This expression is always greater than zero when $b_{\mathrm{T}} > |c|$. It is positive because there is a positive covariance between q_i and $\overline{W}_i$. Kin selection for altruism is thus a special case of Price's model (*16*) of selection based on covariance mathematics. Here, the positive covariance between allele frequency and group fitness exceeds the negative covariance between the number of *a* alleles in a genotype and the genotype's fitness. However, for the altruistic gene to spread, not only must Δq_{G} be positive, but it must also exceed the absolute value of $\overline{\Delta q_{\mathrm{I}}}$. That is, selection between family groups must override the opposing selection within family groups. Setting $\Delta q_{\mathrm{G}} > |\overline{\Delta q_{\mathrm{I}}}|$ and simplifying yields Hamilton's rule for family groups, $b_{\mathrm{T}}/2 > |c|$ (*17*).

The total change in gene frequency under kin selection, Δq, is

$$\Delta q = \Delta q_{\mathrm{G}} + \overline{\Delta q_{\mathrm{I}}} = Npq[(c - b)/N + b/2][q + (1 - h)(p - q)]/\overline{W} \qquad (6)$$

as was given in Eq. 1 and derived from other models (*11*).

This derivation illustrates that kin selection involves individual and group selection as opposing processes. Hamilton's rule specifies the conditions under which group selection in favor of sociality is sufficiently strong to overcome the opposing effects of individual selection against sociality. Whether a family is called a group or a set of kin, this derivation shows that kin selection involves two evolutionary processes (opposing one another in the case of altruism) which have been classically recognized (*13*) as different levels of selection.

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$$\sum_{i=1}^{6} W_i(AA)\Pr(i/AA)$$
where $\Pr(i/AA)$ is the conditional probability that one is in family type i given that one observes an *AA* individual among the offspring. It follows that
$$\sum_{i=1}^{6} \Pr(i/AA) = 1$$
and $\overline{W}(Aa)$ and $\overline{W}(aa)$ can be found in like manner. [See (*11*) for a more detailed discussion.]
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18. I thank S. Arnold, F. Breden, and I. L. Heisler for helpful comments. Supported by NIH grant 22523.

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Adaptive Topography in Family-Structured Models of Kin Selection

Abstract. *Adaptive topographies provide a means of summarizing the qualitative dynamics of evolution. Inclusive fitness serves as an organizing concept in much of sociobiology. Through the use of Sewall Wright's "fitness function," the theoretical equivalence of these concepts for weak selection in family-structured populations is demonstrated.*

One of the most intriguing extensions of the Neo-Darwinian research program is the recent theory of kin selection (*1*). There are two key elements of this theory. First, Hamilton's rule (*1*), $c/b < r$, provides the conditions for increase of an allele that codes for an "altruistic" behavior between two individuals who are related by r. In this rule, c and b are additive increments to the fitnesses of, respectively, the donor and recipient of the altruistic act. Hamilton's rule has revolutionized research on the evolution of behavior, and there has been a considerable amount of theoretical work to determine the precise conditions under which the rule holds (*2–12*).

The second key element of kinship theory has received less theoretical attention, although it plays an important conceptual role in applications. Hamilton (*1*) claimed that gene frequency dynamics proceed along adaptive topographies (*13*) determined by the average inclusive fitness effect (*1*). The inclusive fitness effect of an individual's behavior is defined as the sum of the additive effects of the behavior on the individual fitnesses of the donor and the recipient, the effects on the latter being weighted by the degree of relatedness of recipient and donor. Hamilton's claim is fundamentally important for, if true, it relates kinship theory to Wright's (*13*) adaptive topography, which is one of the most useful theoretical and conceptual tools in evolutionary biology. However, Hamilton (*1*) was not able to demonstrate this claim rigorously. Consequently, inclusive fitness seems to have fallen into disuse in recent family-structured models of kin selection (*3–8, 10–12*). Yet, other studies (*14*) based on Hamilton's original model (*1*) have demonstrated this claim. However, genetic identity coefficients were used in these selection models (*14*). Since these coefficients have concrete meaning only for neutral genes, many workers have been unwilling to accept results of selection models based on them. For this reason, most recent theoretical studies of kin selection have focused on sibling interactions in family-structured models (*3–8, 10–12*). In these models, individual fitness is a function of the social interactions occurring in the

