

## MATHEMATICAL MODELS OF POPULATION INTERACTIONS WITH DISPERSAL. I: STABILITY OF TWO HABITATS WITH AND WITHOUT A PREDATOR\*

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**Abstract.** A system of differential equations is proposed as a model of dispersion between two populations in habitats separated by a barrier. Both strong and weak barriers are considered, and the effect of barrier strength on the limiting populations is analyzed. The case of a predator feeding indiscriminately on these populations is also considered and the effect of barrier strength on the limiting population analyzed.

**1. Introduction.** The study of the existence and the stability properties of stationary solutions of equations governing population growth or population interactions is a subject of considerable interest in the ecological literature; see, for example, the many problems discussed in the books of Maynard Smith [16] and May [15]. The subject of this paper is the effect of dispersion on the equilibrium states of a relatively simple model of two (noncompeting) populations, both with and without a predator. The subject of dispersal is in itself a major area of mathematical ecology and the reader is referred to the excellent bibliographies in the papers of Levin [11], [12] and Segel and Levin [17] for the current state of the literature. The approach here is to treat dispersal as a perturbation of the basic growth equations, in the same spirit as predator-prey models were treated by the authors in [7], [8]. We attempt to express the location of the new equilibria in terms of the perturbation parameter and use the expansion to draw conclusions of a qualitative nature.

We view the problem as two populations of a species separated by a barrier. A parameter in the model can be thought of as measuring the ease with which the barrier may be crossed, zero indicating that such crossing is impossible. With the parameter equal to zero, each population grows according to the characteristics of its local habitat. As the strength of the barrier is weakened, the equilibrium solution changes. We obtain asymptotic estimates for this solution in terms of the parameters of the model. The existence of the equilibrium for the perturbed system is a simple application of the implicit function theorem in the noncritical case (since the equilibrium is interior to the positive quadrant) although in more delicate cases the problem has been studied by Levin [13] and Freedman [6]. However, the expansions are new. We also consider the problem in the critical cases, cases where the Jacobian determinant is zero. Although it can be argued on biological grounds that such a case may be "rare," we feel that these cases are important for often a critical case may indicate a possible bifurcation point. In all but one of the cases considered we show that the solution retains its asymptotic stability and it is not hard to see that, at least in the usual formulation, the Hopf bifurcation theorem does not yield periodic solutions.

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We also study the limiting case as the barrier becomes weak. By analogy this can be viewed as two patches merging into one and as such can yield useful information on the question of the desirability of many small refuges as opposed to one large one. See, for example, the paper by Simberloff and Abele [18]. The work here is perhaps the most interesting biologically, for it indicates that the limiting equilibrium has coordinates less than the arithmetic mean of the individual carrying capacities. This would indicate, by analogy, that several small refuges facilitate increased population size.

Finally we add a predator to the system, a predator which feeds differentially upon each habitat, and obtain an asymptotic expression for the new equilibrium and study its stability.

In the above discussion we have stated the problem in terms of habitat and dispersal, but the equations can be applied to another interesting situation. Bishop and Cook [3] explain how the distribution of peppered and melanic moths can be used as a measure of air pollution. The melanic variety has an advantage in areas of high industrial pollution, where they are harder for the predator to find, and a disadvantage in rural areas where they are easier to locate. Thus the equilibrium point gives a relative measure of the degree of pollution. The models treated here do not strictly apply to this case because we have not introduced a competitive effect between the two, but, with a predator in the system, the total number of moths would be expected to be far below the carrying capacity of the system and the competition effect therefore diminished. In this case, our techniques might be of interest in determining equilibrium states. We also do not wish to claim that the models here reflect the nonlinear complexities of the genetic problem, but such models have been used (Allen [1]) and our analysis is an improvement on that work.

The organization of the paper is as follows: § 2 discusses two noncompetitive species with a strong barrier, § 3, with a weak barrier, and § 4, with a predator. In each section the basic theorems are stated and the qualitative results are discussed. The proofs are deferred to § 5.

Finally the I in the title indicates that a second paper is planned in which more complicated models will be considered.

**2. Dispersion with a strong barrier.** We consider first two populations separated by a strong barrier. Specifically we assume that the "pressure" to disperse is proportional to the population and that the "barrier strength" is inversely proportional to  $\varepsilon > 0$ . As noted in the introduction, this can normally be conceptualized as the same species in two different habitats, and it may also be interpreted as a species with two different forms and the capacity of the offspring to occur in either.

The model is described by

$$(2.1) \quad \begin{aligned} x_1' &= x_1 g_1(x_1) - \varepsilon h_1(x_1) + \varepsilon h_2(x_2), \\ x_2' &= x_2 g_2(x_2) - \varepsilon h_2(x_2) + \varepsilon h_1(x_1). \end{aligned}$$

Concerning the functions  $g$  and  $h$  we shall specifically assume,  $i = 1, 2$ ,

$$(2.2) \quad g_i(0) = \alpha_i > 0,$$

$$(2.3) \quad g_{ix_i}(x_i) \leq 0 \quad \text{for } x_i \geq 0,$$

$$(2.4) \quad \text{there exist numbers } K_i \text{ such that } g_i(K_i) = 0,$$

$$(2.5) \quad h_i(0) = 0, \quad h_{ix_i}(x_i) \geq 0 \quad \text{for } x_i \geq 0.$$

Condition (2.2) states that the birth rate decreases as the population size increases and the  $K_i$ 's in condition (2.4) are the carrying capacities of the respective habitats. Conditions (2.2)–(2.4) include as a special case logistic growth. Condition (2.5) expresses the idea that the larger the population the larger the number who disperse. We investigate the existence and the stability of the equilibria for the system (2.1).

For  $\varepsilon = 0$ , the system (2.1) models two noninteracting, growing populations and there is a nonzero equilibrium at  $(K_1, K_2)$ , the natural carrying capacity of the system. If we further assume that

$$(2.6) \quad g_{ix_i}(K_i) \neq 0,$$

then  $(K_1, K_2)$  is asymptotically stable. For small  $\varepsilon$ , then, if a perturbed equilibrium exists, it will also be asymptotically stable. This corresponds to the result given in Levin [11], [12]. The expansion in  $\varepsilon$  of this equilibrium is given in Theorem 2.1.

**THEOREM 2.1** (noncritical case). *Suppose (2.2)–(2.6) hold. Then for small  $\varepsilon > 0$ , there exists an asymptotically stable equilibrium point  $(x_1^*(\varepsilon), x_2^*(\varepsilon))$  for (2.1) with*

$$(2.7) \quad x_i^*(\varepsilon) = K_i + (-1)^{i+1} \frac{h_1(K_1) - h_2(K_2)}{K_i g_{ix_i}(K_i)} \varepsilon + o(\varepsilon), \quad i = 1, 2.$$

Equation (2.7) says, for example, that if  $h_1(K_1) > h_2(K_2)$ , then for small  $\varepsilon$ ,  $x_1^*(\varepsilon)$  decreases and  $x_2^*(\varepsilon)$  increases. We shall see later in the case of a weak barrier that this trend continues for large  $\varepsilon$ .

We now examine the critical cases. We first suppose that

$$(2.8) \quad g_{1x_1}(K_1) = 0, \quad g_{2x_2}(K_2) \neq 0,$$

and then we shall suppose that

$$(2.9) \quad g_{ix_i}(K_i) = 0, \quad i = 1, 2.$$

The existence, expansions in  $\varepsilon$ , and stability of perturbed equilibria are given in Theorems 2.2 and 2.3 below. The proofs (given in § 5) utilize techniques of critical cases of the implicit function theorem (see Freedman [5], [6]).

