

Appendix 1 Alternative model to test robustness of results

In this appendix we describe a discrete full Wallenius model which was used to test the robustness of the results. This appendix is designed to be read stand-alone, and so overlap between equations here and in the body of text is noted. Code may be found at:

<https://github.com/nadiahpk/settlement-time-game>

A1.1 Model components

A1.1.1 Probability of rank

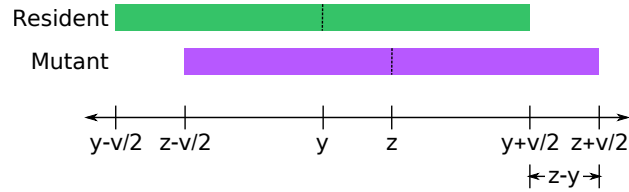


Figure A1: Settling times of individual residents (green) y and mutants (purple) z with uniform arrival distributions of width v .

Consider a population of size N with a resident settling time y over a uniform distribution $[y - v/2, y + v/2]$. Consider a mutant in this population with a settling time z . For a given instance $z + x$ the probability that exactly k of the $N - 1$ residents have already chosen their sites at the moment the mutant makes its choice (at $z + x$) is

$$\psi_k(x, y, z) = \binom{N-1}{k} \left(\frac{1}{2} + \frac{x + z - y}{v} \right)^k \left(\frac{1}{2} - \frac{x + z - y}{v} \right)^{N-1-k} + \left(\frac{z - y}{v} \right) \delta_{z > y, k=N-1} + \left(\frac{y - z}{v} \right) \delta_{z < y, k=0}. \quad (\text{A1})$$

The expression simplifies to a binomial due to the uniform distributions assumed. The δ is the Kronecker symbol; if the conditions in the subscript are satisfied it equals 1, else it equals 0. The last two δ terms take into account the ‘overhanging’ regions (Figure A1).

The probability that a mutant with settling time z chooses when k residents have already chosen is the integral over the arrival distribution of Equation A1

$$P_k(y, z) = \int_{-v/2}^{v/2} \frac{\psi_k(x, y, z)}{v} dx. \quad (\text{A2})$$

If all individuals have the same settling time y , the probability of rank k is equal for all k

$$P_k(y, y) = 1/N. \quad (\text{A3})$$

The probability of rank is calculated numerically in function `calcPkyz.m`.

A1.1.2 Probability of choosing a good territory

As in the main body of the text

$$\omega(y) = w_G/w_B = e^{y(\lambda_B - \lambda_G)}. \quad (\text{A4})$$

The probability that a mutant will choose a good territory, given that k residents have already arrived and they have chosen g good territories is

$$u_{k,g}(z) = \frac{(T_G - g)w_G(z)}{(T_G - g)w_G(z) + (T_B - k + g)w_B(z)} \quad (\text{A5})$$

(equivalent to Eq. 3 in the body of the text).

The probability of choosing a good territory is calculated in the function `calcu.m`.

A1.1.3 Probability of good territories already being chosen

The Wallenius Non-central Hypergeometric Distribution gives the probability distribution for g good territories having been taken given that k residents have already arrived $\mathcal{W}(g; k; T_G, T_B, \omega(y))$:

$$\varphi_k(g, y | T_G, T_B) = \binom{T_G}{g} \binom{T_B}{k-g} \int_0^1 (1 - t^{\omega/d_k(g,y)})^g (1 - t^{1/d_k(g,y)})^{k-g} dt, \quad (\text{A6})$$

where

$$d_k(g, y) = T_B - k + g + \frac{w_G(y)}{w_B(y)}(T_G - g). \quad (\text{A7})$$

In this case the number of good territories (T_G) and bad territories (T_B) take the roles of the familiar numbers of balls of each colour, and the number of each type taken (g and $k - g$) corresponds to the number of balls of each colour taken.

The solution is complicated by the fact that $\varphi_k(g, y)$ is not the correct expression for residents in the presence of the mutant. Typically adaptive dynamics assumes that the number of mutants is so low compared to the number of residents that the dynamics of the residents are not influenced by the mutant, however for population numbers low enough to necessitate a Wallenius distribution, the resident's fitness will be influenced by the mutant. For simplicity, we have made the typical adaptive dynamics assumption and assumed that both the residents and the single mutant are subject to the same $\varphi_k(g, y)$.

The solution is found numerically using the C++ library developed by Fog (2008) within the function `calcphi.m`.

