

Appendix A from M. van de Pol et al., “Variation in Habitat Choice and Delayed Reproduction: Adaptive Queuing Strategies or Individual Quality Differences?”

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Models and Derivation of the Evolutionarily Stable Strategies

The Unconditional Queue Model

The Model

Ens et al. (1995) used a separate demographic and game-theoretical model to quantify the evolutionarily stable queuing strategy. Here we integrate both types of analysis into one coherent model, which—as we show below—has several crucial advantages. The structure of our model is based on the life-cycle plot in figure 1A. The change in density from year t to year $t + 1$ of queuers for high- and low-quality territories (n_{QH} and n_{QL} , respectively) and of high- and low-quality territory owners (n_H and n_L , respectively), is described by the following system of recurrence equations (e.g., Caswell 2001):

$$\begin{pmatrix} n_{QH} \\ n_{QL} \\ n_H \\ n_L \end{pmatrix}_{t+1} = \begin{pmatrix} 1 - \mu_{QH} - a_{QH}^* & 0 & (1-x)(F_H + m_{HN}) & (1-x)(F_L + m_{LN}) \\ 0 & 1 - \mu_{QL} - a_{QL}^* & x(F_H + m_{HN}) & x(F_L + m_{LN}) \\ a_{QH}^* & 0 & m_{HH} & m_{LH} \\ 0 & a_{QL}^* & m_{HL} & m_{LL} \end{pmatrix} \begin{pmatrix} n_{QH} \\ n_{QL} \\ n_H \\ n_L \end{pmatrix}_t. \quad (A1)$$

The matrix elements correspond to the parameters of the life-cycle plot in figure 1A. The strategic parameter x reflects the proportion of nonbreeders following the strategy of queuing for a low-quality territory (QLs), while $1 - x$ corresponds to the proportion of nonbreeders that follows the strategy of queuing for a high-quality territory (QHs). We assess here the performance of a mutant strategy x in a population consisting of individuals playing strategy x^* . The established strategy x^* is indirectly reflected by the annual settlement probabilities in high- and low-quality habitat (a_{QH}^* and a_{QL}^* , respectively). Equation (A1) corresponds to a system of the form $\mathbf{n}_{t+1} = \mathbf{A}(x, x^*)\mathbf{n}_t$, where \mathbf{n} is a vector of the numbers of individuals in each state and $\mathbf{A}(x, x^*)$ is the projection matrix of the population for strategy x in an established population of x^* . In the long term, the population projection reaches an equilibrium with a stable stage distribution given by $\mathbf{n} = (n_{QH}, n_{QL}, n_H, n_L)$ and a growth rate λ . We assume that the numbers of suitable high- and low-quality territories are fixed over time by setting $n_H^* = T_H$ and $n_L^* = T_L$, respectively, which results in a stationary population ($\lambda^* = 1$). Thereby, we introduce density-dependent settlement probabilities because breeding territories are a limiting resource and surplus individuals have to become nonbreeders. By fixing the state variables n_H and n_L , equation (A1) reduces to a system with only two state variables, and we can derive the equilibrium probabilities that a QH or a QL will ever settle (by setting $\mathbf{n}_{t+1} = \mathbf{n}_t$):

$$\frac{a_{QH}^*}{a_{QH}^* + \mu_{QH}} = \frac{T_H(1 - m_{HH}) - T_L m_{LH}}{(1 - x^*)[T_H(F_H + m_{HN}) + T_L(F_L + m_{LN})]} \quad (A2a)$$

and

$$\frac{a_{QL}^*}{a_{QL}^* + \mu_{QL}} = \frac{T_L(1 - m_{LL}) - T_H m_{HL}}{x^*[T_H(F_H + m_{HN}) + T_L(F_L + m_{LN})]}. \quad (A2b)$$

