ROCKY MOUNTAIN
JOURNAL OF MATHEMATICS
Volume 20, Number 4, Fall 1990

LIMITS OF HETEROCLINC ORBITS IN A COMPETITIVE MODEL WITH GENETIC VARIATION

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ABSTRACT. A three-dimensional system of autonomous ordinary differential equations which models the competition between two populations with genetic variation in one population is studied. The competitive interaction is of Lotka/Volterra type. On one allele frequency fixation plane the dynamical behavior is that of stable coexistence and, on the other, mutual exclusion. There are heteroclinic orbits connecting the two fixation planes, and the equilibria which these orbits approach vary depending on the crowding parameter of the genetically invariant population. For a critical value of this parameter, there is a line of polymorphic equilibria. It is shown that portions of this line along with another heteroclinic orbit form the topological limit of the orbits connecting the fixation planes as the parameter approaches its critical value. Hence, this provides a better understanding of the heteroclinic bifurcation occurring at the critical value of the parameter.

1. Introduction. Competition between two populations may be modeled by the two-dimensional system of ordinary differential equations,

$$\begin{aligned} \dot{M} &= \mu(M,N)M \\ \dot{N} &= \eta(M,N)N, \end{aligned} \tag{1}$$

where $M, N \geq 0$ are the population sizes (or densities) and μ, η are C^1 functions with $\partial\mu/\partial N < 0$ and $\partial\eta/\partial M < 0$. The functions μ and η are per capita growth rates for the M and N populations, respectively. We refer to μ and η as *fitness* functions. The competition is said to be Lotka/Volterra if the fitnesses are linear functions of M and N, i.e.,

$$\begin{aligned} \mu(M,N) &= r_M - \alpha M - \beta N \\ \eta(M,N) &= r_N - \delta M - \gamma N, \end{aligned} \tag{2}$$

Research supported by funds provided by a Science and Education Grant to the USDA-Forest Service, Southeastern Forest Experiment Station, Population Genetics of Forest Trees Research Unit, Raleigh, North Carolina

where all parameters are positive. If (1) has an equilibrium in the interior of the positive quadrant, there are two possible outcomes of Lotka/Volterra competition: stable coexistence and mutual exclusion (see Freedman [**9**] or Waltman [**16**]). These two outcomes are distinguished by the difference between the intraspecific competition (the self-repression) and the interspecific competition, i.e.,

$$\alpha\gamma - \beta\delta. \tag{3}$$

If (3) is positive then the interior equilibrium is globally, asymptotically stable in the interior of the positive quadrant; thus, we have stable coexistence. If (3) is negative, then the interior equilibrium is a saddle point with stable manifold separating the regions of asymptotic stability of the single species equilibria on the axes (mutual exclusion).

Changing the outcome of Lotka/Volterra competition from stable coexistence to mutual exclusion involves a two parameter bifurcation, e.g., both the slope and the intercept of an isocline must be changed. However, if one population is allowed to vary genetically, both outcomes may occur in the same dynamical system (see Selgrade and Namkoong [**15**]). Henceforth, we assume that the M population is diploid with two alleles, A and a, at one locus. Thus, the M population is divided into three subpopulations distinguished by the *genotypes* AA, Aa, and aa; and each genotype has a fitness function denoted by μ_{ij}, for $i, j = A, a$. The frequency of the allele A is denoted by the variable p. Hence, the frequency of the allele a is given by $1 - p$. In general, the genotype fitnesses are functions of the population densities, M and N, and of the allele frequency p. The allele fitnesses, μ_A and μ_a, are defined by $\mu_A = p\mu_{AA} + (1-p)\mu_{Aa}$ and $\mu_a = p\mu_{Aa} + (1-p)\mu_{aa}$; and the mean fitness μ for the M population is defined by $\mu = p\mu_A + (1-p)_{\mu_a}$. The fitness for the N population may depend on p as well as M and N. Assuming random mating and slow selection in the M population, the following three-dimensional system of autonomous ordinary differential equations models the interacting populations (see Crow and Kimura [**6**] or Ginzburg [**11**]):

$$\begin{aligned} \dot{p} &= p(1-p)(\mu_A - \mu_a) \\ \dot{M} &= \mu M \\ \dot{N} &= \eta N. \end{aligned} \tag{4}$$

Solutions to (4) of biological interest lie in the three-dimensional region

$$\mathcal{S} \equiv \{(p, M, N) : 0 \le p \le 1,\ M \ge 0,\ N \ge 0\}.$$

If p equals 1 or 0, then one allele is absent from the M population; and on these invariant planes of *allele fixation*, (4) reduces to (1).

In order to simplify (4) somewhat, we assume that the gene action in the M species exhibits *no dominance*, i.e., neither allele in the heterozygote dominates in its phenotypic expression. Hence, we assume that the heterozygote fitness is the average of the homozygote fitnesses:

$$\mu_{Aa} = (\mu_{AA} + \mu_{aa})/2. \tag{A1}$$

Using (A1), the allele and mean fitnesses simplify to

$$\mu_A - \mu_a = (\mu_{AA} - \mu_{aa})/2 \text{ and } \mu = p\mu_{AA} + (1-p)\mu_{aa}. \tag{5}$$

For Lotka/Volterra competition, we assume the following linear fitness functions:

$$\begin{aligned} \mu_{AA} &= 1 - \alpha_{AA}M - \beta_{AA}N \\ \mu_{aa} &= 1 - \alpha_{aa}M - \beta_{aa}N \\ \eta &= 1 - \delta M - \gamma N, \end{aligned} \tag{A2}$$

where all parameters are positive. In (A2), we have taken the intrinsic growth rates for all populations to be equal, and then, by time-scaling, we have assumed that value to be 1. As in [**13**] and [**15**], to obtain stable coexistence between the AA genotype and the N-population (i.e., on the fixation plane $\{p = 1\}$) and mutual exclusion between the aa genotype and the N population (i.e., on $\{p = 0\}$), we assume

$$\alpha_{aa} < \delta < \alpha_{AA} \text{ and } \beta_{AA} < \gamma < \beta_{aa}. \tag{A3}$$

Assuming (A1), (A2), and (A3) in (4) and using (5), we derive the following system of equations which depends on six parameters:

$$\begin{aligned} \dot{p} &= p(1-p)[(\alpha_{aa} - \alpha_{AA})M + (\beta_{aa} - \beta_{AA})N]/2 \\ \dot{M} &= p[1 - \alpha_{AA}M - \beta_{AA}N]M + (1-p)[1 - \alpha_{aa}M - \beta_{aa}N]M \\ \dot{N} &= [1 - \delta M - \gamma N]N. \end{aligned} \tag{6}$$

The right-hand side of (6) is called the *vector field* and is denoted by the vector function $F(p, M, N)$.

In [**15**], a quadratic combination K of the competition parameters in (6) is defined (see equation (8) in Section 2), the sign of which determines the dynamical behavior of the solutions to (6). Munoz and Selgrade [**13**] show that each solution converges to an equilibrium solution regardless of the value of K. If K is positive, the equilibrium C_1 on the plane $\{p = 1\}$ and the M-species equilibrium M_0 on the plane $\{p = 0\}$ are locally, asymptotically stable with respect to the three-dimensional flow of (6), see Figure 1(a). Also, there is a heteroclinic orbit connecting the equilibrium M_1 in $\{p = 1\}$ to the equilibrium C_0 in $\{p = 0\}$. If K is negative, the equilibrium M_0 is globally, asymptotically stable with respect to the interior of $\mathcal{S}$, and there is a heteroclinic orbit connecting C_1 to M_0, see Figure 1(c). If K is zero, there is a line of degenerate equilibria connecting C_1 to C_0 which contains a special equilibrium denoted by C_{p^*}, and there are two heteroclinic orbits, one from M_1 to C_{p^*} and the other from C_{p^*} to M_0, see Figure 1(b).