A1.1.4 Probability of acquiring territory of various types

Bringing together Equations A2, A5 and A6, the probability of a mutant with strategy z acquiring a good territory amongst resident strategy y is

$$e_G(y, z) = \sum_{k=0}^{\min(N-1, T)} \sum_{g=0}^{\min(k, T_G)} P_k(y, z) u_{k,g}(z) \varphi_k(g, y). \quad (\text{A8})$$

When $N \leq T$ every individual acquires either a good or a bad territory, however for $N > T$ the last arriving individuals will acquire no territory. The probability of a bird acquiring no territory is equivalent to the probability of it having arrived after $k = T \dots N - 1$

$$e_0(y, z) = \delta_{T < N} \sum_{k=T}^{N-1} P_k(y, z). \quad (\text{A9})$$

Finally

$$e_B(y, z) = 1 - e_G(y, z) - e_0(y, z). \quad (\text{A10})$$

The probability of acquiring territory of each type is calculated in the function `calce.m`.

A1.2 Singular strategy and its stability

The fitness of a mutant with strategy z in a resident population of strategy y can be rewritten

$$U(y, z) = S_A + S_J R([f_G - f_B]e_G(y, z) + f_B[1 - e_0(y, z)]) \quad (\text{A11})$$

(which is equivalent to Equation 10 in the body of the text).

The fitness gradient can be calculated numerically as in the function `calcnumericdU.m`, which can then be solved numerically to find the singular strategy (function `solveEss.m`). However it is also possible to find an analytic description for it.

The fitness gradient is

$$\left. \frac{\partial U(y, z)}{\partial z} \right|_{z=y} = S_J R \left((f_G - f_B) \left. \frac{\partial e_G}{\partial z} \right|_{z=y} - f_B \left. \frac{\partial e_0}{\partial z} \right|_{z=y} \right) \quad (\text{A12})$$

and the singular strategy y^* is defined when

$$\left. \frac{\partial U(y, z)}{\partial z} \right|_{z=y} = 0 \quad (\text{A13})$$

is satisfied. The criterion for ESS stability is

$$\left. \frac{\partial^2 U(y, z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} = S_J R \left((f_G - f_B) \left. \frac{\partial^2 e_G}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} - f_B \left. \frac{\partial^2 e_0}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} \right) < 0. \quad (\text{A14})$$

We can deal with each component separately.

From Equation A8 and A3

$$\left. \frac{\partial e_G(y, z)}{\partial z} \right|_{z=y} = \frac{\partial}{\partial z} \left[\sum_{k=0}^{\min(N-1, T)} \sum_{g=0}^{\min(k, T_G)} P_k(y, z) u_{k,g}(z) \varphi_k(g, y) \right]_{z=y} \quad (\text{A15})$$

$$= \sum_{k=0}^{\min(N-1, T)} \sum_{g=0}^{\min(k, T_G)} \varphi_k(g, y) \left(\frac{1}{N} \left. \frac{\partial u_{k,g}(z)}{\partial z} \right|_{z=y} + u_{k,g}(y) \left. \frac{\partial P_k(y, z)}{\partial z} \right|_{z=y} \right). \quad (\text{A16})$$

So the selection gradient due to e_G is the sum of two terms:

- The first term (involving $\left. \frac{\partial u_{k,g}(z)}{\partial z} \right|_{z=y}$) is the part of the selection gradient that is due to the effect of changing settlement time on the probability of discerning a good site.
- The second term (involving $\left. \frac{\partial P_k(y, z)}{\partial z} \right|_{z=y}$) is the part of the selection gradient that is due to the effect of changing settlement time on the rank of the individual

These two terms represent the trade-off described in the body of the text.

$$\begin{aligned} \left. \frac{\partial^2 e_G(y, z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} &= \sum_{k=0}^{\min(N-1, T)} \sum_{g=0}^{\min(k, T_G)} \varphi_k(g, y^*) \left(u_{k,g}(y^*) \left. \frac{\partial^2 P_k(y, z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} \right. \\ &\quad \left. + 2 \left[\left. \frac{\partial P_k(y, z)}{\partial z} \right|_{z=y} \left. \frac{\partial u_{k,g}(z)}{\partial z} \right|_{z=y} \right]_{y=y^*} + P_k(y^*, y^*) \left. \frac{\partial^2 u_{k,g}(z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} \right) \end{aligned} \quad (\text{A17})$$

