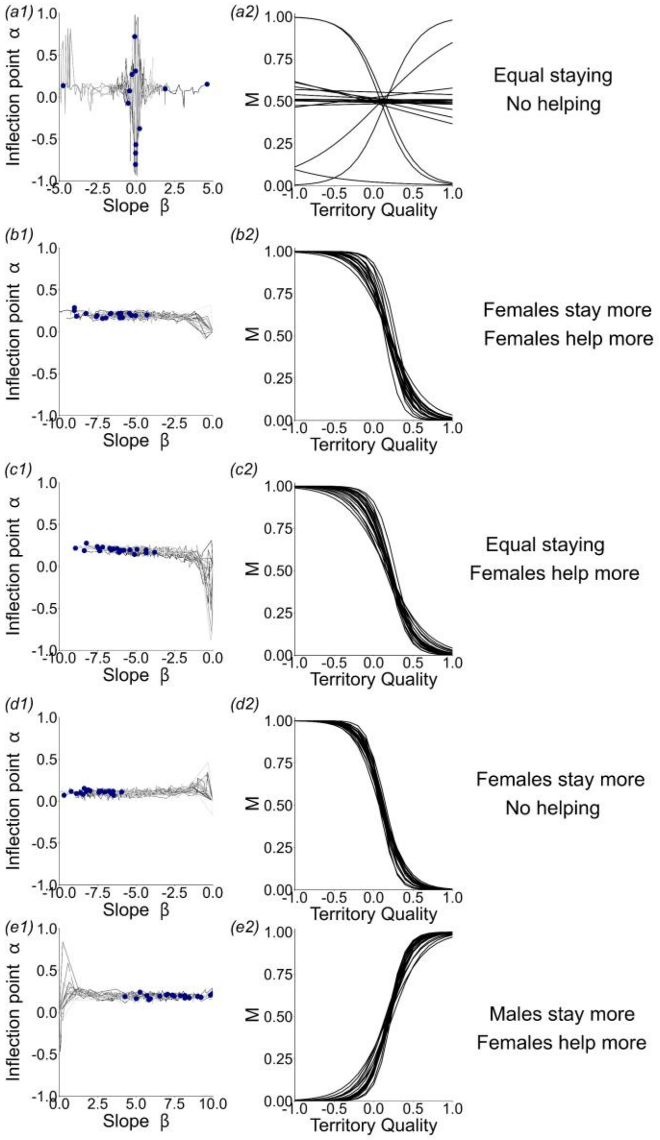

Figure 3: The evolution of sex ratio strategies in five scenarios. The scenarios differ in their assumptions regarding the differences between the sexes. For each scenario, the left panel shows the time course of the population averages of the slopes (β) and inflection points (α) in 20 replicate simulations. Each replicate started in (0,0) and ended in a dark blue dot. The right panel shows for each replicate the average sex ratio trend at the end of the simulation. All scenarios in this figure did not have benefits of philopatry, i.e. breeders and floaters had the same probability to become a breeder. (a) No difference between the sexes. (b) Daughters have a higher probability of staying and a higher helping efficiency than sons. (c) No sex difference in dispersal, but daughters have a higher helping efficiency than sons. (d) No help provided by sons and daughters (i.e., zero helping efficiency), but sons disperse more than daughters. (e) Sons have a higher probability to stay, but daughters have a higher helping efficiency.

Scenario B: Sex difference in helping efficiency and the probability to stay and help. As a second control, we reran the Seychelles warbler simulations (higher helping efficiency for females: 7 vs 3; and a higher staying probability for females: 0.7 vs 0.3), but without a benefit of philopatry (i.e., helpers and floaters have the same probability to obtain a free breeder position). Here again in all 20 replicates a sex ratio strategy evolved where mainly daughters were produced in high-quality territories and mostly sons were produced in low-quality territories (Fig. 3B). The evolved sex-ratio trend is very similar to the one with benefits of philopatry (Fig. 1d), which suggests that benefits of philopatry do not have direct effects driving the sex-ratio trend in Seychelles warblers.

