

The evolution of dispersal from source to sink populations

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ABSTRACT

The evolutionary stability of dispersal from source to sink populations has been demonstrated only for models based on contest competition. Models based on declining reproductive value with density show that dispersal from source to sink populations is only stable when there is temporal heterogeneity. In this note, I show that dispersal from source to sink habitat can be evolutionarily stable in a temporally stable environment provided: (i) there is back-migration to the source and (ii) it is easier to disperse between habitat types than within a habitat type. This second condition is very stringent and is unlikely to be achieved in most conditions but could possibly be realized by the spatial arrangement of habitat. Because of emigration of individuals from source to sink habitat, it is possible for an evolutionarily stable dispersal rate to evolve that means the population in the source habitat becomes dependent on migration from the sink to persist.

Keywords: dispersal, evolution, migration, population models, source–sink, spatial heterogeneity.

INTRODUCTION

The last decade has seen an enormous increase in the attention paid by ecologists to habitat variability and, specifically, to source–sink dynamics (Shmida and Ellner, 1984). This has been fuelled by empirical studies showing that many populations occur in sub-optimal habitats where reproduction is insufficient to balance mortality (e.g. Keddy, 1981; Watkinson, 1985; Bergerud, 1988; Dias *et al.*, 1996; Eriksson, 1996). This has profound implications for population dynamics (Howe *et al.*, 1991; Pulliam and Danielson, 1991), the concept of the ecological niche (Hutchinson, 1958; Kawecki, 1995; Holt, 1996), species conservation (Wootton and Bell, 1992; Doak, 1995; Gaggiotti and Smouse, 1996) and community structure (Holt, 1985; Van Tienderen, 1991; Brown and Pavlovic, 1992). For a review of much of this work, see Dias (1996).

With many recorded examples of populations with source–sink dynamics, it is important to gain an understanding of both the population dynamics and evolution in these systems. One of the most obvious points to be addressed is why some species seem to disperse into unfavourable habitats. Dispersal into sink habitats may just be a by-product of

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organisms attempting to find favourable habitats (e.g. Keddy, 1981). For example, plant seeds may be dispersed randomly, such that some seeds will find favourable habitats while some will fall on barren ground. Here, however, the conditions under which individuals might choose to colonize sink habitat *instead of* attempting to find a source habitat are considered.

Pulliam (1988), in an influential paper, showed that dispersal from source to sink populations could evolve as a consequence of habitat choice. His model was based on a form of contest competition, in which excess individuals in source patches had no access to resources (and, therefore, had zero reproduction) and would therefore benefit from dispersing to sink patches (where average reproduction would be less than one offspring, but more than zero). Thus, a positive dispersal rate from source to sink depends on surplus reproduction in a source habitat with limited breeding resources. Morris (1991), complementing work by Bull *et al.* (1987), used a genetical analysis to show that a positive dispersal rate from source to sink populations would be an evolutionarily stable strategy (ESS) only when there was back-migration from the sink to the source. This was based on the assumption that, once individuals have left a particular habitat, they are unable to return. So, individuals (and the genes they carry) dispersing from source habitats are lost from the source population.

Contest competition, although appropriate to many species, has alternatives. One is where the reproductive success of all individuals declines with increasing density (see, for example, Hassell, 1975). In this case, individuals remaining in populated source habitats face a declining, but always non-zero, reproductive rate. They should disperse instead to sink habitats, if the average number of offspring in the sink habitat exceeds that which would have been produced if they had remained in the source habitat. Dispersal to sink habitats should, therefore, be less likely than with contest competition (Morris, 1991).

In analysing the implications of source-sink dynamics, many authors have focused on declining reproductive success with density (e.g. Holt, 1985, 1986; Holt and Gaines, 1992; McPeck and Holt, 1992; Watkinson and Sutherland, 1995). It is important, therefore, to test whether dispersal from source to sink habitats can evolve in a population whose reproductive rate continuously declines with increasing density. This question has been addressed previously. For example, Holt (1985) showed that optimal habitat selection implies that selection would favour no migration between source and sink. And McPeck and Holt (1992) showed that selection could favour a positive dispersal rate if the dispersal strategy was conditional on the environment (i.e. it varied depending on whether the habitat was a source or sink).