Using Equations A4 and A5

$$\left. \frac{\partial u_{k,g}(z)}{\partial z} \right|_{z=y} = (\lambda_B - \lambda_G) u_{k,g}(y) [1 - u_{k,g}(y)] \quad (\text{A18})$$

$$\left. \frac{\partial^2 u_{k,g}(z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} = (\lambda_B - \lambda_G) u_{k,g}(y^*) [1 - u_{k,g}(y^*)] [1 - 2u_{k,g}(y^*)]. \quad (\text{A19})$$

Using Equation A2

$$\left. \frac{\partial P_k(y, z)}{\partial z} \right|_{z=y} = \frac{1}{v} \left[\int_{-v/2}^{v/2} \frac{\partial \psi_k(x, y, z)}{\partial z} dx \right]_{z=y} \quad (\text{A20})$$

$$\left. \frac{\partial^2 P_k(y, z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} = \frac{1}{v} \left[\frac{\partial}{\partial z} \left(\int_{-v/2}^{v/2} \frac{\partial \psi_k(x, y, z)}{\partial z} dx \right) \right]_{\substack{z=y \\ y=y^*}}. \quad (\text{A21})$$

From Equation A1 it can be seen that

$$\frac{\partial \psi_k(x, y, z)}{\partial z} = \frac{\partial \psi_k(x, y, z)}{\partial x} \quad (\text{A22})$$

so

$$\left. \frac{\partial P_k(y, z)}{\partial z} \right|_{z=y} = \frac{1}{v} \left[\psi_k(v/2, y, z) - \psi_k(-v/2, y, z) \right]_{z=y} \quad (\text{A23})$$

$$\left. \frac{\partial^2 P_k(y, z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} = \frac{1}{v} \left[\frac{\partial \psi_k(v/2, y, z)}{\partial z} - \frac{\partial \psi_k(-v/2, y, z)}{\partial z} \right]_{\substack{z=y \\ y=y^*}}. \quad (\text{A24})$$

Substituting in from Equation A1 and its derivative leads to

$$\left. \frac{\partial P_k(y, z)}{\partial z} \right|_{z=y} = \begin{cases} -\frac{1}{v}, & \text{if } k = 0 \\ \frac{1}{v}, & \text{if } k = N - 1 \\ 0, & \text{otherwise} \end{cases} \quad (\text{A25})$$

$$\left. \frac{\partial^2 P_k(y, z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} = \begin{cases} \frac{N-1}{v^2}, & \text{if } k = 0 \text{ or } k = N - 1 \\ -\frac{N-1}{v^2}, & \text{if } k = 1 \text{ or } k = N - 2 \\ 0, & \text{otherwise} \end{cases} \quad (\text{A26})$$

Substituting the above into Equation A15

$$\begin{aligned} \left. \frac{\partial e_G(y, z)}{\partial z} \right|_{z=y} &= \left(\frac{\lambda_B - \lambda_G}{N} \right) \sum_{k=0}^{\min(N-1, T)} \sum_{g=0}^{\min(k, T_G)} \varphi_k(g, y) u_{k,g}(y) (1 - u_{k,g}(y)) \\ &\quad + \frac{1}{v} \left(\delta_{N \leq T} \sum_{g=0}^{\min(N-1, T_G)} \varphi_{N-1}(g, y) u_{N-1,g}(y) - u_{0,0}(y) \right) \end{aligned} \quad (\text{A27})$$

which reveals that:

- The first term, the effect on the ability to discern a good site, depends upon the difference in the cue signalling rate ($\lambda_B - \lambda_G$) and the variance in individual success amongst the residents in finding a good site.
- The second term, the effect on rank, is simplified to only depend on the difference between choosing first and choosing last.