Scenario C: No sex difference in dispersal, but a sex difference in helping efficiency. Here, we implemented only a difference in helping efficiency, so that females helped more efficiently than males (contributing 7 vs 3 resources to the offspring). Both sexes were assumed to have the same probability of staying and becoming a helper (0.5). Again, a territory-quality-dependent sex ratio strategy evolved (Fig. 3c), and the outcome is very similar to that in Scenario B. Hence, it seems that the sex-ratio trends in the Seychelles warblers are not driven by sex differences in local resource competition due to differences in dispersal.

Scenario D: No helping, but sex difference in dispersal. Next, we implemented only a difference in dispersal, where females had a higher probability of staying in their natal territory than males (0.7 versus 0.3). The helping efficiency of both sexes was set to zero, implying that neither of the sexes helped when they stayed. Once more, a territory-quality-dependent sex ratio strategy evolved (Fig. 3d), that is quite similar to the strategies in Scenarios B and C. Now, the simulation outcome suggests that the sex ratio trend in Seychelles warblers is not driven by local resource enhancement due to helping, but rather by the avoidance of local resource competition on low-quality territories. The production of daughters on high-quality territories is not explained by their helping, but by selection for a 1:1 population sex ratio (Fisher’s principle).

Scenario E: Higher probability of staying and helping in one sex, but a higher helping efficiency in the other sex. In this scenario, we switched the staying probabilities so that males had a higher staying probability than females (0.7 vs 0.3), but we kept the difference in helping efficiency the same as before, so that females had a higher helping efficiency than males (7 vs 3). In this case, a sex ratio strategy evolved in the opposite direction as before, so that mainly males were produced in high-quality territories while mostly females were produced in low-quality territories (Fig. 3E). Thus, for these parameter values, the staying probability had a stronger effect on the evolution of the sex ratio strategy than the helping efficiency.

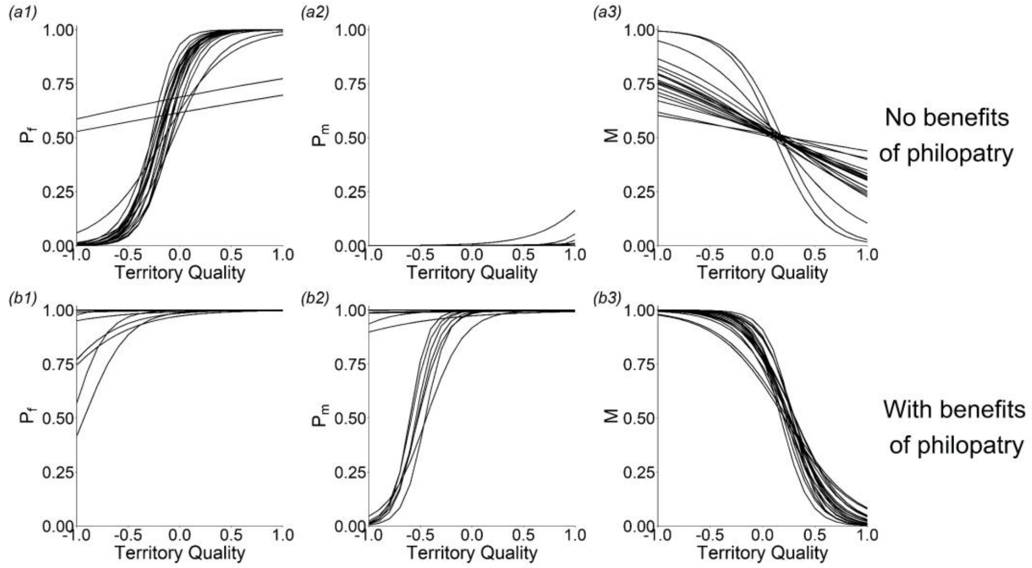

Figure 4: Co-evolution of sex ratio strategies and the probability of staying. (a) No benefits of philopatry. The graphs show the average evolved strategy in 20 replicates regarding the probability of staying in females (a1) and males (a2), and the sex ratio (a3). (b) With benefits of philopatry (helpers have a higher probability of obtaining a free breeder position than floaters). Evolved strategies of staying in females (b1) and males (b2), and the sex ratio strategy.

