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ON THE DISTRIBUTION OF DOMINANCE IN POPULATIONS OF SOCIAL ORGANISMS*

EVA JÄGER[†] AND LEE A. SEGEL[†]

Abstract. Bumble bees may possess a scalar character called dominance, which changes according to certain rules as a result of encounters between pairs of organisms. An equation for the distribution of dominance in a population is derived based on a set of plausible axioms. The resulting Boltzmann-like integrodifferential equation is analyzed, analytically and/or numerically, for certain important special cases.

Key words. dominance, probability distribution, Boltzmann, Fokker–Planck, integrodifferential equation

AMS(MOS) subject classifications. 45K05, 60J, 92

1. Introduction. The idea of dominance is of major importance in studies of animal behavior. Observations of dominance date at least from the work of Schjelderup–Ebbe [16], who established the existence of “peck right” in interactions between hens. This “right” is the expression of the dominance of one of a pair of hens over the other. A considerable portion of the research on dominance has concerned higher organisms wherein individuals recognize one another, leading to the possibility of a great variety of sophisticated behavior (see, e.g., [4] and [3]).

The “animal sociology” induced among N individuals by peck rights has been investigated. For example, Rapaport [14] enumerated the possible social structures (directed graphs) assuming that a first encounter, with equiprobable win or loss, permanently determines the pairs peck order (winner pecks loser). Landau [9] introduced a hierarchy index, a single number that characterized structure, and calculated its mean and variance under various assumptions. (See Landau [10].)

This paper is concerned with the dynamics of dominance in simple situations, such as may occur in beehives, wherein all organisms are anonymous. We show how to derive an equation for the development in time of the distribution of dominance through a large population, and we study certain properties of this equation. The equation is of nonlinear Boltzmann type, and therefore is representative of a class of problems that has considerable mathematical interest (e.g., see [1] and [2]). Thus our exposition here is directed more toward mathematical audiences. In another paper, we plan to present the equations in a less formal, but more intuitive manner and to derive more consequences of them.

The establishment of a dominance distribution in a population is analogous to the establishment of ratings in competitive events such as chess, golf, and bowling. Ratings changes must be designed to produce desirable distributions, not an easy task. A recent reference is Glickman’s Bayesian approach to rating chess players [5].

Turning to the specific subject matter of the present paper, we call attention to Van Honk and Hogeweg’s [21] observations of encounters between individuals in a

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Bombus terrestris (bumble bee) colony. Frequently, bees would meet and antennate each other for a moment, after which one bee would retreat and walk away. Based on these observations, Hogeweg and Hesper [6] developed computer simulations of hive behavior. Although their model contained considerably more detail, the core of their assumptions is captured in the following.

Consider a population of anonymous organisms, where each individual possesses an attribute called *dominance* that is associated with a single nonnegative real number x . Assuming that there is an upper bound to the dominance, with no loss of generality, take $0 \leq x \leq 1$. Assume that the following rules govern the development of dominance.

(i) Individuals continually "encounter" other individuals. Each pairwise encounter results in a winner and a loser.

(ii) Results of an encounter are chance events wherein the probability of winning is greater for the individual with larger dominance.

(iii) After an encounter, the dominance of the winner is incremented, while that of the loser is decremented. The more surprising the result, the bigger are the subsequent changes in dominance. (For example, if A has a much larger dominance than B , and A wins the encounter, then the resulting changes in dominance should be relatively small compared to the case where B wins.)

We assume a stochastic model based on a random variable $X(t)$ that takes a value x , at any time t , from the "dominance space" $[0, 1]$. In this paper, we derive and partially analyze the equation for the probability density function $f(x, t)$, where $f(x, t)dx$ gives the fraction of the population that at time t has dominance values in the interval $(x, x + dx)$. A major point of interest is whether dominance values eventually accumulate only near $x = 0$ and $x = 1$. Hogeweg and Hesper [6] suggested that such a split in the population might be used to organize the hive: low dominants perform one task while high dominants perform another.

2. Formulation of the basic equation. Let $\eta(x, y)dt$ denote the probability that a pair of individuals with dominance x and y , respectively, will have an encounter in the time interval of duration dt , where $dt \ll 1$. More precisely, the probability that exactly one encounter occurs in the time interval $(t, t + dt)$ is $\eta(x, y)dt$, the probability that no encounter takes place is $1 - \eta(x, y)dt$, and the probability that more than one encounter occurs is $o(dt)$. We denote by $\psi(x, y, u)du$ the probability that after an encounter between two individuals with dominance x and y , respectively, the x individual will end up with its dominance in the interval $(u, u + du)$, irrespective of the y individual's change in dominance. Of course, ψ satisfies the normalization condition

$$(2.1) \quad \int_0^1 \psi(x, y, u)du = 1.$$

The probability that an individual with dominance x at time t will have its dominance in $(u, u + du)$ at time $t + dt$ is denoted by $f(u, t + dt | x, t)du$. To derive an equation for f , we note that if $x = u$, then in the time interval $(t, t + dt)$, the x individual should not change its dominance, which means that it should not have an encounter. For $x \neq u$, the only possibility is that an encounter takes place between the individual and some partner y such that the x individual will end up with dominance in $(u, u + du)$. We assume the "law of mass action," according to which the probability of finding a partner for an encounter is directly proportional to the number of available

partners. Accordingly,

$$(2.2) \quad f(u, t + dt | x, t) = \left(1 - dt \int_0^1 \eta(x, y) f(y, t) C dy \right) \delta(u - x) + dt \int_0^1 \eta(x, y) f(y, t) C \psi(x, y, u) dy.$$

Here C stands for the size of the population, and thus $f(y, t) C dy$ is the number of individuals with dominance in $(y, y + dy)$ at time t . Moreover, δ is the Dirac distribution. Note that (2.2) describes a Markov process.

We use two fundamental relations from the theory of Markov processes [20]. The first of these is the Chapman–Kolmogorov equation

$$(2.3) \quad f(x_3, t_3 | x_1, t_1) = \int f(x_3, t_3 | x_2, t_2) f(x_2, t_2 | x_1, t_1) dx_2.$$

The second relation links $f(x_2, t_2 | x_1, t_1)$ with the probability distribution function that we seek, $f(x, t)$,

$$(2.4) \quad f(x_2, t_2) = \int f(x_2, t_2 | x_1, t_1) f(x_1, t_1) dx_1.$$

Below, we write the Chapman–Kolmogorov equation for our process taking $t_1 = 0$, $t_2 = t$ and $t_3 = t + dt$ for $dt \ll 1$:

$$(2.5) \quad f(x, t + dt | u, 0) = \int_0^1 f(x, t + dt | v, t) f(v, t | u, 0) dv.$$

Using (2.2), we find that (2.5) becomes

$$(2.6) \quad f(x, t + dt | u, 0) = \int_0^1 \left[\left(1 - dt \int_0^1 \eta(v, y) f(y, t) C dy \right) \delta(x - v) + dt \int_0^1 \eta(v, y) f(y, t) C \psi(v, y, x) dy \right] f(v, t | u, 0) dv.$$

Subtracting $f(x, t | u, 0)$ from both sides and dividing through by dt , we are led to the *master equation*

$$(2.7) \quad \frac{\partial f(x, t | u, 0)}{\partial t} = - f(x, t | u, 0) \int_0^1 \eta(x, y) f(y, t) dy + \int_0^1 \int_0^1 \eta(v, y) f(y, t) \psi(v, y, x) f(v, t | u, 0) dy dv,$$

where, with no loss of generality, we have equated the total population size C to unity.

To put (2.7) into a more satisfactory form, we use (2.4). Multiplying (2.7) by $f(u, 0)$ and integrating over u , we obtain our *basic equation*

$$(2.8) \quad \frac{\partial f(x, t)}{\partial t} = - f(x, t) \int_0^1 \eta(x, y) f(y, t) dy + \int_0^1 \int_0^1 \eta(v, y) \psi(v, y, x) f(v, t) f(y, t) dv dy.$$

The basic equation (2.8) is a gain-loss equation for each state x . The first term on the right side is the loss due to transitions into other states. (An x individual having an encounter with a y partner will change its dominance as a result and thus will leave the x level.) The second term is the gain due to transitions from other states v . (Because of the definition of the ψ function, a v individual, after an encounter with some y partner will reach the dominance level x .)

As a consistency check, we note that upon integration over x in (2.8) and using (2.1), we obtain

$$(2.9) \quad \frac{d}{dt} \int_0^1 f(x, t) dx = 0,$$

as is appropriate for a probability distribution function. The initial condition

$$(2.10) \quad f(x, 0) = f_0(x)$$

must be prescribed, where

$$(2.11) \quad \int_0^1 f_0(x) dx = 1.$$

3. Wins and losses: The governing equation. Each pairwise encounter between individuals results in a winner and a loser. We therefore introduce the function $\phi(p, q)$, the probability that a $p - q$ encounter is won by p (p and q stand for the dominance values of the two partners). Since ϕ is a probability, we necessarily have that

$$(3.1) \quad 0 \leq \phi(p, q) \leq 1.$$

Because the two events “ p wins, q loses” and “ p loses, q wins” are complementary, the function ϕ must satisfy

$$(3.2) \quad \phi(p, q) + \phi(q, p) = 1.$$

For $p = q$, we obtain from (3.2)

$$(3.3) \quad \phi(p, p) = \frac{1}{2} \quad \text{for any } 0 \leq p \leq 1.$$

(Our individuals are distinguished only by their dominance, so that condition (3.3) is natural.) The “dominant is more likely to win” axiom of (ii), §1 requires ϕ to be an increasing function of its first variable and a decreasing function of its second variable. When ϕ is differentiable, this is expressed by

$$(3.4) \quad \phi_1(p, q) \equiv \frac{\partial \phi(p, q)}{\partial p} \geq 0, \quad \phi_2(p, q) \equiv \frac{\partial \phi(p, q)}{\partial q} \leq 0.$$

We now consider several special cases of ϕ . It is possible that only the difference between the dominances of the two partners is important in determining the outcome of an encounter. In such a case, ϕ satisfies

$$(3.5) \quad \phi(1 - p, 1 - q) = 1 - \phi(q, p).$$

In this case, $\phi(p, q) = g(p - q)$, where g is an increasing function satisfying

$$(3.6) \quad 0 \leq g(x) \leq 1 \quad \text{for } -1 \leq x \leq 1; \quad g(0) = \frac{1}{2}; \quad g(x) + g(-x) = 1.$$

As a simple example of this type, we mention that

$$(3.7) \quad \phi(p, q) = \frac{1}{2} + \frac{p - q}{2}.$$

A large class of ϕ functions is given by

$$(3.8) \quad \phi(p, q) = \frac{1}{2} + \frac{1}{2}(p - q)h(p, q),$$

where h is a symmetric function such that

$$(3.9) \quad |(p - q)h(p, q)| \leq 1, \quad 0 \leq p, q \leq 1.$$

For $h(p, q) \equiv 1$, we recover (3.7).