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family. Although the family-structured models lack the generality of the approaches based on identity coefficients, they have the advantage of explicitly representing the population processes that give rise to the genetic relationship. Up to now, there has been no demonstration of any role for inclusive fitness in these, more traditional, models (*15*). Consequently, inclusive fitness has not been used as a theoretical tool, and there is some concern that this concept may not be firmly rooted in the theory of gene frequencies. In this report we construct a "fitness function" (*16*) for kin selection in family-structured models. The graph of the fitness function is equivalent to the adaptive topography. We show that this fitness function is identical with the mean inclusive fitness effects, provided that these effects are additive and that the adult frequencies can be approximated by their Hardy-Weinberg proportions. The assumption of Hardy-Weinberg proportions at the adult stage is commonplace in these models (*4, 5, 8, 9, 16-18*) and allows the use of a single equation for gene frequency instead of the more rigorous equations for adult genotypic frequency (*3, 6, 7, 10-12*). This assumption holds for weak selection (*19*), as well as in certain special cases of strong selection (*20*).

The basic equation for gene frequency change at a single locus under selection is (*16*)

$$\Delta p = \frac{p(1-p)}{2\overline{W}} \sum_i W_i \frac{df_i}{dp} \qquad (1)$$

In this equation p is the frequency of the allele under consideration A, with $(1 - p)$ the frequency of the alternate allele a. The genotypes are indexed by a single subscript i ($i = 1, 2, 3$ corresponding to the genotypes AA, Aa, aa respectively), with f_i the frequency of genotype i, W_i the fitness of genotype i, and the average fitness

$$\overline{W} = \sum_i f_i W_i$$

The W_i's may be arbitrarily complex functions of environmental or gene frequency variables. Equation 1 gives an accurate picture of selection at a single locus if (i) mating is random, (ii) recombination is high with respect to other interacting or linked loci, and (iii) generations are discrete. Although these conditions limit the theoretical adequacy of the model (*21*), the single-locus approach provides an appealing framework for reconciling the evolutionary roles of the various forces which can change gene frequencies. In so doing, single-locus theory has functioned as a strong "positive heuristic" (*22*) in evolutionary biology (*23*).

Table 1. Family-structured model. $P(i/j)$ is the conditional probability for genotype j to interact with a sibling of genotype i and takes into account the family structure. If the adults are distributed in Hardy-Weinberg proportions, then $P(1/1)={}^1/_4(p+1)^2$, $P(2/1)={}^1/_2(1-p^2)$, $P(3/1)={}^1/_4(1-p)^2$, $P(1/2)={}^1/_4p(1+p)$, $P(2/2)={}^1/_2(-p^2+p+1)$, $P(3/2)={}^1/_4(p-1)(p-2$, $P(1/3)={}^1/_4p^2$, $P(2/3) = p(1-{}^1/_2p)$, $P(3/3)={}^1/_4(p-2)^2$. See text for further explanation.

Genotype	f_i	df_i/dp	W_i
AA	p^2	$2p$	$\sum_i w_{1i}P(i/1)$
Aa	$2p(1-p)$	$2-4p$	$\sum_i w_{2i}P(i/2)$
aa	$(1-p)^2$	$-2+2p$	$\sum_i w_{3i}P(i/3)$

A convenient way of picturing adaptation at this single locus is with Wright's adaptive topography (*13*) concept, generalized by the use of fitness functions (*16*), to study frequency-dependent selection. Kin selection is a form of frequency-dependent selection (*5, 6, 9*). The fitness function $F(p)$ is implicitly defined by Eq. 1 as the indefinite integral

$$F(p) = \int dp \sum_i W_i \frac{df_i}{dp} \qquad (2)$$

so that Eq. 1 becomes

$$\Delta p = \frac{p(1-p)}{2\overline{W}} \frac{dF}{dp} \qquad (3)$$

The problem for a particular case of selection is to evaluate Eq. 2 and then to interpret this integral biologically.