**THEOREM 2.2** (first critical case). *Suppose that (2.2)–(2.5), (2.8) hold. If  $g_{1x_1x_1x_1}(K_1) \neq 0$  and  $h_2(K_2) - h_1(K_1) \neq 0$ , then there exists a perturbed equilibrium  $(x_1^*, x_2^*)$  given by*

$$\begin{aligned} x_1^* &= K_1 + \theta_0 \varepsilon^{1/3} + o(\varepsilon^{1/3}), \\ x_2^* &= K_2 + \frac{h_2(K_2) - h_1(K_1)}{K_2 g_{2x_2}(K_2)} \varepsilon + o(\varepsilon), \end{aligned}$$

where

$$\theta_0 = \left[ \frac{6[h_1(K_1) - h_2(K_2)]}{K_1 g_{1x_1x_1}(K_1)} \right]^{1/3}.$$

If  $h_2(K_2) = h_1(K_1)$ , then an equilibrium is given by

$$x_1^* = K_1, \quad x_2^* = K_2.$$

In either case the equilibrium is asymptotically stable.

**THEOREM 2.3** (second critical case). *Let (2.2)–(2.5), (2.9) hold and suppose that  $g_{ix_ix_i}(K_i) \neq 0$ ,  $i = 1, 2$ . If  $h_1(K_1) - h_2(K_2) \neq 0$ , then for  $\varepsilon > 0$  and sufficiently small there exists an asymptotically stable perturbed equilibrium of the form  $(x_1^*, x_2^*)$ , where*

$$x_i^* = K_i + y_{i,0}\varepsilon^{1/3} + o(\varepsilon^{1/3}),$$

and where

$$y_{i,0} = \left[ \frac{(-1)^i 6(h_2(K_2) - h_1(K_1))}{K_i g_{ix_ix_i}(K_i)} \right]^{1/3}.$$

If  $h_1(K_1) = h_2(K_2)$ , then  $x_i^* = K_i$ ,  $i = 1, 2$ , and this equilibrium is stable.

Qualitatively, Theorems 2.2 and 2.3 state that stability is preserved under appropriate hypotheses even in critical cases.

It has been suggested (by one of the referees) that where a habitat is such that it requires cooperative hunting (see Ghent [9])  $g(x)$  could be taken as

$$(2.10) \quad g(x) = (1 - x/K)^3.$$

In case only one habitat is so construed, Theorem 2.2 would apply. If both habitats are such that (2.10) holds, then Theorem 2.3 may be utilized.

**3. Dispersion with a weak barrier.** In this section we wish to remove the restriction that  $\varepsilon$  be small (the case of a strong barrier) and study the problem for large  $\varepsilon$  (weak barrier). Attention will be restricted to a special case:

$$(3.1) \quad \begin{aligned} x_1' &= \alpha_1 x_1 \left( 1 - \frac{x_1}{K_1} \right) - \varepsilon x_1 + \varepsilon x_2 \\ x_2' &= \alpha_2 x_2 \left( 1 - \frac{x_2}{K_2} \right) - \varepsilon x_2 + \varepsilon x_1. \end{aligned}$$

The general growth term has been replaced by a standard logistic term and the dispersion is assumed to take place directly proportional to the size of the population. We are also assuming the barrier has “equal strength” in both directions— $\varepsilon$  is the coefficient for each dispersion term. This is reasonable since we are concerned about limiting behavior, but some relaxation of this requirement is possible.

The main thrust of this section is given by Theorem 3.1.

**THEOREM 3.1.** *For every  $\varepsilon > 0$ , the system (3.1) has an asymptotically stable critical point  $(x_1^*(\varepsilon), x_2^*(\varepsilon))$  in the interior of the first quadrant. As  $\varepsilon \rightarrow \infty$  the two*

components tend to a common value  $x^*$  given by

$$(3.2) \quad x^* = \frac{\alpha_1 + \alpha_2}{\alpha_1/K_1 + \alpha_2/K_2}.$$

Figure 3.1 illustrates this theorem. There we have plotted the time course of each species for several values of  $\epsilon$ . The species with the larger carrying capacity is approaching a smaller limiting population as  $\epsilon$  increases; the other species is approaching a larger limiting value.

If one thinks of  $K_1$  and  $K_2$  as the maximal attainable populations of habitats 1 and 2 respectively in the case of an insurmountable barrier, and  $2x^*$  as the maximal attainable population in the case of no barrier, then it is of interest to compute  $K_1 + K_2 - 2x^*$ , which, using (3.2) and some simple algebra, gives

$$(3.3) \quad K_1 + K_2 - 2x^* = \frac{(K_1 - K_2)(\alpha_1 K_1 - \alpha_2 K_2)}{\alpha_1 K_1 + \alpha_2 K_2}.$$

The meaning of (3.3) is perhaps best understood in case  $\alpha_1 = \alpha_2$ ,  $K_1 \neq K_2$ , in which case

$$(3.4) \quad K_1 + K_2 - 2x^* = \frac{(K_1 - K_2)^2}{K_1 + K_2} > 0.$$

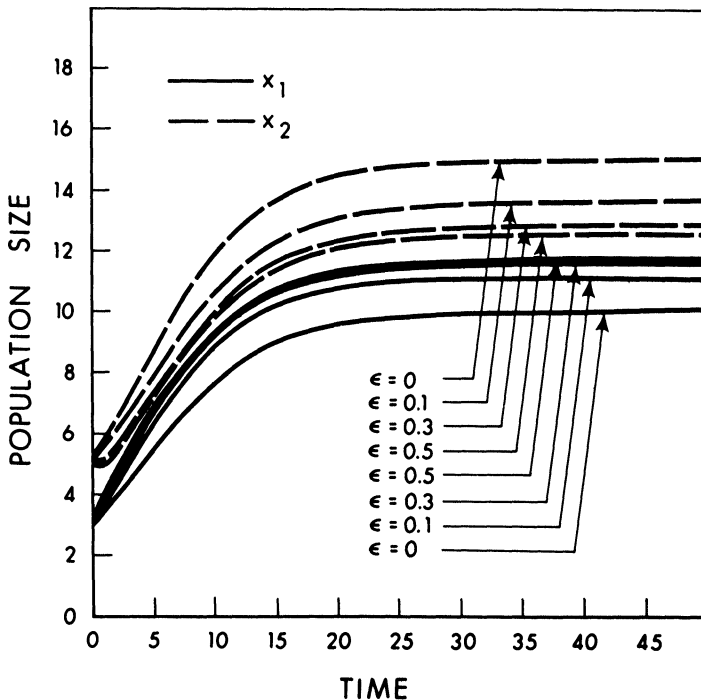


FIG. 3.1. The case of a weak barrier and two species; as  $\epsilon$  increases, the two populations tend to a common limiting value.

Equation (3.4) may be interpreted as giving support to the theory of Simberloff and Abele [18], who state on ecological grounds that several smaller refuges may be preferable to one large refuge. Formula (3.4) shows that the total population attainable in two habitats giving similar initial growth rates but having different carrying capacities is larger than the attainable population when the habitats are combined.