A special case of ϕ corresponds to the deterministic rule "dominant always wins," i.e.,

$$(3.10) \quad \phi(p, q) = 1, \quad p > q; \quad \phi(p, q) = \frac{1}{2}, \quad p = q; \quad \phi(p, q) = 0, \quad p < q.$$

This is an example of (3.8).

The above "dominant always wins" function can be obtained as a limit of functions $\phi_\alpha(p, q)$ for $\alpha \rightarrow \infty$, where

$$(3.11) \quad \phi_\alpha(p, q) = \begin{cases} \frac{1}{2} + T \left[\frac{\alpha(p-q)}{pq(1-p)(1-q)} \right] & p, q \neq 0, 1, \\ \frac{1}{2} & p = q = 0 \text{ or } p = q = 1, \\ 0 & p = 0, q \neq 0 \text{ or } p \neq 1, q = 1, \\ 1 & p = 1, q \neq 1 \text{ or } p \neq 0, q = 0. \end{cases}$$

Here the function T must satisfy

$$\lim_{x \rightarrow -\infty} T(x) = -\frac{1}{2}, \quad \frac{d}{dt} T(x) > 0, \quad T(-x) = T(x), \quad \lim_{x \rightarrow \infty} T(x) = \frac{1}{2}.$$

For example,

$$(3.12) \quad T(x) = \frac{1}{\pi} \arctan x \quad \text{or} \quad T(x) = \frac{1}{2} \tanh x.$$

Even when α is as small as unity, the dominant "almost always" wins (see Fig. 1).

Hogeweg and Hesper [6] use

$$(3.13) \quad \phi(p, q) = \frac{p}{p + q},$$

which can be obtained from (3.8), by taking $h(p, q) = (p + q)^{-1}$.

We now focus on the effective changes in dominance produced by an encounter. Let $\hat{W}(\alpha, \beta, x)dx$ and $\hat{L}(\alpha, \beta, x)dx$ denote the probability that, if α is the winner or the loser, respectively, of an $\alpha - \beta$ encounter, then α acquires a dominance in the interval

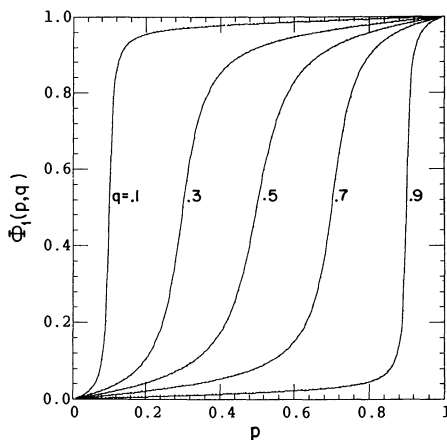


FIG. 1. Graph of $\phi(p, q) = \frac{1}{2} + (1/\pi) \arctan(p - q/pq(1-p)(1-q))$ for several fixed values of q .

$(x, x + dx)$. (Major notations are summarized in Table 1.) Using the probability $\phi(\alpha, \beta)$ just defined, we have that

$$(3.14) \quad \psi(\alpha, \beta, x) = \phi(\alpha, \beta)\hat{W}(\alpha, \beta, x) + \phi(\beta, \alpha)\hat{L}(\alpha, \beta, x),$$

where ψ is defined in §2. Of course, we assume that

$$(3.15) \quad \int_0^1 \hat{W}(\alpha, \beta, x)dx = 1, \quad \int_0^1 \hat{L}(\alpha, \beta, x)dx = 1,$$

guaranteeing the normalization condition (2.1) on ψ .

Let $W(\alpha, \beta)$ be the expected increase of α 's dominance if α wins a α -encounter, while $L(\alpha, \beta)$ is the expected decrease if α loses. Then an interesting choice for $\hat{W}(\alpha, \beta, x)$ would be

$$(3.16) \quad \hat{W}(\alpha, \beta, x) = g(\alpha + W(\alpha, \beta); \sigma, x).$$

In (3.16) g denotes a "near Gaussian," by which we mean a density function obtained by normalizing the restriction to the interval $[0, 1]$ of a Gaussian with mean value $\alpha + W(\alpha, \beta)$ and standard deviation σ ($\sigma \ll 1$). The exact expression for g does not influence our further discussion.

Of particular interest is the limiting case wherein $\sigma \rightarrow 0$, so that the winner α attains a dominance of exactly $\alpha + W(\alpha, \beta)$. Thus, in this case,

$$(3.17) \quad \hat{W}(\alpha, \beta, x) = \delta(\alpha + W(\alpha, \beta) - x), \quad \hat{L}(\alpha, \beta, x) = \delta(\alpha - L(\alpha, \beta) - x).$$

Let us now examine the consequences of specializing the basic equation (2.8) to the case where (3.14) and (3.17) hold. Let us first perform the y integration in (2.8) for the term

$$(3.18) \quad \int_0^1 \phi(v, y)\delta(v + W(v, y) - x)f(y, t)dy.$$

TABLE 1
Major notations.

Symbol	Discrete correspondent	Definition
$f(x, t)dx$	$f_i(t)$	Fraction of population that at time t has dominance values in $(x, x + dx)$;
$\psi(x, y, u)du$	ψ_{ijk}	Probability that after an encounter between the individuals x and y , x ends up in $(u, u + du)$;
$\eta(x, y)dt$	$\eta_{ij}dt$	Probability that individuals x and y will have an encounter in $(t, t + dt)$;
$\phi(p, q)$	ϕ_{ij}	Probability that a $p - q$ encounter is won by p ;
$\hat{W}(\alpha, \beta, x)dx, \hat{L}(\alpha, \beta, x)dx$		Probability that α by winning or losing, respectively, an $\alpha - \beta$ encounter acquires dominance in $(x, x + dx)$;
$W(\alpha, \beta), L(\alpha, \beta)$	W_{ij}, L_{ij}	Expected increase or decrease, respectively of α 's dominance after an encounter with a β partner;
$\alpha_n(x, t)$		The n th derivate moment of the stochastic process;
$\lambda(x, t)$		Flux function representing the amount of probability crossing x in the positive direction per unit time;
$M(x, t)$		First derivate moment, i.e., $\alpha_1(x, t)$;
$D(x, t)$		Second derivate moment, i.e., $\alpha_2(x, t)$

We make the substitution

$$(3.19a) \quad s \equiv v + W(v, y) - x,$$

$$(3.19b) \quad ds = W_2(v, y)dy,$$

where the subscript i indicates the partial derivative with respect to the i th argument; $i = 1, 2$. Assume that (3.19a) can be solved for y to give

$$(3.20) \quad y = y_W(s; v, x).$$

Then the integral in (3.18) becomes

$$(3.21) \quad \int_0^1 \phi[v, y_W(s; v, x)]\delta(s)f[y_W(s; v, x), t][W_2(v, y_W(s; v, x))]^{-1}\chi(y_W(s; v, x))ds \\ = \phi[v, y_W(0; v, x)]f(y_W(0; v, x), t)[W_2(v, y_W(0; v, x))]^{-1}\chi(y_W(0; v, x)).$$

Here χ is the characteristic function for $[0, 1]$, shown below:

$$\chi(x) = 1 \text{ for } 0 \leq x \leq 1; \quad \chi(x) = 0 \text{ for } x < 0, x > 1.$$

The factor $\chi(y_W(s; v, x))$ must appear in (3.21) to ensure that we are integrating well-defined quantities on $[0, 1]$. See (3.38) and (3.39), below.

Performing the y integration for the term involving $\hat{L}(v, y, x)$, we obtain

$$(3.22) \quad \phi(y_L(0; v, x), v)f(y_L(0; v, x), t)[-L_2(v, y_L(0; v, x))]^{-1}\chi(y_L(0; v, x)),$$

where now $y_L(0; v, x)$ is the solution of

$$(3.23) \quad v - L(v, y) = 0.$$

With the notations

$$(3.24) \quad v \equiv w, \quad y_W(0; v, x) = p(w, x)$$

for the term involving W , and

$$(3.25) \quad v \equiv \ell, \quad y_L(0; v, x) = q(\ell, x)$$

for the term involving L , we find that (2.8) becomes the *governing equation*

$$(3.26) \quad \begin{aligned} \frac{\partial f(x, t)}{\partial t} = & - f(x, t) \int_0^1 \eta(x, y) f(y, t) dy \\ & + \int_0^1 \eta(w, p(w, x)) \phi(w, p(w, x)) \frac{f(p(w, x), t)}{W_2(w, p(w, x))} f(w, t) \chi(p(w, x)) dw \\ & - \int_0^1 \eta(\ell, q(\ell, x)) \phi(q(\ell, x), \ell) \frac{f(q(\ell, x), t)}{L_2(\ell, q(\ell, x))} f(\ell, t) \chi(q(\ell, x)) d\ell. \end{aligned}$$

The second term on the right side of (3.26) gives the fraction of the population that attains dominance level x by winning an encounter, while the third term is that of the losers.