These equations have a clear-cut interpretation: for example, the probability a QH will ever settle (left-hand

side of eq. [A2a]) depends on the number of vacant high-quality territories divided by the total number of individuals following the QH strategy (right-hand side of eq. [A2a]). To perform an evolutionary cost-benefit analysis, we calculated the reproductive values (v), which can be found by solving $\mathbf{v}^T = \mathbf{v}^T \mathbf{A}$ (e.g., Taylor 1990):

$$v_{QH}^* = (1 - a_{QH}^* - \mu_{QH})v_{QH}^* + a_{QH}^*v_H^*, \quad (\text{A3a})$$

$$v_{QL}^* = (1 - a_{QL}^* - \mu_{QL})v_{QL}^* + a_{QL}^*v_L^*, \quad (\text{A3b})$$

$$v_H^* = (1 - x^*)(F_H + m_{HN})v_{QH}^* + x^*(F_H + m_{HN})v_{QL}^* + m_{HH}v_H^* + m_{HL}v_L^*, \quad (\text{A3c})$$

$$v_L^* = (1 - x^*)(F_L + m_{LN})v_{QH}^* + x^*(F_L + m_{LN})v_{HL}^* + m_{LH}v_H^* + m_{LL}v_L^*. \quad (\text{A3d})$$

The interpretation of the reproductive values is straightforward. For example, the reproductive value of an individual queuing for a high-quality territory (v_{QH}) equals the probability of remaining a QH times the reproductive value of a QH plus the probability of becoming a high-quality territory owner times the reproductive value of high-quality territory owners (v_H). Similarly, the reproductive value of a high-quality territory owner (v_H) is the sum of (1) the number of offspring produced that become QHs times v_{QH} , (2) the number of offspring produced that become QLs times v_{QL} , (3) the probability of staying a high-quality territory owner times v_H , and (4) the probability of moving to a low-quality territory times v_L . Equations (A3a) and (A3b) can be expressed in simpler form:

$$v_{QH}^* = \frac{a_{QH}^*}{a_{QH}^* + \mu_{QH}} v_H^* \quad (\text{A4a})$$

and

$$v_{QL}^* = \frac{a_{QL}^*}{a_{QL}^* + \mu_{QL}} v_L^*. \quad (\text{A4b})$$

Again, these equations have an intuitive meaning: the reproductive values of individuals queuing for high- or low-quality territories equal the probability of ever settling in high- or low-quality habitat times the reproductive value in high- or low-quality habitat, respectively (see also eqq. [11], [12] in EWD). Furthermore, because we are interested only in comparisons between groups of individuals, we can normalize all reproductive values to the reproductive value of low-quality territory owners. By inserting equations (A4a) and (A4b) into equations (A3c) and (A3d), respectively, solving for v_H and v_L and dividing the resulting equations, we find

$$\frac{v_H^*}{v_L^*} = \frac{(1 - m_{LL})p + m_{HL}}{1 - m_{HH} + m_{LH}p}, \quad (\text{A4c})$$

where $p = (F_H + m_{HN})/(F_L + m_{LN})$.

Calculating the Evolutionarily Stable Strategy

We can find the evolutionarily stable strategy (ESS) by calculating the value of x^* where no mutant strategy $x \neq x^*$ can invade. At an ESS, the fitness $\lambda(x, x^*)$ of each mutant is smaller than the fitness $\lambda(x^*, x^*)$ of the predominant strategy. Here, $\lambda(x, x^*)$ is defined as the relative growth rate of a mutant x in the established population x^* and is given by the dominant eigenvalue of \mathbf{A} . At an ESS, the selection gradient has to be 0 (e.g., Taylor 1990). This equilibrium condition can be expressed in terms of reproductive values and the deviations of the elements of matrix $\mathbf{A}(x, x^*)$ with respect to the strategic variable x :

$$\left. \frac{\partial \lambda(x, x^*)}{\partial x} \right|_{x=x^*} \propto \sum_{ij} \left(\left. \frac{\partial A_{ij}}{\partial x} \right|_{x=x^*} v_i^* n_j^* \right) = 0. \quad (\text{A5})$$