**4. Two prey and one predator.** We now add a predator to the system (3.1) and obtain

$$\begin{aligned}
 (4.1) \quad x_1' &= \alpha_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - \beta_1 x_1 y - \varepsilon x_1 + \varepsilon x_2, \\
 x_2' &= \alpha_2 x_2 \left(1 - \frac{x_2}{K_2}\right) - \beta_2 x_2 y - \varepsilon x_2 + \varepsilon x_1, \\
 y' &= -\gamma y + \delta_1 x_1 y + \delta_2 x_2 y.
 \end{aligned}$$

$\beta_1$  and  $\beta_2$  measure the feeding rates of the predator on each species,  $\gamma$  the death rate of the predator, and  $\delta_1, \delta_2$  the conversion rates of prey to predator. In the case of the two moths discussed in the introduction, better cover is provided by the environment for one population and this would be reflected in  $\beta_1 \neq \beta_2$  while  $\delta_1 = \delta_2$  reflects the fact that they are the same except for color. We seek to find equilibria of (4.1), interior to the first octant, as a function of  $\varepsilon$ .

At  $\varepsilon = 0$ , equilibria are solutions of

$$\begin{aligned}
 (4.2) \quad \alpha_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - \beta_1 x_1 y &= 0, \\
 \alpha_2 x_2 \left(1 - \frac{x_2}{K_2}\right) - \beta_2 x_2 y &= 0, \\
 \delta_1 x_1 + \delta_2 x_2 &= \gamma.
 \end{aligned}$$

Denote the solutions of (4.2) by  $x_{10}, x_{20}, y_0$ , respectively. Routine algebraic manipulation yields

$$\begin{aligned}
 (4.3) \quad x_{10} &= \frac{K_1(\alpha_1 \beta_2 \delta_2 K_2 - \alpha_2 \beta_1 \delta_2 K_2 + \alpha_2 \beta_1 \gamma)}{\alpha_1 \beta_2 \delta_2 K_2 + \alpha_2 \beta_1 \delta_1 K_1}, \\
 x_{20} &= \frac{K_2(\alpha_1 \beta_2 \gamma + \alpha_2 \beta_1 \delta_1 K_1 - \alpha_1 \beta_2 \delta_1 K_1)}{\alpha_1 \beta_2 \delta_2 K_2 + \alpha_2 \beta_1 \delta_1 K_1}, \\
 y_0 &= \alpha_1 \alpha_2 \left[ \frac{\delta_1 K_1 + \delta_2 K_2 - \gamma}{\alpha_1 \beta_2 \delta_2 K_2 + \alpha_2 \beta_1 \delta_1 K_1} \right].
 \end{aligned}$$

For these quantities to be positive it must be the case that

$$(4.4) \quad -\frac{\alpha_2 \gamma}{\beta_2 \delta_2 K_2} < \frac{\alpha_1}{\beta_1} - \frac{\alpha_2}{\beta_2} < \frac{\alpha_1 \gamma}{\beta_1 \delta_1 K_1},$$

$$(4.5) \quad \delta_1 K_1 + \delta_2 K_2 > \gamma.$$

Note that if the ratios of initial growth rates to predation rates for the two populations are sufficiently close (a not unreasonable assumption for two populations of the same species), then (4.4) is automatically satisfied.

**THEOREM 4.1.** *Suppose the coefficients in the system (4.1) are such that (4.4) holds. Then, for  $\varepsilon > 0$  and sufficiently small, there exists a constant solution of (4.1), interior to the first octant. This solution is represented by*

$$(4.6) \quad \begin{aligned} x_1^*(\varepsilon) &= x_{10} + \frac{\delta_2 K_1 K_2 (x_{20} - x_{10}) (\beta_1 / x_{20} + \beta_2 / x_{10})}{\alpha_1 \beta_2 \delta_2 K_2 + \alpha_2 \beta_1 \delta_1 K_1} \varepsilon + o(\varepsilon), \\ x_2^*(\varepsilon) &= x_{20} + \frac{\delta_1 K_1 K_2 (x_{20} - x_{10}) (\beta_1 / x_{20} + \beta_2 / x_{10})}{\alpha_1 \beta_2 \delta_2 K_2 + \alpha_2 \beta_1 \delta_1 K_1} \varepsilon + o(\varepsilon), \\ y^*(\varepsilon) &= y_0 + \frac{K_1 K_2 (x_{20} - x_{10}) (\alpha_2 \delta_1 / K_2 x_{10} - \alpha_1 \delta_2 / K_1 y_{20})}{\alpha_1 \beta_2 \delta_2 K_2 + \alpha_2 \beta_1 \delta_1 K_1} \varepsilon + o(\varepsilon), \end{aligned}$$

where  $(x_{10}, x_{20}, y_0)$  are given by (4.3). This interior critical point is asymptotically stable.

Figures 4.1–4.3 illustrate the theorem. In Figure 4.1, the inequality (4.4) has been satisfied and all species tend to positive elements. In Figure 4.2 the last inequality in (4.4) is violated and the predator becomes extinct. In Figure 4.3, the second inequality in (4.4) is violated and the second prey species becomes extinct.

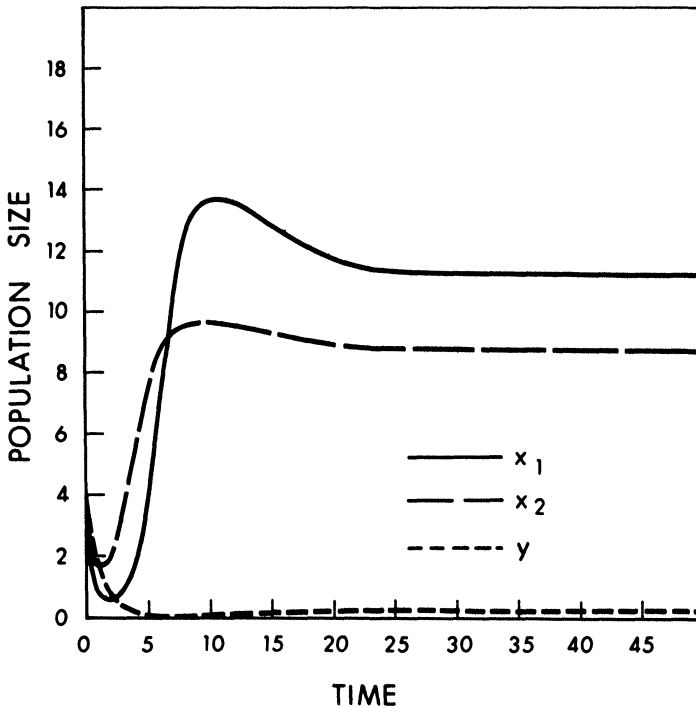


FIG. 4.1. Inequality (4.4) is satisfied and all limiting values are positive.