Evolution of the probability of staying

Until now, the probability of staying (and becoming a helper) was a fixed parameter. Next, we investigated a scenario where the probability of staying and the sex ratio strategy could co-evolve. As before, females had a higher helping efficiency than males (7 vs 3). Figure 4a shows the evolutionary outcome in the absence of benefits of philopatry (helpers and floaters have the same probability of obtaining a free breeder position). Females evolved a philopatry strategy, where they mostly stay in high-quality territories, while they mostly disperse from low-quality territories. Males evolved a strategy where they almost always disperse, although in high-quality territories their probability of staying is a bit higher than 0. A sex ratio strategy evolved where daughters are produced in high-quality territories and sons in low-quality territories, but the replicates differ in the slope of this strategy. We think that this strategy evolved because it is beneficial for low-quality territory parents to produce the dispersing sex (sons), while for high-quality territory parents it is beneficial to produce the opposite sex (daughters) due to Fisher's principle and because daughters were more efficient helpers.

With benefits of philopatry (Fig. 4b), females evolved to almost always stay (to become a helper), although in the lowest territory qualities, this probability was a bit lower than one. Males tended to evolve a similar strategy, although in some replicates a strategy evolved where males disperse from territories of very low quality, while staying and becoming a helper in high-quality territories. Again, a sex ratio strategy evolved where mainly daughters were produced in high-quality territories and mostly sons in low-quality territories. Presumably, this sex ratio strategy has evolved because it is beneficial for high-quality territory parents to produce daughters, as these are the more efficient helpers, while it is beneficial for low-quality territory parents to produce sons due to Fisher's principle.

Discussion

In our model, situation-dependent sex ratio strategies evolved readily and consistently. For the model variant tailored to the Seychelles warbler (where sons disperse more and daughters help more efficiently), a sex ratio trend evolved where sons are overproduced on low-quality territories and daughters are overproduced on high-quality territories. If the number of present helpers could be considered in the sex-ratio decision, daughters were only produced when helpers were absent or in the highest-quality territories. All this makes intuitive sense, and the evolved trends are qualitatively in line with the sex ratio trend reported for the Seychelles warbler (Komdeur et al., 1997).

However, we also found that virtually identical sex ratio trends evolved under different conditions. For example, in our simulations without helping, and only a sex difference in dispersal, we also found that daughters were produced in high-quality territories and sons in low-quality territories. In this scenario, local resource enhancement does not play a role, and the sex ratio trend is most likely caused by selection to reduce local resource competition in low-quality territories. Indeed, from the perspective of the local resource competition hypothesis, the evolved trend makes perfect sense: the more dispersing sex (males) is overproduced under highly competitive conditions (i.e., when territory quality is low), while females are overproduced when competition is less intense (on high-quality territories). In the opposite scenario, with only a sex difference in helping and no sex difference in dispersal, virtually the same sex ratio trend evolved as in the previous scenario. Now, sex differences in local resource competition do not play a role, and the trend is most likely caused by selection to enhance the productivity on high-quality territories. Again, the evolved sex ratio strategy makes sense: the more helpful sex (females) is produced in high-quality territories, while males are overproduced in the other (low-quality) territories.

Interestingly, significant sex ratio trends also evolved in (some of the) simulations of a control scenario, where neither sons nor daughters help and where the sexes do not differ in dispersal tendency. A detailed explanation why these trends can still evolve, even when there are no differences between the sexes, can be found in the results section. However, the implications of this are important. If a situation-dependent sex ratio trend is found in nature, it means that the sexes do not necessarily have to differ in a fitness-relevant manner, nor that the cue a situation-dependent sex ratio trend is based on is necessarily relevant for fitness. Moreover, we also showed with this example that the absence of a sex ratio trend at the population level does not automatically imply the absence of such trends at the individual level. In the absence of other selective pressures, selection is in the direction of an even sex ratio at the population level (Fisher’s principle). This can be reached in many ways, including in situation-dependent and independent ways.

