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Existence and nonexistence of steady-state solutions for a selection-migration model in population genetics

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Abstract. We discuss a selection-migration model in population genetics, involving two alleles A_1 and A_2 such that A_1 is at an advantage over A_2 in certain subregions and at a disadvantage in others. It is shown that if A_1 is at an overall disadvantage to A_2 and the rate of gene flow is sufficiently large than A_1 must die out; on the other hand, if the two alleles are in some sense equally advantaged overall, then A_1 and A_2 can coexist no matter how great the rate of gene flow.

Key words: Population genetics — Bifurcation theory — Indefinite weight functions — Sub- and supersolutions

1. Introduction

In this paper we discuss solutions of a semilinear elliptic equation arising in population genetics introduced by Fleming in [6]. Consider a model with two alleles A_1 and A_2 corresponding to three possible genotypes A_1A_1, A_1A_2, A_2A_2. The population lives in a region D in R^n. Let $u(x, t)$ denote the frequency of the allele A_1 at time t at the point x in D. Changes in gene frequency are assumed to be caused only by the flow of genes within D and selective advantages for certain genotypes in certain sub-regions of D. Then u satisfies the semilinear parabolic equation

$$u_t(x, t) = d\Delta u + g(x)f(u) \quad \text{in } D$$

where Δ denotes the Laplacian and $f(u) = u(1-u)[h(1-u)+(1-h)u]$ for some constants $d > 0$, $0 < h < 1$. The term $d\Delta u$ represents the effect of gene flow. The term $g(x)f(u)$ represents the effect of natural selection where the fitness coefficients of the genotypes A_1A_2 and A_2A_2 relative to A_1A_1 are respectively $1 - hg(x)$ and $1 - g(x)$. We assume that g takes on both positive and negative values on the region D; this corresponds to the allele A_1 having an advantage over A_2 in some parts of D and being at a disadvantage in other parts.

Population geneticists have discussed the possibility of genetic differentiation, i.e. of obtaining a steady state solution of the above equation with $u \neq 0$ and $u \neq 1$, see Slatkin [14]. In an allopatric speciation theory (see Mayr [9]) it is proposed that genetic differentiation is impossible if the rate of gene flow is sufficiently large whereas in a sympatric speciation theory genetic differentiation occurs even if the rate of gene flow is very large. (see Pimentel et al. [11]). In this paper we determine sufficient conditions for the allopatric and sympatric cases to occur both in the cases where D is a bounded region and $D = R^n$. We study the semilinear elliptic equation

$$-\Delta u(x) = \lambda g(x) f(u) \quad \text{for } x \text{ in } D \tag{1.1}$$

corresponding to steady-state solutions of the parabolic equation above where small λ corresponds to a large rate of gene flow. Roughly speaking we find that the allopatric case occurs when one allele has a definite overall advantage (e.g. when $\int_D g(x)\,dx > 0$) and that the sympatric case occurs when the alleles are in some sense equally advantaged.

In Sect. 2 we study (1.1) when D is a bounded region. Fleming [6] discussed this case when $D = [-1, 1]$ and u satisfies Neumann boundary conditions. Brown and Lin [2] studied the case where $D \subset R^n$ and u may satisfy either Neumann boundary conditions or Dirichlet boundary conditions of the form $u|_{\partial D} = 0$ or $u|_{\partial D} = 1$. In [2] the existence of eigenvalues of the linearisation of (1.1) corresponding to eigenfunctions which do not change sign on D is discussed. Such eigenvalues correspond to bifurcation points of (1.1) from which emanate physically meaningful solutions u, i.e. solutions such that $0 \leq u \leq 1$. The global properties of such bifurcation curves have been studied by Hess and Kato in [8]. In Sect. 2 we recall and extend some of the results of [2] and [8] and show that genetic differentiation is impossible if the rate of gene flow is sufficiently large (i.e. we are in the allopatric case) except in the special case of Neumann boundary conditions when $\int_D g(x)\,dx = 0$, i.e. when neither allele has an overall advantage.

In the remainder of the paper we consider the case where $D = R^n$, $n = 1, 2$. It is shown that the existence of solutions for small values of λ depends on

$$\gamma = \lim_{R\to\infty} \inf\left\{ \int_{B_R} (\nabla u)^2\,dx \Big/ \int_{B_R} g(x)u^2\,dx \colon u \in H_0^1(B_R), \int_{B_R} g(x)u^2\,dx > 0 \right\}$$

where $B_R = \{x \in R^n \colon |x| \leq R\}$.

In Sect. 3 we consider the case where allele A_2 has the advantage over allele A_1 in the sense that $\int_{R^n} g(x)\,dx < 0$ and $g(x) < 0$ whenever $|x|$ is sufficiently large. Roughly speaking we show that in this case $\gamma > 0$ and deduce that there are no non-trivial solutions in $H^1(R^n)$. If, moreover, g is bounded away from zero at ∞, we show that all physically meaningful solutions must be in $H^1(R^n)$. Thus it can be seen that, if A_2 has an advantage for sufficiently large $|x|$, then genetic differentiation does not occur when the rate of gene flow is sufficiently large.

In Sect. 4 we use sub and supersolutions to prove the existence of non-trivial solutions of (1.1). First we prove the existence of nontrivial solutions when λ is sufficiently large by constructing sub and supersolutions by using solutions of the equation on bounded regions satisfying the boundary conditions $u = 0$ or $u = 1$. Then we show that nontrivial solutions exist for all $\lambda > 0$ (i.e. no matter how large the rate of gene flow) in the case where allele A_1 has an overall advantage, viz. $\int_{R^n} g(x)\,dx > 0$ but allele A_2 has an advantage at infinity, viz. $g(x)$ is sufficiently negative when $|x|$ is sufficiently large.