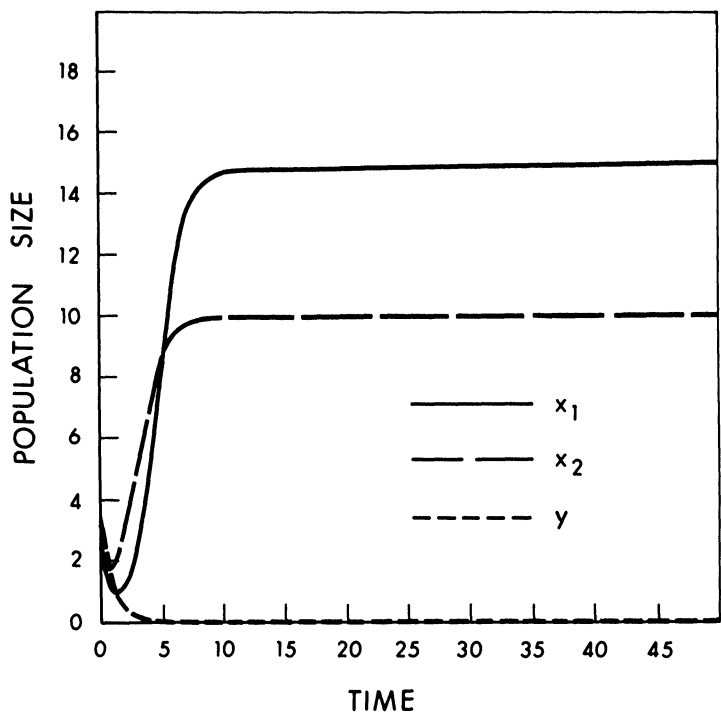


FIG. 4.2. *The last inequality in (4.4) is violated and the predator becomes extinct.*

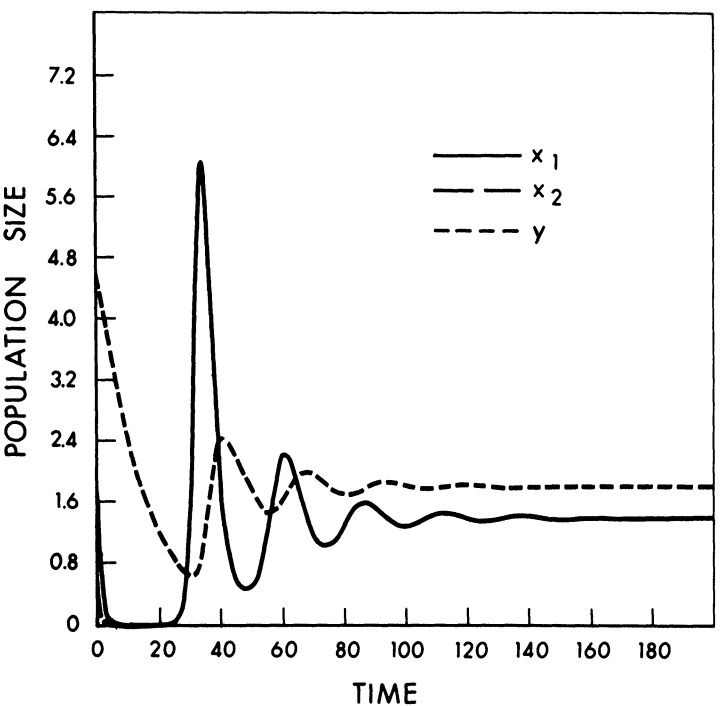


FIG. 4.3. *The second inequality in (4.4) is violated and the second prey species becomes extinct.*



In the basic equation (4.1) it was assumed implicitly that the dispersal pressure was the same for both species. The way the equations are nondimensionalized can affect this, so we note here that the technique in no way depends on the sameness of these coefficients. For example, if we were to rewrite (4.1) as

$$(4.1)' \quad \begin{aligned} x_1' &= \alpha_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - \beta_1 x_1 y + \varepsilon (\mu_2 x_2 - \mu_1 x_1), \\ x_2' &= \alpha_2 x_2 \left(1 - \frac{x_2}{K_2}\right) - \beta_2 x_2 y + \varepsilon (\mu_1 x_1 - \mu_2 x_2), \\ y' &= -\gamma y + \delta_1 x_1 y + \delta_2 x_2 y, \end{aligned}$$

then  $\mu_i$  can be thought of as a measure of “relative dispersal pressure” and the  $\varepsilon$  as a measure of barrier strength. The final result is (4.6) with the factor  $(x_{20} - x_{10})$  replaced by  $(\mu_2 x_{20} - \mu_1 x_{10})$ . An advantage of the result in this form is that one of the  $\mu_i$ 's can be zero—the dispersion can be in one direction only. In the case of the moths, the mutation can be in one direction. For the case of two habitats, the barrier may be more easily crossed in one direction than in the other; for example, movement downstream may be easier than upstream.

**5. Proofs.** We provide here the proofs of the theorems stated in §§2–4.

*Proof of Theorem 2.1.* Let

$$(5.1) \quad \begin{aligned} F_1(x_1, x_2, \varepsilon) &= x_1 g_1(x_1) - \varepsilon h_1(x_1) + \varepsilon h_2(x_2), \\ F_2(x_1, x_2, \varepsilon) &= x_2 g_2(x_2) - \varepsilon h_2(x_2) + \varepsilon h_1(x_1). \end{aligned}$$

Then

$$F_i(K_1, K_2, 0) = 0$$

and

$$F_x(x_1, x_2, \varepsilon) = \begin{bmatrix} x_1 g_{1x_1}(x_1) + g_1(x_1) - \varepsilon h_{1x_1}(x_1) & \varepsilon h_{2x_2}(x_2) \\ \varepsilon h_{1x_1}(x_1) & x_2 g_{2x_2}(x_2) + g_2(x_2) - \varepsilon h_{2x_2}(x_2) \end{bmatrix}$$

or

$$\det |F_x(K_1, K_2, 0)| = K_1 K_2 g_{1x_1}(K_1) g_{2x_2}(K_2) \neq 0.$$

Hence by the implicit function theorem there exist critical points  $x_i^*(\varepsilon)$ ,  $i = 1, 2$ , given by

$$\begin{pmatrix} x_1^*(\varepsilon) \\ x_2^*(\varepsilon) \end{pmatrix} = \begin{pmatrix} K_1 \\ K_2 \end{pmatrix} - [F_x(K_1, K_2, 0)]^{-1} \begin{bmatrix} -h_1(K_1) + h_2(K_2) \\ -h_2(K_2) + h_1(K_1) \end{bmatrix} \varepsilon + o(\varepsilon),$$

which may be simplified to

$$x_i^*(\varepsilon) = K_i + (-1)^{i+1} \frac{h_1(K_1) - h_2(K_2)}{K_i g_{ix_i}(K_i)} \varepsilon + o(\varepsilon), \quad i = 1, 2.$$

*Proof of Theorem 2.2.* Since  $F_{2x_2}(K_1, K_2, 0) \neq 0$ , the second equation of (2.7) may be solved for  $x_2 = \phi(x_1, \varepsilon)$ . It follows that ( $x_2 \neq 0$ )

$$\begin{aligned}\phi(K_1, 0) &= K_2, \\ \phi_{x_1}(K_1, 0) &= 0, \\ \phi_\varepsilon(K_1, 0) &= \frac{h_2(K_2) - h_1(K_1)}{K_2 g_{2x_2}(K_2)}.\end{aligned}$$

Thus  $\phi(x, \varepsilon)$  can be expanded as

$$x_2 = \phi(x_1, \varepsilon) = K_2 + \phi_\varepsilon(K_1, 0)\varepsilon + o(r)$$

where  $r = \sqrt{(x_1 - K_1)^2 + \varepsilon^2}$ .