If we first perform the v integration in (2.8), we obtain our governing equation with integration over the “partners” as follows:

$$(3.27) \quad \begin{aligned} \frac{\partial f(x, t)}{\partial t} = & - f(x, t) \int_0^1 \eta(x, y) f(y, t) dy \\ & + \int_0^1 \eta(w(p, x), p) \phi(w(p, x), p) \frac{f(w(p, x), t)}{1 + W_1(w(p, x), p)} f(p, t) \chi(w(p, x)) dp \\ & + \int_0^1 \eta(\ell(q, x), q) \phi(q, \ell(q, x)) \frac{f(\ell(q, x), t)}{1 - L_1(\ell(q, x), q)} f(q, t) \chi(\ell(q, x)) dq. \end{aligned}$$

In (3.27) $w(p, x)$ and $\ell(q, x)$ denote the solutions of the equations

$$(3.28a) \quad w + W(w, p) = x,$$

$$(3.28b) \quad \ell - L(\ell, q) = x.$$

Let us now consider particular possible examples for the function W and L . The basic restrictions on $W(\alpha, \beta)$ and $L(\alpha, \beta)$ are their nonnegativity, and also

$$(3.29a) \quad 0 \leq w + W(w, p) \leq 1, \quad 0 \leq w, p \leq 1,$$

$$(3.29b) \quad 0 \leq \ell - L(\ell, q) \leq 1, \quad 0 \leq \ell, q \leq 1,$$

to assure that dominance values range between zero and unity. Other conditions stem from the rules (iii) enunciated in §1. Thus we expect that a winner w wins more if

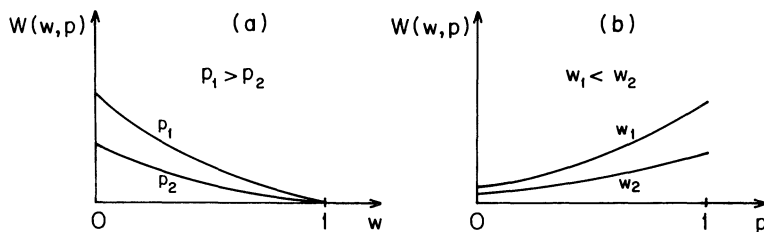


FIG. 2. Typical graph of the function $W(w, p)$, the dominance increase of the winner w in a $w - p$ encounter, as a function of w with p fixed (a) and as function of p with w fixed (b).

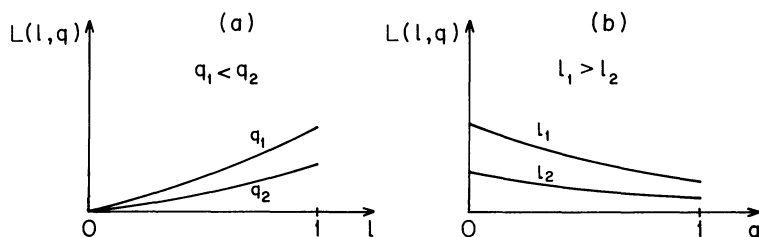


FIG. 3. Typical graph of the function $L(l, q)$, the dominance decrease of the loser l in an $l - q$ encounter as a function of l with q fixed (a) and as a function of q with l fixed (b).

partner p is more dominant (so that a win is less expected). By the same token, w wins less if w itself is more dominant. In mathematical terms, we take as axioms

$$(3.30) \quad W_1(w, p) \equiv \frac{\partial W(w, p)}{\partial w} < 0, \quad W_2(w, p) \equiv \frac{\partial W(w, p)}{\partial p} > 0.$$

Parallel with (3.30), we expect that a biologically plausible loss function satisfies

$$(3.31) \quad L_1(\ell, q) \equiv \frac{\partial L(\ell, q)}{\partial \ell} > 0, \quad L_2(\ell, q) \equiv \frac{\partial L(\ell, q)}{\partial q} < 0.$$

Condition (3.29) on W , in particular, requires $W(1, p) \leq 0$ for any p . Since W is nonnegative, it follows that

$$(3.32) \quad W(1, p) = 0 \quad \text{for } 0 \leq p \leq 1.$$

Indeed, a winner with dominance unity cannot raise his dominance. In like manner, from (3.29), taking $\ell = 0$, we obtain $L(0, q) \leq 0$, for any q . Using the nonnegativity condition on L , it follows that

$$(3.33) \quad L(0, q) = 0 \quad \text{for } 0 \leq q \leq 1;$$

i.e., no loss is suffered by a loser whose dominance is already zero. See Figs. 2 and 3 for typical graphs of $W(w, p)$ and $L(\ell, q)$.

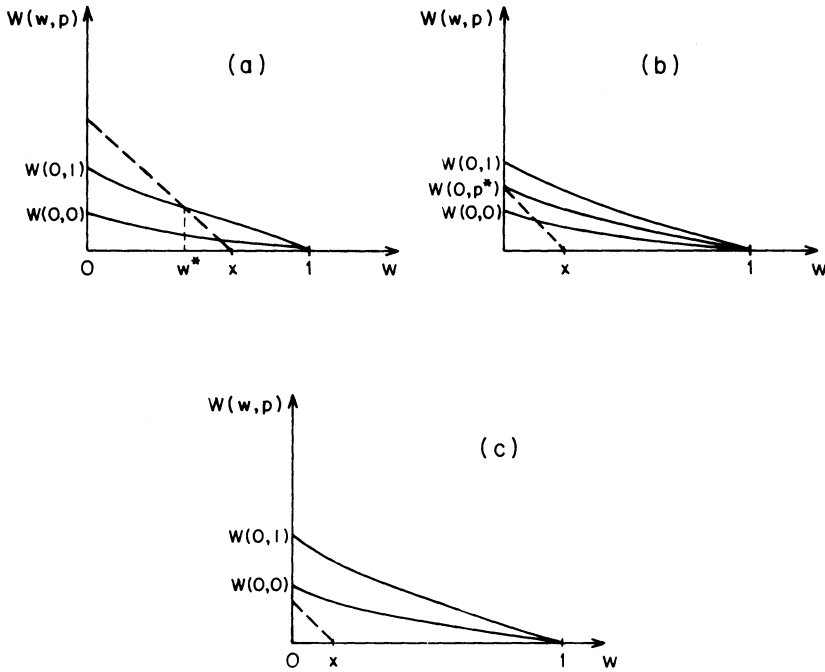


FIG. 4. Graphs for determining w^* and p^* (defined in (3.40) and (3.36)), the limits of integration in (3.38) and (3.39) in the "winner-term" for (a) $W(0, 1) \leq x \leq 1$; (b) $W(0, 0) \leq x < W(0, 1)$; and (c) $0 \leq x < W(0, 0)$.

If we assume that the equations of (3.28) have unique solutions in $[0, 1]$, then more conditions on functions W and L follow. More precisely, so that a unique solution $w(p, x)$ to (3.28a) exists, we impose

$$(3.34) \quad 1 + W_1(w, p) > 0, \quad 0 \leq w, p \leq 1.$$

Similarly, to obtain a unique solution $\ell(q, x)$ of (3.28b), we require that

$$(3.35) \quad 1 - L_1(\ell, q) < 0, \quad 0 \leq \ell, q \leq 1.$$

Conditions (3.30) are sufficient to assure uniqueness of the solutions of the equations (3.28a) and (3.28b) when solved for p and q , respectively.

To find the values of p for which $w(p, x)$ is between zero and unity, we refer to Fig. 4. We see that a unique $w(p, x)$ exists for

$$(3.36) \quad 0 \leq p \leq p^*(x) \quad \text{where} \quad \begin{cases} p^*(x) \equiv 1, & 1 \geq x \geq W(0, 1), \\ W(0, p^*) = x, & W(0, 0) \leq x < W(0, 1), \\ p^* \equiv 0, & 0 \leq x < W(0, 0). \end{cases}$$

Similarly, to find the values of q for which $\ell(q, x)$ is between 0 and 1, we refer to Fig. 5. A unique $\ell(q, x)$ exists for

$$(3.37) \quad q^*(x) \leq q \leq 1 \quad \text{where} \quad \begin{cases} q^*(x) \equiv 0, & 1 \geq 1 - x \geq L(1, 0), \\ L(1, q^*) = 1 - x, & L(1, 0) > 1 - x \geq L(1, 1), \\ q^*(x) \equiv 1, & L(1, 1) \geq 1 - x > 0. \end{cases}$$

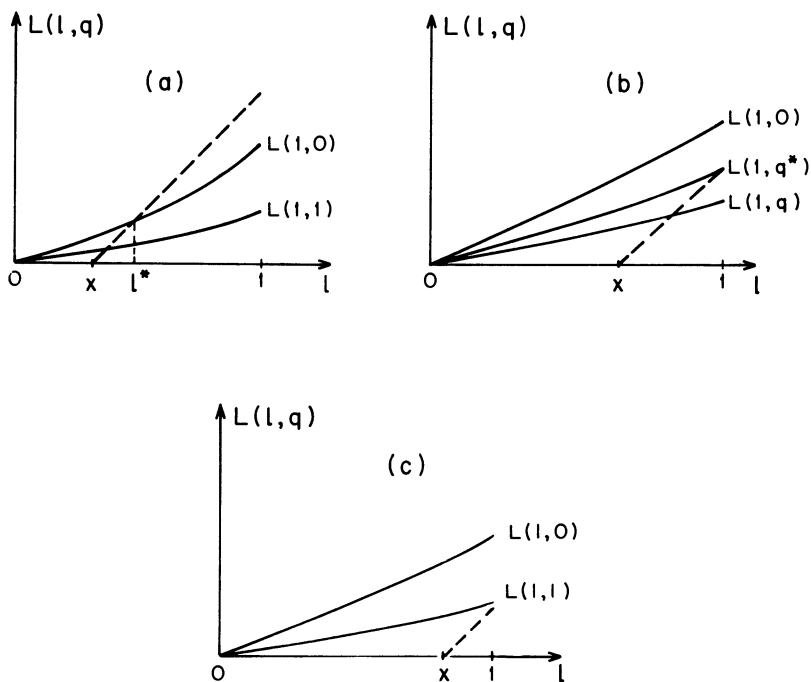


FIG. 5. Graphs for determining l^* and q^* (defined in (3.41) and (3.37)), the limits of integration in (3.38) and (3.39) in the "losers-term" for (a) $1 \geq 1 - x \geq L(1, 0)$; (b) $L(1, 0) > 1 - x \geq L(1, 1)$; and (c) $L(1, 1) > 1 - x \geq 0$.