Because of the lack of compactness in the problem it seems difficult to prove bifurcation results for (1.1) in the case $D = R^n$ analogous to the results of Sect. 2 for bounded D. In [4], however, we obtain such results by using shooting arguments in the case where g is radially symmetric and f is concave. In this special case it can be proved that bifurcation occurs from the zero solution at some $\lambda_1 > 0$ when $\int_{R^n} g(x)\,dx < 0$ and that a branch of solutions approaches the solution $u \equiv 1$ as $\lambda \to 0$ when $\int_{R^n} g(x)\,dx > 0$.

2. The bounded region case

We shall assume throughout this section that D is an open bounded region in R^n with sufficiently smooth boundary and that $g: D \to R$ is a continuous function which attains both positive and negative values on D. The function $f(u) = u(1-u)[h(1-u)+(1-h)u]$ clearly satisfies

$$f(0)=f(1)=0, \qquad f(u)>0 \quad \text{for } 0<u<1, \qquad f'(0)>0, \qquad f'(1)<0.$$

We consider solutions u such that $0 \leqslant u \leqslant 1$ (recall that u represents the frequency of the allele A_1) of

$$-\Delta u(x) = \lambda g(x) f(u) \quad \text{for } x \text{ in } D \tag{2.1$_\lambda$}$$

subject to one of the following boundary conditions

$$u(x) = 0 \quad \text{for } x \text{ on } \partial D \tag{2.2}$$

$$u(x) = 1 \quad \text{for } x \text{ on } \partial D \tag{2.3}$$

$$\frac{\partial u}{\partial n}(x) = 0 \quad \text{for } x \text{ on } \partial D. \tag{2.4}$$

The no flux problem $(2.1)_\lambda$, (2.4) studied in [6] is the most natural from the viewpoint of population genetics but we require results on $(2.1)_\lambda$, (2.2) and $(2.1)_\lambda$, (2.3) in order to discuss the existence of solutions on all of R^n in Sect. 4.

We first show that solutions must be strictly between 0 and 1 on D by using the following strengthened version of the maximum principle.

Lemma 2.1. *Let v be a C^2 function on D such that $v(x) \geqslant 0$ and $-\Delta v(x) + q(x)v(x) \geqslant 0$ for all x in D for some uniformly bounded function $q: D \to R$. Then*

(i) *If v vanishes at some point in D, $v \equiv 0$ on D;*

(ii) *If $v \not\equiv 0$ on D and $v(x_0) = 0$ for some $x_0 \in \partial D$, then $\partial v/\partial n(x_0) < 0$.*

The result is well known when $q \geqslant 0$ and the general result can be found in Serrin [13] or Gidas et al. [7].

Lemma 2.2. *Suppose that u is a solution of $(2.1)_\lambda$ such that $0 \leqslant u \leqslant 1$ on D.*

(i) *If $u(x_0) = 0$ for some $x_0 \in D$, then $u \equiv 0$ on D.*

(ii) *If $u(x_0) = 1$ for some $x_0 \in D$, then $u \equiv 1$ on D.*

(iii) *If $u \not\equiv 0$ and $u(x_0) = 0$ for some $x_0 \in \partial D$, then $\partial u/\partial n(x_0) < 0$.*

(iv) *If $u \not\equiv 1$ and $u(x_0) = 1$ for some $x_0 \in \partial D$, then $\partial u/\partial n(x_0) > 0$.*

Proof. Parts (i) and (iii) follow directly from Lemma 2.1 as u satisfies $-\Delta u + q(x)u = 0$ where $q(x) = -\lambda g(x)f(u(x))/u(x)$. Parts (ii) and (iv) follow similarly from Lemma 2.1 by considering $v = 1 - u$.

We now discuss the problem with zero Dirichlet boundary conditions. Consider the linearization of $(2.1)_\lambda$, (2.2), viz.,

$$\begin{aligned} -\Delta u(x) &= \lambda g(x) h u \quad \text{for } x \text{ in } D \\ u(x) &= 0 \quad \text{for } x \text{ on } \partial D. \end{aligned} \tag{2.5}$$

It is shown in [8] that there exists a sequence of eigenvalues $\{\lambda_n\}$, $0 < \lambda_1 < \lambda_2 \leqslant \cdots$, such that λ_1 is a simple eigenvalue and is the only eigenvalue possessing an eigenfunction which does not change sign on D. Clearly $\nu = 0$ is the least eigenvalue of the linear eigenvalue problem

$$-\Delta u(x) - \lambda_1 g(x) h u = \nu u \quad \text{on } D; \qquad u|_{\partial D} = 0$$

and so

$$0 = \inf\left\{ \int_D |\nabla u|^2 \, dx - \lambda_1 h \int_D g(x) u^2 \, dx \colon u \in H_0^1(D), \int_D u^2 \, dx = 1 \right\}.$$

Hence

$$\lambda_1 = h^{-1} \inf\left\{ \int_D |\nabla u|^2 \, dx \Big/ \int_D g(x) u^2 \, dx \colon u \in H_0^1(D), \int_D g(x) u^2 \, dx > 0 \right\}.$$

It is shown in [8] that a branch of positive solutions for $(2.1)_\lambda$, (2.2) bifurcates from the branch of zero solutions at $\lambda = \lambda_1$ and this branch $C \subset C(D) \times R$ is such that C joins $(0, \lambda_1)$ to ∞ in $C(D) \times R$.

The following two lemmas give further information about C.

Lemma 2.3. *If* $(u, \lambda) \in C$ *and* $u \not\equiv 0$, *then* $0 < u(x) < 1$ *for all* $x \in D$.