Define

$$G(x_1, \varepsilon) = F_1(x_1, \phi(x_1, \varepsilon), \varepsilon).$$

We wish to solve the equation  $G(x_1, \varepsilon) = 0$  for  $x_1$  as a function of  $\varepsilon$ . First of all,

$$G(K_1, 0) = F_1(K_1, \phi(K_1, 0), 0) = F_1(K_1, K_2, 0) = 0$$

and

$$(5.2) \quad G_{x_1}(K_1, 0) = F_{1x_1}(K_1, K_2, 0) + F_{1x_2}(K_1, K_2, 0) \frac{\partial \phi}{\partial x_1}(K_1, 0).$$

The first term on the right-hand side of (5.2) is zero since by hypothesis  $g_{1x_1}(K_1) = 0$ , and the second term is also zero since  $\phi_{x_1}(K_1, 0) = 0$ , as shown above. However,

$$\begin{aligned}G_\varepsilon(K_1, 0) &= F_{1\varepsilon}(K_1, K_2, 0) + F_{1x_2}(K_1, K_2, 0)\phi_\varepsilon(K_1, 0) \\ &= h_2(K_2) - h_1(K_1).\end{aligned}$$

We suppose first

$$(5.3) \quad h_2(K_2) - h_1(K_1) \neq 0.$$

Since  $G_{x_1}(K_1, 0) = 0$ , we compute

$$\begin{aligned}G_{x_1 x_1}(K_1, 0) &= F_{1x_1 x_1}(K_1, K_2, 0) + 2F_{1x_1 x_2}(K_1, K_2, 0) \frac{\partial \phi}{\partial x_1}(K_1, 0) \\ &\quad + F_{1x_2}(K_1, K_2, 0) \frac{\partial^2 \phi}{\partial x_1^2}(K_1, 0) + F_{1x_2 x_2}(K_1, K_2, 0) \left( \frac{\partial \phi}{\partial x_1}(K_1, 0) \right)^2.\end{aligned}$$

However, since, as noted above,  $\partial \phi(K_1, 0)/\partial x_1$  and  $F_{1x_2}(K_1, K_2, 0)$  are zero, it follows that

$$G_{x_1 x_1}(K_1, 0) = F_{1x_1 x_1}(K_1, K_2, 0).$$

However,

$$F_{1x_1 x_1} = x_1 g_{1x_1 x_1} + 2g_{1x_1} - \varepsilon h_{1x_1 x_1}$$

and at  $(K_1, K_2, 0)$  we have

$$F_{1x_1x_1}(K_1, K_2, 0) = K_1 g_{1x_1x_1}(K_1).$$

Since  $g_{1x_1}(x_1) \leq 0$ ,  $g_1(K_1) = g_{1x_1}(K_1) = 0$ , and  $g(x_1) < 0$  for  $x_1 > K_1$ , it follows that  $g_{1x_1x_1}(K_1) = 0$ . This turn of events means that it is necessary to compute  $G_{x_1x_1x_1}(K_1, 0)$ . A straightforward computation yields

$$\begin{aligned} G_{x_1x_1x_1}(K_1, 0) &= F_{1x_1x_1x_1}(K_1, K_2, 0) \\ &= K_1 g_{1x_1x_1x_1}(K_1). \end{aligned}$$

If we assume that  $g_{1x_1x_1x_1}(K_1) \neq 0$  (and hence necessarily that  $g_{1x_1x_1x_1}(K_1) < 0$  by (2, 3)), then we are in a position to apply the technique of Freedman [5, Case iv,  $n = 3$ ]. In the notation of that paper,

$$\begin{aligned} \theta_0 &= \left[ \frac{-6G_\varepsilon(K_1, 0)}{G_{x_1x_1x_1}(K_1, 0)} \right]^{1/3} \\ &= \left[ \frac{6[h_1(K_1) - h_2(K_2)]}{K_1 g_{1x_1x_1x_1}(K_1)} \right]^{1/3} \end{aligned}$$

and

$$(5.4) \quad x_1^* = K_1 + \theta_0 \varepsilon^{1/3} + o(\varepsilon^{1/3}).$$

Since  $x_2 = \phi(x_1, \varepsilon)$  and  $x_1$  is given as a function of  $\varepsilon$  by (5.4) we have effectively found  $x_2^*$ . The computations are straightforward but somewhat tedious and we spare the reader the details. The simple form of  $x_2^*$  given in the statement of the theorem results because in the Taylor expansion of  $\phi(x, \varepsilon)$ , all derivatives involving  $\varepsilon$  are multiplied by  $\varepsilon$  (obviously) and all derivatives not involving  $\varepsilon$  are zero, i.e.,  $\phi_{x_1 \dots x_1}(K_1, 0) = 0$ . This latter fact can be seen by successively differentiating both sides of  $F_2(x_1, \phi(x_1, \varepsilon), \varepsilon) = 0$ , and using the basic assumption  $F_{2x_2}(K_1, K_2, 0) \neq 0$ .

We examine the stability of this critical point for small  $\varepsilon$ . The variational matrix at  $x_1^*, x_2^*$  is given by

$$(5.5) \quad M(\varepsilon) = \begin{bmatrix} x_1^* g_{1x_1}(x_1^*) + g_1(x_1^*) - \varepsilon h_{1x_1}(x_1^*) & \varepsilon h_{2x_2}(x_2^*) \\ \varepsilon h_{1x_1}(x_1^*) & x_2^* g_{2x_2}(x_2^*) + g_2(x_2^*) - \varepsilon h_{2x_2}(x_2^*) \end{bmatrix}.$$

If we put in the asymptotic form of  $x_1^*, x_2^*$  and expand to order  $\varepsilon^{2/3}$  we find (making use of  $g_{1x_1}(K_1) = g_{1x_1x_1}(K_1) = 0$ ),

$$M(\varepsilon) = \begin{bmatrix} \frac{1}{2} K_1 g_{1x_1x_1x_1}(K_1) \varepsilon^{2/3} + o(\varepsilon^{2/3}) & o(\varepsilon^{2/3}) \\ o(\varepsilon^{2/3}) & K_2 g_{2x_2}(K_2) + o(\varepsilon^{2/3}) \end{bmatrix}.$$

By the Gerschgorin circle theorem, Isaacson and Keller [10, p. 135], the eigenvalues lie in a neighborhood of radius  $o(\varepsilon^{2/3})$  about  $\frac{1}{2} K_1 g_{1x_1x_1x_1}(K_1) \varepsilon^{2/3} + o(\varepsilon^{2/3})$  and  $K_2 g_{2x_2}(K_2) + o(\varepsilon^{2/3})$ . Both  $g_{1x_1x_1x_1}(K_1)$  and  $g_{2x_2}(K_2)$  are negative. As remarked previously, if  $g_{1x_1x_1x_1}(K_1) \neq 0$ , then  $g_{1x_1x_1x_1}(K_1) < 0$ .  $g_{2x_2}(K_2) < 0$  from (2.3) and (2.9). Hence  $\lambda(\varepsilon) < 0$  for small  $\varepsilon > 0$ , and the critical point retains its asymptotic stability under small perturbations.