To check the stability of such an equilibrium, higher-order conditions have to be checked as well, which we

skip here to avoid technical detail. In our case, all but four terms in equation (A5) vanish, and in view of $n_H^* = T_H$ and $n_L^* = T_L$, we obtain

$$(v_{QL}^* - v_{QH}^*)[T_H(F_H + m_{HN}) + T_L(F_L + m_{LN})] = 0, \quad (A6)$$

from which it can be seen that at an ESS, $v_{QH}^* = v_{QL}^*$; in other words, individuals that decide to queue for high- and low-quality habitat can coexist at equilibrium only if they have the same reproductive value. This corresponds to the result of EWD that at an ESS, both strategies must yield equal fitness payoffs. The ESS x^* can be found by finding the value of x^* where the condition $v_{QH}^* = v_{QL}^*$ is satisfied. For comparison reasons, we first express this equality condition in a form similar to EWD’s. By equating equation (A3a) with equation (A3b), we find

$$\frac{x^*}{1 - x^*} = \frac{m_{NL}(v_L^* - v_{QL}^*)}{m_{NH}(v_H^* - v_{QH}^*)}, \quad (A7)$$

where $m_{NH} = (1 - x^*)a_{QH}^*$ and $m_{NL} = x^*a_{QL}^*$, which is equivalent to equation (15) in EWD (although EWD used expected future reproductive success instead of reproductive values). Equation (A7) (also given as eq. [1]) shows that in evolutionary equilibrium, the ratio of QH individuals to QLs reflects the ratio of the expected benefits of the two types of strategies. Ens et al. (1995) subsequently calculated x^* using settlement probabilities of nonbreeders derived from field data (m_{NH} and m_{NL}). However, this approach has two important disadvantages. First, life-history parameters of nonbreeders, such as m_{NH} and m_{NL} , are notoriously difficult to reliably estimate in the field because of the incomplete site fidelity of nonbreeders in many species. Second, the use of estimates of settlement probabilities from field data to calculate the ESS is not ideal because these same parameters are also indirectly used for model validation (i.e., they determine the age of first reproduction and recruitment probabilities). Therefore, we took a different approach to calculating x^* , one that takes full advantage of the fact that we have incorporated population limitation in our model. Because the total number of suitable territories is fixed, the availability of empty suitable territories for nonbreeders and thereby settlement probabilities can also be predicted from the behavior of the breeders (see eqq. [A2]). In other words, in our model, settlement probabilities are generated by the model itself, resulting in an internally consistent model, while this was not the case in the EWD model. By equating equation (A4a) to equation (A4b) and using equations (A2a), (A2b), and (A4c), as well as the reparameterization $q = T_H/T_L$, we find

$$x^* = \frac{(1 - m_{HH} + m_{LH}p)(1 - m_{LL} - m_{HL}q)}{[(1 - m_{HH})(1 - m_{LL}) - m_{HL}m_{LH}](1 + pq)}, \quad (A8)$$

(also given as eq. [2]), which shows that the evolutionarily stable queuing strategy x^* is dependent on the relative—rather than absolute—number of territories ($q = T_H/T_L$) as well as on the relative—rather than absolute—influx of new nonbreeders from high- and low-quality territories ($p = (F_H + m_{HN})/(F_L + m_{LN})$). More importantly, x^* is expressed as a function of several life-history parameters of breeders, which can be more reliably estimated than those of nonbreeders (as in eq. [A7]). The average time it takes a successful QH to acquire a high-quality territory is given by $1/(a_{QH}^* + \mu_{QH})$ (EWD). From this, we can calculate the predicted age at first reproduction of successful QHs by adding the age of sexual maturity to this value (similar for QLs).

The Conditional Queue Model

The Model

We extend the previous model by allowing nonbreeders born in high- (N_H) or low-quality territories (N_L) to make an independent choice of which strategy to follow (x_H or x_L ; see fig. 1B). In addition, we incorporate a new parameter, c , that represents differences in competitive abilities between N_H and N_L . We now get the following set of recurrence equations:

