

Chapter 2

Competition for Limiting Resources, Hamilton's Rule, and Chesson's R^*

Competition is an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth, and/or reproduction of the competing individuals concerned.

Begon et al. (1990)

Social evolution is facilitated in proportion to the coincidence of fitness interests experienced, through sociality, by the component sub-units (partners). Such a coincidence may come about through two basic methods, namely shared genes (relatedness) or shared reproductive fate.

Bourke (2011)

The expected evolution obeys an adaptive topography defined by the long-run growth rate of the population. The expected fitness of a genotype is its Malthusian fitness in the average environment minus the covariance of its growth rate with that of the population.

Engen et al. (2009)

Abstract This chapter links Chesson's R^* with inclusive fitness theory, arguing that competition for limiting resources within and between groups underlies both formulations. Chesson's R^* determines the strengths of interspecific compared to intraspecific competition, the balance of which is determined by the species having the highest rate of increase when conditions are at their worst. The latter formulation is generalized to the within- and between-group levels, l^*_{within} and l^*_{between} , where types compete for the lowest l^* values in the most severe regimes. Conditionally, entities with the highest growth (group, population) or reproductive (types) rates are, theoretically, the superior or dominant types. It is argued that l^* values are linked to Hamilton's rule via a formulation advanced in 2002 showing when kin should remain in groups and when they should leave, states determined by intensities of within-group compared to between-group competition.

Keywords Hamilton's rule · Inclusive fitness theory · Direct reproduction · Indirect reproduction · Ecological constraints · Hebbian "decisions" · Chesson's R^*

Immediate or future consequences of fitness-maximizing “decisions” will often be unpredictable and uncontrollable, even in stable conditions, defined as persisting benefits from relatedness or from shared reproductive interests (Bourke 2011). For example, if one type dies or locates a mate of higher quality, fitness optima of Actor, Recipient, or the offspring of either type may change. Large-brained mammals should be selected to utilize a set of “decision rules” about when, under what conditions, and how to help a conspecific. *Ceteris paribus*, male helping will limit male mates, increasing the intensity of competition among females for mates; female helping will limit availability of female mates, increasing competition among males for mates; and, helping by both sexes will yield intense competition within both sexes for mates. An organism's “decisions” are expected to be influenced by factors in addition to self-interest, such as predation, resource dispersion, and interspecific competition (Fig. 2.1). The latter effects may, at some “decision” points, overwhelm self-interest so that “ego” loses or fails to gain inclusive reproductive benefits. Bourke (2011) stressed that benefits parameterized in Hamilton's rule are in the form of offspring produced in the future, and that the outcomes “are effects at the level of the entity (e.g., cell, organism, “type”) performing the behavior, which is why they are expressed in terms of offspring number.” The current section links inclusive fitness theory with competition theory as presented by Chesson's (Chesson's 2000; Chesson and Kuang 2008; also see, Amarasekare 2003, 2009; Amarasekare et al. 2004) treatments of “competitive coexistence.” These two traditions are connected via the reproductive consequences to types from competition within and between groups for limiting resources convertible to direct or indirect reproduction (West-Eberhard 1975), where competition is a function of genotype $\times$ environment (including social environment) interactions in a type's thermal zone.

2.1 West et al. (2002) Places Hamilton's Rule in the Context of Intraspecific Competition

As Bourke (2011) made clear, Actors will generally prefer to facilitate the reproductive interests of kin since such choices will represent the highest likelihoods of increasing the representation of an allele in a population. However, variations in resource dispersion and quality change a type's costs and benefits and, possibly, response thresholds and hierarchies. An extension of Hamilton's (1964) treatment was advanced by West et al. (2002), showing that where within-group (local or “patch”) competition exceeds (some threshold level of) between-group (“global” or population) competition, selection will favor phenotypes dispersing from natal groups, thereby, avoiding direct, genetically deleterious, competition with kin whose ecological requirements are most likely to overlap. West et al. (2002) presented a model predicting conditions under which individuals should (weak within-group competition relative to strong between-group competition) and should not (strong within-group competition relative to between-group competition) cooperate with or demonstrate altruism toward kin. This formulation takes into account all agents affected by an act, not only the relatives of an Actor (Hamilton's rule: Fig. 1.2).