In this note, I wish to explore the case where it may be easier for offspring leaving a source to find and colonize a sink, instead of continuing to actively search for another source habitat. For example, consider a fragmented source habitat where each source is surrounded by sink habitat. For offspring leaving a source, it would be easier to find a sink because of the fragmentation and spatial arrangement of the environment. Does this scenario make for the easier evolution of an evolutionarily stable dispersal rate from source to sink habitat?

Next, the model is outlined in more detail and then the results are presented. The mathematical calculations underpinning these results have been collected, for clarity of presentation, in the Appendix.

MODEL AND METHODS

Assume the environment is divided into the fraction of habitat, S , that is of type 1 and the fraction of the habitat, K , that is of type 2, so that $S + K = 1$. Consider the following model:

$$\begin{aligned}\frac{dp_1}{dt} &= (1 - E)\lambda_1 p_1 (S - p_1) - m_1 p_1 + I\lambda_2 p_2 \beta (S - p_1) \\ \frac{dp_2}{dt} &= E\lambda_1 p_1 \alpha (K - p_2) + (1 - I)\lambda_2 p_2 (K - p_2) - m_2 p_2\end{aligned}\quad (1)$$

where p_1 and p_2 are the fractions of each type of habitat occupied and λ_1 , λ_2 and m_1 , m_2 are the fecundities and mortality rates in each type of habitat. The parameters I and E represent immigration into and emigration from habitat 1. E is the fraction of individuals that are born in habitat 1 and emigrate and attempt to colonize habitat 2. The parameter I represents the fraction of individuals that are born in habitat 2, but leave and attempt to colonize habitat 1. The terms α and β represent the difficulty or ease of colonizing one habitat type from the other. When α (or β) < 1 , then individuals are not as effective at colonizing the alternative habitat as they would be at colonizing habitat similar to that in which they were born. For example, this could reflect an additional degree of mortality due to dispersing further distances between habitat types. Alternatively, when α (or β) > 1 , then individuals are more effective at colonizing the alternative habitat than colonizing the habitat in which they were born. This could be the case when the habitat types are fragmented so that, for example, habitat type 1 could be surrounded by habitat type 2 so that an individual from habitat 1 would encounter habitat 2 sooner than habitat 1.

Sources are defined as habitats where the birth rate exceeds the death rate or, alternatively, where the intrinsic growth rate is greater than zero. Conversely, sinks are habitats where the death rate exceeds the birth rate. When there is no dispersal between the habitats ($E = 0$ and $I = 0$), the equilibrium fraction of habitat occupied is given by:

$$p_1^* = S - \frac{m_1}{\lambda_1} \quad (2)$$

$$p_2^* = K - \frac{m_2}{\lambda_2} \quad (3)$$

Source habitat is thus defined to be where $S > m_1/\lambda_1$ and sinks where $K < m_2/\lambda_2$. When $S = 1$, it is sufficient that $\lambda_1 > m_1$ (Hastings, 1980) – that is, the reproductive rate is larger than the death rate – for habitat 1 to be a source habitat. When $S < 1$, the reproductive rate must be larger than the death rate by some margin. Habitat of type 2 will always be a sink when $m_2 > \lambda_2$.

Now I enquire whether it is an evolutionarily stable strategy for some individuals to disperse from source habitat to sink habitat *instead of* attempting to colonize another source habitat (i.e. is there an ESS where $E > 0$). This considers active dispersal from source to sink habitat, not when offspring disperse into sink habitats as a by-product of their dispersal from one source to another. To answer the question, one needs to ascertain whether a small invading population with strategy $E_I > 0$ can invade a resident population adopting the strategy $E_R = 0$. The answer is ‘yes’ when the invading population has a positive growth rate.

The necessary mathematics are outlined in the Appendix. For clarity, in the next section I present only the results.

RESULTS

The invading population will have a positive growth rate if either of the two following inequalities holds true (see Appendix):

$$0 > (E_I - E_R)E_R m_1 \lambda_1^2 a p_1^* p_1^* + (E_I - E_R) m_1 \lambda_1 (1 - I) \lambda_2 p_1^* p_2^* + (1 - E_R)E_R m_2 \lambda_1^2 a p_1^* p_1^* + (m_1 + m_2)E_R I \lambda_1 \lambda_2 a \beta p_1^* p_2^* + m_1 I (1 - I) \lambda_2^2 \beta p_2^* p_2^* \quad (4)$$

$$0 < (E_I - E_R)(I \lambda_2 \beta p_2^* - E_R \lambda_1 p_1^*) \quad (5)$$

Condition (4) is never met if $E_I > E_R$. It is only sometimes met when $E_I < E_R$. The second condition now depends on the equilibrium fractions of each habitat occupied. The ESS is $E \lambda_1 p_1^* = I \lambda_2 \beta p_2^*$. This ESS, when $E = E^*$, is stable and can always be achieved (because, when $E < E^*$, a population with E higher than the resident population can always invade, and when $E > E^*$, a population with E smaller than the resident population can always invade).