The utility of the fitness function can be seen in Eq. 3. The term $p(1 - p)/2\overline{W}$ on the right is always nonnegative and is 0 only if the allele frequency is 0 or 1. This term can affect the rate of selection, but not the qualitative dynamics, which are determined by dF/dp. Consequently, the surface of F controls the evolutionary outcome of selection at this locus. The allele increases in frequency if dF/dp is positive and decreases in frequency if dF/dp is negative. In addition, internal equilibria must satisfy $dF/dp = 0$. The fitness function plays a role in evolution similar to a potential function in physics.

In the basic family-structured model (Table 1), the association-specific fitness w_{ij} is the fitness of i in association with j. The w_{ij}'s can be decomposed into specific models of behavior. In particular, Hamilton (*1*) defined behavior in terms of the increments in fitness accrued by both participants of an interaction. Let c_i be the additive effect of i's behavior on its own fitness and b_i the additive effect of i's behavior on its associate's fitness. We then have

$$w_{ij} = 1 + c_i + b_j \qquad (4)$$

Substituting Eq. 4 into the W_i's of Table 1 and evaluating the integral in Eq. 2, yields

$$\begin{aligned} F(p) = p^2(c_1 + {}^1/_2b_1 - \\ 2c_2 - b_2 + c_3 + {}^1/_2b_3) + \\ p(2c_2 + b_2 - 2c_3 - b_3) + C \qquad (5) \end{aligned}$$

where C is the constant of integration.

Following Hamilton (*1*) we define $e_i = c_i + {}^1/_2b_i$ as the inclusive fitness effect of the ith genotype when i is interacting with outbred siblings to whom it is related by 1/2. Taking the constant of integration $C = e_3$, we can express Eq. 5 as

$$F(p) = \bar{e} \equiv \sum_i f_i e_i \qquad (6)$$

where $\bar{e}$ is the average inclusive fitness effect. Consequently, in these models, evolution does proceed along topographies determined by the mean inclusive fitness effect.

By setting the derivative of Eq. 6 equal to zero, an internal equilibrium $\hat{p}$ satisfies

$$\hat{p} = \frac{e_3 - e_2}{e_1 + e_3 - 2e_2} \qquad (7)$$

From Eq. 7, for there to be an internal equilibrium there must be heterozygote superiority or inferiority in the inclusive fitness effects. When Eq. 6 is differentiated twice, we find that $\hat{p}$ (Eq. 7) is a global maximum in the mean inclusive fitness effect if there is heterozygote superiority in these effects. Consequently, the standard equilibrium equation of population genetics can be used to study social selection in family-structured populations, so long as inclusive fitness is substituted for individual fitness.

To extract Hamilton's rule from this model, let A be the altruistic allele and a the nonaltruistic allele, by assuming $e_1 = c + {}^1/_2b$, $e_2 = h(c + {}^1/_2b)$, and $e_3 = 0$ (*24*). The fitness function (Eq. 6) then becomes $F(p) = p^2(1 - 2h)(c + {}^1/_2b) + 2ph(c + {}^1/_2b)$ (*25*) and so $dF/dp = 2(c + {}^1/_2b)[p + h(q - p)]$, where $q = 1 - p$. If h is interpreted as the probability that a heterozygote performs an altruistic act ($0 \leq h \leq 1$), then dF/dp is positive so long as $-c/b < 1/2$ (*26, 27*).

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25. Under the stated assumptions of this report, this expression equals the "adaptive function" [Eq. 53 of (*12*)] proposed elsewhere.
26. There is no internal equilibrium possible for this case $(0 \leq h \leq 1)$. However, if there is overdominance so that heterozygotes are more altruistic than homozygotes $(h > 1)$, then an internal equilibrium exists at $\hat{p} = h/(2h - 1)$ and it is stable if $-c/b < 1/2$. The existence of this equilibrium with strong selection has been confirmed [Eq. 49 of (*12*)].
27. This research was supported by NSF grant DEB-79 10191. We are grateful to M. Wade and S. Wright for criticism and comments.