In this paper, we intend to explain how the transition in the heteroclinic orbits occurs as K passes through 0. Roughly speaking, we show that the heteroclinic orbits from C_1 to M_0, when $K < 0$, approach the union of the equilibria from C_1 to C_{p^*} and the heteroclinic orbit from C_{p^*} to M_0 at $K = 0$. Similarly, the heteroclinic orbits from M_1 to C_0, when $K > 0$, approach the union of the equilibria from C_{p^*} to C_0 and the heteroclinic orbit from M_1 to C_{p^*} at $K = 0$. Hence, the heteroclinic orbits "jump" from connecting C_1 and M_0 to connecting M_1 and C_0 by passing through these unions of orbits when $K = 0$. Our arguments use global topological results and a local analysis of the perturbation at $K = 0$.

2. Background results needed to obtain Figure 1. There are several equilibria of (6) on the boundary of $\mathcal{S}$ with stability characteristics determined by (A3). The p-axis consists of equilibria which are unstable into the interior of $\mathcal{S}$. $M_0 = (0, 1/\alpha_{aa}, 0)$ is locally stable, and $M_1 = (1, 1/\alpha_{AA}, 0)$ is a saddle point with one-dimensional stable manifold parallel to the M-axis and two-dimensional unstable manifold intersecting the interior of $\mathcal{S}$. $N_0 = (0, 0, 1/\gamma)$ is a saddle with two-dimensional stable manifold in the MN-plane and one-dimensional unstable manifold in the pN-plane, and $N_1 = (1, 0, 1/\gamma)$

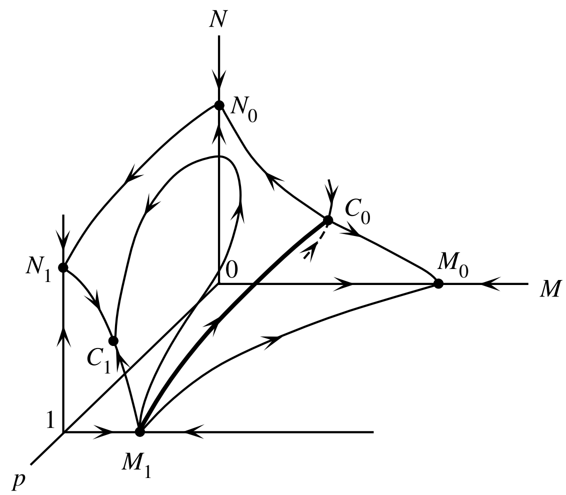

FIGURE 1(a). $K > 0$ $(\gamma < \gamma_0)$, M_0 and C_1 stable.

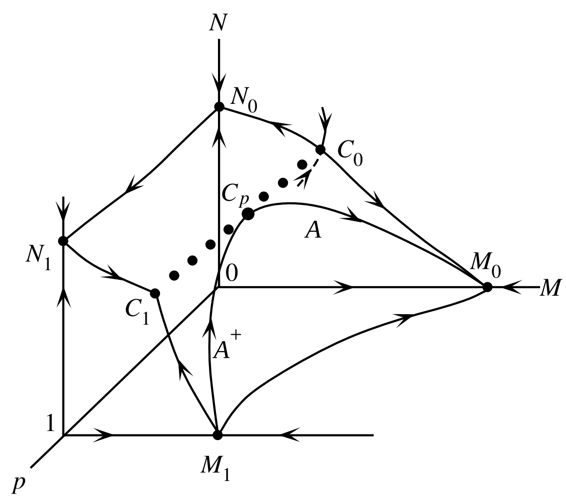

FIGURE 1(b). $K = 0$ $(\gamma = \gamma_0)$.

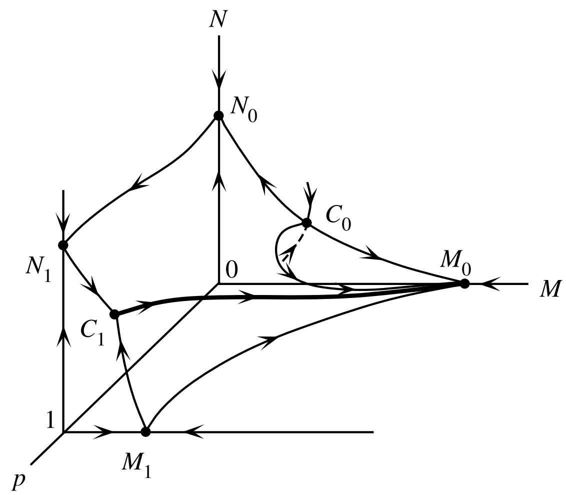

FIGURE 1(c). $K < 0\ (\gamma > \gamma_0)$, M_0 stable.

has a two-dimensional stable manifold in the pN-plane and a one-dimensional unstable manifold in $\{p = 1\}$. Each fixation plane contains an equilibrium in its interior, $C_0 = (0, (\gamma - \beta_{aa})/\sigma_a, (\alpha_{aa} - \delta)/\sigma_a)$ and $C_1 = (1, (\gamma - \beta_{AA})/\sigma_A, (\alpha_{AA} - \delta)/\sigma_A)$, where $\sigma_i \equiv \alpha_{ii}\gamma - \beta_{ii}\delta$ for $i = A, a$. C_0 is a saddle in $\{p = 0\}$ and C_1 is stable in $\{p = 1\}$; but the eigenvalues of both equilibria corresponding to eigenvectors in the p-direction have the same sign, and this sign varies with the parameters of (A2). If $K < 0$ (see equation (8)), then C_0 and C_1 are unstable in the p-direction, and if $K > 0$, then C_0 and C_1 are stable in the p-direction.

An equilibrium for (6), interior to $\mathcal{S}$, is a solution to the following system of three linear equations in the two unknowns M and N:

$$\mu_{AA} = 0,\ \mu_{aa} = 0, \quad \text{and} \quad \eta = 0. \tag{7}$$

Generically, (7) has no solution and, hence, (6) has no interior equilibrium (see Figure 1(a) and 1(c)). But there is a consistency condition which guarantees solutions to (7), i.e., (7) has solutions if the constant K is zero, where

$$K \equiv \alpha_{AA}\beta_{aa} - \alpha_{aa}\beta_{AA} + \alpha_{aa}\gamma - \beta_{aa}\delta + \beta_{AA}\delta - \alpha_{AA}\gamma. \tag{8}$$

Geometrically, K is the scalar triple product of vectors associated with the linear map in (7). If $K = 0$, then (6) has a line of equilibria given by

$$\mathcal{L} \equiv \{(p, M, N) : 0 \leq p \leq 1,\ M = (\beta_{aa} - \beta_{AA})/\sigma,\ N = (\alpha_{AA} - \alpha_{aa})/\sigma\},$$

where $\sigma \equiv \alpha_{AA}\beta_{aa} - \alpha_{aa}\beta_{AA}$. Since $\mathcal{L}$ is parameterized by p, we let C_p denote the equilibrium on $\mathcal{L}$ given by p. K is a measurement of the total competition in the ecological system. Note that

$$K = \sigma + \sigma_a - \sigma_A.$$

From (A3), we see that σ_a is negative, which asserts that the interspecific competition between the aa genotype and the N population is greater than the self-repression. Note that σ_a corresponds to the value in (3); and, hence, $\sigma_a < 0$ implies mutual exclusion on the plane $\{p = 0\}$. Also, σ_A is positive, which asserts that the self-repression is greater than the interspecific competition between the AA genotype and the N population and guarantees stable coexistence on $\{p = 1\}$. Hence, the term in (8) which determines the sign of K is the first term, $\alpha_{AA}\beta_{aa}$, which is the product of the self-repression on the AA genotype and the interspecific competition on the aa genotype.