If case (5.3) fails, i.e.,  $h_1(K_1) = h_2(K_2)$ , it follows that  $(K_1, K_2)$  is a constant solution of (2.1), or  $x_1^*(\varepsilon) = K_1$ ,  $x_2^*(\varepsilon) = K_2$ . It is also the only solution. Suppose there existed a second constant solution  $(\hat{x}_1^*(\varepsilon), \hat{x}_2^*(\varepsilon))$ , i.e., suppose  $G(\hat{x}_1^*(\varepsilon), \varepsilon) \equiv 0$ . For sufficiently small  $\varepsilon > 0$ , expand  $G$  about  $(K_1, 0)$  through quadratic terms. All of the coefficients must be zero; all are, except

$$G_{x_1\varepsilon}(K_1, 0) = F_{1x_1\varepsilon}(K_1, K_2, 0) = h_{1x_1}(K_1) \neq 0.$$

Thus  $G(\hat{x}_1^*(\varepsilon), \varepsilon) \not\equiv 0$  unless  $\hat{x}_1^*(\varepsilon) = x_1^*(\varepsilon)$ .

To examine the stability we note that in evaluating the variational matrix  $x_1^* = K_1$ ,  $x_2^* = K_2$ , and hence we must show that the eigenvalues of

$$(5.6) \quad M(\varepsilon) = \begin{bmatrix} -\varepsilon h_{1x_1}(K_1) & \varepsilon h_{2x_2}(K_2) \\ \varepsilon h_{1x_1}(K_1) & K_2 g_{2x_2}(K_2) - \varepsilon h_{2x_2}(K_2) \end{bmatrix}$$

have negative real part. Since  $g_{2x_2}(K_2) < 0$ , the same arguments as before would yield the fact that one eigenvalue is negative but the other terms are of the same order and the Gerschgorin theorem does not yield useful information. The characteristic polynomial of (5.6) takes the form

$$\begin{aligned} &\lambda^2 + \lambda(\varepsilon h_{1x_1}(K_1) + \varepsilon h_{2x_2}(K_2) - K_2 g_{2x_2}(K_2)) \\ &+ \varepsilon h_{1x_1}(K_1)(\varepsilon h_{2x_2}(K_2) - K_2 g_{2x_2}(K_2)) - \varepsilon^2 h_{1x_1}(K_1) h_{2x_2}(K_2) = 0. \end{aligned}$$

For small  $\varepsilon > 0$ , the multiplier of  $\lambda$  is positive. In the constant term the multiplier of  $\varepsilon$  is positive and the one negative term is multiplied by  $\varepsilon^2$ . Thus for sufficiently small  $\varepsilon$  all coefficients in the quadratic are positive. Thus the roots must have negative real part. (In fact, both are real and have the form  $\lambda_1 = K_2 g_{2x_2}(K_2) + o(1)$ ,  $\lambda_2 = -h_{1x_1}(K_1)\varepsilon + o(\varepsilon)$ , although this fact is not needed here.) Thus the perturbed critical point is asymptotically stable and the proof of Theorem 2.2 is complete.

*Proof of Theorem 2.3.* We note first that with  $g_{ix_i}(K_i) = 0$ , the assumptions on  $g$  require  $g_{ix_i x_i}(K_i) = 0$ ,  $i = 1, 2$ ,  $F_i(x_1, x_2, \varepsilon)$  may be expanded up to cubic terms to yield

$$\begin{aligned} (5.7) \quad F_i(x_1, x_2, \varepsilon) &= F_{i\varepsilon}(K_1, K_2, 0)\varepsilon + F_{ix_i\varepsilon}(K_1, K_2, 0)(x_i - K_i)\varepsilon \\ &\quad + F_{ix_i^2\varepsilon}(K_1, K_2, 0)(x_i - K_i)^2\varepsilon \\ &\quad + \frac{1}{6}F_{ix_1x_1x_1}(K_1, K_2, 0)(x_1 - K_1)^3 \\ &\quad + \frac{1}{6}F_{ix_2x_2x_2}(K_1, K_2, 0)(x_2 - K_2)^3 \\ &\quad + \frac{1}{2}F_{ix_1x_1\varepsilon}(K_1, K_2, 0)(x_1 - K_1)^2\varepsilon \\ &\quad + \frac{1}{2}F_{ix_1x_2\varepsilon}(K_1, K_2, 0)(x_2 - K_2)^2\varepsilon + \text{H.O.T.} \end{aligned}$$

If  $h_1(K_1) - h_2(K_2) \neq 0$ , then  $F_{1\varepsilon}(K_1, K_2, 0) \neq 0$  and  $F_{2\varepsilon}(K_1, K_2, 0) \neq 0$ . Let  $y_i$  be defined by  $x_i - K_i = y_i \varepsilon^{1/3}$ ,  $i = 1, 2$ . If we can find  $y_i$  as a function of  $\varepsilon$  such that  $F_i(K_1 + y_1 \varepsilon^{1/3}, K_2 + y_2 \varepsilon^{1/3}, \varepsilon) = 0$  we have found the requisite critical point. Define

$$J_i(y_1, y_2, \varepsilon) = \varepsilon^{-1} F_i(K_1 + y_1 \varepsilon^{1/3}, K_2 + y_2 \varepsilon^{1/3}, \varepsilon), \quad i = 1, 2,$$

or, making use of (5.7),

$$J_1(y_1, y_2, \varepsilon) = F_{1\varepsilon}(K_1, K_2, 0) + \frac{1}{6}F_{1x_1x_1x_1}(K_1, K_2, 0)y_1^3 + o(\varepsilon^{1/3}),$$

$$J_2(y_1, y_2, \varepsilon) = F_{2\varepsilon}(K_1, K_2, 0) + \frac{1}{6}F_{2x_2x_2x_2}(K_1, K_2, 0)y_2^3 + o(\varepsilon^{1/3}).$$

Let  $J = (J_1, J_2)$  and we seek to solve  $J = 0$  for  $y_1, y_2$  as functions of  $\varepsilon$ . If  $y_{i0}$  are roots of

$$F_{i\varepsilon}(K_1, K_2, 0) + \frac{1}{6}F_{ix_1x_1x_1}(K_1, K_2, 0)y_i^3 = 0$$

then  $J(y_{10}, y_{20}, 0) = 0$ . Further,  $\det(J_y(y_{10}, y_{20}, 0)) \neq 0$ . Thus

$$y_i = y_{i0} + o(1), \quad i = 1, 2,$$

and

$$x_i = K_i + y_{i0}\varepsilon^{1/3} + o(\varepsilon^{1/3})$$

where

$$y_{i0} = \left[ \frac{(-1)^i 6(h_2(K_2) - h_1(K_1))}{K_i g_{ix_ix_ix_i}(K_i)} \right]^{1/3}.$$

The variational matrix now takes the form

$$M(\varepsilon) = \begin{bmatrix} \frac{1}{2}K_1 g_{1x_1x_1x_1}(K_1)y_{10}^2\varepsilon^{2/3} + o(\varepsilon^{2/3}) & o(\varepsilon^{2/3}) \\ o(\varepsilon^{2/3}) & \frac{1}{2}K_2 g_{2x_2x_2x_2}(K_2)y_{20}^2\varepsilon^{2/3} + o(\varepsilon^{2/3}) \end{bmatrix}.$$

Since  $g_{1x_1x_1x_1}(K_1) < 0$  and  $g_{2x_2x_2x_2}(K_2) < 0$ , the Gerschgorin circle argument can be applied and the critical point is asymptotically stable.