We also studied what happened when sex ratio strategies could co-evolve with offspring philopatry strategies. In our simulations we found similar results when we included or excluded the co-evolution of sex ratio strategies and offspring natal dispersal strategies and again found that a similar offspring sex ratio strategy evolved. When there were benefits of philopatry, both sons and daughters evolved to always stay (to become helper), while in the absence of such benefits, daughters evolved to mostly stay, while sons evolved to mostly disperse. Without benefits of philopatry, the evolved sex ratio strategies varied more across replicates and did not look exactly like those in the other scenarios, so potentially selection is weaker in that case.

Previous studies on the topic of sex ratio strategies focused on the population offspring sex ratio (Frank & Swingland, 1988; Pen & Weissing, 2000; Wild, 2006; Wild & West, 2007). These studies generally concluded that at the population level an overproduction of the sex that is produced under unfavourable conditions is to be expected (Frank & Swingland, 1988). In the case of cooperative breeders, this means that the non-helping sex should be overrepresented at conception (Pen & Weissing, 2000). We found an overproduction of sons (the sex produced in low-quality territories) at the population level in most of our scenarios (see Supplement 3), and that this was consistent between all replicates. We also found that the population offspring sex ratio changed considerably at the end of the season (after checking offspring survival). After survival, all scenarios showed a distribution around 0.5 or one that is slightly female-biased. This seems logical, as the offspring in the low-quality environments have a lower survival rate than in the high-quality environments. Hence, in most of our simulations, sons have a lower survival probability than daughters (because they are more likely to be born on a low-quality territory), which consequently reduces the skew that was found at conception.

The predictions of this model are based on assumptions, of which some need further research. Importantly, we assume that our individuals have a mechanism to skew the sex ratio of their offspring in an adaptive manner. In animals with chromosomal sex ratio determination (like birds), this is, however, not a clear-cut assumption. Hypothesised mechanisms include sex-specific resorption of eggs (Emlen, 1997), sex-specific ripening speeds of ova, selective abortion of the unwanted sex either before or after fertilisation (Gosling, 1986), and non-random ovulation (Krackow, 1995). However, consistent evidence has not been found for any of these ways to manipulate the offspring sex ratio. We also assumed that such a sex ratio manipulation mechanism was cost-free. This assumption seems feasible in, for example, haplodiploid animals, where females can simply ‘choose’ to fertilise an egg or not. Yet, in animals with chromosomal sex determination this seems less likely and depends on the mechanism that is used to skew the sex ratio. If there are costs to manipulation of the offspring sex ratio, this has considerable effects on the evolution of sex ratio strategies (Pen & Weissing, 2002).

An important feature of our modelling approach is that we used a logistic function, with a linear exponential, to represent the offspring sex ratio strategy. We purposefully chose to do so, as offspring sex ratio data is often analysed using logistic regression models. Hence, logistic functions reflect empirical findings well. However, because of this choice, the evolved curves will automatically have an S-shape. To some extent, this limits the possible sex ratio strategies that can evolve, but as shown in our Supplement 2, it was still possible for many different types of strategies to emerge. When the inflection point (α) evolved to be outside of the territory quality range that was used in the simulation, or when the slope value stayed close to 0, linear relationships were also possible, or strategies where only sons (or only daughters) were produced. We could have added extra genes (e.g. add a quadratic term of territory quality with a corresponding gene) to allow for more freedom in the shapes of sex ratio strategies that could evolve (Botero et al., 2010), but as this is not common in the analysis of sex ratio trends, we decided against it.

In conclusion, we found that an offspring sex ratio trend in nature can evolve through many processes, also involving co-evolution, and that most of these sex ratio trends look virtually identical. This makes it virtually impossible to disentangle the relative importance of quite different factors like local resource enhancement and or local resource competition. Hence, it is far from trivial to understand which processes have caused an empirical sex ratio trend.

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Conflict of Interest

The authors declare to have no competing interests.

Author contributions

MJB and FJW designed the project. MJB, HH and MK developed the simulation code. MJB and MK ran all the simulations and did the data visualisation. MJB wrote the first version of this manuscript, and FJW and MK revised the manuscript multiple times. All authors agree on its publication.

Data availability

Data will be publicly available on the University of Groningen Dataverse, once the paper is accepted. The simulation code will be available on GitHub once the paper is accepted.

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