Munoz and Selgrade [**13**] show that the sign of K determines the dynamical behavior of (6). The invariance properties of the plane where $\dot{p}$ equals zero in the interior of $\mathcal{S}$ are particularly useful in their analysis. Define this plane by

$$\mathcal{H} \equiv \{(p, M, N) : (\alpha_{aa} - \alpha_{AA})M + (\beta_{aa} - \beta_{AA})N = 0\} = \{\mu_{AA} - \mu_{aa} = 0\}.$$

$\mathcal{H}$ separates the interior of $\mathcal{S}$ and contains the p-axis; $\dot{p}$ equals zero in the interior of $\mathcal{S}$ precisely along $\mathcal{H}$; is negative below $\mathcal{H}$; and is positive above $\mathcal{H}$. Studying the vector field F of (6) along $\mathcal{H}$ shows that F points upward along $\mathcal{H}$ if $K > 0$, that F points downward along $\mathcal{H}$ if $K < 0$, and that F is tangent to $\mathcal{H}$ if $K = 0$. Hence, after at most one change in direction, the p-component of each solution in the interior of $\mathcal{S}$ becomes monotone and converges to a constant. Then, using the Butler/McGehee Lemma (see Appendix 1 in Freedman and Waltman [**10**]), it follows that

THEOREM 2.1 (MUNOZ/SELGRADE). *Assume* (A1), (A2), *and* (A3). *Then each solution to* (6) *converges to an equilibrium as* $t \to \infty$, *i.e., for each* $x \in \mathcal{S}$, $\omega(x)$ *is one point.*

The existence of the heteroclinic orbits in Figures 1(a) and 1(c) follows from Theorem 2.1 and a "shooting" argument.

Center manifold theory is needed to obtain Figure 1(b) for $K = 0$. Each equilibrium of $\mathcal{L}$ has a zero eigenvalue with corresponding eigenvector parallel to the p-axis. For p near 1, C_p has two negative eigenvalues, and, for p near 0, C_p has one negative and one positive eigenvalue. If we define

$$p^* \equiv (\alpha_{aa} - \delta)/(\alpha_{aa} - \alpha_{AA}),$$

then C_{p^*} has two zero eigenvalues and one negative eigenvalue. Every equilibrium on $\mathcal{L}$ has one eigenvalue equal to -1. In fact, the invariant plane $\mathcal{H}$ consists of points of $\mathcal{L}$ and stable manifolds (which are lines) of these points corresponding to the eigenvalue -1. For $p \neq p^*$, the center manifold of C_p is a subset of $\mathcal{L}$. Munoz and Selgrade [**13**] show that, for $p > p^*$, the orbit structure near C_p is that of a cylinder foliated by the strong stable manifolds of points of $\mathcal{L}$. For $p < p^*$, the orbit structure near C_p is that of a cylinder foliated by two-dimensional disks on which there is saddle behavior. This result is summarized by

LEMMA 2.2. *Assume* (A1), (A2), *and* (A3) *and that* $K = 0$. *Let* $p_0 \neq p^*$. *There is an open segment* $\mathcal{L}' \subset \mathcal{L} \backslash C_{p^*}$ *containing* C_{p_0}, *a two-dimensional disk* D, *and a neighborhood* B *of* C_{p_0} *which is* C^1 *diffeomorphic to* $\mathcal{L}' \times D$. *If* $p_0 > p^*$, *then the positive orbit of each point in* B *remains in* B *and is asymptotic to some* $C_p \in L'$ *as* $t \to \infty$. *If* $p_0 < p^*$, *then the positive orbit of* $x \in B$ *is asymptotic to some* $C_p \in L'$ *if and only if* $x \in \mathcal{H} \cap B$.

In order to understand orbit behavior near C_{p^*}, Munoz and Selgrade [**13**] analyze the flow on the center manifold using an approach discussed in Carr [**1**]. The following quadratic approximation is obtained:

$$\begin{aligned} \dot{u}_1 &= (1 + a_1 u_1 + O(\|u\|^2))u_2 \\ \dot{u}_2 &= (a_2 u_1 + O(\|u\|^2))u_2, \end{aligned} \tag{9}$$

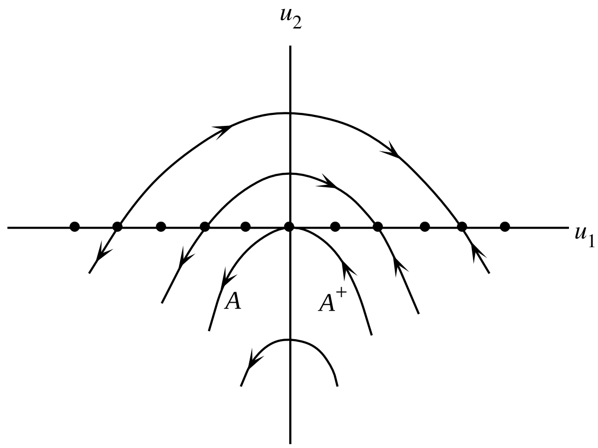

FIGURE 2.

where (u_1, u_2) are the variables on the center manifold of C_{p^*}, which is the origin in the (u_1, u_2)-system. It is important that $a_2 < 0$ and that the u_1 variable is just a translation of the p variable. The flow for (9) near the origin is given in Figure 2.

Hence, Munoz and Selgrade [**13**] conclude:

LEMMA 2.3. *Assume* (A1), (A2) *and* (A3) *and that* $K = 0$. *Then each center manifold of* C_{p^*} *contains a unique orbit* $\mathcal{A}^+$ *which is asymptotic to* C_{p^*} *as* $t \to \infty$ *and a unique orbit* $\mathcal{A}^-$ *which is asymptotic to* C_{p^*} *as* $t \to -\infty$. *In addition, the* p*-components of* $\mathcal{A}^+$ *and* $\mathcal{A}^-$ *are decreasing functions of* t.

Although the center manifold of C_{p^*} may not be unique, a recent result of Chow and Lin (see Appendix A in [**3**]) implies that each orbit negative asymptotic to C_{p^*} ultimately belongs to every center unstable manifold. Thus, since C_{p^*} has no strong unstable manifold and Lemma 2.3 implies that each center manifold contains a unique orbit negatively asymptotic to C_{p^*}, there is only one orbit in $\mathcal{S}$ negatively asymptotic to C_{p^*}, i.e., $\mathcal{A}^-$ is unique in $\mathcal{S}$. On the other hand, $\mathcal{A}^+$ may not be unique in $\mathcal{S}$ because C_{p^*} has a three-dimensional center stable manifold and so the $\mathcal{A}^+$'s in each center manifold need not coincide.

Using Lemmas 2.2 and 2.3 and the previous uniqueness remark, we have the following:

THEOREM 2.4 (MUNOZ/SELGRADE). *Assume* (A1), (A2)*, and* (A3) *and* $K = 0$. *There exist heteroclinic orbits from* M_1 *to* C_{p^*} *and a unique orbit,* $\mathcal{A}^-$*, from* C_{p^*} *to* M_0.