We see that (3.27) can be rewritten without the characteristic functions by changing the limits of integration in the three integrals to

$$(3.38) \quad \int_0^1 dy, \quad \int_0^{p^*} dp, \quad \text{and} \quad \int_{q^*}^1 dq.$$

Similarly, the characteristic functions of (3.26) can be eliminated by changing the limits of integration to

$$(3.39) \quad \int_0^1 dy, \quad \int_{w^*}^x dw, \quad \text{and} \quad \int_x^{\ell^*} d\ell,$$

where

$$(3.40) \quad \begin{aligned} w^* + W(w^*, 1) &= x, & 1 \geq x \geq W(0, 1), \\ w^* &\equiv 0, & W(0, 1) > x \geq W(0, 0), \\ w^* &\equiv x, & W(0, 0) > x \geq 0 \end{aligned}$$

and

$$(3.41) \quad \begin{aligned} \ell^* - L(\ell^*, 0) &= x, & 1 \geq 1 - x \geq L(1, 0), \\ \ell^* &\equiv 1, & L(1, 0) > 1 - x \geq L(1, 1), \\ \ell^* &\equiv x, & L(1, 1) > 1 - x \geq 0. \end{aligned}$$

Again, see Figs. 4 and 5. (Note that if (3.28a) and (3.28b) do not have unique solutions, then additional integrals appear in (3.38) and (3.39).)

Let us now consider particular possible examples for the functions W and L . A first example for W might be

$$(3.42) \quad W(w, p) = \epsilon_1 p(1 - w),$$

where $0 \leq \epsilon_1 \leq 1$. The nonnegativity condition is automatically satisfied, and condition (3.29a) is also, since $\epsilon_1 p(1 - w) \leq 1 - w$. Similarly, a possible choice for L is

$$(3.43) \quad L(\ell, q) = \epsilon_2 \ell(1 - q),$$

where $0 \leq \epsilon_2 \leq 1$.

A reasonable symmetry constraint to place on the function $W(w, p)$ and $L(\ell, q)$ is that the reward of winning bears the same relation to the minimal dominance value (zero) as does the penalty of losing to the maximal dominance value (unity). That is,

$$(3.44) \quad W(w, p) = L(1 - w, 1 - p),$$

or, equivalently,

$$(3.45) \quad W(1 - \ell, 1 - q) = L(\ell, q).$$

The example of (3.42) and (3.43) satisfies this symmetry constraint if $\epsilon_1 = \epsilon_2$. A general pair of win-increment and loss-decrement functions that satisfy the symmetry constraint is

$$(3.46) \quad W(w, p) = h[p(1 - w)], \quad L(\ell, q) = h[\ell(1 - q)],$$

for a function h such that

$$(3.47) \quad 0 \leq h(x), \quad 0 < h'(x), \quad h(x) \leq x, \quad h(0) = 0, \quad 0 \leq x \leq 1.$$

These conditions follow from (3.30), (3.31), and (3.46).

We remark that $W(w, 0) = L(\ell, 1) = 0$ for (3.42) and (3.43). This is not the case for

$$(3.48a) \quad W(w, p) = (1 - w)\phi(p, w),$$

$$(3.48b) \quad L(\ell, q) = \ell\phi(\ell, q)$$

(where $\phi(w, p)$ is the probability that w wins a $w - p$ encounter, as defined in §3). According to (3.48a), for example, if p is virtually certain to win [$\phi(p, w) \approx 1$], yet w actually does win, then w 's new dominance value, $w + W(w, p)$ becomes the highest possible (virtually unity). By contrast, if ℓ is virtually certain to lose an $\ell - q$ encounter [$\phi(\ell, q) \approx 0$], and ℓ indeed loses, then ℓ 's dominance is virtually unchanged.

Similar rules to (3.48a) and (3.48b) are

$$(3.49a) \quad W(w, p) = (1 - w) \exp[-\mu\phi(w, p)],$$

$$(3.49b) \quad L(\ell, q) = \ell \exp[-\mu\phi(q, \ell)].$$

Here, if the positive parameter μ is made large, only for very unlikely victories does w 's dominance become nearly unity; otherwise, w 's rewards are small.

Hogeweg and Hesper [6] consider the win-loss functions

$$(3.50) \quad W(p, q) \equiv L(q, p) = \Delta\phi(q, p),$$

where ϕ is defined in (3.13) and Δ is a positive constant. If $w + W(w, p) > 1$ or $\ell - L(\ell, q) < 0$, "legal" alternatives to (3.50) are

$$(3.51) \quad W(w, p) = L(p, q) = 0$$

or

$$(3.52) \quad W(w, p) = 1 - w, \quad L(\ell, q) = \ell.$$

In chess, similar rules are used to establish the changes in rating. The win-loss functions are given by (3.50) for some specific Δ , and ϕ is given by

$$(3.53) \quad \phi(p, q) = \frac{1}{1 + 10^{-(15(p-q)/2)}}.$$

Formula (3.53) is essentially the same as that given by Kazic, Keene, and Lim [7], except that we have normalized the ratings so that they fall in $[0, 1]$.

4. A discrete model. For the process under consideration, a discrete model can be constructed on its own, but we prefer one that approximates the continuous model. Such a discrete model proves itself to be useful in our later numerical analysis. Our exposition therefore closely follows the continuous model's construction.

At this point, we shift to a dominance space that comprises the whole real line $(-\infty, \infty)$ instead of the closed interval $[0, 1]$. With this, the general theory of stochastic processes is much easier to apply. Moreover, we need not be concerned about limits of integrations in our equations (as in (3.38) and (3.39)). We still want to preserve our previous rule that active individuals are only those with dominance in $[0, 1]$ that remain in $[0, 1]$ even after encounters (i.e., our win-loss function W and L remain as we defined them). Therefore we make the following assumptions.

Assumption 1. $\eta(x, y) = 0$ if x or y is outside $[0, 1]$ (i.e., individuals with dominance outside $[0, 1]$ are inactive).

Assumption 2. $f(x, t_0) = f_0(x)$, the initial distribution, is zero outside $[0, 1]$.

Assumption 3. $\psi(\alpha, \beta, x) = \delta(\alpha - x)$ for α or β outside $[0, 1]$ (inactive individuals do not change their dominance).

With these assumptions, the governing equation (2.8) gives

$$(4.1) \quad \frac{\partial f(x, t)}{\partial t} \equiv 0 \quad \text{for } x \notin [0, 1].$$

It follows that $f(x, t) = 0$ for any t , if we start with $f(x, t_0) = 0$, $x \notin [0, 1]$. In this way, $f(x, t)$ is well defined on the whole real line. Therefore we henceforth consider the dominance space to be $(-\infty, \infty)$. We must note, however, the possible existence of discontinuities at $x = 0$ and $x = 1$.

In formulating a discrete model, let us consider the dominance space to be the set of all the real numbers, and, for any integer i , let $f_i(t)$ denote the fraction of

“*i*-organisms” whose dominance x is the range $(i - 1)\Delta \leq x < i\Delta$, where Δ is a positive real number. Let $\eta_{ij}dt$ denote the probability that a pair of individuals with dominance in the i th and j th interval respectively, will have an encounter in the time interval $(t, t + dt)$ where $dt \ll 1$.

To characterize encounters, we introduce the probability ψ_{pqi} . Here ψ_{pqi} is the probability that, after an encounter between two individuals with dominance in the p th and q th interval, respectively, the p individual will end up with its dominance in the i th interval regardless of the final dominance of the partner. Necessarily,

$$(4.2) \quad \sum_i \psi_{pqi} = 1.$$

Here and below, unless otherwise indicated, summations are to be performed over all integers.

Let $f_{ij}(t + dt | t)$ denote the probability that an individual that was in state j at time t will be in state i at time $t + dt$. (By “state i ,” we mean having dominance in the i th interval.) As for the continuous case, we assume the law of mass action and therefore write

$$(4.3) \quad f_{ij}(t + dt | t) = \left[1 - dt \sum_k \eta_{jk} f_k(t) \right] \delta_{ij} + dt \sum_k \eta_{jk} f_k(t) \psi_{jki},$$

where δ_{ij} is the Kronecker symbol and the population size has been taken to be unity.