$$\begin{pmatrix} n_{QH(H)} \\ n_{QL(H)} \\ n_{QH(L)} \\ n_{QL(L)} \\ n_H \\ n_L \end{pmatrix}_{t+1} = \begin{pmatrix} 1 - \mu_{QH} - ca_{QH}^* & 0 & 0 & 0 & (1 - x_H)(F_H + m_{HN}) & 0 \\ 0 & 1 - \mu_{QL} - ca_{QL}^* & 0 & 0 & x_H(F_H + m_{HN}) & 0 \\ 0 & 0 & 1 - \mu_{QH} - a_{QH}^* & 0 & 0 & (1 - x_L)(F_L + m_{LN}) \\ 0 & 0 & 0 & 1 - \mu_{QL} - a_{QL}^* & 0 & x_L(F_L + m_{LN}) \\ ca_{QH}^* & 0 & a_{QH}^* & 0 & m_{HH} & m_{LH} \\ 0 & ca_{QL}^* & 0 & a_{QL}^* & m_{HL} & m_{LL} \end{pmatrix} \begin{pmatrix} n_{QH(H)} \\ n_{QL(H)} \\ n_{QH(L)} \\ n_{QL(L)} \\ n_H \\ n_L \end{pmatrix}, \quad (A9)$$

where $n_{QH(H)}$ refers to nonbreeders born in high-quality territories that follow a QH strategy, and so forth. When $c = 1$, there are no competitive asymmetries; when $c > 1$, N_H are competitively superior to N_L , so that they have a c times higher annual probability of acquiring a high- or low-quality territory; the opposite holds when $c < 1$. Reproductive values are now given by

$$v_{QH(H)}^* = \frac{ca_{QH}^*}{ca_{QH}^* + \mu_{QH}} v_H^* = \frac{q(1 - m_{HH}) - m_{LH} - (1 - x_L^*)(F_L + m_{LN})a_{QH}^*/(a_{QH}^* + \mu_{QH})}{(1 - x_H^*)(F_H + m_{HN})q} v_H^*, \quad (A10a)$$

$$v_{QL(H)}^* = \frac{ca_{QL}^*}{ca_{QL}^* + \mu_{QL}} v_L^* = \frac{1 - m_{LL} - m_{HL}q - x_L^*(F_L + m_{LN})a_{QL}^*/(a_{QL}^* + \mu_{QL})}{x_H^*(F_H + m_{HN})q} v_L^*, \quad (A10b)$$

$$v_{QH(L)}^* = \frac{a_{QH}^*}{a_{QH}^* + \mu_{QH}} v_H^* = \frac{q(1 - m_{HH}) - m_{LH} - (1 - x_H^*)(F_H + m_{HN})qca_{QH}^*/(ca_{QH}^* + \mu_{QH})}{(1 - x_L^*)(F_L + m_{LN})} v_H^*, \quad (A10c)$$

$$v_{QL(L)}^* = \frac{a_{QL}^*}{a_{QL}^* + \mu_{QL}} v_L^* = \frac{1 - m_{LL} - m_{HL}q - x_H^*(F_H + m_{HN})qca_{QL}^*/(ca_{QL}^* + \mu_{QL})}{x_L^*(F_L + m_{LN})} v_L^*, \quad (A10d)$$

$$\frac{v_H^*}{v_L^*} = \frac{1 - m_{LL} - x_L^*(F_L + m_{LN})a_{QL}^*/(a_{QL}^* + \mu_{QL})}{m_{LH} + (1 - x_L^*)(F_L + m_{LN})a_{QH}^*/(a_{QH}^* + \mu_{QH})}. \quad (A10e)$$

Note that if competitive asymmetries affected nonbreeder mortality (μ_{QH}/c'), for example, because of competition over food, this would result in qualitatively the same reproductive values as in the case of competitive asymmetries in settlement probabilities (ca_{QH}^* and ca_{QL}^*); this is a matter of rescaling.

Calculating the Evolutionarily Stable Strategy

We now have to evaluate the selection gradients for both strategic parameters, x_H and x_L , simultaneously:

$$\left. \frac{\partial \lambda(x_H, x_H^*)}{\partial x_H} \right|_{x_H = x_H^*} \propto (v_{QL(H)} - v_{QH(H)})T_H(F_H + m_{HN}) = 0 \quad (A11a)$$

and

$$\left. \frac{\partial \lambda(x_L, x_L^*)}{\partial x_L} \right|_{x_L = x_L^*} \propto (v_{QL(L)} - v_{QH(L)})T_L(F_L + m_{LN}) = 0. \quad (A11b)$$