Proof. It follows from the implicit function theorem (see Crandall and Rabinowitz [5]) that $0 < u(x) < 1$ for all $x \in D$ whenever $(u, \lambda) \in C$ lies in a sufficiently small neighbourhood of $(0, \lambda_1)$. Suppose that the result is false. Then, because of the connectedness of C, there exists a sequence $\{(u_n, \lambda_n)\}$ in C lying outside a neighbourhood of $(0, \lambda_1)$ converging to $(u, \lambda) \in D$ and $u(x_0) = 0$ or 1 for some $x_0 \in D$. Therefore by Lemma 2.2 we must have $u \equiv 0$ or $u \equiv 1$. Since $u|_{\partial D} = 0$, we cannot have $u \equiv 1$. If $u \equiv 0$, then $(0, \lambda)$ is a bifurcation point for $(2.1)_\lambda$, (2.2) to which converges a sequence of positive solutions and so λ must be an eigenvalue of (2.5) corresponding to a positive eigenfunction. Thus $\lambda = \lambda_1$ and we have obtained a contradiction.

Theorem 2.4. *There exists* $\lambda_0 > 0$ *such that* $\lambda \geqslant \lambda_0$ *whenever* u *is a solution of* $(2.1)_\lambda$, (2.2) *such that* $0 < u(x) < 1$ *for all* $x \in D$.

Proof. Choose M and K such that $g(x) \leqslant M$ for all $x \in D$ and $f(u) \leqslant Ku$ for $0 \leqslant u \leqslant 1$. Suppose u is a solution of $(2.1)_\lambda$, (2.2). Then

$$\int_D |\nabla u|^2 \, dx = -\int_D u \, \Delta u \, dx = \lambda \int_D g(x) f(u) u \, dx \leqslant \lambda K M \int_D u^2 \, dx.$$

But by the spectral theorem

$$\int_D |\nabla u|^2 \, dx \geqslant \nu_1 \int_D u^2 \, dx \tag{2.6}$$

where ν_1 is the least eigenvalue on D of $-\Delta u$ with Dirichlet boundary conditions. Hence $\lambda \geqslant \nu_1/KM$.

Since C joins $(0, \lambda_1)$ to ∞ in $C(D)\times R$ and $\|u\|<1$ and $\lambda>\lambda_0$ for all $(u, \lambda)\in C$, it follows that C can become unbounded only by λ approaching $+\infty$. Thus we have

Theorem 2.5. *There exists a solution* u *of* $(2.1)_\lambda$, (2.2) *such that* $0<u(x)<1$ *for all* $x\in D$ *whenever* $\lambda>\lambda_1$.

Similar results hold for the problem $(2.1)_\lambda$, (2.3) if and only if $v=1-u$ satisfies

$$-\Delta v(x)=\lambda \hat{g}(x)v(1-v)[hv+(1-h)(1-v)] \quad \text{for } x \text{ in } D$$
$$v(x)=0 \quad \text{for } x \text{ on } \partial D, \tag{2.7}$$

where $\hat{g}=-g$ which has exactly the same form as (2.1) apart from the sign change in g and replacement of h by $1-h$. Arguing as above, we can prove that there exists a continuum C of solutions of (2.7) joining $(0, \gamma_1)$ to ∞ in $C(D)\times R$ where

$$\gamma_1=(1-h)^{-1}\inf\left\{\int_D |\nabla u|^2\,dx \Big/ \int_D \hat{g}(x)u^2\,dx \colon u\in H_0^1(D), \int_D \hat{g}(x)u^2\,dx>0\right\}.$$

Moreover Lemma 2.3 and Theorem 2.4 apply to Eq. (2.7) and so C becomes unbounded by λ approaching ∞. Thus we have

Theorem 2.6. *There exists a solution* u *of* $(2.1)_\lambda$, (2.3) *such that* $0<u(x)<1$ *for all* $x\in D$ *whenever* $\lambda>\gamma_1$.

Theorem 2.4 shows that genetic differentiation cannot occur under Dirichlet boundary conditions (2.2) or (2.3) whenever the rate of gene flow is sufficiently large; in this case the concentration of genes throughout D must coincide with the concentration specified by the boundary condition on ∂D (see Fig. 1).

The existence of solutions of $(2.1)_\lambda$, (2.4) depends on the sign of $\int_D g(x)\,dx$. Suppose $\int_D g(x)\,dx<0$. It is shown in [2] that the linearisation

$$-\Delta u(x)=\lambda h g(x)u \quad \text{on } D; \qquad \frac{\partial u}{\partial n}=0 \quad \text{on } \partial D$$

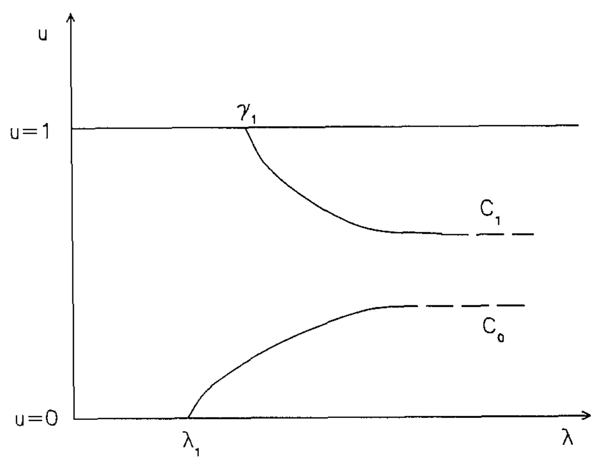

Fig. 1. Bifurcation curves in the case of Dirichlet boundary conditions

has a unique positive eigenvalue μ_1 corresponding to an eigenfunction which does not change sign on D if and only if $\int_D g(x)\,dx<0$. There is a continuum of solutions C emanating from $(0, \mu_1)$ such that $0<u(x)<1$ for all $(u, \lambda)\in C$ in a neighbourhood of $(0, \mu_1)$.