As in the continuous case, there follows the discrete master equation

$$(4.4) \quad \frac{df_i(t)}{dt} = -f_i(t) \sum_\ell \eta_{i\ell} f_\ell(t) + \sum_{j,\ell} \eta_{j\ell} f_j(t) f_\ell(t) \psi_{j\ell i}.$$

To link with our continuous model, we define

$$(4.5) \quad \Theta(i\Delta, t) \equiv f_i(t), \quad \psi(p\Delta, q\Delta, i\Delta) \equiv \psi_{pqi}, \quad \eta(i\Delta, j\Delta) \equiv \eta_{ij}.$$

We consider the limits $\Delta \rightarrow 0$, $i, j, p, q \rightarrow \infty$ such that $i\Delta = x$, $j\Delta = y$, $p\Delta = \alpha$, $q\Delta = \beta$ are fixed, and

$$(4.6) \quad \begin{aligned} \Theta(i\Delta, t)/\Delta &\rightarrow f(x, t), \\ \psi(p\Delta, q\Delta, i\Delta)/\Delta &\rightarrow \psi(\alpha, \beta, x), \quad \eta(i\Delta, j\Delta) \rightarrow \eta(x, y). \end{aligned}$$

It can be seen that $\Theta(i\Delta, t)$ and $\psi(p\Delta, q\Delta, i\Delta)$ play roles of probability distributions whose probability densities are $f(x, t)$ and $\psi(\alpha, \beta, x)$, respectively. Consequently, for small Δ , (4.4) is an approximation of the continuous basic equation (2.8). For simplicity, we take $\Delta = 1/N$, N being some positive integer.

In line with our previous assumption (i.e., all the encounters take place only between individuals with dominance in $[0, 1]$), we assume that

$$\begin{aligned} f_i(0) &= 0, & i &\notin \{1, 2, 3, \dots, N\}, \\ \eta_{ij} &= 0, \psi_{ijk} = \delta_{ik} & i \text{ or } j &\notin \{1, 2, 3, \dots, N\}. \end{aligned}$$

From (4.4), it follows that

$$\frac{d}{dt} f_i(t) = 0, \quad i \notin \{1, 2, \dots, N\}.$$

Therefore $f_i(t) = f_i(0) = 0$, for any time t . That is, if we start with a population distributed over $[0, 1]$, this property will be preserved if we ensure that encounters between individuals with dominance in $[0, 1]$ will result in changes that do not take dominance values outside this interval.

We now define discrete counterparts of the probability functions ϕ and ψ and of the win-loss functions W and L . For the probability ϕ_{ij} , we can take any particular ϕ from our continuous model and define

$$(4.7) \quad \phi_{ij} = \phi(i/N, j/N), \quad 1 \leq i, j \leq N.$$

Thus we preserve the monotonicity properties of ϕ .

The discrete win-loss function W_{ij} and L_{ij} for the case of exact win and loss are integer-valued functions such that

$$(4.8) \quad \psi_{ijk} = \phi_{ij}\delta_{k, i+W_{ij}} + \phi_{ji}\delta_{k, i-L_{ij}}.$$

The functions W_{ij} and L_{ij} are taken to satisfy the requirements

$$(4.9) \quad 0 \leq W_{ij}, L_{ij} \leq N - 1, \quad 1 \leq i, j \leq N.$$

According to (3.30) and (3.31), the win and loss functions in the discrete case must also satisfy monotonicity requirements. Therefore $W_{ij}(L_{ij})$ is a decreasing (increasing) function of the first variable, and an increasing (decreasing) function of the second variable. An illuminating example is the discrete counterpart of (3.42) and (3.43)

$$(4.10) \quad W_{ij} = \left\lfloor \frac{(N-i)(j-1)}{a(N-1)} \right\rfloor, \quad L_{ij} = \left\lfloor \frac{(i-1)(N-j)}{b(N-1)} \right\rfloor, \quad 1 \leq i, j \leq N.$$

The brackets denote the integer part of the expressions and a, b are positive integers, $1 \leq a, b \leq N-1$. ($a = b = 1$ corresponds to $\epsilon_1 = \epsilon_2 = 1$ and $a, b > 1$ for $0 < \epsilon_1, \epsilon_2 < 1$.)

From (3.2) and (4.7), $\phi_{ij} + \phi_{ji} = 1$. If (4.8) holds, then (4.2) is satisfied, for there are unique integers k_1, k_2 such that $i + W_{ij} = k_1$ and $i - L_{ij} = k_2$ for i and j fixed, which implies that

$$(4.11) \quad \sum_{k=1}^N \psi_{ijk} = \sum_{k=1}^N (\phi_{ij}\delta_{k, k_1} + \phi_{ji}\delta_{k, k_2}) = \phi_{ij} + \phi_{ji} = 1.$$

In the discrete case, it follows that we must deal with the following system of ordinary differential equations, for $1, 2, \dots, N$:

$$(4.12) \quad \frac{df_i(t)}{dt} = -f_i(t) \sum_{j=1}^N \eta_{ij} f_j(t) + \sum_{j,k=1}^N \eta_{jk} f_j(t) f_k(t) \psi_{jki}.$$

Using (4.2), we can check that (4.12), the discrete counterpart of our basic equation (2.8), implies that

$$(4.13) \quad \sum_{i=1}^N f_i(t) = \text{constant}.$$

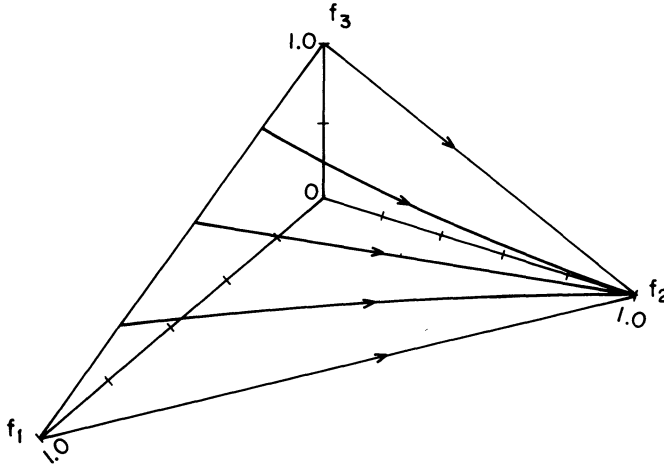


FIG. 6. Typical phase portrait of system (5.2) restricted to the domain $D = \{(x_1, x_2, x_3) \mid x_1 + x_2 + x_3 = 1, x_i \geq 0, i = 1, 2, 3\}$.

The constant is, of course, taken equal to unity.

5. Discrete models when $N=2$ and $N=3$. We examine discrete models for $N = 2$ and $N = 3$, for they provide the simplest examples of the phenomena in which we are interested. When $N = 2$ (two dominance values), the fraction f_1 of individuals with low dominance satisfies

$$df_1/dt = (a - b + c)f_1^2 + (b - 2c - 1)f_1 + c,$$

where $a \equiv \psi_{111}$, $b = \psi_{121} + \psi_{211}$, $c = \psi_{221}$. There is a unique globally stable steady state: Arbitrary ratios of high to low dominants can be obtained by suitable parameter choices.

When $N = 3$, there is an intermediate dominance value: We can see if and when there are situations when the population nonetheless tends to a situation where only high and low dominants are present. It is sufficient to illustrate matters with specific examples.

For the first example, we take the following discrete counterpart of (3.48):

$$(5.1) \quad \phi_{ij} = \frac{1}{2} + \frac{i-j}{6}, \quad W_{ij} = [(3-i)\phi_{ji}], \quad L_{ij} = [(i-1)\phi_{ij}].$$

Using $f_2 = 1 - (f_1 + f_3)$, we obtain from (4.12) with $\eta_{ij} \equiv 1$

$$(5.2) \quad \begin{aligned} \frac{df_1}{dt} &= -f_1 + \frac{1}{2}f_1^2 + \frac{2}{3}f_1(1 - f_1 - f_3) + \frac{5}{6}f_1f_3, \\ \frac{df_3}{dt} &= -f_3 + \frac{1}{2}f_3^2 + \frac{5}{6}f_1f_3 + \frac{2}{3}f_3(1 - f_1 - f_3). \end{aligned}$$

The unique nonnegative steady state of system (5.2) is $f_1 = f_3 = 0$. Linear analysis shows that this steady state is stable. Simulations, such as that illustrated in Fig. 6, indicate that all the individuals will reach dominance level 2 (i.e., $f_2 = 1$). This is a case where dominance cannot be used to organize the society. It is a useless property, since it soon attains a single value for all members of the population.

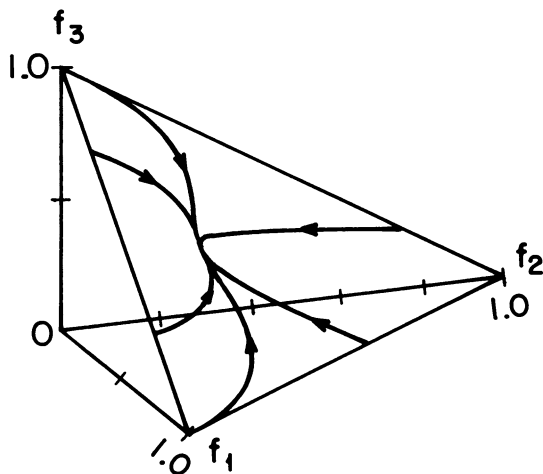


FIG. 7. Similar to Fig. 6 for system (5.3).

The second example concerns the “dominant always wins” case (3.10). Given the definition of the function ϕ , we must consider only the values W_{ij} for $i \geq j$ and L_{ij} for $i \leq j$. From these values, $W_{3j} = 0$ and $L_{1j} = 0$ for any j . Let us first consider the situation where $W_{11} = W_{21} = W_{22} = L_{22} = L_{23} = L_{33} = 1$. System (4.12) in this case becomes

$$(5.3) \quad \frac{df_1}{dt} = -\frac{1}{2}f_1^2 + \frac{1}{2}f_2^2 + f_2(1 - f_1 - f_2), \quad \frac{df_2}{dt} = -f_2 + \frac{1}{2}f_1^2 + \frac{1}{2}(1 - f_1 - f_2)^2.$$

System (5.3) has a nonnegative steady state $f_1 = -1 + \sqrt{2}$ and $f_2 = 3 - 2\sqrt{2}$ (necessarily $f_3 = -1 + \sqrt{2}$), which proves to be stable. A typical phase portrait is depicted in Fig. 7. Here, there is a differentiation of the population into high and low dominants, but there is no gap in the distribution ($f_2 \neq 0$).