3. Limits of heteroclinic orbits. For all results in the next two sections, we tacitly assume (A1), (A2), and (A3).

A large change in the vector field F may not be reflected by a changed in K, so we may not use K as a bifurcation parameter in studying limits of heteroclinic orbits as a parameter varies. Henceforth, we fix all parameters except γ, which measures the self-repression in the genetically invariant population N; and we consider the family of vector fields F_γ which vary C^r with γ for any $r \geq 0$. From (8) it is clear that K is a decreasing, linear function of γ. Let γ_0 be the value of γ between β_{AA} and β_{aa} where $K = 0$. For $\gamma < \gamma_0$, $K > 0$ and there are heteroclinic orbits from M_1 to C_0. For $\gamma > \gamma_0$, $K < 0$ and there is a unique heteroclinic orbit from C_1 to M_0 for each γ. We suggest that, as γ decreases to γ_0, the family of heteroclinic orbits from C_1 to M_0 approaches the union of the line segment of equilibria from C_1 to C_{p^*} and the unique orbit $\mathcal{A}^-$ from C_{p^*} to M_0. Also, as γ increases to γ_0, any one-parameter family of orbits from M_1 to C_0 approaches the union of the line segment of equilibria from C_{p^*} to C_0 and one of the orbits from M_1 to C_{p^*}.

For each γ, $\gamma_0 < \gamma < \beta_{aa}$, let $\mathcal{O}(\gamma)$ denote the unique heteroclinic orbit from C_1 to M_0. For $\beta_{AA} < \gamma < \gamma_0$, let $\mathcal{O}'(\gamma)$ denote one of the heteroclinic orbits from M_1 to C_0. The " $'$ " notation is used to indicate a choice has been made; and " $'$ " will be omitted when the meaning is clear from the context. When $\gamma > \gamma_0$, C_1 is below $\mathcal{H}$ and orbits starting below $\mathcal{H}$ stay below $\mathcal{H}$. When $\gamma < \gamma_0$, C_0 is below $\mathcal{H}$ and an orbit ending below $\mathcal{H}$ must have always been below $\mathcal{H}$. Hence, $\mathcal{O}(\gamma)$ has a decreasing p-component. Let $\mathcal{P}_c$ be the vertical plane determined by fixing p equal to c, $0 \le c \le 1$, i.e.,

$$\mathcal{P}_c \equiv \{(p, M, N) \in \mathcal{S} : p = c\}.$$

Then $\mathcal{O}(\gamma)$ meets $\mathcal{P}_c$ exactly once. So we define this point of intersection as

$$\mathcal{O}_c(\gamma) \equiv \mathcal{O}(\gamma) \cap \mathcal{P}_c.$$

Note that $\mathcal{O}_c(\gamma)$ always lies below $\mathcal{H}$.

In order to study $\lim_{\gamma \to \gamma_0} \mathcal{O}_p(\gamma)$ for $0 < p < 1$, we need several geometric results about the vector field F_γ. There is an attracting, positively invariant, compact set A for F_γ for all γ, $\beta_{AA} < \gamma < \beta_{aa}$. A is the region between two planes—one where η is a positive constant and the other where η is a negative constant. These planes are chosen so that one is just below (i.e., closer to the origin) the region between the planes $\{\mu_{AA} = 0\}$ and $\{\mu_{aa} = 0\}$, and the other is just above this region. Since the surface $\{\mu = 0\}$ lies between $\{\mu_{AA} = 0\}$ and $\{\mu_{aa} = 0\}$, F_γ points into A on its boundary. Also, it is easy to see that all solutions to (6), except the p-axis, ultimately enter A.

For notational convenience, let $x = (p, M, N) \in \mathcal{S}$. Also, we treat the parameter γ as an additional variable, i.e., consider the four-dimensional system of equations:

$$\begin{aligned} \dot{x} &= F_\gamma(x) \\ \dot{\gamma} &= 0. \end{aligned} \tag{10}$$

The x-component of the flow of (10) is denoted by $\phi(x, \gamma, t)$, i.e., $\phi(x, \gamma, t)$ is the flow of $F_\gamma(x)$. Clearly, the vector field of (10) is C^r on A for any $r \ge 0$, and so the flow ϕ depends smoothly on x and γ.

Many of our subsequent lemmas are stated for sequences $\gamma_n \to \gamma_0$ as $n \to \infty$.

LEMMA 3.1. *Fix* $p_0 \in (0, 1)$. *Suppose* $z \in \mathcal{H}$ *and* $\lim_{\gamma_n \to \gamma_0} \mathcal{O}_{p_0}(\gamma_n) = z$. *Then* $z = C_{p_0}$.

PROOF. If $z \ne C_{p_0}$, then, for $\gamma = \gamma_0$, the negative-time orbit of z leaves the attractor A and never returns. By continuity of ϕ, this is also true for the negative-time orbit of $\mathcal{O}_{p_0}(\gamma_n)$ for γ_n close to γ_0.

This contradicts the fact that $\mathcal{O}(\gamma_n)$ is negatively asymptotic to C_1 if $\gamma_n > \gamma_0$ or to M_1 if $\gamma_n < \gamma_0$. $\square$

LEMMA 3.2. *Fix* $p_0 \in (0,1)$. *Suppose* $z \notin \mathcal{H}$ *and* $\lim_{\gamma_n \to \gamma_0} \mathcal{O}_{p_0}(\gamma_n) = z$. *Take* $T > 0$. *Then, for each* $t \in [-T, T]$, *there is a* $p_t \in (0,1)$ *so that* $\phi(z, \gamma_0, t) \in \mathcal{P}_{p_t}$ *and* $\lim_{\gamma_n \to \gamma_0} \mathcal{O}_{p_t}(\gamma_n) = \phi(z, \gamma_0, t)$.

PROOF. We prove this result for positive t and a similar argument works for negative t.

Since z is below $\mathcal{H}$, the p-component of the orbit of z is decreasing. Let p_t be the value of p so that $\phi(z, \gamma_0, t) \in \mathcal{P}_{p_t}$. Take $\epsilon > 0$. Construct a tubular neighborhood of radius ϵ around the orbit of z extending beyond $\mathcal{P}_{p_t}$ so that orbits in this neighborhood cross through $\mathcal{P}_{p_t}$. Then take a neighborhood B of (z, γ_0) so that the x-component of solutions to (10) starting in B stay in the tubular neighborhood until they pass through $\mathcal{P}_{p_t}$. But, for γ_n close to γ_0, $(\mathcal{O}_{p_0}(\gamma_n), \gamma_n)$ belongs to B, and, hence, $\mathcal{O}_{p_t}(\gamma_n)$ is within ϵ of $\phi(z, \gamma_0, t)$. Since ϵ is arbitrary, we have the result. $\square$

The next result about α- and ω-limit sets, when $\gamma = \gamma_0$, follows from Theorem 2.1 and Lemma 2.2.

LEMMA 3.3. *Suppose* $\gamma = \gamma_0$ *and* z *lies below* $\mathcal{H}$ *in the interior of* $\mathcal{S}$. *Then* $\alpha(z) = M_1$, $\alpha(z) = C_p$ *for some* $p \le p^*$, *or* $\alpha(z) \cap A = \phi$. *Also,* $\omega(z) = M_0$ *or* $\omega(z) = C_p$ *for some* $p \ge p^*$.

Next we show which of the points in Lemma 3.3 may be α- and ω-limit sets for points which are limits of the heteroclinic orbits.

LEMMA 3.4. *Suppose* $z \notin \mathcal{H}$ *and* $z = \lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_{p_0}(\gamma_n)$ *for some* $p_0 \in (0,1)$. *Then* $\alpha(z) = C_p$ *for some* $p \le p^*$.