Substituting the above into Equation A17 gives

$$\begin{aligned}
\left. \frac{\partial^2 e_G(y, z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} = & 2 \left(\frac{\lambda_B - \lambda_G}{v} \right) \left(\delta_{N \leq T} \sum_{g=0}^{\min(N-1, T_G)} \varphi_{N-1}(g, y^*) u_{N-1,g}(y^*) (1 - u_{N-1,g}(y^*)) - u_{0,0} (1 - u_{0,0}(y^*)) \right) \\
& + \left(\frac{(\lambda_B - \lambda_G)^2}{N} \right) \sum_{k=0}^{\min(N-1, T)} \sum_{g=0}^{\min(k, T_G)} \varphi_k(g, y^*) u_{k,g}(y^*) (1 - u_{k,g}(y^*)) (1 - 2u_{k,g}(y^*)) \\
& + \left(\frac{N-1}{v^2} \right) \left(u_{0,0}(y^*) + \delta_{N \leq T} \sum_{g=0}^{\min(N-1, T_G)} \varphi_{N-1}(g, y^*) u_{N-1,g}(y^*) \right. \\
& \quad \left. - \sum_{g=0}^1 \varphi_1(g, y^*) u_{1,g}(y^*) - \delta_{N \leq T+1} \sum_{g=0}^{\min(N-2, T_G)} \varphi_{N-2}(g, y^*) u_{N-2,g}(y^*) \right). \quad (\text{A28})
\end{aligned}$$

From Equation A9, using Equation A25 and A26

$$\left. \frac{\partial e_0}{\partial z} \right|_{z=y} = \frac{\delta_{T < N}}{v} \quad (\text{A29})$$

$$\left. \frac{\partial^2 e_0}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} = \left(\frac{N-1}{v^2} \right) (\delta_{T < N} - \delta_{T < N-1}). \quad (\text{A30})$$

Substituting Equation A29 and A27 into Equation A12, we can obtain the final expression for the fitness gradient

$$\begin{aligned}
\left. \frac{\partial U(y, z)}{\partial z} \right|_{z=y} = S_J R \left[(f_G - f_B) \left(\frac{\lambda_B - \lambda_G}{N} \right) \sum_{k=0}^{\min(N-1, T)} \sum_{g=0}^{\min(k, T_G)} \varphi_k(g, y) u_{k,g}(y) (1 - u_{k,g}(y)) + \right. \\
\left. \frac{f_G - f_B}{v} \left(\delta_{N \leq T} \sum_{g=0}^{\min(N-1, T_G)} \varphi_{N-1}(g, y) u_{N-1,g}(y) - u_{0,0}(y) \right) - f_B \frac{\delta_{T < N}}{v} \right]. \quad (\text{A31})
\end{aligned}$$

The analytic expression for the fitness gradient in Equation A31 is used in function `calcanalyticdU.m`, which can be used as an alternative feeder function for the numerical solution to the singular strategy (function `solveEss.m`).

Substituting Equation A30 and A28 into Equation A14 gives the ESS-stability criterion

$$\begin{aligned}
\left. \frac{\partial^2 U(y, z)}{\partial z^2} \right|_{\substack{z=y \\ y=y^*}} &= S_J R \left\{ (f_G - f_B) \left[\right. \right. \\
&2 \left(\frac{\lambda_B - \lambda_G}{v} \right) \left(\delta_{N \leq T} \sum_{g=0}^{\min(N-1, T_G)} \varphi_{N-1}(g, y^*) u_{N-1,g}(y^*) (1 - u_{N-1,g}(y^*)) - u_{0,0} (1 - u_{0,0}(y^*)) \right) \\
&+ \left(\frac{(\lambda_B - \lambda_G)^2}{N} \right) \sum_{k=0}^{\min(N-1, T)} \sum_{g=0}^{\min(k, T_G)} \varphi_k(g, y^*) u_{k,g}(y^*) (1 - u_{k,g}(y^*)) (1 - 2u_{k,g}(y^*)) \\
&+ \left(\frac{N-1}{v^2} \right) \left(u_{0,0}(y^*) + \delta_{N \leq T} \sum_{g=0}^{\min(N-1, T_G)} \varphi_{N-1}(g, y^*) u_{N-1,g}(y^*) \right. \\
&\left. \left. - \sum_{g=0}^1 \varphi_1(g, y^*) u_{1,g}(y^*) - \delta_{N \leq T+1} \sum_{g=0}^{\min(N-2, T_G)} \varphi_{N-2}(g, y^*) u_{N-2,g}(y^*) \right) \right] \\
&\left. - f_B \left(\frac{N-1}{v^2} \right) (\delta_{T < N} - \delta_{T < N-1}) \right\} < 0. \quad (\text{A32})
\end{aligned}$$

The analytic expression for the ESS-stability criterion in Equation A32 is implemented in the function `calcdU.m`.