If we slightly modify the win-loss functions by taking $W_{11} = L_{33} = 2$, we obtain

$$(5.4) \quad \frac{df_1}{dt} = -f_1 + \frac{1}{2}, \quad \frac{df_2}{dt} = -f_2.$$

The unique and globally attracting steady state is $f_1 = \frac{1}{2}$, $f_2 = 0$, and hence $f_3 = \frac{1}{2}$. Again, this state is stable. Now there are only high dominants and low dominants. (See Fig. 8.)

6. Weak interactions. To make further analytic progress, we consider situations where an individual encounter has only a small effect on dominance. To study this case, we recall that for the Markovian transition density function f (defined under (2.1)) we can write the so-called Kramers–Moyal expansion [20], [19]

$$(6.1) \quad \frac{\partial f(x, t | x_0, t_0)}{\partial t} = -\frac{\partial \lambda(x, t)}{\partial x},$$

where

$$(6.2) \quad \lambda(x, t) = \sum_{n=1}^{\infty} \frac{(-1)^n}{n!} \frac{\partial^{n-1}}{\partial x^{n-1}} [\alpha_n(x, t) f(x, t | x_0, t_0)].$$

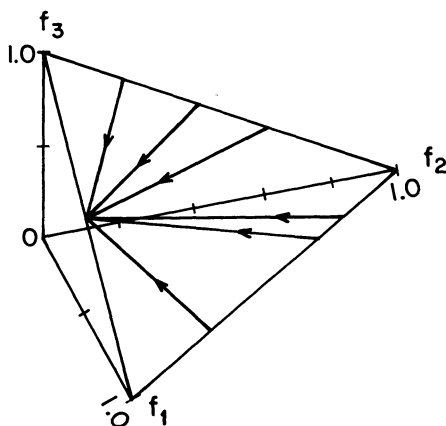


FIG. 8. Similar to Fig. 6 for system (5.4).

The derivate moments of the stochastic process $X(t)$ are defined by

$$(6.3) \quad \alpha_n(x, t) = \lim_{\Delta t \rightarrow 0} (1/\Delta t) E\{(X(t + \Delta t) - X(t))^n \mid X(t) = x\}, \quad n = 1, 2, \dots$$

The symbol E is used in (6.3) to indicate an expected-value operation. Multiplying by $f(x_0, t_0)$ and integrating over x in (6.1), we can see that the probability density function $f(x, t)$ also satisfies (6.1). Equation (6.1) describes the convection of probability. The flux function $\lambda(x, t)$ represents the amount of probability crossing x in the positive direction per unit time.

To approximate (6.1), let us now analyze our master equation (2.7) in the case of "small jumps," i.e., for exact and small wins and losses, as follows:

$$(6.4) \quad W(w, p) = \epsilon \bar{W}(w, p), \quad L(\ell, q) = \epsilon \bar{L}(\ell, q); \quad 0 < \epsilon \ll 1.$$

We assume that the larger of the maxima of $\bar{W}(w, p)$ and $\bar{L}(\ell, q)$ for $0 \leq w, \ell, p, q \leq 1$ is unity, so that ϵ gives the scale of the wins and losses. We accomplish this here with the following assumption, in the important special case of symmetric maximum wins and losses:

$$(6.5) \quad \bar{W}(0, 1) = 1, \quad \bar{L}(1, 0) = 1.$$

To write the Kramers-Moyal expansion, we must first determine the incremental moments $\alpha_n(x, t)$. With the aid of a suitable version of (2.2), the expression of $\alpha_n(x, t)$ can be written as

$$(6.6) \quad \begin{aligned} \alpha_n(x, t) &= \lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \int_{-\infty}^{\infty} (y - x)^n f(y, t + \Delta t \mid x, t) dy \\ &= \int_{-\infty}^{\infty} (y - x)^n \left(\int_{-\infty}^{\infty} \eta(x, u) f(u, t) \psi(x, u, y) du \right) dy, \quad n = 1, 2, \dots \end{aligned}$$

Hence

$$(6.7) \quad \frac{\partial f(x, t)}{\partial t} = \sum_{n=1}^{\infty} \frac{(-1)^n}{n!} \epsilon^n \frac{\partial^n}{\partial x^n} \left\{ \left[\int_0^1 \eta(x, u) U_n(x, u) f(u, t) du \right] f(x, t) \right\},$$

$x \in [0, 1],$

where

$$(6.8) \quad U_n(x, u) = \phi(x, u) \bar{W}^n(x, u) + (-1)^n \phi(u, x) \bar{L}^n(x, u).$$

For $\epsilon \ll 1$, it is of interest to examine the first two terms in the Kramers–Moyal expansion

$$(6.9) \quad \frac{\partial f(x, t)}{\partial t} = -\epsilon \frac{\partial}{\partial x} [M(x, t) f(x, t)] + \frac{\epsilon^2}{2} \frac{\partial^2}{\partial x^2} [D(x, t) f(x, t)],$$

where M and D denote the first two incremental moments, i.e.,

$$(6.10a) \quad M(x, t) \equiv \alpha_1(x, t),$$

$$(6.10b) \quad D(x, t) \equiv \alpha_2(x, t).$$

Alternatively,

$$(6.11) \quad \frac{\partial f(x, t)}{\partial t} = -\epsilon \frac{\partial}{\partial x} \left[\left(M(x, t) - \frac{\epsilon}{2} \frac{\partial D(x, t)}{\partial x} \right) f(x, t) - \frac{\epsilon}{2} D(x, t) \frac{\partial f(x, t)}{\partial x} \right].$$

Equation (6.11) exhibits a convection with velocity ϵM , together with a small $O(\epsilon^2)$ correction, and also a weak diffusion $\frac{1}{2}\epsilon^2 D$.

The convection-diffusion equation (6.11) requires an initial condition

$$(6.12) \quad f(x, t_0) = f_0(x)$$

at some initial time t_0 . To determine the boundary conditions, we reconsider (6.4). Integrating over x from 0 to 1, we obtain

$$(6.13) \quad \int_0^1 \frac{\partial f(x, t)}{\partial t} dx = - \int_0^1 \frac{\partial}{\partial x} \lambda(x, t) dx = 0,$$

since $\int_0^1 f(x, t) dx = 1$. It follows that

$$(6.14) \quad \lambda(0, t) = \lambda(1, t) \quad \text{for any time } t.$$

Because we do not allow jumps from $[0, 1]$ to outside $[0, 1]$, we necessarily have that

$$(6.15) \quad \lambda(0, t) \geq 0, \quad \lambda(1, t) \leq 0.$$

Relations (6.14) and (6.15) imply that

$$(6.16) \quad \lambda(0, t) = \lambda(1, t) = 0 \quad \text{for any time } t.$$

(As expected, conservation of material is associated with zero-flux conditions at the boundaries.) For (6.9), (6.16) is equivalent to

$$(6.17) \quad M(x, t)f(x, t) - \frac{\epsilon}{2} \frac{\partial}{\partial x} [D(x, t)f(x, t)] \Big|_{x=0,1} = 0.$$

As is discussed further below, solutions to (6.9) exhibit a variety of defects as approximations to (3.26) for small ϵ . In the present paper, we view (6.9) as a heuristic that can lead to conjectures concerning qualitative behavior that can be tested by numerical analysis.

With its interpretation as the governing equation of a convective-diffusive flow, (6.9) sometimes permits immediate characterization of the development with time of the dominance distribution. Consider, for example, hypothesis (3.48) for the win and loss functions, preceded by a parameter, ϵ :

$$(6.18) \quad W(w, p) = \epsilon(1 - w)\phi(p, w), \quad L(\ell, q) = \epsilon\ell\phi(\ell, q); \quad 0 < \epsilon \ll 1.$$

When $0 < \epsilon \ll 1$, by (6.8) and (6.10) with $\eta \equiv 1$ the convection speed is given by

$$(6.19) \quad M(x, t) = (1 - 2x) \int_0^1 \phi(x, u)\phi(u, x)f(u, t)du.$$

Since ϕ and f are positive,

$$(6.20) \quad M(x, t) > 0 \quad \text{if } x < \frac{1}{2}, \quad M(x, t) < 0 \quad \text{if } x > \frac{1}{2}.$$

Consequently (to first approximation) according to (6.9) all dominance is “swept” to $x = \frac{1}{2}$. (The diffusion will “soften” the delta function at $x = \frac{1}{2}$ to a peaked function.) That is, most organisms will eventually attain a common dominance value near to $\frac{1}{2}$. In this case, dominance cannot produce a social hierarchy.