The equilibrium values, p_1^* and p_2^* for general E , are very complicated equations and substituting for these values gives little insight into the biology. However, there are other informative questions that can be addressed. First, what are the conditions for a population with positive E_I to invade a resident population with $E_R = 0$? To determine this, the values for p_1^* and p_2^* can be approximated arbitrarily close to $E_R = 0$ (see Appendix). Then, the second condition is:

$$K > \frac{m_2}{\lambda_2 [I(a\beta - 1) + 1]} \quad (6)$$

For this to be true, I must be greater than zero – that is, there must be back-migration from the sink to the source (which confirms the result of Morris, 1991) – and $a\beta > 1$.

Given that a population with a positive emigration rate E can invade, then what is the value of E at the ESS? To determine this, the values of p_1^* and p_2^* at the ESS can be calculated using the fact that $E \lambda_1 p_1^* = I \lambda_2 \beta p_2^*$. This then gives the equilibrium population sizes at E^* as:

$$p_1^* = S - \frac{m_1}{\lambda_1}$$

$$p_2^* = K - \frac{m_2}{\lambda_2 [I(a\beta - 1) + 1]} \quad (7)$$

Surprisingly, the equilibrium fraction of source habitat occupied at the ESS is exactly the same as when there is no dispersal between sources and sinks (equation 2). The equilibrium fraction of sink habitat occupied is only positive when the condition for invasion is also positive, as expected. Using these two expressions, the value of E at the ESS can now be found:

$$E^* = \frac{I \lambda_2 \beta}{S \lambda_1 - m_1} \left(K - \frac{m_2}{\lambda_2 [I(a\beta - 1) + 1]} \right) \quad (8)$$

Depending on parameter values, the expression for E^* above can be larger than 1. In these circumstances, the condition that $E\lambda_1 p_1^* = I\lambda_2 \beta p_2^*$, upon which equation (8) is based, cannot be achieved for $E < 1$ and the ESS value for E is its maximum value of 1.

Earlier, a source habitat was defined to be one where, in the absence of dispersal between source and sink habitats, the reproductive rate was greater than the death rate. This translated into the condition $S\lambda_1 > m_1$. However, when some individuals from source habitats attempt to colonize sink habitats, then that condition may be inadequate to maintain a population in the source habitat. If the emigration rate E is high enough, and there is no back-migration from sink to source, then there will not be enough individuals colonizing the source habitat to compensate for emigration. The fraction of source habitat occupied will go to zero. Depending on parameter values, this condition is sometimes met at the ESS (equation 8). The situation could arise, therefore, that dispersal from source to sink habitat can evolve, but the source habitat can then no longer maintain itself in the absence of back-migration from the sink habitat. It would no longer act as a classical source habitat. Suppose the corresponding sink habitat were removed, or a barrier were imposed so that back-migration became impossible or substantially reduced. Now suppose the organism could not evolve a quick response to that change. The organism would go extinct from the source and then, afterwards, from the sink habitat. In other words, manipulating the sink habitat can cause dramatic changes within the source as well as vice versa.

DISCUSSION

A number of conclusions can be drawn from the above results:

1. For a positive evolutionarily stable dispersal rate from source to sink habitats to exist, there must be: (i) back-migration from the sink to the source habitat ($I > 0$) and (ii) it must be easier for individuals to colonize habitat of the alternative type to that in which they were born ($a\beta > 1$).

This confirms the result of Morris (1991) based on a genetic analysis and contest competition. It is also in line with previous work by Holt and Gaines (1992) and Holt (1996). They studied a two-patch model in which reproductive rate declines continuously with density. Holt (1996) showed that evolution, in terms of selection on the basic reproductive rate in each habitat, would completely favour adaptation to the source at the expense of the sink when there was only unidirectional dispersal. In this case, unidirectional dispersal favours $E = 0$, which can be interpreted as a bias towards source habitats.