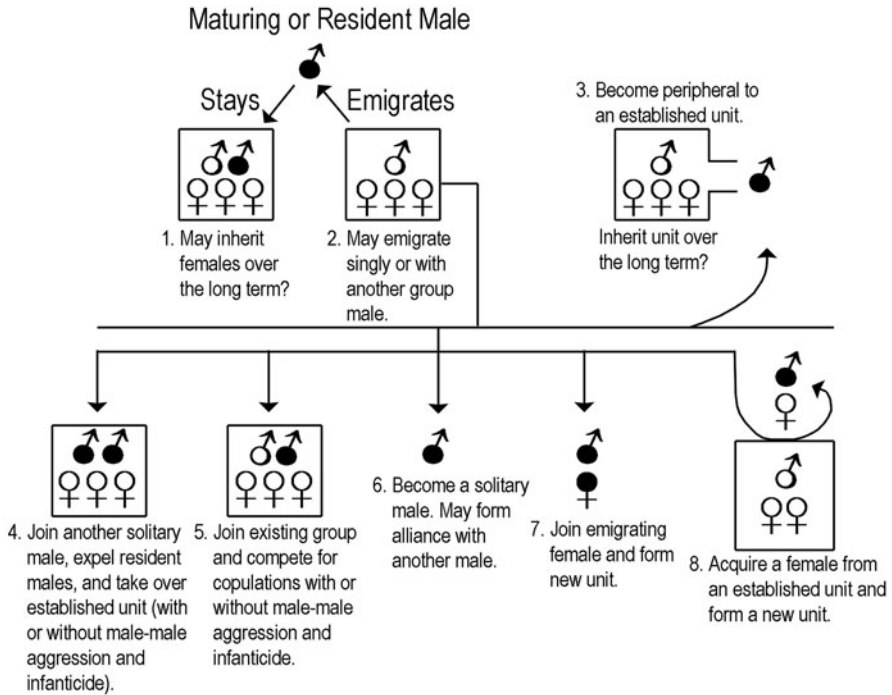


Fig. 2.1 Selected alternative reproductive “decisions” (Chap. 3) available to mammalian males of one species (*Alouatta palliata*, based on real data: Jones 2005) remaining in or after emigration from natal or resident groups. “Decision” 6 may lead to a “solitary” (“sexually segregated”) population structure, and options 2, 7, and 8 may lead to varieties of polygyny or to monogamy in which a single reproductive male (related or unrelated) monopolizes one or more than one reproductive female. Strategies 1, 4, as well as 5 affect multimale–multifemale groups requiring male–male tolerance, possibly, leading to sociality (e.g., alliances, coalitions, dominance hierarchies or other forms of aggressive and/or reproductive restraint, possibly imposed by dominants). Other potential options are not represented in this figure (e.g., colonization). All alternative reproductive “decisions” should occur in response to condition-dependent, within- and between-group competition for limiting resources (e.g., for group membership, for mates: see Jones et al. 2008), and the potential for social evolution will be a function of differential reproductive costs and benefits in association with shared reproductive interests with kin or non-kin. Hystricognath rodents would provide a large and various group for tests of the previous topics, including the role of adult sex ratios in groups and populations as determinants of differential reproductive tactics and strategies expressed by adult females and males. In sum, abiotic and biotic characteristics of “local” and “global” regimes, including conspecific and conspecific interactions, will determine condition-dependent “decisions” made by types. © Clara B. Jones