PROOF. We need to eliminate the possibility of $\alpha(z) = M_1$ or of $\alpha(z) \cap A = \phi$. If the negative-time orbit of z leaves A, then so

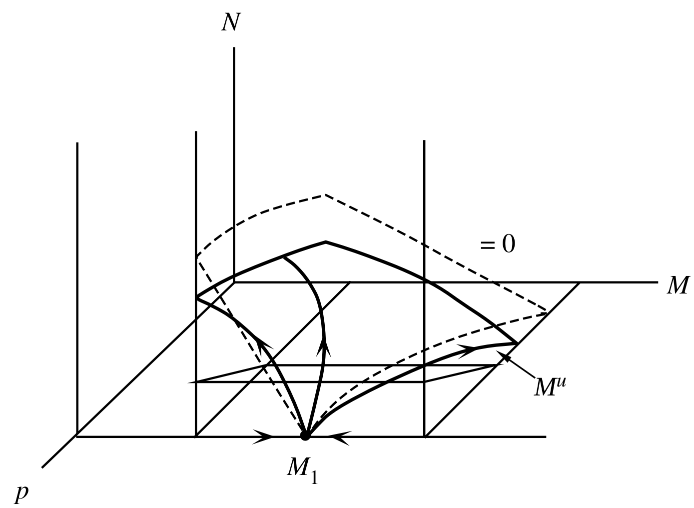

FIGURE 3(a).

does $\mathcal{O}(\gamma_n)$ for γ_n near γ_0, but this contradicts the fact that $\mathcal{O}(\gamma_n)$ is negatively asymptotic to C_1 for $\gamma_n > \gamma_0$. Hence, $\alpha(z) \subset A$.

Assume $\alpha(z) = M_1 = (1, 1/\alpha_{AA}, 0)$. For all γ, M_1 is a hyperbolic equilibrium with a one-dimensional stable manifold parallel to the M-axis in $\{p = 1\}$ and a two-dimensional unstable manifold $\mathcal{M}^u$ meeting the interior of $\mathcal{S}$. We need to control the long-term behavior of negative-time orbits passing near M_1 for γ near γ_0. For this, we construct an isolating block [**2, 4, 5, 12**] relative to the set $\mathcal{S}$ for M_1. Normally, an isolating block for a flow is not a block for all nearby flows; however, the block B we use will work for flows F_γ if γ is close to γ_0. B is a five-sided wedge, see Figure 3, with vertical front face in $\{p = 1\}$, with bottom in the plane $\{N = 0\}$, with triangular vertical sides perpendicular to $\{N = 0\}$, and with rectangular top slanted from $\{p = 1\}$ to $\{N = 0\}$. The triangular sides are the entrance set (where orbits enter B), the top is the exit set, and the line segments common to the top and the triangular sides are the tangency set, see Figure 3(b). To construct B

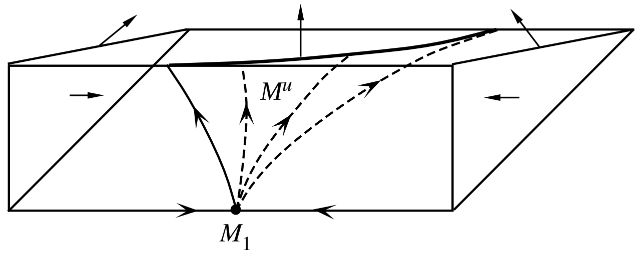

FIGURE 3(b).

this way, notice that $\{\mu = 0\}$ and $\mathcal{M}^u$ are both transverse to $\{N = 0\}$ and to $\{p = 1\}$. Thus the top can be chosen transverse to $\{\mu = 0\}$ and to $\mathcal{M}^u$ so that $\{\mu = 0\}$ and $\mathcal{M}^u$ intersect the top in its interior, see Figure 3(a). The choice of top essentially determines B. Since the triangles are on opposite sides of $\{\mu = 0\}$, F_γ points to the left on the right triangle and to the right on the left triangle. Hence, the triangles are entrance sets. By taking γ close to γ_0 and by shrinking B (i.e., choosing M closer to $1/\alpha_{AA}$ and N closer to 0), we get that F_γ points out on the top of B. The crucial property which we need for B is that the negative-time orbits of points on the triangular sides leave A. This is obtained by shrinking B again so that the triangles are close to the stable manifold of M_1 which leaves A in negative time.

Recall that $\alpha(z) = M_1$, and so $z \in \mathcal{M}^u$. By continuity, there is a neighborhood of (z, γ_0) which has negative-time ϕ orbits entering B. In particular, $\mathcal{O}(\gamma_n)$ enters B for γ_n near γ_0. But negative-time orbits in B are negatively asymptotic to M_1 or leave B through the triangular sides and, hence, leave A in negative time. This contradicts the fact that $\mathcal{O}(\gamma_n)$ is negatively asymptotic to C_1. The conclusion of this lemma now follows from Lemma 3.3. $\square$

LEMMA 3.5. *Suppose $z \notin \mathcal{H}$ and $z = \lim_{\gamma_n \nearrow \gamma_0} \mathcal{O}'_{p_0}(\gamma_n)$ for some $p_0 \in (0,1)$. Then $\omega(z) = C_p$ for some $p \geq p^*$.*

PROOF. Assume $\omega(z) = M_0$. M_0 is locally, asymptotically stable for all γ, so, for γ near γ_0, there is an attracting neighborhood U of M_0. Hence, there is a neighborhood of (z, γ_0) with orbits entering U; for γ_n near γ_0, $\mathcal{O}'(\gamma_n)$ enters U and is asymptotic to M_0. This contradicts the fact that $\mathcal{O}'(\gamma_n)$ is asymptotic to C_0 for $\gamma_n < \gamma_0$. The result now follows from Lemma 3.3. $\square$

Using the previous two lemmas, we show that portions of the heteroclinic orbits converge to subsegments of the line of equilibria.

THEOREM 3.6. *For each* $p_0 \geq p^*$, $\lim_{\gamma \searrow \gamma_0} \mathcal{O}_{p_0}(\gamma) = C_{p_0}$. *For each* $p_0 \leq p^*$, $\lim_{\gamma \nearrow \gamma_0} \mathcal{O}'_{p_0}(\gamma) = C_{p_0}$.

PROOF. To establish the first limit, we show that the assertion is true for every sequence $\gamma_n \searrow \gamma_0$. Assume there is a $z \neq C_{p_0}$ so that $\lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_{p_0}(\gamma_n) = z$. By Lemma 3.1, $z \notin \mathcal{H}$ so the p-component of the orbit of z is decreasing. Lemma 3.4 implies that $\alpha(z) = C_p$ for some $p \leq p^*$, but this is impossible since the negative-time orbit of z lies in the region where $p > p^*$.

To prove the second assertion, take a sequence $\gamma_n \nearrow \gamma_0$ and assume that $\lim_{\gamma_n \nearrow \gamma_0} \mathcal{O}'_{p_0}(\gamma_n) = z \neq C_{p_0}$. Lemma 3.5 gives that $\omega(z) = C_p$ for some $p \geq p^*$. But the positive orbit of z lies in the region where $p < p^*$. Hence, we have a contradiction. $\square$

LEMMA 3.7. *If* $p_0 < p^*$ *and* $\lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_{p_0}(\gamma_n) = C_{p_0}$, *then* $\lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_p(\gamma_n) = C_p$ *for all* $p \geq p_0$. *Also, if* $p_0 > p^*$ *and* $\lim_{\gamma_n \nearrow \gamma_0} \mathcal{O}'_{p_0}(\gamma_n) = C_{p_0}$, *then* $\lim_{\gamma_n \nearrow \gamma_0} \mathcal{O}'_p(\gamma_n) = C_p$ *for all* $p \leq p_0$.

PROOF. To prove the first assertion, we need to consider only $p \in (p_0, p^*)$ because of Theorem 3.6. Assume there is a $z \in \mathcal{P}_p$ with $z \neq C_p$ so that $z = \lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_p(\gamma_n)$. From Lemmas 3.1 and 3.3, $\omega(z) = M_0$. Let $T > 0$ be the time so that $\phi(z, \gamma_0, T) \in \mathcal{P}_{p_0}$. Lemma 3.2 implies that $\lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_{p_0}(\gamma_n) = \phi(z, \gamma_0, T)$, which is a contradiction.