At an interior equilibrium ($0 < x_H^* < 1$, $0 < x_L^* < 1$), both conditions have to be satisfied, yielding $v_{QH(H)} = v_{QL(H)}$ and $v_{QH(L)} = v_{QL(L)}$. These conditions can be rewritten using equation (A10):

$$\frac{v_H}{v_L} = \frac{ca_{QL}^*}{ca_{QL}^* + \mu_{QL}} \frac{ca_{QH}^* + \mu_{QH}}{ca_{QH}^*} \quad (A12a)$$

and

$$\frac{v_H}{v_L} = \frac{a_{QL}^*}{a_{QL}^* + \mu_{QL}} \frac{a_{QH}^* + \mu_{QH}}{a_{QH}^*}. \quad (\text{A12b})$$

When $c = 1$, these conditions are identical; consequently, both fitness functions are simultaneously optimized. Proceeding as before, we can show that both equation (A12a) and equation (A12b) imply that

$$x_L^* = \frac{(1 - m_{HH} + m_{LH}p)(1 - m_{LL} - m_{HL}q)}{(1 - m_{HH})(1 - m_{LL}) - m_{LH}m_{HL}} - pqx_H^* \quad (\text{A13})$$

(also given as eq. [3]). When $c = 1$, there is no asymmetry in the model parameters between N_H and N_L ; hence, the strategy space is overparameterized, which results in a line of neutral equilibria of many different combinations of x_H^* and x_L^* . We verified whether the two conditional strategies x_H^* and x_L^* yield the same queuing strategy at the population level as the unconditional model (x^*) by describing the population strategy in the conditional model as a weighted average of the conditional strategies:

$$x^* = \frac{x_L^*N_L + x_H^*N_H}{N_L + N_H} = \frac{x_L^* + pqx_H^*}{1 + pq}. \quad (\text{A14})$$

If we insert x_L^* from equation (A13) in equation (A14), we return to the x^* from the unconditional queue model (eq. [A8]), thereby demonstrating that all different combinations of x_H^* and x_L^* in the conditional model yield the same population strategy x^* as in the unconditional model. In the absence of competitive differences, there is no mathematical reason to assume that one combination of x_H^* and x_L^* is more likely than any other. However, starting out with a monomorphic population that plays strategy x^* , there is no selection pressure that results in x_H^* being different from x_L^* in the unconditional model without competitive asymmetries (i.e., $x_H^* = x_L^* = x^*$).

When $c \neq 1$, there is an asymmetry in competitive abilities that directly affects the settlement probabilities in both types of habitat. When an asymmetry is included, the two conditions required for an interior equilibrium (eqq. [A12a], [A12b]) cannot be simultaneously met, and their solutions will be generically different if $c \neq 1$. Hence, we recover the principle that asymmetric conflicts do not allow a completely mixed ESS (Maynard Smith and Parker 1976). At an ESS, either x_H^* have to play a pure strategy (i.e., $x_H^* = 0$ or $x_H^* = 1$) or x_L^* have to play a pure strategy (i.e., $x_L^* = 0$ or $x_L^* = 1$), resulting in four candidate ESSs. If x_H^* plays a pure strategy, the selection gradient $[\partial\lambda(x_H, x_H^*)/\partial x_H]_{x_H=x_H^*}$ is not required to be 0. Instead, $x_H^* = 0$ will be stable if $[\partial\lambda(x_H, x_H^*)/\partial x_H]_{x_H=0} < 0$ (i.e., selection favors smaller values of x_H); the corresponding ESS x_L^* can be found by solving $[\partial\lambda(x_L, x_L^*)/\partial x_L]_{x_L=x_L^*, x_H^*=0} = 0$. Similarly, $x_H^* = 1$ will be stable if $[\partial\lambda(x_H, x_H^*)/\partial x_H]_{x_H=1} > 0$ (i.e., selection favors larger values of x_H); the corresponding ESS x_L^* can be found by solving $[\partial\lambda(x_L, x_L^*)/\partial x_L]_{x_L=x_L^*, x_H^*=1} = 0$. The ESS conditions for $x_L^* = 0$ and $x_L^* = 1$ are analogous.