West et al. (2002) extended Hamilton's rule so that $r_{xy}b - c - r_{xe}d > 0$, with r_{xy} representing an Actor's relatedness to an act's Recipient (Hamilton's r), r_{xe} , an Actor's relatedness to individuals whose fitness is decreased by the act, and d represents the positive or negative effects of the act for within-group competition. In the expanded formulation, b and c are defined as in Hamilton's equation. If d increases

as a result of an act, fitness may be negatively influenced, whereas, if d decreases as a result of an act, fitness may be positively influenced (relative to values of r_{xy} and r_{xe}). Thus, when applied to group maintenance subsequent to the formation of groups, a “decision” to cooperate or otherwise help a member of an aggregation or existing group will be a function of a helper’s potential benefits and costs from the consequences of helping for the inclusive fitness of relatives and non-relatives in the aggregation. r_{xe} will be associated with local (single patch) competition, increasing as within-patch (density-dependent) competition for limiting resources intensifies. The extended formulation shows that helping is not inevitable, but that it is a function of its effects upon all affected types in an aggregation (see Sect. 2.2). This model, thus, demonstrates how groups of related or unrelated types might arise from aggregations, possibly forming stable maintenance of groups given constraints imposed by Hamilton’s rule. Furthermore, like Hamilton’s original treatment (1964), the parameters advanced by West et al. (West et al. 2002; Rodrigues and Gardner 2012, 2013) are measurable or can be estimated in Nature; thus, technically, they are testable with further theoretical treatments and by field and laboratory experimentation. The extensive dataset on within- and between-group interactions of polygynandrous African lions (*Panthera leo*) assembled by Mosser and Packer (2009) may provide tests of the previous model.

Crespi’s (2006) discussion of West et al. (2006) applies, as well, to West et al. (2002) by emphasizing the necessity to consider the spatial scale (environmental context) of competition and its effect upon the differential costs and benefits of cooperation for individuals of a population. As Crespi (2006) pointed out, the dispersion of limiting resources may “create opportunities to compete and to cheat.” The social potential of a given “patch,” in theory, should be measurable. The previous author considered the spatiotemporal distribution and abundance of limiting resources hypothesized to favor groups. A fundamental theoretical problem has been explaining how cooperation is sustained once it is expressed since the benefits of cheating and self-interested behavior are expected to outweigh the benefits of cooperation or altruism (Maynard Smith 1974) since Actor is related to itself by an r of 1.00. West et al. (2006) showed that the “spatial scale of competition can drive evolutionary dynamics of social interactions among non-kin,” conditions hypothesized to be a function of whether competition is local or global. Emphasizing the relative nature of inclusive-fitness maximizing, Crespi (2006) expressed the (spatial) ideas of West et al. (2006) schematically, as follows:

- Cooperation Local, Competition Global $\rightarrow$ Local Cooperation Favored by Selection
- Competition Local, Cooperation Global $\rightarrow$ Local Competition Favored by Selection

where Local implies competition for limiting resources within “patches” or within groups, and Global implies competition in the population at large (between groups). The treatments of West et al. (West et al. 2002, 2006; Rodrigues and Gardner 2012,

2013), thus, expand Hamilton's (1964) work by defining the population-level contexts of cooperation and altruism and conditions under which those responses by Actors should conform to Hamilton's rule and be favored by selection.

2.2 Generalizing Chesson's R^* and Linking it to Hamilton's Rule

The logic of "competitive coexistence" theory holds that where two species are in competition for the same resource, the dominant species will have the higher rate of increase "at the lowest resource level" (Stearns 1989; Schoener 1974). Discussing the evolution of stable coexistence among species, Chesson (Chesson 2000; Amarasekare 2003, 2009; Amarasekare et al. 2004) proposed that mechanisms of coexistence ("stabilizing mechanisms") involve (condition-dependent) facilitation of an inferior species by a superior species, classifying promoters of coexistence as mechanisms of resource partitioning, predation ("natural enemies"), and spatiotemporal fluctuations in population densities (e.g., along environmental gradients). Chesson (2000) pointed out that (condition-dependent) facilitation via "stabilizing mechanisms" promotes "long-term per capita growth rate" of inferior species by facilitating an increase in the density (rate of increase, growth rate) of the inferior species, decreasing stochasticity in their population numbers.