For the second assertion, we consider $p \in (p^*, p_0)$ and assume there is a $z \in \mathcal{P}_p$ with $z \neq C_p$ so that $\lim_{\gamma_n \nearrow \gamma_0} \mathcal{O}'_p(\gamma_n) = z$. It follows that

$\alpha(z) = M_1$, and, hence, there is a $T > 0$ so that $\phi(z, \gamma_0, -T) \in \mathcal{P}_{p_0}$. Applying Lemma 3.2 again, we reach a contradiction. $\square$

Theorem 3.6 and Lemma 3.7 show that, for $\gamma \searrow \gamma_0$, the heteroclinic orbits $\mathcal{O}(\gamma)$ approach the subsegment of equilibria of $\mathcal{L}$ from $p = 1$ to $p = p_0$ for some $p_0 \leq p^*$. Lemma 3.2 and Lemma 3.4 can be used to show that the rest of $\mathcal{O}(\gamma)$ approach the unstable manifold of C_{p_0}. In the next section we use perturbation analysis of the dynamical behavior of F_γ near C_{p^*} to conclude that $p_0 = p^*$. Hence, the rest of $\mathcal{O}(\gamma)$ approaches $\mathcal{A}^-$ as $\gamma \searrow \gamma_0$.

4. Perturbation analysis. In order to complete the analysis of the limiting behavior of $\mathcal{O}(\gamma)$, we need to study carefully these heteroclinic orbits as they pass near C_{p^*}. Our approach is to consider (6) a perturbation problem for γ close to γ_0. The behavior of F_{γ_0} on the center manifold of C_{p^*} is reminiscent of the degenerate behavior in two-dimensional singularly perturbed systems, e.g., see Eckhaus [**7**] and Schecter [**14**]. Intuitively, the orbits $\mathcal{O}(\gamma)$ remain close to the center manifold because of the strong contraction along the line $\mathcal{L}$ of equilibria transverse to the center manifold, see Fenichel [**8**]. $\mathcal{L}$ is the "slow manifold," and, for $\gamma \geq \gamma_0$ and $\gamma \sim \gamma_0$, an orbit $\mathcal{O}(\gamma)$ leaves C_1 and remains close to $\mathcal{L}$ as a consequence of Theorem 3.6. As $\mathcal{O}(\gamma)$ passes $C_{p^*}, \mathcal{O}(\gamma)$ moves away from $\mathcal{L}$ along $\mathcal{A}^-$. To see this, we need a coordinate change in a neighborhood of C_{p^*} for $\gamma \sim \gamma_0$ which illustrates how the flow curves slide off the slow manifold at C_{p^*}. Here we argue for $\gamma > \gamma_0$; however, a similar argument may be given for $\gamma < \gamma_0$ by reversing the time as discussed at the end of this section. The difficulty with $\gamma < \gamma_0$ is the nonuniqueness of $\mathcal{A}^+$. We introduce a small parameter ϵ in (6) by defining $\epsilon \equiv \gamma - \gamma_0$. A translation, a linear transformation, and then a nonlinear map are performed on the variables in (6) in order to render the system in a more workable form. To simplify the expressions, we use the following notation:

$$\alpha \equiv \alpha_{aa} - \alpha_{AA} < 0, \quad \sigma \equiv \alpha_{AA}\beta_{aa} - \alpha_{aa}\beta_{AA} > 0,$$
$$\beta \equiv \beta_{aa} - \beta_{AA} > 0, \quad \tau \equiv (\alpha_{AA} - \delta)(\delta - \alpha_{aa}) > 0,$$

$$\sigma_i \equiv \alpha_{ii}\gamma_0 - \beta_{ii}\delta \quad \text{for } i = A, a.$$

In the (p, M, N) coordinates, $C_{p^*} = ((\alpha_{aa} - \delta)/\alpha, \beta/\sigma, -\alpha/\sigma)$. Notice that C_{p^*} does not depend on ϵ. Recall that x denotes a point in (p, M, N)-space. Let T_1 translate C_{p^*} to the origin in y-space, i.e., $y = T_1(x)$. The linear transformation T_2 maps the two-dimensional center subspace at C_{p^*} to the $\{z_3 = 0\}$ plane in the z-space. So $z = T_2(y)$, where

$$T_2 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & \sigma\tau(\delta - \alpha_{aa})/(2\alpha^2\sigma_a) & \sigma\tau(\gamma_0 - \beta_{aa})/(2\alpha^2\sigma_a) \\ 0 & -\delta/\sigma_a & -\gamma_0/\sigma_a \end{pmatrix}.$$

In the z-coordinate system, (6) becomes

(11)

$$\begin{aligned}
\dot{z}_1 &= z_2 - \alpha(\alpha_{aa} + \alpha_{AA} - 2\delta)z_1 z_2/\tau - \alpha^2 z_1^2 z_2/\tau \\
\dot{z}_2 &= \epsilon(\beta_{aa} - \gamma_0)[\tau/(2\sigma) - \tau(\delta - \alpha_{aa})z_3/\alpha - 2\delta\alpha z_2 \\
&\qquad + 2\delta(\delta - \alpha_{aa})z_2 z_3 + 2\delta^2\alpha^2 z_2^2/(\sigma\tau) \\
&\qquad + \sigma\tau(\delta - \alpha_{aa})^2 z_3^2/(2\alpha^2)]/\sigma_a \\
&\quad + \beta(\delta - \alpha_{aa})z_1 z_2/\sigma_a + \sigma_a z_2 z_3 \\
&\quad - 2\gamma_0\alpha^2(\delta - \alpha_{aa})z_1 z_2^2/(\tau\sigma_a) + \sigma(\delta - \alpha_{aa})(\beta_{aa} - \gamma_0)z_1 z_2 z_3/\sigma_a \\
\dot{z}_3 &= \epsilon\gamma_0[\alpha^2 - 4\delta\alpha^3 z_2/\tau - 2\alpha\sigma(\delta - \alpha_{aa})z_3 \\
&\qquad + 4\delta\sigma\alpha^2(\delta - \alpha_{aa})z_2 z_3/\tau + 4\delta^2\alpha^4 z_2^2/\tau^2 \\
&\qquad + \sigma^2(\delta - \alpha_{aa})^2 z_3^2]/(\sigma^2\sigma_a) \\
&\quad - z_3 - 2\beta\delta\alpha^2 z_1 z_2/(\tau\sigma\sigma_a) + \sigma_a z_3^2 \\
&\quad + 4\delta\gamma_0\alpha^4 z_1 z_2^2/(\tau^2\sigma\sigma_a) - 2\delta\alpha^2(\beta_{aa} - \gamma_0)z_1 z_2 z_3/(\tau\sigma_a).
\end{aligned}$$

If $\epsilon = 0$, (11) corresponds to equation (9) in [**13**] and, hence, describes the behavior of solutions to (6) when $K = 0$. The composite transformation $T_2 \circ T_1$ maps $\mathcal{L}$ to the z_1-axis and maps the plane $\mathcal{H}$ to the plane $\{z_2 = 0\}$ with the region below $\mathcal{H}$ mapped to the region where $z_2 < 0$. The center manifold of the origin is a surface tangent to the plane $\{z_3 = 0\}$. The flow on this manifold may be obtained from the first two equations in (11) by setting $\epsilon = 0$ and by using the fact that, on this manifold, z_3 has a quadratic approximation in terms of z_1 and z_2 (see [**13**]). Grouping the higher order terms gives (9), where

$$a_2 \equiv \beta(\delta - \alpha_{aa})/\sigma_a < 0.$$

From Figure 2, notice that the orbits near zero form curves which are given approximately by parabolas. The last transformation T_3 is chosen