2. The evolutionarily stable dispersal rate, E^* , is larger when (i) a and/or β are large; (ii) when back-migration (I) is large; (iii) when there is a large proportion of sink habitat (i.e. K is large); and (iv) when a source is close to being a sink (i.e. when $S - m_1/\lambda_1$ is small).

This last condition basically states that the smaller the productivity of source sites, then the less it pays individuals to seek out a share of some of the source resources. This contrasts with cases of contest competition (where resources are not shared, but are captured by some individuals, while the remaining have zero reproduction). In this case, higher productivity means that there are more individuals for whom it would pay to find sink habitat as an alternative to zero reproduction in the source. For contest competition, dispersal to sinks should therefore increase with the productivity of the source habitat, whereas, in the case I have studied, it pays for individuals to compete more strongly for source habitat when productivity is high.

3. A dispersal rate from source to sink habitat can evolve such that the organism depends on back-migration from the sink to persist in both habitats. This scenario has similarities with the concept of 'pseudo-sinks' introduced by Watkinson and Sutherland (1995). There are circumstances in which, if the migration rate from source to sink were high enough, then the population in both habitats would go extinct (as in Holt, 1985). However, when this migration rate is under evolutionary control, this is never possible. The total fraction of habitat occupied (source and sink) is always higher at the ESS migration rate compared to when $E = 0$.

Biologically, my conclusions can be summarized as follows. The conditions that favour a positive dispersal rate are: (i) back-migration from sink to source; (ii) offspring can more easily colonize the alternative habitat compared to the one in which they were born; (iii) a high proportion of sink habitat; and (iv) a source is close to being a sink.

The main aim of this paper was to establish the conditions (stated above) under which dispersal from source to sink habitats can evolve in a population where the per capita probability of colonizing new habitat continuously decreases with the density of occupied habitat. The conditions for dispersal from a source to a sink to evolve are clearly (and were expected to be) far more stringent than in Pulliam's scenario. They compare with Holt's (1985) work looking at a continuously decreasing reproductive rate with density, when $a = \beta = 1$. In this case, dispersal from source to sink cannot evolve in a temporally stable environment. The condition that $a\beta > 1$ (for dispersal to evolve) implies that it must, on average, be easier for offspring to colonize the alternative habitat to the one in which they were born. This is a condition on dispersal from source to sinks (a) and sink to source (β). As such, the condition is very stringent and I would not expect it to be met under most conditions. It agrees, therefore, with Holt's condition that dispersal from source to sinks is unlikely to evolve in a temporally unchanging environment (Holt, 1985; McPeck and Holt, 1992).

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REFERENCES

- Bergerud, A.T. 1988. Caribou, wolves and man. *TREE*, **3**: 68–73.
- Brown, J.S. and Pavlovic, N.B. 1992. Evolution in heterogeneous environments: Effects of migration on habitat specialisation. *Evol. Ecol.*, **6**: 360–382.
- Bull, J.J., Thompson, D.N. and Moore, R. 1987. A model for natural selection of genetic migration. *Am. Nat.*, **129**: 143–157.
- Dias, P.C. 1996. Sources and sinks in population biology. *TREE*, **11**: 326–330.
- Dias, P.C., Verheyen, G.R. and Raymond, M. 1996. Source–sink populations in Mediterranean blue tits: Evidence using single locus mini-satellite probes. *J. Evol. Biol.*, **9**: 965–978.
- Doak, D.F. 1995. Source–sink models and the problem of habitat degradation – general models and applications to the Yellowstone grizzly. *Conserv. Biol.*, **9**: 1370–1379.
- Doebeli, M. 1991. Dispersal and dynamics. *Theor. Pop. Biol.*, **47**: 82–106.
- Eriksson, O. 1996. Regional dynamics of plants – a review of evidence for remnant, source–sink metapopulations. *Oikos*, **77**: 248–258.