Moreover

$$\mu_1 = h^{-1}\inf\left\{\int_D |\nabla u|^2\,dx \Big/ \int_D g(x)u^2\,dx\colon u\in H^1(D),\ \int_D g(x)u^2\,dx>0\right\}.$$

Using arguments similar to those used previously, it can be shown that $0<u(x)<1$ whenever $(u, \lambda)\in C$ and $u\not\equiv 0, 1$. The possibility that C joins up with the trivial branch of solutions corresponding to $u\equiv 1$ is precluded by the fact that there can be no bifurcation of solutions satisfying $0<u<1$ from this branch as for the corresponding linearisation (2.6) with Neumann boundary conditions we have $\int_D \hat{g}(x)\,dx>0$ and so there are no positive eigenvalues corresponding to eigenfunctions which do not change sign on D. The fact that C is bounded away from $\lambda=0$ is a consequence of the following results.

Lemma 2.7. Suppose $\int_D g(x)\,dx<0$. *Then there exists* $k>0$ *such that* $\int_D |\nabla u|^2\,dx > k\int_D u^2\,dx$ *for all* $u\in H^1(D)$ *such that* $\int_D g(x)u^2\,dx>0$.

Proof. Suppose that the result does not hold. Then there exists a sequence $\{u_n\}$ in $H^1(D)$ such that $\int_D g(x)u_n^2\,dx>0$ and $\int_D |\nabla u_n|^2\,dx \leq 1/n \int_D u_n^2\,dx$ for all n. We may assume without loss of generality that $\int_D u_n^2\,dx=1$. Clearly $\{u_n\}$ is a bounded sequence in $H^1(D)$ and so has a convergent subsequence which we again denote by $\{u_n\}$ converging to u in $L^2(D)$. Since

$$\|u_n-u_m\|_{H^1}^2 = \|u_n-u_m\|_{L^2}^2 + \|\nabla u_n - \nabla u_m\|_{L^2}^2$$

and

$$\|\nabla u_n - \nabla u_m\|_{L^2}^2 \leq (\|\nabla u_n\|_{L^2} + \|\nabla u_m\|_{L^2})^2 \leq \left(\frac{1}{\sqrt{n}}+\frac{1}{\sqrt{m}}\right)^2,$$

it follows that $\{u_n\}$ is a Cauchy sequence in $H^1(D)$. Hence $\{u_n\}$ converges to u in $H^1(D)$. Moreover

$$\int_D |\nabla u|^2\,dx = \lim_{n\to\infty}\int_D |\nabla u_n|^2\,dx = 0$$

and so u must be a constant function, i.e., $u\equiv c$ for some c. But $c^2\int_D g(x)\,dx = \lim_{n\to\infty}\int_D g(x)u_n^2\,dx \geq 0$ and so we must have $c=0$. Since $\int_D u^2\,dx = \lim_{n\to\infty}\int_D u_n^2\,dx=1$, we have obtained a contradiction and the proof is complete.

It is easy to see that a similar result holds when the signs of $\int_D g(x)\,dx$ and $\int_D g(x)u^2\,dx$ are reversed.

By using the same proof as in Theorem 2.4 but using Lemma 2.7 in place of Eq. (2.6), it is straightforward to establish the following result.

Theorem 2.8. *Suppose* $\int_D g(x)\,dx<0$. *Then there exists* $\lambda_0>0$ *such that* $\lambda\geq\lambda_0$ *whenever* u *is a solution of* $(2.1)_\lambda$, (2.4) *such that* $0<u(x)<1$ *for all* $x\in D$.

Thus the continuum C must join $(0, \mu_1)$ to ∞ in $C(D)\times R$ by λ approaching $+\infty$ and therefore we obtain the following existence result.

Theorem 2.9. *Suppose that* $\int_D g(x)\,dx<0$. *Then there exists a solution* u *of* $(2.1)_\lambda$, (2.4) *such that* $0<u(x)<1$ *for all* $x\in D$ *whenever* $\lambda>\mu_1$.

Similar results can be obtained when $\int_D g(x)\,dx>0$. In this case a continuum of solutions bifurcates from the trivial branch of solutions corresponding to $u\equiv 1$ and theorems analogous to 2.8 and 2.9 can be established. Thus, when $\int_D g(x)\,dx\neq 0$, $(2.1)_\lambda$, (2.4) does not have physically interesting solutions when λ is sufficiently small. If, however, $\int_D g(x)\,dx=0$, then bifurcation occurs at $(c, 0)$ on the branch of constant solutiosn corresponding to $\lambda=0$ where $f'(c)=0$ (see [3]). Hence, non-constant solutions exist for arbitrarily small λ, i.e., genetic differentiation is possible no matter how great the rate of gene flow in the case where neither allele has an overall advantage in the sense that $\int_D g(x)\,dx=0$.

3. Non-existence of solutions

For the rest of the paper we shall consider the case where $D=R^2$. All of the results we prove hold for the case $D=R$ with similar but simpler proofs. The case $D=R^n$, $n\geq 3$, seems more complicated; it is harder to describe the asymptotics of solutions in this case (see [4]) and the method used to prove existence in the next section fails if $n\geq 3$.

We shall suppose that allele A_2 has an advantage at infinity in the sense that

(G1) there exists $R_0>0$ such that $g(x)<0$ whenever $|x|>R_0$.

We consider the problem

$$\begin{aligned} -\Delta u(x)&=\lambda g(x)f(u) \quad \text{for } x \text{ in } R^2\\ 0\leq u(x)&\leq 1 \quad \text{for } x \text{ in } R^2. \end{aligned} \tag{3.1$_\lambda$}$$

Clearly $(3.1)_\lambda$ has solutions $u\equiv 0$ and $u\equiv 1$; we shall refer to all other solutions as being nontrivial.

Lemma 3.1. *Let* g *satisfy* (G1) *and let* u *be a nontrivial solution of* $(3.1)_\lambda$. *Then there exists a constant* $k<1$ *such that* $0<u(x)<k$ *for all* $x\in R^2$.