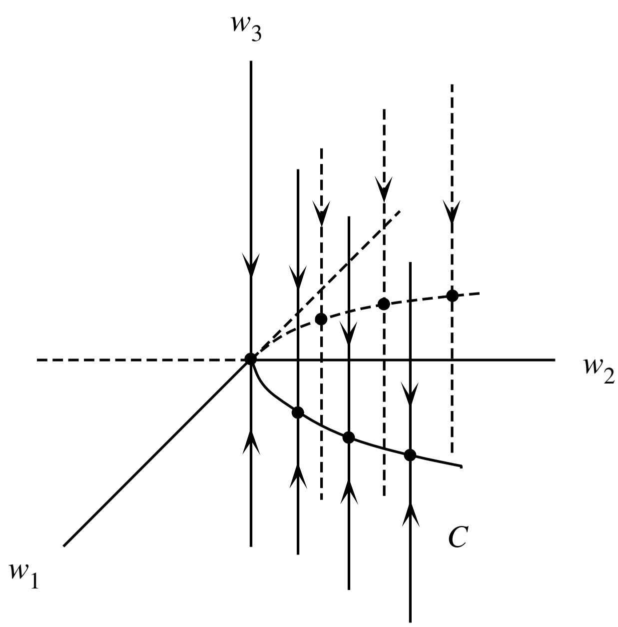

FIGURE 4.

so that these curves are approximately horizontal lines, and the line of equilibria is a parabola, see Figure 4. Define $w = T_3(z)$ by

$$T_3(z_1, z_2, z_3) = (z_1, z_2 - a_2 z_1^2/2, z_3).$$

T_3 maps the z_1-axis to the parabola $\{(w_1, w_2, w_3) : w_2 = -a_2 w_1^2/2, w_3 = 0\}$ and maps the plane $\{z_2 = 0\}$ to the parabolic cylinder $\mathbf{C} \equiv \{(w_1, w_2, w_3) : w_2 = -a_2 w_1^2/2\}$, see Figure 4.

Hence, $T \equiv T_3 \circ T_2 \circ T_1$ is a change of variables for (6) yielding the system

(12)

$$
\begin{aligned}
\dot{w}_1 &= (w_2 + a_1 w_1^2/2)[1 - \alpha(\alpha_{aa} + \alpha_{AA} - 2\delta)w_1/\tau - \alpha^2 w_1^2/\tau] \\
\dot{w}_2 &= \epsilon\tau(\beta_{aa} - \gamma_0)/(2\sigma\sigma_a) - \epsilon\tau(\beta_{aa} - \gamma_0)(\delta - \alpha_{aa})w_3/(\alpha\sigma_a) \\
&\quad + \epsilon\sigma\tau(\delta - \alpha_{aa})^2(\beta_{aa} - \gamma_0)w_3^2/(2\alpha^2\sigma_a) \\
&\quad + (w_2 + a_2 w_1^2/2)[-2\epsilon\delta\alpha(\beta_{aa} - \gamma_0)/\sigma_a \\
&\qquad\qquad + 2\epsilon\delta(\beta_{aa} - \gamma_0)(\delta - \alpha_{aa})w_3/\sigma_a \\
&\qquad\qquad + 2\epsilon\delta^2\alpha^2(\beta_{aa} - \gamma_0)(w_2 + a_2 w_1^2/2)/(\tau\sigma\sigma_a) \\
&\qquad\qquad + \sigma_a w_3 \\
&\qquad\qquad - 2\gamma_0\alpha^2(\delta - \alpha_{aa})w_1(w_2 + a_2 w_1^2/2)/(\tau\sigma_a) \\
&\qquad\qquad + \sigma(\delta - \alpha_{aa})(\beta_{aa} - \gamma_0)w_1 w_3/\sigma_a \\
&\qquad\qquad + a_2\alpha(\alpha_{aa} + \alpha_{AA} - 2\delta)w_1^2/\tau + a_2\alpha^2 w_1^3/\tau] \\
\dot{w}_3 &= \epsilon\gamma_0\alpha^2/(\sigma^2\sigma_a) - w_3 + \sigma_a w_3^2 - 2\epsilon\gamma_0\alpha(\delta - \alpha_{aa})w_3/(\sigma\sigma_a) \\
&\quad + \epsilon\gamma_0(\delta - \alpha_{aa})^2 w_3^2/\sigma_a \\
&\quad + (w_2 + a_2 w_1^2/2)[-4\epsilon\gamma_0\delta\alpha^3/\sigma - 2\beta\delta\alpha^2 w_1 \\
&\qquad\qquad + 4\epsilon\gamma_0\delta\alpha^2(\delta - \alpha_{aa})w_3 \\
&\qquad\qquad + 4\epsilon\gamma_0\delta^2\alpha^4(w_2 + a_2 w_1^2/2)/(\tau\sigma) \\
&\quad + 4\delta\gamma_0\alpha^4 w_1(w_2 + a_2 w_1^2/2)/\tau - 2\delta\sigma\alpha^2(\beta_{aa} - \gamma_0)w_1 w_3]/(\tau\sigma\sigma_a).
\end{aligned}
$$

Since $w = T(x)$, the vector field of (12) is given by $TF_\epsilon T^{-1}$, where F_ϵ is the vector field of (6). T maps $\mathcal{H}$ to $\mathbf{C}$, and, since F_ϵ points down on $\mathcal{H}$ when $\epsilon > 0$, $TF_\epsilon T^{-1}$ points to the left on $\mathbf{C}$. Also, the w_1 variable is a translation of the p variable. The image of the heteroclinic orbits $\mathcal{O}(\epsilon)$ under T are orbits staying close to $T(\mathcal{L})$ just to the left of $\mathbf{C}$ with w_1-coordinate decreasing to zero. The orbits $T(\mathcal{O}(\epsilon))$ meet the plane $\{w_1 = 0\}$ at points with negative w_2-coordinates. These intersection points converge to the origin as $\epsilon \searrow 0$ by Theorem 3.6.

Now we show that the orbits $T(\mathcal{O}(\epsilon))$ may not approach any equilibrium on the back side of $\mathbf{C}$, i.e., with negative w_1-coordinate. We do this by exhibiting a small region on a plane with w_2 equal to a constant near $T(\mathcal{L})$ on which the w_2-component of $TF_\epsilon T^{-1}$ is negative. Intuitively, $T(\mathcal{O}(\epsilon))$ is being pushed away from $T(\mathcal{L})$ on the back side of $\mathbf{C}$ because these equilibria have unstable manifolds.

LEMMA 4.1. *Assume* $\alpha_{aa} + \alpha_{AA} \geq 2\delta$. *If* $\bar{p} < p^*$ *and* $\gamma_n \searrow \gamma_0$, *then* $\lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_{\bar{p}}(\gamma_n) \neq C_{\bar{p}}$.