A1.3 Comparison result

Fig. A2 shows the response of the discrete full Wallenius model to changes in parameter values. The results in Figure A2 were also generated using a numerical solution to the fitness gradient in order to verify the correctness of the analytic solution (Equation A31). The approximation in the body of the paper assumes large values for N^* , however even at low N^* both the quantitative and the qualitative behaviour of the full Wallenius treatment shows good agreement with the approximation (compare Fig. A2 with Fig. 4 in body of text).

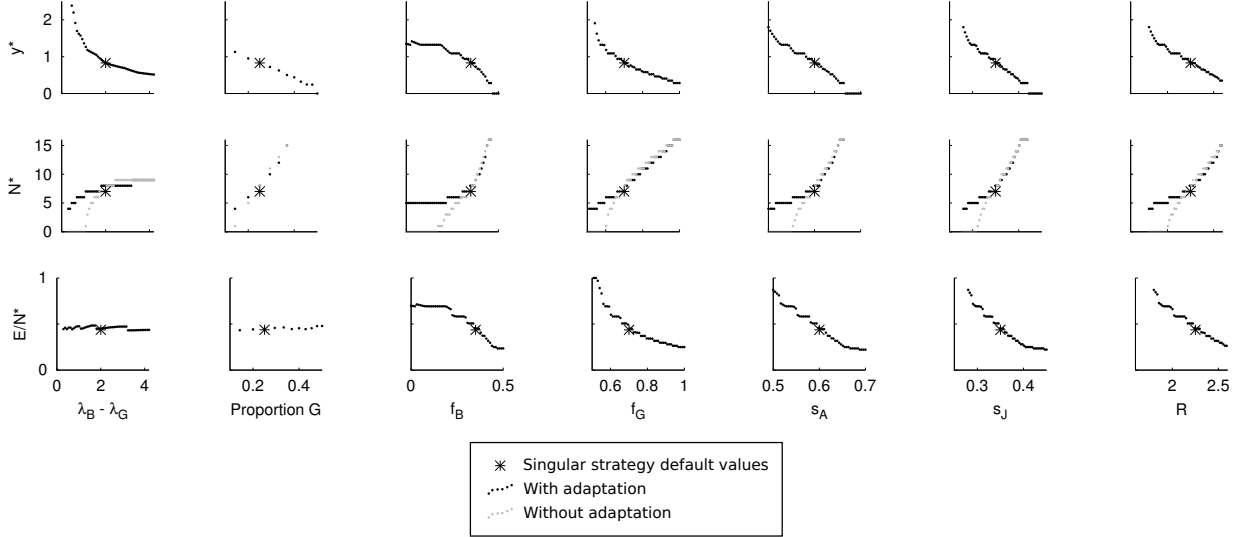


Figure A2: Ecological and evolutionary responses to changes in information, habitat-specific fledging rates, and demographic parameters. These results were produced by the discrete full-Wallenius model, for comparison with the simplified model in the body of the text in Figure 4. Default parameter values are: $S_A = 0.6$, $v = 1$, $R = 2.25$, $\lambda_G = 0.2$, $\lambda_B = 2.2$, $f_B = 0.35$, $f_G = 0.7$, $S_J = .35$, $T_G = 4$, and $T_B = 12$.

A1.4 A note about evolutionary stability

For all settling time strategies found above that were *not* on the cusp of a transition from one population size to another, both visual inspection of the fitness landscape and the analytic criterion for ESS-stability (Equation A32) showed that the singular strategy was ESS-stable. However the singular strategy is not a global maximum, and for low N^* , invasion is possible by rare strategies of very high z , corresponding to a thorough search for the remaining good strategies missed by earlier-settling residents (Figure A3(a)).

Further, for some parameter values (typically high y^* low N^* regions in Figure A2) the ‘singular’ strategy identified was at the transition from one (discrete) population size to another, with both alternate population sizes resulting in y^* estimates with fitness gradients (of opposite signs) some distance from 0 (Figure A3(b)). Therefore neither a numerical approach nor the analytic expression could be used to verify ESS-stability for these cases, as it presupposes evaluation at y^* .