In the case  $h_1(K_1) = h_2(K_2)$  we again have that  $x_i^* = K_i$ ,  $i = 1, 2$ . Uniqueness can be shown (we omit the details). The variational matrix takes the form

$$M(\varepsilon) = \begin{bmatrix} -\varepsilon h_{1x_1}(K_1) & \varepsilon h_{2x_2}(K_2) \\ \varepsilon h_{1x_1}(K_1) & -\varepsilon h_{2x_2}(K_2) \end{bmatrix}$$

and is singular. Thus one root is zero; the other is  $\lambda = -\varepsilon(h_{1x_1}(K_1) + h_{2x_2}(K_2)) < 0$ .

*Proof of Theorem 3.1.* If interior equilibria exist, they must satisfy

$$(5.8) \quad \begin{aligned} \alpha_1 x_1 \left( 1 - \frac{x_1}{K_1} \right) - \varepsilon x_1 + \varepsilon x_2 &= 0, \\ \alpha_2 x_2 \left( 1 - \frac{x_2}{K_2} \right) - \varepsilon x_2 + \varepsilon x_1 &= 0. \end{aligned}$$

Solving the first for  $x_2$  yields

$$(5.9) \quad \begin{aligned} x_2 &= x_1 \left[ -\frac{\alpha_1}{\varepsilon} \left( 1 - \frac{x_1}{K_1} \right) + 1 \right] \\ &= \frac{\alpha_1 x_1}{\varepsilon K_1} \left[ x_1 - \frac{K_1}{\alpha_1} (\alpha_1 - \varepsilon) \right], \end{aligned}$$

which may be put back into (5.8). After some algebraic manipulation this reduces to

$$\begin{aligned} f(x_1) &= \alpha_1^2 \alpha_2 x_1^3 - 2\alpha_1 \alpha_2 K_1 (\alpha_1 - \varepsilon) x_1^2 \\ &\quad + K_1 (\alpha_2 K_1 (\alpha_1 - \varepsilon) - \alpha_1 K_2 \varepsilon (\alpha_2 - \varepsilon)) x_1 - K_1^2 K_2 \varepsilon (\alpha_1 \varepsilon + \alpha_2 \varepsilon - \alpha_1 \alpha_2) \\ &= \alpha_2 x_1 [\alpha_1 x_1 - K_1 (\alpha_1 - \varepsilon)]^2 \\ &\quad - K_1 K_2 \varepsilon [\alpha_1 (\alpha_2 - \varepsilon) x_1 + K_1 (\alpha_1 \varepsilon + \alpha_2 \varepsilon - \alpha_1 \alpha_2)] \\ &= 0. \end{aligned}$$

Clearly,  $\lim_{x \rightarrow \infty} f(x) = \infty$ . Further,

$$f(0) = -K_1^2 K_2 \varepsilon (\alpha_1 \varepsilon + \alpha_2 (\varepsilon - \alpha_1))$$

and

$$f\left(\frac{K_1}{\alpha_1}(\alpha_1 - \varepsilon)\right) = -K_1^2 K_2 \varepsilon^3 < 0.$$

If  $\varepsilon > \alpha_1$ ,  $f(0) < 0$  and there is a positive root. If  $\alpha_1 > \varepsilon$ , then  $(K_1/\alpha_1)(\alpha_1 - \varepsilon) > 0$  and  $f$  is negative at  $(K_1/\alpha_1)(\alpha_1 - \varepsilon)$ . Hence  $f$  must have a positive root, and if there are two we take the one larger than  $(K_1/\alpha_1)(\alpha_1 - \varepsilon)$ . In either case there is a positive number,  $x_2$ , corresponding to  $x_1$  given by (5.9).  $x_2 > 0$  since  $x_1 > (K_1/\alpha_1)(\alpha_1 - \varepsilon)$ .

To analyze stability we note that the variational matrix has the form

$$\begin{aligned} M(\varepsilon) &= \begin{bmatrix} \alpha_1 - \frac{2x_1^*}{K_1} - \varepsilon & \varepsilon \\ \varepsilon & \alpha_2 - \frac{2x_2^*}{K_2} - \varepsilon \end{bmatrix} \\ &= \begin{bmatrix} -\frac{\varepsilon x_2^*}{x_1^*} - \frac{\alpha_1 x_1^*}{K_1} & \varepsilon \\ \varepsilon & -\frac{\varepsilon x_1^*}{x_2^*} - \frac{\alpha_2 x_2^*}{K_2} \end{bmatrix}. \end{aligned}$$

The characteristic equation is then

$$\left(\frac{\varepsilon x_2^*}{x_1^*} + \frac{\alpha_1 x_1^*}{K_1} + \lambda\right) \left(\frac{\varepsilon x_1^*}{x_2^*} + \frac{\alpha_2 x_2^*}{K_2} + \lambda\right) - \varepsilon^2 = 0.$$

Note that the  $-\varepsilon^2$  is canceled by the product of the first term in each parentheses and that all remaining coefficients in the quadratic will be positive since every term is. Therefore the eigenvalues will have negative real parts and the equilibrium is asymptotically stable.

To establish that  $\lim_{\varepsilon \rightarrow \infty} x_i^*(\varepsilon)$  exists, we first show that the quantities in question are bounded. Suppose  $\limsup_{\varepsilon \rightarrow \infty} x_1(\varepsilon) = \infty$ , i.e., let  $\varepsilon_n \rightarrow \infty$  as  $n \rightarrow \infty$  and  $\lim_{n \rightarrow \infty} x_1(\varepsilon_n) = \infty$ . By adding the equations in (5.8) one obtains

$$(5.10) \quad \alpha_1 x_1 \left(1 - \frac{x_2}{K_1}\right) + \alpha_2 x_2 \left(1 - \frac{x_2}{K_2}\right) = 0.$$

As  $n \rightarrow \infty$ ,  $x_1(\varepsilon_n) \rightarrow \infty$ , so the first term in the sum tends to  $-\infty$ . Therefore

$$\lim_{n \rightarrow \infty} x_2(\varepsilon_n)(K_2 - x_2(\varepsilon_n)) = \infty.$$

If for a subsequence of  $\varepsilon_n$ , again called  $\varepsilon_n$ ,  $x_2(\varepsilon_n) \rightarrow \infty$ , the first term is positive and the second is negative, a contradiction. If  $x_2(\varepsilon_n)$  is finite for some subsequence, then the left side is finite and the right infinite. Thus  $x_1(\varepsilon)$  is bounded for all  $\varepsilon$  and the symmetric argument works for  $x_2(\varepsilon)$ .