Proof. It follows from Lemma 2.2 that $0<u(x)<1$ for all $x\in R^2$. Since $-\Delta u=\lambda g(x)f(u)\leq 0$ for $|x|>R_0$, u is subharmonic for $|x|>R_0$ and so it follows from the Hadamard three circles theorem (see Protter and Weinberger [12], p. 129) that $M(r)\leq M(R_0)$ whenever $r>R_0$ where $M(r)=\sup\{u(x): |x|=r\}$. Hence $u(x)\leq \sup\{u(y): |y|\leq R_0\}<1$ for all $x\in R^2$.

In the remainder of this section we show first that $(3.1)_\lambda$ has no nontrivial solutions $u\in H^1(R^2)$ for small λ when allele A_2 also has an overall advantage in the sense that $\int_{R^2} g(x)\,dx<0$ and then that all non-trivial solutions must lie in $H^1(R^2)$ when g is bounded away from zero at infinity.

Theorem 3.2. *Suppose* g *satisfies* (G1) and $\int_{R^2} g(x)\,dx<0$. *Then there exists* $\lambda_0>0$ *such that for all* $\lambda<\lambda_0$ *Eq.* $(3.1)_\lambda$ *has no nontrivial solution* $u\in H^1(R^2)$.

Proof. Suppose that $u\in H^1(R^2)$ is a nontrivial solution of $(3.1)_\lambda$. Multiplying $(3.1)_\lambda$ by u and integrating, we obtain

$$\int_{R^2} |\nabla u|^2\,dx=\lambda\int_{R^2} g(x)f(u)u\,dx. \tag{3.2}$$

We shall obtain a lower bound on λ by using Lemma 2.7. Choose $R > R_0$ such that $\int_B g(x)\,dx < 0$ where $B = \{x \in R^2 : |x| \leq R\}$. Then by Lemma 2.7 there exists $k > 0$ such that

$$\int_B |\nabla v|^2\,dx \geq k \int_B v^2\,dx \tag{3.3}$$

for all $v \in H^1(B)$ such that $\int_B g(x)v^2\,dx > 0$.

We now prove that $\int_B g(x)u^2\,dx > 0$. Let $w = u^2/f(u)$. By Lemma 3.1 u is bounded away from 1 and so $f(u) \geq Ku$, i.e. $w \leq K^{-1}u$, for some positive constant K. Thus $w \in L^2(R^2)$. Moreover $\nabla w = (u/f^2(u))(2f(u) - uf'(u))\nabla u$ and so $\nabla w \in L^2(R^2)$. Multiplying $(3.1)_\lambda$ by w and integrating gives

$$\lambda \int_{R^2} g(x)u^2\,dx = -\int_{R^2} w\,\Delta u\,dx = \int_{R^2} \nabla w \cdot \nabla u\,dx$$

$$= \int_{R^2} (u/f^2(u))[2f(u) - uf'(u)]|\nabla u|^2\,dx > 0$$

as $2f(u) - uf'(u) > 0$ for $0 < u < 1$. Hence

$$\int_B g(x)u^2\,dx > \int_{R^2} g(x)u^2\,dx > 0$$

as $g(x) < 0$ on R^2/B and so u satisfies (3.3).

There exist positive constants M and K such that $g(x) \leq M$ for all x in R^2 and $f(u) \leq Ku$ for all u, $0 \leq u \leq 1$. Hence

$$\int_B u^2\,dx \geq K^{-1}M^{-1} \int_B g(x)f(u)u\,dx.$$

Therefore

$$\int_{R^2} |\nabla u|^2\,dx \geq \int_B |\nabla u|^2\,dx \geq k \int_B u^2\,dx$$

$$\geq kK^{-1}M^{-1} \int_B g(x)f(u)u\,dx \geq kK^{-1}M^{-1} \int_{R^2} g(x)f(u)u\,dx.$$

Hence by (3.2) we have $\lambda \geq kK^{-1}M^{-1}$ and the proof is complete.

We now give a sufficient condition to ensure that all nontrivial solutions of $(3.1)_\lambda$ lie in $H^1(R^2)$.

Theorem 3.3. *Suppose g is uniformly bounded and there exist k, $R_0 > 0$ such that $g(x) \leq -k$ whenever $|x| \geq R_0$. Then every nontrivial solution of $(3.1)_\lambda$ lies in $H^1(R^2)$.*

Proof. Suppose that u is a nontrivial solution of $(3.1)_\lambda$. By Lemma 3.1 u is bounded away from 1 and so there exists a positive constant k_1 such that $f(u(x)) \geq k_1 u(x)$ for all x in R^2. Hence, if $|x| \geq R_0$,

$$-\Delta u = \lambda g(x)f(u) \leq -\lambda k k_1 u = -Ku \tag{3.4}$$

for some constant $K>0$. In order to study the asymptotic properties of u we study the symmetrisation v of u given by

$$v(r)=\int_{|x|=1} u(rx)\, dS.$$

Since u is bounded, so is v and it follows from (3.4) that

$$-v''-\frac{1}{r}v'+Kv\leqslant 0 \quad \text{for } r\geqslant R_0. \tag{3.5}$$

We first show that v is decreasing for $r\geqslant R_0$. We can write (3.5) as

$$-(rv')'+Krv\leqslant 0 \quad \text{for } r\geqslant R_0.$$

Hence $(rv')'>0$ and so rv' is an increasing function for $r\geqslant R_0$. Suppose there exists $r_0>R_0$ such that $v'(r_0)>0$. Then $v'(r)>(1/r)r_0v(r_0)$ for all $r>r_0$ and so $\lim_{r\to\infty} v(r)=\infty$ which is impossible. Hence $v'(r)\leqslant 0$ for all $r\geqslant R_0$ and so it follows from (3.5) that