Relying upon previous quantitative treatments, Chesson (2000) argued that mechanisms of coexistence reflect "direct competition" and "resource dynamics" where species are limited by a single resource. Such conditions are governed by the R^* rule whereby R^* "is the resource level at which a species is just able to persist." The previous author goes on to note that, "The winner [sic] in competition is the species with the lowest R^* value," comprising the relative potential for types in low-density conditions to survive and reproduce. The same author pointed out that the ability to persist at low resource levels can be partitioned into causes such as success of foraging strategies and rates of predation. The potentially destabilizing effects of interspecific competition can be kept in check via mechanisms of coexistence (e.g., facilitation), yielding a condition whereby interspecific competition would be, *ceteris paribus*, less intense than intraspecific competition.

It follows logically that intraspecific competition applies to direct competition between groups and between types in groups where (condition-dependent) niche space of a type overlaps with niche space of other groups. Social biology, then, pertains to mechanisms whereby types manage direct competition with other types via interindividual actions (Table 1.1, Fig. 2.2). By analogy with Chesson's (2000) formulations, a dominant type is the one with the highest growth rate when a resource is sparsely distributed or least abundant (= low resource dispersion), and facilitation by a dominant or subordinate type are expected to increase the low growth rate of a subordinate type, relative to local ("patch") or "global" (population) regimes (Table 2.1). It follows that, because types within groups are more likely to be similar

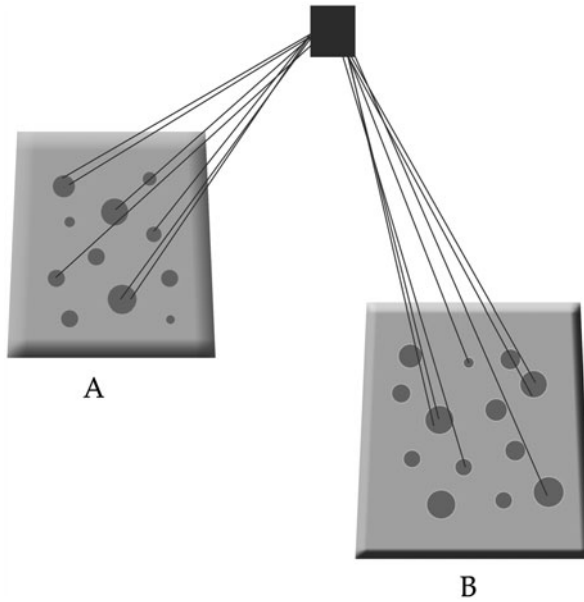


Fig. 2.2 A “nested vision,” 3D map, conceptualizing a type (*black square*) interacting with two environments, *A* and *B* (e.g., local regimes, “patches,” habitats, or different regions of a gradient). In each landscape, each *line* represents a trade-off of two traits, x vs. y , whereby a trade-off indicates that expression of one or a suite of traits decreases energy available for allocation to traits associated with survival, reproduction, or growth. Sizes of different circles (*dark grey*) represent differences in relative reproductive success of each trade-off, and performance in each patch has different optimal tradeoffs determined by condition-dependent features. Alternatively, each *dark grey circle* may be envisioned as the relative reproductive benefit gained from each trade-off (each line, x vs. y) when interacting with two group members, *A* and *B* (“social competition”: Crook 1972; West-Eberhard 1979). Imagine that the trade-offs are survival (x) and reproduction (y) of two social traits where x = care of one’s own offspring, y = “helping” the reproduction of another group member. In “fine-grained” conditions (environmental changes less than generation time), single optima will be favored in both locales (*A* and *B*), a scenario descriptive of the reproductive optimum of many large mammals. In other conditions, specialization to the separate locales will obtain (“coarse-grained” conditions: environment changes occur longer than generation time, characteristic of many small mammals). In other regimes, polymorphism is selected, for example, in predictable, heterogeneous environments such as seasonal regimes.