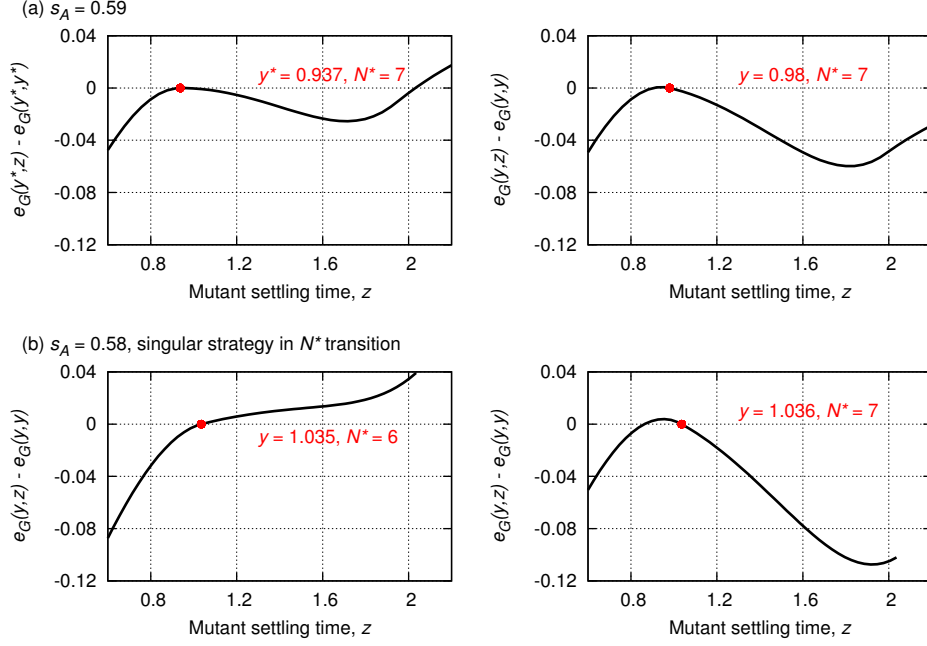


Figure A3: The fitness landscape around the resident strategy y^* for (a) $S_A = 0.59$ and (b) $S_A = 0.58$. In case (a), the singular strategy y^* can be found at it is ESS-stable. There is a region of higher fitness for higher values of y , however it is separated by a valley and a resident strategy in this region has negative fitness slope. In case (b), the singular strategy cannot be found. There is a discrete jump transition from population size $N^* = 6$ to $N^* = 7$ at the point near where the singular strategy should be, and so the test for ESS-stability cannot be applied. Other parameter values are the same as in Figure A2: $v = 1$, $R = 2.25$, $\lambda_G = 0.2$, $\lambda_B = 2.2$, $f_B = 0.35$, $f_G = 0.7$, $S_J = .35$, $T_G = 4$, and $T_B = 12$.

At the very least, this finding opens the possibility for invasion by strategies some distance away from the singular strategy, which may result in speciations and mixed strategies. Unfortunately the issue of evolutionary outcomes in such cases cannot be settled here. Such analysis is outside the scope of the current study, but the possibility is noted here for future workers.

Appendix 2 Demography of the model

The adaptive dynamics approach as used in this investigation assumes the population is close to equilibrium between invasion attempts (e.g. Dieckmann and Law (1996)). In order to verify this assumption, and ensure that the model does not exhibit large demographic variability, in which case other methods would be more appropriate (Doebeli 1995, Champagnat et al. 2006), we studied the demographic dynamic of a stochastic version of the population dynamic model. We proceeded as follows. We let the individuals choose sites following their ranking and with the probability to choose a good habitat as specified by eq. 8:

$$P_G = \frac{gw_G}{gw_G + bw_B}$$

After the individual has made its choice we subtracted 1 from g or b depending on whether it picked a good or a bad habitat. We modelled births and deaths as Poisson and binomial processes respectively. The number of offspring of each individual was obtained as a Poisson-distributed number with Rf_G and Rf_B as the parameter in good and bad nest sites respectively. Survival of an adult or juvenile individual occurred with probabilities given by S_A and S_J respectively, such that the mortality in the population was binomially distributed.

In this way we calculated population time series and extracted the variance. Specifically, we ran the model for 1000 time steps and calculated the variance of the population sizes in the last 500 time steps. We studied the coefficient of variation (CV, i.e. standard deviation divided by mean) since this enables comparisons across population sizes.