$$-v''+Kv\leqslant 0 \quad \text{for } r\geqslant R_0. \tag{3.6}$$

Let $w(r)=e^{\sqrt{K}r}v(r)$. Substituting in (3.6) we obtain

$$w''-2\sqrt{K}w'\geqslant 0 \quad \text{for } r\geqslant R_0.$$

Hence $d/dr(e^{-2\sqrt{K}r}w')\geqslant 0$ and so $e^{-2\sqrt{K}r}w'$ is increasing for $r\geqslant R_0$. Supose there exists $r_1>R_0$ such that $w'(r_1)>0$. Then $w'(r)\geqslant e^{2\sqrt{K}(r-r_1)}w'(r_1)$ and so $w(r)\geqslant w(r_1)+M\,e^{2\sqrt{K}r}$ for $r\geqslant R_0$ for some constant $M>0$. Therefore

$$v(r)=e^{-\sqrt{K}r}w(r)\geqslant M\,e^{\sqrt{K}r} \quad \text{for } r\geqslant R_0$$

which is impossible as v is bounded. Thus $w'(r)\leqslant 0$ for all $r\geqslant R_0$ and so w is bounded. Therefore there exists a constant $N>0$ such that

$$v(r)\leqslant N\,e^{-\sqrt{K}r} \quad \text{for all } r. \tag{3.7}$$

We now deduce that u also decays exponentially. Suppose $|x|>R_0+1$ and let B_x denote the ball $\{y\in R^2\colon |x-y|<1\}$ and A_x denote the annulus $\{y\in R^2\colon |x|-1\leqslant |y|\leqslant |x|+1\}$. Since $g<0$ on B_x, $-\Delta u=\lambda g(x)f(u)<0$, i.e. u is subharmonic on B_x. Hence

$$u(x)\leqslant \pi^{-1}\int_{B_x} u(y)\, dy\leqslant \pi^{-1}\int_{A_x} u(y)\, dy=\pi^{-1}\int_{|x|-1}^{|x|+1} rv(r)\, dr.$$

Thus it follows from (3.7) that there exist positive constants P and α such that

$$u(x)\leqslant P\,e^{-\alpha|x|} \quad \text{for all } x \text{ such that } |x|>R_0.$$

Moreover since u satisfies $(3.1)_\lambda$, there exists a positive constant Q such that

$$|\Delta u(x)|\leqslant Q\,e^{-\alpha|x|} \quad \text{for all } x \text{ such that } |x|>R_0.$$

Therefore we can obtain L_p bounds for u and Δu in B_x where $p>2$ of the form

$$\|u\|_{L^p},\ \|\Delta u\|_{L^p}\leqslant \mathrm{R}\, e^{-\alpha|x|},$$

and so by standard interior estimates we can obtain a bound for u in the $W^{2,p}$ norm on $B'_x = \{y \in R^2: |x-y| < \frac{3}{4}\}$ in terms of $e^{-\alpha|x|}$. Since $W^{2,p}(B'_x)$ can be embedded continuously in $C^1(B'_x)$, we obtain the bound

$$|\text{grad}\, u(x)| \leq S\, e^{-\alpha|x|}.$$

Hence $u \in H^1(R^2)$ and the proof is complete.

Corollary 3.4. *Suppose g satisfies the hypotheses of Theorem* 3.3. *Then there exists* $\lambda_0 > 0$ *such that for all* $\lambda < \lambda_0$ *Eq.* $(3.1)_\lambda$ *has no nontrivial solutions.*

4. Existence of solutions

We shall prove the existence of solutions by constructing appropriate weak sub and supersolutions. If u_1 and u_2 are smooth subsolutions of $(3.1)_\lambda$ on $B_R = \{x \in R^2: |x| \leq R\}$ and $B_R^* = \{x \in R^2: |x| \geq R\}$ respectively, i.e., $-\Delta u_i \leq \lambda g(x) f(u_i)$, such that

$$u_1(x) = u_2(x) \text{ and } \partial u_1/\partial r(x) \leq \partial u_2/\partial r(x) \text{ whenever } |x| = R,$$

we say that u is a weak subsolution of $(3.1)_\lambda$ if

$$u(x) = \begin{cases} u_1(x) \text{ for } |x| \leq R \\ u_2(x) \text{ for } |x| > R \end{cases}.$$

Roughly speaking u can be regarded as the supremum of the two subsolutions u_1 and u_2. Weak supersolutions can be defined similarly. Similar weak sub and supersolutions are discussed by Berysticki and Lions in [1] in the case of bounded regions and the existence of solutions lying between weak subsolutions and weak supersolutions is obtained. Ni in [10] proves the existence of a solution lying between smooth sub and supersolutions for semilinear elliptic equations on all of R^n; the solution is obtained as the limit of solutions on bounded regions and so the proof in [10] can be adapted to apply to the case of weak sub and supersolutions. Thus we have the following result.

Lemma 4.1. *Let* $\underline{u}$ *and* $\bar{u}$ *be a weak subsolution and a weak supersolution respectively for* $(3.1)_\lambda$ *such that* $\underline{u}(x) \leq \bar{u}(x)$ *for all x in* R^2. *Then there exists a solution u of* $(3.1)_\lambda$ *such that* $\underline{u} \leq u \leq \bar{u}$.

We assume throughout this section that g satisfies the condition (G1) given at the start of Sect. 3. Let $R > R_0$ and let $B = \{x \in R^2: |x| \leq R\}$. We construct appropriate weak sub and super solutions using solutions of the Dirichlet problems $(2.1)_\lambda$, (2.2) and $(2.1)_\lambda$, (2.3) on B. In Sect. 2 we discussed continua of solutions for these problems. We showed that there is a continuum C_0 in $C(B) \times R$ joining $(0, \lambda_1)$ to ∞ such that u is a solution of $(2.1)_\lambda$, (2.2) satisfying $0 \leq u < 1$ whenever $(u, \lambda) \in C_0$ and a continuum C_1 joining $(1, \gamma_1)$ to ∞ such that u is a solution of $(2.1)_\lambda$, (2.3) satisfying $0 < u \leq 1$ whenever $(u, \lambda) \in C_1$.