Changes in values of trade-offs across each performance curve (single optimum trade-off, specialization to *A* and *B*, or polymorphism) represent responses to competition within groups (Maharjan et al. 2013; Adler et al. 2013). These changes may be detected by differential interaction rates of types. Thus, these relationships should be testable. Intensity of within-group competition relative to between-group competition will determine relative costs and benefits to types (in this case, a type expressing traits x and y) of residing with kin or with unrelated types. Where groups of reproductive kin coreside, altruism may be favored (Fig. 1.2). Where groups of unrelated reproductive types are favored, social evolution will depend upon shared reproductive interests (“fates”) of group members, constraining evolutionary potential for the rise of altruism but with the capacity for the rise of cooperation in the Hamiltonian sense (Bourke 2011). For reasons that are poorly understood, social evolution has been retarded in most mammalian taxa, even where groups of related reproductive types coreside, possibly because competitive regimes have disfavored coresidence of kin (i.e., where within-group competition is intense compared to between-group competition: Chap. 2).

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Table 2.1 Assuming two types (a “dyad”) compete for a limiting resource, three possibilities obtain to manage competition: Positive, Neutral, or Negative interactions. Each of the three mechanisms has the potential to induce group-formation or, in some conditions, to maintain groups once they have formed (see examples). The evolution of sociality (Fig. 1.2) may arise initially *via* facilitation (e.g., daughters helping mothers), *via* tolerance (e.g., mothers tolerating presence of daughters), or *via* inhibition (usually) *via* a superior type repressing reproduction of an inferior type (e.g., mothers repressing the reproduction of daughters). Care must be taken to precisely identify whether only one type in a dyadic interaction facilitates the reproduction of the other type or whether both types facilitate reproduction of the other type in the dyad. © Clara B. Jones Based on Begon et al. (1990)

Potential responses to limiting resource available for monopolization

Mechanism employed by focal type (Actor) to manage competition with recipient and/or recipient's kin	Effect of interaction on recipient and/or recipient's kin	Description of response
Facilitation (positive interactions)	+	Contest competition or exploitative competition initially; only certain types in group capable of monopolizing resource Management of competition with Recipient increases Hamiltonian fitness of Actor and Recipient or increases Recipient's Hamiltonian fitness at expense of Actor's, e.g., some avoidance responses; restraint by Actor; change in status or rank; dispersal; death; cooperation, altruism; reciprocity, alliances, coalitions; increase or decrease thermal tolerance (niche space), possibly, via roles or division of labor (intermediate or high levels of competition or stress)
Tolerance (neutral interactions)	0	No attempt to manage competition with Recipient or no competition, e.g., aggregation?; some avoidance responses; standoff, “cold war,” <i>détante</i> ; “social facilitation” may be precursor to facilitation or inhibition
Inhibition (negative interactions)	—	Management of competition increases or does not change Actor's Hamiltonian fitness but decreases Recipient's Hamiltonian fitness, e.g., “parental control”; “parental manipulation”; ejection; repression of reproduction or other selfishness by Recipient or Recipient's kin (low or high levels of competition or stress?); the role of negative interactions requires close inspection for its ability to induce “altruism” (“helping”) in potential helpers (“donors”; see this brief, Coda) Older types in good condition may persist in some groups until types in poorer condition disperse or are ejected or die Younger or older types in good condition may inhibit types in poor condition

Table 2.1 (continued)