If we wish to construct a model that will divide the organisms into two groups (one group with dominance near zero and one group with dominance near unity), then the convection speed $M(x, t)$ should satisfy

$$(6.21) \quad M(x, t) < 0 \quad \text{for } 0 < x < x^*, \quad M(x, t) > 0 \quad \text{for } x^* < x < 1,$$

where x^* is some constant between zero and unity. By (3.32) and (3.33),

$$(6.22) \quad \overline{W}(1, u) = \overline{L}(0, u) = 0,$$

so that (6.8) yields

$$(6.23) \quad M(0, t) \geq 0, \quad M(1, t) \leq 0.$$

Comparing (6.21) and (6.23), we see that if we wish to achieve (6.21) with a function M that is continuous in x , it is necessary that

$$(6.24a) \quad M(0, t) = 0,$$

$$(6.24b) \quad M(1, t) = 0,$$

$$(6.24c) \quad M_1(0, t) < 0,$$

$$(6.24d) \quad M_1(1, t) < 0.$$

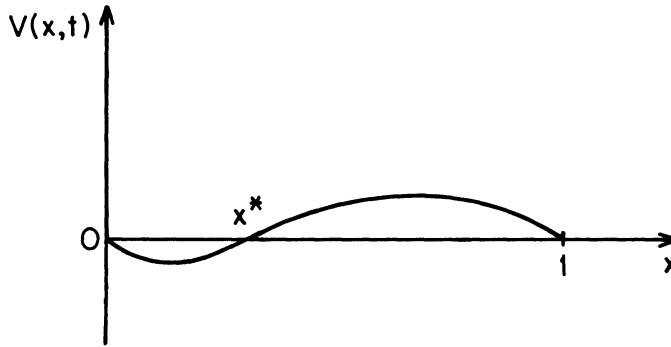


FIG. 9. The shape of a "convection function" M (defined in (6.10a)) that divides the population into high and low dominants.

See Fig. 9.

To achieve (6.24a) and (6.24b), we see from the definition of M that we must require that

$$(6.25) \quad \phi(0, u) = \phi(u, 1).$$

For the expression of $M_1(x, t)$, we obtain

$$(6.26) \quad M_1(x, t) = \int_0^1 [\overline{W}_1(x, u)\phi(x, u) + \overline{W}(x, p)\phi_1(x, u) - \overline{L}_1(x, u)\phi(u, x) - \overline{L}(x, u)\phi_2(u, x)]f(u, t)du.$$

Using (6.22) and (6.25), we find that

$$(6.27) \quad M_1(z, t) = \int_0^1 [\overline{W}(z, u)\phi_1(z, u) - \overline{L}_1(z, u)\phi(u, z)]f(u, t)du, \quad z = 0, 1.$$

From (3.4), (3.30), and (3.31), recall the assumptions

$$(6.28) \quad \phi_1 \geq 0, \quad \phi_2 \leq 0, \quad W_1 \leq 0, \quad L_1 \geq 0.$$

To guarantee (6.24c) and (6.24d), we further assume that

$$(6.29) \quad \phi_1(0, u) = \phi_2(u, 1) = 0.$$

As an example, the functions ϕ_α given by (3.11) can be shown to satisfy (6.25) and (6.29).

A model that yields a division of the organisms into two groups proves to be the "dominant always wins" case for which, as mentioned in the paragraph following (3.10), the function ϕ is the limit of ϕ_α as $\alpha \rightarrow \infty$. Here

$$(6.30) \quad M(x, t) = \int_0^x \overline{W}(x, u)f(u, t)du - \int_x^1 \overline{L}(x, u)f(u, t)du.$$

By (6.22), (6.24a) and (6.24b) are satisfied. Also,

$$(6.31) \quad M_1(x, t) = [\overline{W}(x, x) + \overline{L}(x, x)]f(x, t) + \int_0^x \overline{W}_1(x, u)f(u, t)du - \int_x^1 \overline{L}_1(x, u)f(u, t)du.$$

Let us assume that

$$(6.32) \quad \overline{W}(0, 0) = \overline{L}(1, 1) = 0.$$

Then, since $\overline{W}_1 < 0$, $\overline{L}_1 > 0$, all the necessary conditions of (6.24) are satisfied in this case as well. An example of where our conditions appear sufficient is provided in the next section.

7. Numerical analysis. To supplement our analytical results, we present numerical results for two examples. Our basic tool is the discrete model presented in §4 and, more precisely, system (4.12) of ordinary differential equations. As we mentioned in §4, system (4.12) can be considered as an approximation of the basic equation (2.8). How good is the above approximation? In trying to answer this question, we must look carefully at the discrete win-loss functions.

Parallel with (3.29), the functions W_{ij} and L_{ij} must satisfy the following restrictions:

$$(7.1) \quad i + W_{ij} \leq N, \quad 1 \leq i - L_{ij}, \quad 1 \leq i, j \leq N.$$

From (7.1) for $i = N$, it follows that $W_{Nj} \leq 0$, which requires that $W_{Nj} = 0$ for any j . This means that the most dominant individual cannot jump to a higher dominance level. Similarly, the less dominant individual cannot jump to a lower dominance level. Therefore $L_{1j} = 0$. It follows that states 1 and N in the discrete model play similar roles to dominance 0 and 1, respectively, for the continuous case. There is one essential difference, however. In the continuous case, the dominance values 0 and 1 can be reached only after an infinite number of encounters. This follows from the fact that the equations

$$(7.2) \quad w + W(w, p) = 1, \quad \ell - L(\ell, q) = 0$$

have unique solutions $w(p, 1)$ and $\ell(q, 0)$ for some appropriate partners p, q if conditions (3.34) and (3.35) are fulfilled; these solutions are 1 and 0, respectively. In the discrete case, states 1 and N either can be reached directly from some state i or they cannot be reached at all.

We treat the case of exact wins and losses for which the functions ψ_{ijk} are given by (4.8). Because of the conservation law (4.13) for the f_i , we should solve the system of ordinary differential equations obtained from (4.4) by eliminating the k_0 th equation and taking

$$(7.3) \quad f_{k_0} = 1 - \sum_{\substack{i=1 \\ i \neq k_0}}^N f_i.$$

Initial conditions $f_i(0) = f_i$ are given. In our simulations, $N = 101$.

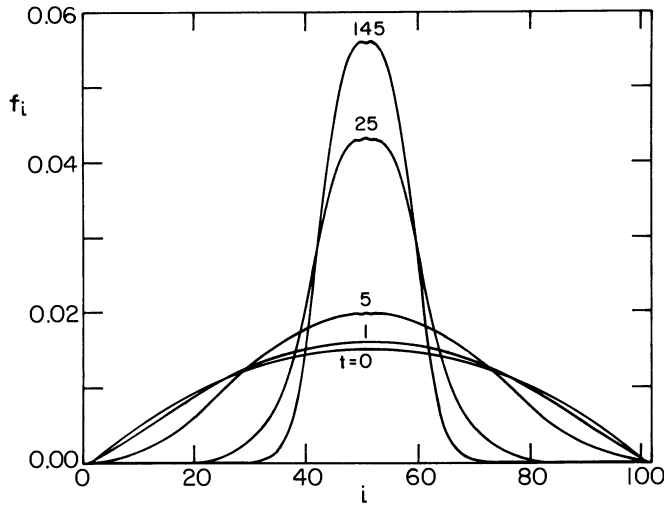


FIG. 10. Evolution in time of the solution for system (4.12), using discrete versions of (3.7) and (3.48). Initial condition obtained by normalizing the quadratic polynomial $(i - 1)(N - i)$; $N = 101$, $\epsilon \approx 0.09$.

We concern ourselves with the special case of “weak interactions” for which the maximum ϵ dominance change is given (in the discrete case) by

$$(7.4) \quad \epsilon = \max_{\substack{i,j \\ \phi_{ij} \neq 0}} \frac{W_{ij}}{N} = \max_{\substack{i,j \\ \phi_{ij} \neq 0}} \frac{L_{ij}}{N}.$$

The win-loss functions W_{ij} and L_{ij} are integer-valued. Therefore ϵ should be greater than 0.01. (We must allow jumps at least to the neighboring levels.) Moreover, we must note that choosing ϵ too small causes W_{ij} and L_{ij} , for a given i , to be the same for many partners “ j .”

Figure 10 shows the evolution in time of the solution for system (4.12) in our first example. Below, we use the discrete counterparts of the win-loss functions of (3.48) and ϕ of (3.7):

$$(7.5) \quad W_{ij} = \left\lceil \frac{N - i}{10} \phi_{ji} \right\rceil, \quad L_{ij} = \left\lceil \frac{i - 1}{10} \phi_{ij} \right\rceil, \quad \phi_{ij} = \frac{1}{2} + \frac{i - j}{2N}.$$

Computations of the ψ_{ijk} show that

$$(7.6) \quad \psi_{ij1} = 0 \quad \text{for all } i \neq 1, \quad \psi_{ijN} = 0 \quad \text{for all } i \neq N.$$

According to (7.6), no organism is pushed to the ends. Therefore, if we start with $f_1 = f_N = 0$, these values will be preserved. More generally, we can see the accumulation around the dominance value $\frac{1}{2}$, verifying the assertions following (6.23).

Our second example is a case where the dominant always wins. In particular, we use discrete counterparts of (3.42), (3.43), and (3.10), as follows:

$$(7.7) \quad W_{ij} = \left\lceil \frac{(N - i)(j - 1)}{N - 1} \right\rceil, \quad L_{ij} = \left\lceil \frac{(i - 1)(N - j)}{N - 1} \right\rceil, \quad \phi_{ij} = \begin{cases} 1 & i > j, \\ \frac{1}{2} & i = j, \\ 0 & i < j. \end{cases}$$

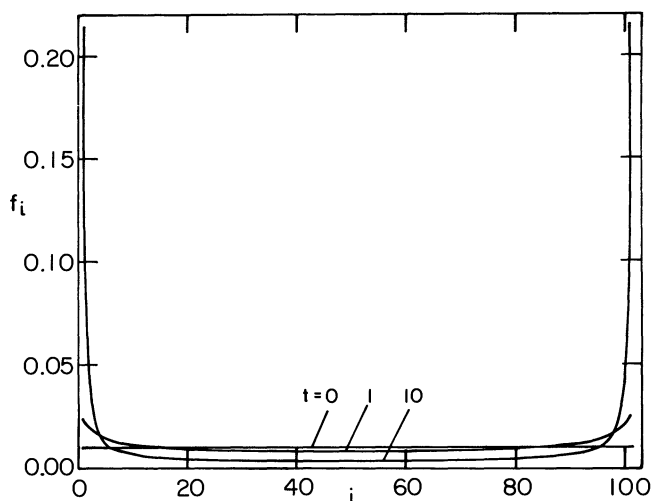


FIG. 11. Similar to Fig. 10 for the DAW case. Uniform initial condition $f_i = 1/N$, $\epsilon \approx 0.24$.