Lemma 4.2. *Suppose* $(u, \lambda) \in C_0$ *and* $(v, \lambda) \in C_1$. *Then* $u(x) \leq v(x)$ *for all* $x \in B$.

Proof. It is clear that the result must be true when either (u, λ) or (v, λ) lie in a sufficiently small neighbourhood of the bifurcation points $(0, \lambda_1)$ or $(1, \gamma_1)$.

Suppose that the theorem does not hold. Then a continuity argument shows that there must exist $(u, \lambda) \in C_0$ and $(v, \lambda) \in C_1$ such that $u(x) \leq v(x)$ for all $x \in B$ but $u(x_0) = v(x_0)$ for some $x_0 \in B$. Let $w = v - u$. Then

$$-\Delta w = \lambda g(x)[f(v(x)) - f(u(x))] = \lambda g(x) c(x) w(x)$$

where c is the continuous function such that $c(x) = \int_0^1 f'(u(x) + tw(x))\, dt$. Since $w \geq 0$ on B and $w(x_0) = 0$, it follows from Lemma 2.1 that $w \equiv 0$ on B but this is impossible as $w|_{\partial B} = 1$ and so the proof is complete.

Theorem 4.3. *There exists a nontrivial solution of* $(3.1)_\lambda$ *whenever* $\lambda > \max\{\lambda_1, \gamma_1\}$.

Proof. Suppose $\lambda > \max\{\lambda_1, \gamma_1\}$. Since the continua of solutions C_0 and C_1 join $(0, \lambda_1)$ and $(1, \gamma_1)$ to ∞ by λ becoming unbounded, there exist $(u, \lambda) \in C_0$ and $(v, \lambda) \in C_1$. By Lemma 4.2, $u(x) \leq v(x)$ for all $x \in B$. Let

$$\underline{u}(x) = \begin{cases} u(x) & \text{for } |x| \leq R \\ 0 & \text{for } |x| > R \end{cases}$$

and

$$\bar{u}(x) = \begin{cases} v(x) & \text{for } |x| \leq R \\ 1 & \text{for } |x| > R^{\cdot} \end{cases}$$

Then $\underline{u}$ $(\bar{u})$ is a weak subsolution (supersolution) of $(3.1)_\lambda$ and $\underline{u}(x) \leq \bar{u}(x)$ for all $x \in R^2$. The theorem now follows from Lemma 4.1.

Let us denote the numbers λ_1 and γ_1, the bifurcation points for problems $(2.1)_\lambda$ (2.2) and $(2.1)_\lambda$, (2.3) on $B_R = \{x \in R^2\colon |x| \leq R\}$ by $\lambda_1(R)$ and $\gamma_1(R)$. It is easy to see from the variational characterizations in Sect. 2 that $\lambda_1(R)$ and $\gamma_1(R)$ are decreasing functions of R. The existence of solutions for $(3.1)_\lambda$ depends on $\lim_{R\to\infty} \lambda_1(R)$ which in turn depends on the sign of $\int_{R^2} g(x)\, dx$.

Lemma 4.4. *Suppose g satisfies* (G1) and $\int_{R^2} g(x)\, dx > 0$. *Then* $\lim_{R\to\infty} \lambda_1(R) = 0$.

Proof. Let $\varepsilon > 0$. Choose $R > R_0$ such that

$$\left| \int_{|x| \geq R} g(x)\, dx \right| \leq \tfrac{1}{2} \int_{R^2} g(x)\, dx.$$

Define a continuous, radially symmetric function u as follows

$$\begin{aligned} u(r) &= 1 && \text{if } r \leq R \\ u'(r) &= -\varepsilon / r && \text{if } R \leq r \leq Z \\ u(r) &= 0 && \text{if } r \geq Z. \end{aligned}$$

Then u is a decreasing function for $R \leq r \leq Z$ with $u(R) = 1$ and $u(Z) = 0$; clearly Z is a function of R and ε. Since $u(r) = -\varepsilon \ln r + b$ on $[R, Z]$ for some positive constant b we must have that

$$-\varepsilon \ln R + b = 1; \qquad -\varepsilon \ln Z + b = 0$$

and so

$$\varepsilon(\ln Z - \ln R) = 1.$$

If $r > Z$,

$$\int_{B_r} |\nabla u|^2\,dx = \int_0^r r u_r^2\,dr = \int_R^Z \varepsilon^2/r\,dr = \varepsilon^2(\ln Z - \ln R) = \varepsilon.$$

Moreover

$$\int_{B_r} g(x)u^2\,dx = \int_{B_R} g(x)\,dx + \int_{R \le |x| \le r} g(x)u^2\,dx$$
$$\ge \int_{R^2} g(x)\,dx - \left|\int_{|x| \ge R} g(x)\,dx\right| \ge \tfrac{1}{2}\int_{R^2} g(x)\,dx.$$

Hence, using $u \in H_0^1(B_r)$ as a test function, we have $\lambda_1(r) \le 2\varepsilon/\int_{R^2} g(x)\,dx$. Thus $\lim_{r\to\infty} \lambda_1(r) = 0$.

The preceding lemmas show that, if g satisfies (G1) and $\int_{R^2} g(x)\,dx > 0$, then there exists a weak subsolution of $(3.1)_\lambda$ for all $\lambda > 0$. It remains to investigate the existence of corresponding supersolutions. Unfortunately, it appears that $\lim_{R\to\infty} \gamma_1(R) \ne 0$ but we can, however, obtain weak supersolutions for arbitrarily small λ by using the solutions of appropriate ODE's provided that g does not approach 0 too rapidly as $|x| \to \infty$.