- Gaggiotti, O.E. and Smouse, P.E. 1996. Stochastic migration and the maintenance of genetic variation in sink populations. *Am. Nat.*, **147**: 919–945.
- Hassell, M.P. 1975. Density dependence in single-species populations. *J. Anim. Ecol.*, **44**: 283–295.
- Hastings, A. 1980. Disturbance, coexistence, history and competition for space. *Theor. Pop. Biol.*, **18**: 363–373.
- Holt, R.D. 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theor. Pop. Biol.*, **28**: 181–208.
- Holt, R.D. 1996. Adaptive evolution in source–sink environments: Direct and indirect effects of density-dependence on niche evolution. *Oikos*, **75**: 182–192.
- Holt, R.D. and Gaines, M.S. 1992. Analysis of adaptation in heterogeneous landscapes: Implications for the evolution of fundamental niches. *Evol. Ecol.*, **6**: 433–447.
- Howe, R.W., Davis, G.J. and Mosca, V. 1991. The demographic significance of sink populations. *Biol. Conserv.*, **57**: 239–255.
- Hutchinson, G.E. 1958. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.*, **22**: 415–427.
- Kawecki, T.J. 1995. Demography of source–sink populations and the evolution of ecological niches. *Evol. Ecol.*, **9**: 38–44.
- Keddy, P.A. 1981. Experimental demography of the sand-dune annual *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *J. Ecol.*, **69**: 615–630.
- McPeck, M.A. and Holt, R.D. 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.*, **140**: 1010–1027.
- Morris, D.W. 1991. On the evolutionary stability of dispersal to sink habitats. *Am. Nat.*, **137**: 907–911.
- Pulliam, H.R. 1988. Sources, sinks and population regulation. *Am. Nat.*, **132**: 652–661.
- Pulliam, H.R. and Danielson, B.J. 1991. Sources, sinks and habitat selection – a landscape perspective on population dynamics. *Am. Nat.*, **137**: S50–S66.
- Shmida, A. and Ellner, S. 1984. Coexistence of plant species with similar niches. *Vegetatio*, **58**: 29–55.
- Van Tienderen, P.H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution*, **45**: 1317–1331.
- Watkinson, A.R. 1985. On the abundance of plants along an environmental gradient. *J. Ecol.*, **73**: 569–578.
- Watkinson, A.R. and Sutherland, W.J. 1995. Sources, sinks and pseudo-sinks. *J. Anim. Ecol.*, **64**: 126–130.
- Wootton, J.T. and Bell, D.A. 1992. A metapopulation model of the peregrine falcon in California: Viability and management strategies. *Ecol. Appl.*, **2**: 307–321.

APPENDIX: DETERMINING WHEN SMALL POPULATIONS CAN INVADE

The invading population's dynamics are given by:

$$\frac{dq_1}{dt} = (1 - E)\lambda_1 q_1 (S - (p_1 + q_1)) - m_1 q_1 + I\lambda_2 q_2 \beta (S - (p_1 + q_1))$$

$$\frac{dq_2}{dt} = E\lambda_1 q_1 a (K - (p_2 + q_2)) + (1 - I)\lambda_2 q_2 (K - (p_2 + q_2)) - m_2 p_2$$

where q_1 and q_2 are the fraction of habitat of types 1 and 2 occupied by the invading population.

As the invading population size is small, one can linearize around a zero population size for the invading population and the equilibrium population size for the resident. The mutant dynamics are thus:

$$\frac{dq_1}{dt} = f(q_1, q_2) = (1 - E)\lambda_1 q_1 (S - p_1^*) - m_1 q_1 + I\lambda_2 q_2 \beta (S - p_1^*)$$

$$\frac{dq_2}{dt} = g(q_1, q_2) = E\lambda_1 q_1 a (K - p_2^*) + (1 - I)\lambda_2 q_2 (K - p_2^*) - m_2 p_2$$

The growth rate of the invading population is given by the largest eigenvalue of the Jacobian matrix. The only requirement for the invading population to grow is that the largest eigenvalue of the Jacobian is positive. The Jacobian matrix, $\mathbf{J}$, is given by:

$$\begin{pmatrix} \frac{df(q_1, q_2)}{dq_1} - a_{11} & \frac{df(q_1, q_2)}{dq_2} = a_{12} \\ \frac{dg(q_1, q_2)}{dq_1} = a_{21} & \frac{dg(q_1, q_2)}{dq_2} = a_{22} \end{pmatrix}$$

The Routh-Hurwitz criteria are given by:

$$-(a_{11} + a_{22}) < 0$$

$$a_{11}a_{22} - a_{12}a_{21} < 0$$

If either of these two inequalities is met, then at least one of the eigenvalues of $\mathbf{J}$ is positive.