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Male *Photuris* Fireflies Mimic Sexual Signals of Their Females' Prey

Abstract. Photuris *males emit flashed signals matching those of unrelated sympatric forms (*Photinus *and* Pyractomena *species). Some have only one flash pattern matching that of another species, others mimic at least two species, as well as emitting "their own" species-specific pattern. They tend to restrict the mimicking signals, but not their own, to the habitats, seasons, and daily periods of the mimicked species. Since* Photuris *females prey on males of other firefly species by mimicking their females' flashes, the* Photuris *males may be using their mimicry to locate and seduce their own hunting females. This mimicry is without known parallel in other animal communicative systems. It explains why the genus* Photuris *has been a frustrating mystery to taxonomists, who have long used flash patterns to distinguish sibling species in other genera.*

Fireflies of the American genera *Photinus, Pyractomena,* and *Photuris* (beetle family Lampyridae) use flashes of light for sexual communication. In general, flying males flash a species-typical pattern to which perched females of their species respond with a specific flashed answer. Males fly toward respondents and, after a few flash-exchanges, reach and mate with them (*1*). Numerous sibling species have been discovered through studies of male flash patterns (*2*). Females of the genus *Photuris*, in addition to using flashed signals in their own sexual communication, mimic females of other species, attract males, and eat them (*3*).

Barber (*2*) suspected that males of *Photuris lucicrescens* emit two distinct patterns. My field studies over the past 13 years show that, in addition to their own species-specific flashes, males of several *Photuris* species have two or more patterns (*4*) that mirror the patterns of males of *Photinus* and *Pyractomena* active at the same time and place. [Figure 1 shows model and mimic flash patterns (and the *Photuris*' own patterns).] This similarity probably evolved as a consequence of the aggressive mimicry of the *Photuris* females (*3*). Such a complex of behavioral mimicries is without known parallel in the animal kingdom.

Male flash pattern similarities are most obvious when they involve distinctive patterns, flickers with specific modulation rates (M rates), or flashes that are paired at specific time intervals. Most dramatic is the shifting back and forth by some *Photuris* males between their own species-typical pattern and the patterns of other species active at the same time and place. This report records and discusses this behavior in *Photuris* males (*5*).

In early spring in northwest peninsular Florida, males of an unnamed *Photuris* (VR) (*6*) mimic two species of *Pyractomena*: namely, *P. barberi* (short flickers) and *P. angustata* (minutes-long bright glows). Each mimicked species signals in pine and grassland less than 3 meters above the ground, while *Photuris* VR males produce a slow three- to seven-flash phrase (Fig. 1b) at much higher altitudes, especially around the crowns of pines. During the *Pyractomena* season, VR males descend into the *Pyractomena* flight space (*7*) and there emit flickers and glows closely resembling those of the *Pyractomena*. Individual *Photuris* males can often be seen to change their altitude and signaling pattern at the same time. Near the end of VR's season both *Pyractomena* are gone, and VR males then emit flickers and glows only occasionally. The M rate of VR's flicker is identical to that of *P. barberi* at comparable temperatures (Fig. 1, a and c; Table 1) (*8*).

Photuris AR (Florida panhandle) also mimics *P. angustata*'s glow in the appropriate space and season and otherwise emits its own single flash pattern at high altitudes (Fig. 1h).

At least five *Photuris* mimic the flicker of widespread and common *Pyractomena angulata* (Fig. 1, compare d with e, f, i, k, and l; Table 1). Three of these have their own distinctive pattern (Fig. 1, g, j, and n), but *Photuris* B emits only the mimicked pattern (Fig. 1e). The B females prey on *P. angulata* and at least two other species (*9*).

One of *angulata*'s mimics (in Maryland), *Photuris cinctipennis* (*10*), occurs in Florida and there emits its own pattern (Fig. 1n) (*11*), and mimics two *Photinus* (Fig. 1, p to u). Its mimicry is statistically indistinguishable from the model patterns in both cases.

Other examples of *Photuris* convergence on firefly associates include: (i) A flickering grassland *Photinus* in Colombia, South America, is mimicked by a *Photuris* that occurs with it, and its females have been observed answering the *Photinus* males (Fig. 1, v and w; Table 1). (ii) *Photuris jamaicensis* appears to mimic several *Photinus* in Jamaica, including some that are known prey of *jamaicensis* females (*12*), *P. evanescens* and *P. commissus* among them (Fig. 1, x to z; Table 1). (iii) *Photuris* A (Florida) emits a long single flash during the early evening activity period of its dusk-active associate and prey *Photinus collustrans*, and later switches to a one- to five-pulse pattern like that of another associate *Photinus lineellus* (Fig. 1, a′ and b′). Their patterns are statistically indistinguishable. (iv) Florida *Photuris versicolor*

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