We showed at the end of §6 that, according to (6.9), this case embodies various necessary conditions for the population to be convected to the two ends of the interval. Figure 11 shows that, indeed, such convection occurs. Perhaps the individuals are pushed to the ends somewhat quickly (i.e., after a finite number of jumps), but the general picture should be correct both qualitatively and semiquantitatively. Indeed, the overall conclusion from these numerical examples is the usefulness of the “weak-interaction” convection-diffusion approximation. This approximate often permits considerable insight into the general form of the solution, even when interactions are not especially weak.

8. Summary and discussion. Computer simulations show that the existence of a single variable that affects the experience of each individual is sufficient to generate a social hierarchy in a population of interacting organisms [6]. In the present work, we focused on simple interactions between individuals that affect the hypothetical attribute called dominance attached to each individual. This attribute was treated as a real-valued one-dimensional stochastic variable.

Taking advantage of the fact that the process under consideration is Markovian, its master equation was derived. Several biologically reasonable examples of win-loss functions W and L and probability functions ϕ that govern the interactions were provided. The governing equation (3.26) for the dominance probability distribution function $f(x, t)$ was derived in terms of ϕ , W , L , and the probability per unit time η that a pair of individuals interact.

Equation (3.26) is a highly nonlinear integrodifferential equation of the Boltzmann type. Two approaches were used to obtain information concerning the solutions of this equation. In one approach, it was hypothesized that each interaction can, at most, slightly change the dominance distribution. The resulting approximate Fokker-Planck equation is still nonlinear, with effective convection and diffusion coefficients that depend on the overall probability distribution. Nevertheless, certain qualitative conclusions concerning the behavior of the solutions could be drawn.

A second approach was numerical. A naive approach to the numerical analysis would not conserve the size of the total population. To accomplish this conservation, we performed our space discretization by constructing a discrete model whose structure paralleled the continuous model. The resulting system of ordinary differential equations was integrated numerically in two cases. One case paralleled our analytic results in providing an example where the initial distribution of dominance collapsed to essentially a single value. This shows that, for a class of interaction rules, dominance cannot be used as an automatic organizing variable for the population.

By contrast, the second numerical example, which also supplemented some of our analytic work, exhibited rules that *did* split the population into two groups. The “dominance always wins” rule that was used in the second example was different from the rule used by Hogeweg and Hesper [6], whose simulations also provided an example of a population splitting into two groups, one with high dominance and one with low.

The splitting property of “dominance always wins” is not obvious. In this case, the result of any given encounter is determinate, but stochasticity enters in the random encounters of individuals with various dominances. Biologists have expressed uneasiness with a probabilistic model that occasionally permits a less dominant individual to win an encounter—although such a rule seems necessary if uncontrolled factors other than dominance also have an influence. This example, however, shows that the splitting property can be achieved even if dominance is the sole factor that influences the result of an encounter.

Certain related investigations must still be performed to obtain a reasonably satisfactory analysis of our model. To explain what is involved, we first note that in the language of asymptotics, (see e.g., [13, Chap. 9]), the Fokker–Planck equation (6.14) that was derived above is an “outer” equation. It can be shown that the velocity and diffusivity take different forms in inner “boundary layers” near $x = 0$ and $x = 1$. When the “outer” convection velocity M is not zero, as in the examples treated above, we do not expect that interactions in the thin boundary layers will have a major effect on the results. In two important cases, however, the rules used by Hogeweg and Hesper [6] and the rules used in chess, in fact, used $M = 0$. Thus it is important to derive the boundary layer equations and to examine their effects.

The case where $M = 0$ gives rise to another complication—for in this case, total dominance is preserved in the population. We wish to know whether we can construct a discrete version of the governing equation (3.26) that is suitable for numerical analysis and that will exactly conserve both total population and total dominance. Another approach to the numerical analysis is the construction of a collocation scheme by writing $f(x, t) = \sum_n \alpha_n(t) \phi_n(x)$, where the ϕ_n are suitably chosen polynomials [1]. Comparison of the various schemes will be of considerable interest.

It is planned, in a future publication, to report on the matters raised in the previous two paragraphs. It is hoped that the formal theory of the steady-state dominance distribution will thereby be brought to an initially satisfactory state.

There are other more profound questions that can be asked. For example, when the population is essentially composed of high and low dominants, e.g., as in the situation of Fig. 11, we might wish to know the frequency at which an individual bee is likely to switch from the high group to the low group or vice versa. Estimates of such frequencies are possible in the weak interaction limit. However, this theory has recently been shown to be one of considerable subtlety, where, for example, the truncated Kramers–Moyal expansion can lead to large errors. (See a series of papers,

the latest of which is Knessl et al. [8].) Full elucidation of the properties of the dominance equations thus poses a rather stern challenge. Enthusiasm to take up the gauntlet might only be tempered by the realization that evidence is as yet inconclusive that the underlying model is based on correct biological hypotheses.

As a final remark, we note that the present investigation can be regarded as a contribution to the question of structure in aspect space, particularly within biological contexts. (Aspect is an independent variable that characterizes some population, see the review by Levin and Segel [12].) In other examples such as predator-prey interactions [11] or shape-space models of the immune system [18], aspect space is high-dimensional; one-dimensional models are a gross simplification. As is the case for certain other aspect variables, however, such as maturity [15], dominance may well vary in a one-dimensional space. From this point of view at least, analysis of structure in dominance space can be regarded as of likely relevance to ethology. It remains to be seen if nature takes advantage of the "opportunity" to use dominance as an automatic social-organizing principle.

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REFERENCES

- [1] N. BELLOMO AND M. LACHOWICZ, *Mathematical biology and kinetic theory: evolution of dominance in a population of interacting organisms*, in *Hyperbolic Systems and Kinetic Theories*, V. Boffi, ed., World Scientific, Teaneck, NJ, 1992, in press.
- [2] N. BELLOMO AND Z. LACHOWICZ, *Lyapunov functionals and dissipativity properties for a nonlinear kinetic model in mathematical biology*, *Ricerche di Matematica* 1992, in press.
- [3] F. DE WAAL, *Chimpanzee Politics: Power and Sex Among Apes*, Johns Hopkins University Press, Baltimore, MD, 1989.
- [4] I. M. DUNBAR, *Primate Social Systems*, Cornell University Press, Ithaca, NY, 1988.
- [5] M. E. GLICKMAN, *A Bayesian paired comparison model for rating chess players*, Tech. Report NSF-C-7, Dept. of Statistics, Harvard University, Cambridge, MA, 1991.
- [6] P. HOGEWEG AND P. HESPER, *The ontogeny of the interaction structure in bumble bee colonies: A MIRROR model*, *Behav. Ecol. Sociobiol.*, 12 (1983), pp. 271–283.
- [7] B. KAŽIĆ, R. D. KEENE, AND K. A. LIM, *The Official Laws of Chess*, Macmillan, New York, 1986.
- [8] C. KNESSL, M. MANGEL, M. MATKOWSKY, Z. SCHUSS, AND C. TIER, *Boundary behavior of diffusion approximations to Markov jump processes*, *J. Statist. Phys.*, 45 (1986), pp. 245–266.
- [9] H. G. LANDAU, *On dominance relations and the structure of animal societies: I. Effect of inherent characteristics*, *Bull. Math. Biophys.*, 13 (1951), pp. 1–19.
- [10] ———, *On dominance relations and the structure of animal societies: III. The condition for a score structure*, *Bull. Math. Biophys.*, 15 (1953), pp. 143–148.
- [11] S. A. LEVIN AND L. A. SEGEL, *Models of the influence of predation on aspect diversity in prey populations*, *J. Math. Biol.*, 14 (1982), pp. 253–285.
- [12] ———, *Pattern generation in space and aspect by interaction and redistribution*, *SIAM Rev.*, 27 (1985), pp. 45–67.

- [13] C. C. LIN AND L. A. SEGEL, *Mathematics Applied to Deterministic Problems in the Natural Sciences*, Macmillan, New York, 1974.
- [14] A. RAPAPORT, *Outline of a probabilistic approach to animal sociology: I*, Bull. Math. Biophys., 11 (1949), pp. 183–196.
- [15] S. I. RUBINOW, *A maturity-time representation for cell populations*, Biophys. J., 8 (1968), pp. 1055–1073.
- [16] T. SCHJELDERUP-EBBE, *Bieträge zum Sozialpsychologie des Haushuhns*, Zeit. für Psychologie, 88 (1922), pp. 225–252.
- [17] L. A. SEGEL, *Modelling Dynamic Phenomena in Molecular and Cellular Biology*, Cambridge University Press, Cambridge, UK, 1984.
- [18] L. A. SEGEL AND A. S. PERELSON, *Computations in Shape Space: An Approach to Network Theory*, in Theoretical Immunology, Part Two, SFI Studies in the Sciences of Complexity, A. S. Perelson, ed., Addison-Wesley, Reading, MA, 1988, pp. 321–343.
- [19] T. T. SOONG, *Random Differential Equations in Science and Engineering*, Academic Press, New York, 1973.
- [20] N. G. VAN KAMPEN, *Stochastic Processes in Physics and Chemistry*, North-Holland, Amsterdam, 1981.
- [21] C. VAN HONK AND P. HOGEWEG, *The ontogeny of the social structure in a captive Bombus terrestris colony*, Behav. Ecol. Sociobiol., 9 (1981), pp. 111–119.