The Jacobian is given by:

$$\begin{pmatrix} (1 - E)\lambda_1 (S - p_1^*) - m_1 & I\lambda_2 \beta (S - p_1^*) \\ E\lambda_1 a (K - p_2^*) & (1 - I)\lambda_2 (K - p_2^*) - m_2 \end{pmatrix}$$

The first condition is thus:

$$-((1 - E)\lambda_1 (S - p_1^*) - m_1 + (1 - I)\lambda_2 (K - p_2^*) - m_2) < 0$$

At equilibrium, $(S - p_1^*) = (m_1 p_1^*) / ((1 - E_R)\lambda_1 p_1^* + I\lambda_2 \beta p_2^*)$ and $(K - p_2^*) = (m_2 p_2^*) / (E_R \lambda_1 a p_1^* + (1 - I)\lambda_2 p_2^*)$. Substituting and rearranging gives:

$$\frac{(1 - E)\lambda_1 m_1 p_1^*}{(1 - E_R)\lambda_1 p_1^* + I\lambda_2 \beta p_2^*} + \frac{(1 - I)\lambda_2 m_2 p_2^*}{E_R \lambda_1 a p_1^* + (1 - I)\lambda_2 p_2^*} > m_1 + m_2$$

After multiplying through by $((1 - E_R)\lambda_1 p_1^* + I\lambda_2 \beta p_2^*)(E_R \lambda_1 a p_1^* + (1 - I)\lambda_2 p_2^*)$ and employing some algebra, this gives inequality (4) in the text.

The second condition is given by:

$$((1 - E)\lambda_1 (S - p_1^*) - m_1)((1 - I)\lambda_2 (K - p_2^*) - m_2) - I\lambda_2 \beta (S - p_1^*) E\lambda_1 a (K - p_2^*) < 0$$

After substitution for $(S - p_1^*)$ and $(K - p_2^*)$ as above and rearranging, this gives inequality (5) in the text.

As $E_R \rightarrow 0$, then $p_2^* \rightarrow 0$, so that when E_R is small, the equilibrium fraction p_2^* is also small. In this case, the equilibrium fractions p_1^* and p_2^* can be approximated by assuming $(K - p_2^*) \approx K$. As E_R is reduced, this becomes a better and better approximation. Using this approximation, inequality (5) can be solved for p_1^* and p_2^* :

$$p_1^* = S - \frac{m_1}{(1 - E_R)\lambda_1 + I\lambda_2 \beta E_R \lambda_1 a K / (m_2 - (1 - I)\lambda_2 K)}$$

$$p_2^* = \frac{E_R \lambda_1 a K}{m_2 - (1 - I)\lambda_2 K} p_1^*$$

Substituting these values into inequality (5) in the text gives inequality (6).

From equation (1):

$$m_1 - (1 - E)\lambda_1 S = SE\lambda_1 - (1 - E)\lambda_1 p_1^* - E\lambda_1 p_1^*$$

Using the ESS condition $p_2^* = E\lambda_1 p_1^* / I\lambda_2 \beta$ and substituting for p_2^* gives:

$$m_1 - (1 - E)\lambda_1 S = SE\lambda_1 - \lambda_1 p_1^*$$

Rearranging this equation gives equation (7) in the text. Also from equation (1):

$$m_2 = E\lambda_1 aK \frac{p_1^*}{p_2^*} - E\lambda_1 a p_1^* + (1 - I)\lambda_2 K - (1 - I)\lambda_2 p_2^*$$

Using the ESS condition $p_1^* = I\lambda_2 \beta p_2^* / (E\lambda_1)$ and substituting for p_1^* gives:

$$m_2 = \frac{\lambda_1 a I \lambda_2 \beta K}{\lambda_1} - \frac{\lambda_1 a I \lambda_2 \beta p_2^*}{\lambda_1} + (1 - I)\lambda_2 K - (1 - I)\lambda_2 p_2^*$$

Rearranging this equation and solving for p_2^* directly gives equation (8) in the text.

Substituting for p_1^* and p_2^* (using equations 7 in the text) in the ESS condition $I\lambda_2 \beta p_2^* = E\lambda_1 p_1^*$ gives directly the condition for E^* in the text.