PROOF. Suppose $\lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_{\bar{p}}(\gamma_n) = C_{\bar{p}}$. Lemma 3.7 implies that $\lim_{\gamma_n \searrow \gamma_0} \mathcal{O}(\gamma_n) = C_p$ for all $p \geq \bar{p}$. Let $(\bar{w}_1, -a_2\bar{w}_1^2/2, 0) = T(C_{\bar{p}})$. Consider the equilibrium on $T(\mathcal{L})$ closer to the origin than $T(C_{\bar{p}})$, given by $(\hat{w}_1, -a_2\hat{w}_1^2/2, 0) = T(C_{\hat{p}})$ for some $\hat{w}_1 \in (\bar{w}_1, 0)$ and some $\hat{p} > \bar{p}$. Since $\lim_{\gamma_n \searrow \gamma_0} T(\mathcal{O}_{\hat{p}}(\gamma_n)) = T(C_{\hat{p}})$, the points $T(\mathcal{O}_{\hat{p}}(\gamma_n))$ approach $T(C_{\hat{p}})$ to the left of the cylinder $\mathbf{C}$ and near the plane $\{w_3 = 0\}$. The orbits $T(\mathcal{O}(\gamma_n))$ stay close to $\{w_3 = 0\}$ because of the strong contraction normal to $\{w_3 = 0\}$. In order to limit on $T(C_{\bar{p}})$ as $\gamma_n \searrow \gamma_0$ (i.e., $\epsilon \searrow 0$), the orbits $T(\mathcal{O}(\gamma_n))$ must cross through $\{w_2 = -a_2\hat{w}_1^2/2\}$ in the positive w_2-direction between $\{w_1 = \hat{w}_1\}$ and $\{w_1 = \bar{w}_1\}$. But we show that $TF_\epsilon T^{-1}$ points in the negative w_2-direction for (w_1, w_3) near $(\bar{w}_1, 0)$, i.e, for $\hat{w}_1$ near $\bar{w}_1$, and for all ϵ small.

To see this, rewrite the w_2-component of $TF_\epsilon T^{-1}$ on $\{w_3 = -a_2\hat{w}_1^2/2\}$ where the ϵ terms are grouped together:

$$\dot{w}_2 = \epsilon h(w_1, w_3) + g(w_1, w_3). \tag{13}$$

From (12) note that

$$\begin{aligned} h(w_1, 0) =& \tau(\beta_{aa} - \gamma_0)/(2\sigma\sigma_a) - \delta\alpha(\beta_{aa} - \gamma_0)(w_1^2 - \hat{w}_1^2)a_2/\sigma_a \\ &+ \delta^2\alpha^2(\beta_{aa} - \gamma_0)(w_1^2 - \hat{w}_1^2)^2 a_2^2/(2\tau\sigma\sigma_a), \end{aligned}$$

where the first term is a negative constant, the third term is not positive since $(w_1^2 - \hat{w}_1^2) \geq 0$ for $w_1 \in [\bar{w}_1, \hat{w}_1]$, and the second term is made small by taking $\hat{w}_1$ near $\bar{w}_1$. Hence, for $\hat{w}_1 \sim \bar{w}_1$ and $w_3 \sim 0$, $h(w_1, w_3)$ is bounded above by a negative constant for all $w_1 \in [\bar{w}_1, \hat{w}_1]$. Also, $g(w_1, w_3) \leq 0$ for all $w_1 \in [\bar{w}_1, \hat{w}_1]$ if $w_3 \sim 0$ and $\hat{w}_1 \sim \bar{w}_1$. This can be seen from the formula

$$\begin{aligned} g(w_1, w_3) = a_2(w_1^2 - \hat{w}_1^2)[&\sigma_a w_3 + \sigma(\delta - \alpha_{aa})(\beta_{aa} - \gamma_0)w_1 w_3/\sigma_a \\ &+ a_2\alpha^2 w_1^3/\tau \\ &- \gamma_0\alpha^2(\delta - \alpha_{aa})w_1(w_1^2 - \hat{w}_1^2)a_2/(\tau\sigma_a) \\ &+ a_2\alpha(\alpha_{aa} + \alpha_{AA} - 2\delta)w_1^2/\tau]/2, \end{aligned}$$

where the sum inside the bracket is positive for $w_3 \sim 0$ because of the third term and the assumption that $\alpha_{aa} + \alpha_{AA} \geq 2\delta$, and the term outside the bracket is not positive. This completes the proof. $\square$

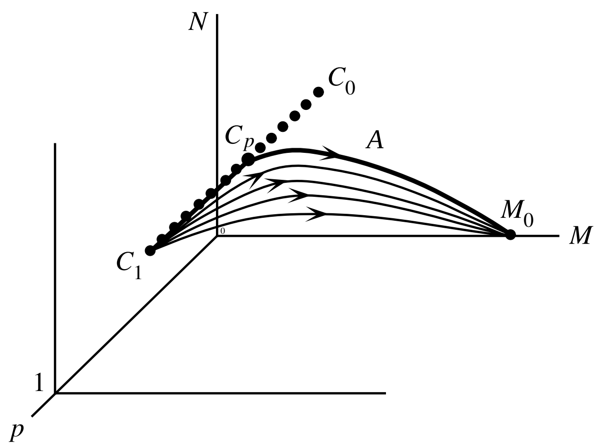

FIGURE 5(a). $\gamma \searrow \gamma_0$ $(K < 0)$.

THEOREM 4.2. *Assume* $\alpha_{aa} + \alpha_{AA} \geq 2\delta$. *Then* $\lim_{\gamma \searrow \gamma_0} \mathcal{O}_p(\gamma) = C_p$ *for all* $p \geq p^*$ *and* $\lim_{\gamma \searrow \gamma_0} \mathcal{O}_p(\gamma) = \mathcal{A}^- \cap \mathcal{P}_p$ *for all* $p < p^*$.

PROOF. Fix $p < p^*$ and assume there is a $\gamma_n \searrow \gamma_0$ so that $\lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_p(\gamma_n) = z \neq \mathcal{A}^- \cap \mathcal{P}_p$. Lemma 3.4 and the uniqueness of $\mathcal{A}^-$ imply that $\alpha(z) = C_{p_0}$ for some $p_0 < p^*$. Using Lemma 3.2, we see that $\lim_{\gamma_n \searrow \gamma_0} \mathcal{O}_{p_0}(\gamma_n) = C_{p_0}$. But this contradicts Lemma 4.1. With Theorem 3.6, the result is proved. □

Theorem 4.2 gives a complete description of the limit of the heteroclinic orbits for $\gamma > \gamma_0$, see Figure 5(a). For $\gamma < \gamma_0$ and a family of orbits $\mathcal{O}'(\gamma)$, a similar argument may be used to obtain a result like Lemma 4.1 by reversing the time and analyzing the flow near the front face of the cylinder **C**, see Figure 4. But, because of the nonuniqueness of $\mathcal{A}^+$, for $\gamma_n \nearrow \gamma_0$, we get that $\mathcal{O}'(\gamma_n)$ converges to some $\mathcal{A}^+$ which may depend on γ_n, see Figure 5(b). Also, although the condition $\alpha_{aa} + \alpha_{AA} \geq 2\delta$ is used in our proof, we do not believe it is necessary for the result.

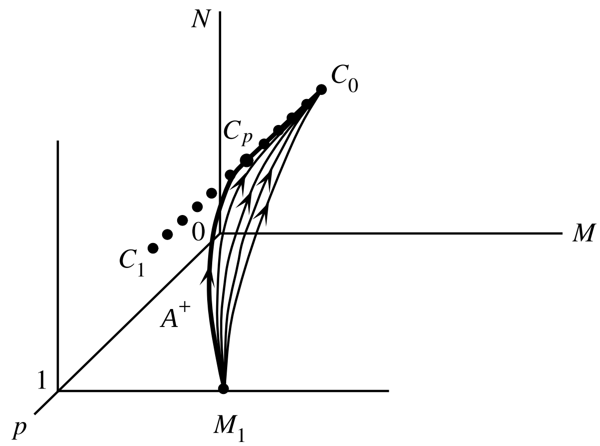

FIGURE 5(b). $\gamma \nearrow \gamma_0$ $(K > 0)$.

Acknowledgment. The author would like to thank X.-B. Lin and S. Schecter for helpful conversations and C. Carothers for drawing the figures.

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