Lemma 4.5. *Suppose* $4kf'(1) < -1$ *and let* $R > 0$. *Then there exists a decreasing solution of*

$$w''(x) - (k/x^2)f(w(x)) = 0 \quad \textit{for } x > R \tag{4.1}$$
$$w(R) = 1; \qquad \lim_{x\to\infty} w(x) = 0.$$

Proof. By making the transformation $s = \ln x$, $v(s) = w(x)$ we see that (4.1) is equivalent to

$$\begin{aligned} &v''(s) - v'(s) - kf(v(s)) = 0 \quad \text{for } s > \ln R \\ &v(\ln R) = 1, \qquad \lim_{s\to\infty} v(s) = 0. \end{aligned} \tag{4.2}$$

Since (4.2) is an autonomous equation it can be discussed by using phase plane methods. We can write (4.2) as a system

$$\begin{aligned} v'(s) &= y(s) \\ y'(s) &= y(s) + kf(v(s)). \end{aligned} \tag{4.3}$$

It is easy to check that (4.3) has a saddle point at $(0, 0)$ with a stable manifold which corresponds to a solution v of (4.2) such that $v'(s) < 0$ for s large enough and $\lim_{s\to\infty} v(s) = \lim_{s\to\infty} v'(s) = 0$. We follow this trajectory backwards and show that it hits the line $v = 1$ without leaving the fourth quadrant in the phase plane.

Suppose that the trajectory corresponds to a solution v of (4.2) on (S_0, ∞) such that $0 < v(s) < 1$. Suppose $v'(s_1) = 0$ for some $s_1 > S_0$. Then $v''(s_1) = kf(v(s_1)) > 0$ and so v has a local minimum at s_1. Since v is eventually decreasing, it follows that if v has critical points in (S_0, ∞) they cannot all be local minima. Hence $v'(s) < 0$ for all $s \ge S_0$. Multiplying (4.2) by v', gives

$$\frac{d}{ds}\left[\tfrac{1}{2}[v'(s)]^2 - kF(v(s))\right] = [v'(s)]^2 > 0 \quad \text{for } s \ge S_0$$

where $F(v)=\int_0^v f(t)\,dt$. Since $\lim_{s\to\infty} v(s)=\lim_{s\to\infty} v'(s)=0$, we have

$$\tfrac{1}{2}[v'(s)]^2<kF(v(s))<kF(1)$$

for $s\geqslant S_0$. Thus we have shown that the trajectory corresponding to the stable manifold cannot cut the v axis (where $v'=0$) and cannot become unbounded in the v' direction as long as $0<v<1$.

There remain two possibilities for the stable manifold; either it hits the line $v=1$ or stays to the left of the line $v=1$ and approaches the equilibrium point $(1,0)$ as $s\to\infty$. However the condition $4kf'(1)<-1$ ensures that $(1,0)$ is an unstable spiral point and so the latter possibility cannot occur. Thus the stable manifold yields a solution of (4.2) and so of (4.1).

Lemma 4.6. *Suppose that* $\lim_{|x|\to\infty}|x|^2(\ln|x|)^2 g(x)=-\infty$. *Then there exists a weak supersolution for* $(3.1)_\lambda$ *for all* $\lambda>0$.

Proof. Let $\lambda>0$. Choose k, $R>0$ such that $|x|^2(\ln|x|)^2 g(x)<-k$ for $|x|>R$ and $4\lambda kf'(1)<-1$. Consider the ODE

$$w''(r)+\frac{1}{r}\,w'(r)-\frac{\lambda k}{r^2(\ln r)^2}f(w)=0 \quad \text{for } r>R \tag{4.4}$$

$$w(R)=1; \qquad \lim_{r\to\infty} w(r)=0.$$

Substituting $s=\ln r$, Eq. (4.4) can be transformed into

$$w''(s)-\frac{\lambda k}{s^2}f(w(s))=0$$

$$w(\ln R)=1; \qquad \lim_{s\to\infty} w(s)=0$$

which has a decreasing solution by Lemma 4.5. Hence Eq. (4.4) has a decreasing solution which we denote by $w(r)$. Let

$$\bar{u}(r)=\begin{cases}1 & \text{if } r\leqslant R\\ w(r) & \text{if } r>R.\end{cases}$$

Then, if $|x|\geqslant R$,

$$-\Delta\bar{u}(x)=-w''(r)-\frac{1}{r}w'(r)=-\frac{\lambda k}{r^2(\ln r)^2}f(w)>\lambda g(x)f(\bar{u}).$$

Hence $\bar{u}$ is a weak supersolution of $(3.1)_\lambda$.

A similar but simpler and shorter argument shows that we can construct a weak supersolution of $(3.1)_\lambda$ for the case $D=R$ when g satisfies the slightly stronger hypothesis $\lim_{|x|\to\infty}|x|^2 g(x)=-\infty$.

Thus we have established the following existence theorem.

Theorem 4.7. *Suppose that* $\int_{R^2} g(x)\,dx>0$ *and*

(i) $n=1$ *and* $\lim_{|x|\to\infty} x^2 g(x)=-\infty$ *or*

(ii) $n=2$ *and* $\lim_{|x|\to\infty}|x|^2(\ln x)^2 g(x)=-\infty$.

Then $(3.1)_\lambda$ *has a nontrivial solution for all* $\lambda>0$.

In the case $n=2$ the conditions that $\lim_{|x|\to\infty}|x|^2(\ln x)^2 g(x)=-\infty$ and $\int_{R^2} g(x)\,dx>0$ (i.e., the integral converges) are very restrictive. However, if $0<\beta<1$, the function $g(x)=-1/|x|^2(\ln x)^{1+\beta}$ for large $|x|$ satisfies both conditions.

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