Subtracting the equations in (5.8) and dividing by  $\varepsilon$  yields

$$(5.11) \quad \frac{1}{\varepsilon} \left[ \alpha_1 x_1^*(\varepsilon) \left( 1 - \frac{x_1^*(\varepsilon)}{K_1} \right) + \alpha_2 x_2^*(\varepsilon) \left( 1 - \frac{x_2^*(\varepsilon)}{K_2} \right) \right] = 2(x_1^*(\varepsilon) - x_2^*(\varepsilon)).$$

As  $\varepsilon \rightarrow \infty$ , the left-hand side of (5.11) tends to zero, hence

$$\lim_{\varepsilon \rightarrow \infty} [x_1^*(\varepsilon) - x_2^*(\varepsilon)] = 0.$$

Let  $x^*$  denote the common value (finite by the preceding arguments). If  $\varepsilon \rightarrow \infty$  in (5.10), then

$$\alpha_1 x^* \left( 1 - \frac{x^*}{K_1} \right) = -\alpha_2 x^* \left( 1 - \frac{x^*}{K_2} \right),$$

or

$$x^* = \frac{\alpha_1 + \alpha_2}{\alpha_1/K_1 + \alpha_2/K_2}.$$

*Proof of Theorem 4.1.* Define

$$F(x_1, x_2, y, \varepsilon) = \begin{bmatrix} \alpha_1 x_1 \left( 1 - \frac{x_1}{K_1} \right) - \beta_1 x_1 y - \varepsilon x_1 + \varepsilon x_2 \\ \alpha_2 x_2 \left( 1 - \frac{x_2}{K_2} \right) - \beta_2 x_2 y - \varepsilon x_2 + \varepsilon x_1 \\ \delta_1 x_1 y + \delta_2 x_2 y - \gamma y \end{bmatrix}.$$

We seek to solve

$$F(x_1, x_2, y, \varepsilon) = 0$$

for  $x_1^*(\varepsilon)$ ,  $x_2^*(\varepsilon)$ ,  $y^*(\varepsilon)$  via the implicit function theorem. (See also Levin [11], [12]. We include some of the calculations so as to make the asymptotic form clear.)  $F(x_{10}, x_{20}, y_0, 0) = 0$ , as shown above. The relevant Jacobian is

$$J(x_{10}, x_{20}, y_0, 0) = \begin{bmatrix} \frac{-\alpha_1 x_{10}}{K_1} & 0 & -\beta_2 x_{10} \\ 0 & \frac{-\alpha_2 x_{20}}{K_2} & -\beta_2 x_{20} \\ \delta_1 y_0 & \delta_2 y_0 & 0 \end{bmatrix}.$$

Since

$$\begin{aligned}\det [J(x_{10}, x_{20}, y_0, 0)] &= \frac{-\beta_1 \alpha_2 \delta_1}{K_2} x_{10} x_{20} y_0 - \frac{\alpha_1 \delta_2 \beta_2}{K_1} x_{10} x_{20} y_0 \\ &= -x_{10} x_{20} y_0 \left( \frac{\alpha_1 \beta_2 \delta_2}{K_1} + \frac{\alpha_2 \beta_1 \delta_1}{K_2} \right) \\ &\neq 0,\end{aligned}$$

the inverse matrix exists, and a straightforward computation gives

$$\begin{aligned}[J(x_{10}, x_{20}, y_0, 0)]^{-1} \\ = 1/(\alpha_1 \beta_2 \delta_2 / K_1 + \alpha_2 \beta_1 \delta_1 / K_2) \begin{bmatrix} \frac{-\beta_2 \delta_2}{x_{10}} & \frac{\beta_1 \delta_2}{x_{20}} & \frac{\alpha_2 \beta_1}{K_2 y_0} \\ \frac{\beta_2 \delta_1}{x_{10}} & \frac{-\beta_1 \delta_1}{x_{20}} & \frac{\alpha_1 \beta_2}{K_1 y_0} \\ \frac{-\alpha_2 \delta_1}{K_2 x_{10}} & \frac{-\alpha_1 \delta_2}{K_1 x_{20}} & \frac{-\alpha_1 \delta_2}{K_1 K_2 y_0} \end{bmatrix}.\end{aligned}$$

Since

$$F_\varepsilon(x_{10}, x_{20}, y_0, 0) = \begin{pmatrix} -x_{10} + x_{20} \\ x_{10} - x_{20} \\ 0 \end{pmatrix},$$

then computing

$$\begin{pmatrix} x_1^*(\varepsilon) \\ x_2^*(\varepsilon) \\ x_3^*(\varepsilon) \end{pmatrix} = \begin{pmatrix} x_{10} \\ x_{20} \\ y_0 \end{pmatrix} - [J(x_{10}, x_{20}, y_0, 0)]^{-1} F_\varepsilon(x_{10}, x_{20}, y_0, 0) \varepsilon + o(\varepsilon)$$

yields the asserted asymptotic expansion.

The relevant characteristic equation is

$$\begin{aligned}f(\lambda) &= \lambda \left( \lambda + \frac{\alpha_1 x_{10}}{K_1} \right) \left( \lambda + \frac{\alpha_2 x_{20}}{K_2} \right) + \beta_1 \delta_1 x_{10} y_0 \left( \lambda + \frac{\alpha_2 x_{20}}{K_2} \right) \\ &\quad + \beta_2 \delta_2 x_{20} y_0 \left( \lambda + \frac{\alpha_1 x_{10}}{K_1} \right) \\ &= \lambda^3 + \left( \frac{\alpha_1 x_{10}}{K_1} + \frac{\alpha_2 x_{20}}{K_2} \right) \lambda^2 + \left( \frac{\alpha_1 \alpha_2 x_{10} x_{20}}{K_1 K_2} + \beta_1 \delta_1 x_{10} y_0 + \beta_2 \delta_2 x_{20} y_0 \right) \lambda \\ &\quad + \left( \frac{\alpha_2 \beta_1 \delta_1}{K_2} + \frac{\alpha_1 \beta_2 \delta_2}{K_1} \right) x_{10} x_{20} y_0 = 0.\end{aligned}$$

Since all coefficients of the cubic are positive, all real roots are negative, and, of course, there is at least one real root. If all roots are real there is nothing further to prove. Suppose not. Then let  $r$  be the unique negative root. We first bound  $r$ .



From the first expression for  $f(\lambda)$ , it follows that

$$f\left(-\frac{\alpha_1 x_{10}}{K_1}\right) = \beta_1 \delta_1 x_{10} y_0 \left(-\frac{\alpha_1 x_{10}}{K_1} + \frac{\alpha_2 x_{20}}{K_2}\right)$$

and

$$f\left(-\frac{\alpha_2 x_{20}}{K_2}\right) = \beta_2 \delta_2 x_{20} y_0 \left(-\frac{\alpha_2 x_{20}}{K_2} + \frac{\alpha_1 x_{10}}{K_1}\right).$$

Since the quantities outside the parentheses are positive, one of the above quantities is nonpositive and one nonnegative; therefore  $r$  lies between  $-\alpha_1 x_{10}/K_1$  and  $-\alpha_2 x_{20}/K_2$ . For definiteness suppose the first quantity is larger. Then  $r = -\alpha_1 x_{10}/K_1 - a$ , where

$$(5.12) \quad a = \alpha \left( \frac{\alpha_2 x_{20}}{K_2} - \frac{\alpha_1 x_{10}}{K_1} \right), \quad 0 \leq \alpha < 1.$$

Then

$$f(\lambda) = (\lambda - r) \left( \lambda^2 + \left( \frac{\alpha_2 x_{20}}{K_2} - a \right) \lambda + q \right),$$

where necessarily  $q > 0$  since the constant term in the original cubic is positive. Further,

$$\frac{\alpha_2 x_{20}}{K_2} > a$$

by (5.12). All coefficients in the quadratic factor are positive so it has only roots with negative real part.

To verify the statements for (4.1)' note that the derivative of  $F$  with respect to  $\varepsilon$  now becomes

$$F_\varepsilon(x_{10}, x_{20}, y_0, 0) = \begin{pmatrix} -\mu_1 x_{10} + \mu_2 x_{20} \\ \mu_1 x_{10} + \mu_2 x_{20} \\ 0 \end{pmatrix}$$

which replaces the factor  $(x_{20} - x_{10})$  by  $(\mu_2 x_{20} - \mu_1 x_{10})$  in (4.6).

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