Figure 3 in the main text shows an example time series produced using this method for the default parameters. Figure A4A-G shows the CV and mean population size for the parameter values used in Fig. 4 in the main document. Figure A4H shows an example time series produced using this method for the default parameters (see Fig. 3 main text). We also performed additional simulations with other parameter values. We studied a case with a large reproductive output R (Fig. A4I). This was chosen because a large intrinsic growth rate in related models (e.g. May (1976)) have been shown to lead to sustained periods with large variance. We also studied a case with increased number of territories (Fig. A4J). As shown by the Figure A4A-G and A4I-J, CV becomes large only for parameter values where population size is low. Under those circumstances, the method used may be inaccurate. However, since high CV and low population size is indicative of large extinction risk (e.g. Nisbet and Gurney (1982), Newman et al. (2004)) it is nevertheless not so meaningful to consider adaptive evolution there. For the remainder of the parameter space CV is relatively low (0.1) and can furthermore be reduced by increasing the population size by increasing the number of nest sites (Fig A4J). Hence, for the ecologically relevant parameter space (low extinction risk), and as long as the number of nests is sufficiently large, population sizes are expected to vary relatively little around a population dynamic equilibrium, in line with the standard assumptions of adaptive dynamics.

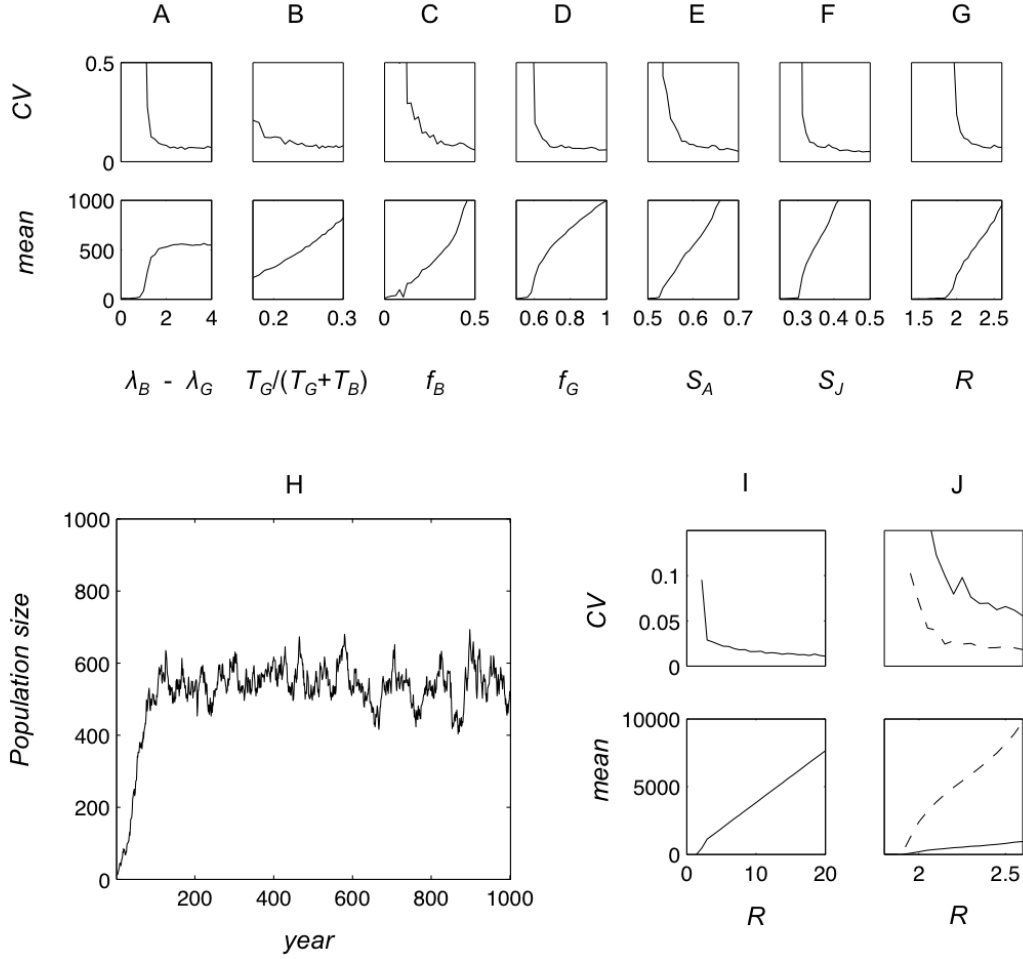


Figure A4: A-G. CV and mean population size for parameters in Fig. 4 in the main text. H. An example of a population time series for the default parameters (as in Fig. 2 main text). I-J. CV and mean population size for larger variation in reproductive output R (I) and effects of increasing the number of territories with a factor 10 (dashed lines) compared to default values (solid lines) (J).

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