Potential responses to limiting resource available for monopolization		
Mechanism employed by focal type (Actor) to manage competition with recipient and/or recipient's kin	Effect of interaction on recipient and/or recipient's kin	Description of response
Facilitation, tolerance, or inhibition	+, 0, or –	Management of competition may change group competition and/or mean levels of competition in group
Facilitation and tolerance	+ and/or 0	Focal type may facilitate Recipient by mere presence
Tolerance and inhibition	0 and/or –	Any type in group capable of monopolizing resource ("scramble" competition initially"?)

than types between groups, their niche spaces will be more likely to overlap. Thus, *ceteris paribus*, within-group competition will be more intense than between-group competition, and the differential reproductive costs and benefits to types within groups will determine, in part, whether a type "decides" to stay or to leave its group of origin. This scenario, based upon West et al. (2002), may explain, in part, why most mammals are "solitary"; however, the latter authors do not parameterize within-group factors that may lead to coresidence of kin or unrelated types. The schema previously formulated assumes that inter- and intraspecific assemblies arise from cumulative effects of the reproductive rates of types (conspecifics) whose reproductive interests overlap. This "transference" from a higher level of organization to another, lower, scale demands quantitative, including experimental, testing. The emphasis herein highlights the similar ways in which phenomena at each scale function.

Herein, I use notation, l^* (level), derived from Chesson's R^* : l^*_{between} and l^*_{within} where l^*_{between} is defined as the lowest resource level at which a type's mean reproductive rate continues to increase when its resident group competes with other groups composed of an overlapping or nonoverlapping set of types. l^*_{within} is defined as the lowest resource level at which a type's mean reproductive rate continues to increase in competition with other types in its resident group. Thus, the type with the lowest l^*_{between} or l^*_{within} is the dominant (superior) type, *in a condition*. Since the expression of social actions (whereby one type facilitates the reproduction of a conspecific type) is density dependent, since social actions directly impact rates of increase or decrease of individuals, groups, and populations, and since Hamilton's rule is fundamental to the operation of social actions, inclusive fitness theory is inherently tied to the competition of individuals for limiting resources, to competition for the lowest l^*_{between} and l^*_{within} , and to the evolution of sociality, herein, the evolution of mammalian sociality.

Groups are composed of types and a type's discrete actions will affect within- and between-group competitive regimes. The actions of a social type may decrease intensity of within-group competition, on average, as long as the response is not

neutralized or outweighed by another type's counterstrategy (e.g., rejection of copulation). In mammals and some other vertebrates, elaborate signals and displays are components of, often lengthy, behavioral sequences serving to increase likelihoods that a social action will more than return its energetic (reproductive) investment to the Actor. The relevant point is that social traits expressed by types will determine whether intensity of competition is higher within or between groups. In the heterogeneous regimes in which mammalian evolution occurred, there would likely have been a dynamic and shifting balance of within- and between-group intensities with consequences for l^*_{between} and l^*_{within} , for patterns of immigration and emigration of types, as well as for the potential for cooperation or altruism between types.

After Chesson's (2000) treatment, social mechanisms may stabilize interactions between and within groups by decreasing stochasticity of one or more type's reproductive rates since l^*_{between} and l^*_{within} impact the reproductive potential of other types. It must be kept in mind, however, that a social act that stabilizes one or more types within or between groups will not necessarily be beneficial to all types concerned (e.g., "desperados," social parasites, the spiteful). Obviously, then, it would seem unlikely to find a group of pure altruists, since there seems always some benefit of retaining genes designed to repress the selfishness of others. As already stated, "decisions" made by types and the consequences of these decisions for resources and for other types (competitors) are limited by the parameters of Hamilton's rule (Bourke 2011; Lehmann and Keller 2006; Frank 2013). West et al. (2002) showed that Hamilton's rule reflects "decisions" available to focal types (Actors: Table 1.1) in ecological regimes (Figs. 1.1 and 2.1, Table 2.1), determining differential, condition-dependent reproductive costs and benefits to types (Fig. 1.2). "Decisions" obtain where types compete for limiting resources in their thermal zones.

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