Appendix A: The Standard Model of Population Growth

Although most writers acknowledge that humans are capable of population growth that if left unchecked would have greatly exceeded today's population, the issue, implicit or explicit, is the mechanism(s) for providing that check. Some see a kind of "natural fertility" in which births and deaths are so closely matched that things just somehow work out (e.g., Fagan 1998). Others posit vague mechanisms that keep populations stable and well below resource stress, much less competition or starvation. Often population size is not coupled with the availability of resources in these models, and we consider this separation highly unlikely for most human populations. Other models acknowledge the necessity of such links (e.g., Hassan 1981) but posit vague control mechanisms such as the feeling on the part of some members of society that their standard of living has become depressed. These models grade into other models that posit a clear linkage to availability of resources but view homeostasis as being attained with little stress and ultimately into the argument that there is no evidence that homeostatic mechanisms have ever worked adequately. We consider all these models versions of the standard model (that is, we believe that the standard model is implicit in many models that do not address the issue directly). The standard model seems to have at its heart the unrealistic assumption that population size is decoupled from carrying capacity or, to put it another way, density-independent. The argument against density-independent population equilibrium as a feature of human ecological adaptation is well summed up by Bates and Lees (1979:274): "So pervasive are explanations based upon this notion, and yet so lacking is it in empirical documentation, that we feel justified in calling it the 'myth of population regulation.' " Yet this seems implicitly to be the model in use in much of anthropology today.

Rather than attempt to characterize the positions of individual writers, we simply list

examples that we consider as using some form of the standard model, either explicitly or implicitly: Benedict (1970), Bettinger (1999), Binford (1968), Binford and Chasko (1976), Birdsell (1968), Blanton (1975), Carneiro (1978), Cowgill (1975*a*, *b*, 1996), Ehrlich, Ehrlich, and Daily (1995), Engelbrecht (1987), Flannery (1969), Gross (1975), Handwerker (1983), Harris and Ross (1987), Hassan (1975, 1981), Hayden (1972, 1975), Layton, Foley, and Williams(1991), Maschner (1992), O'Brien (1987), Polgar (1972), and Sahlins (1972). These writers assume that but do not show how and why stabilization (K^*) would take place far below K and still be linked to it. The issue is subtle but important. For example, Hassan (1981) argues for populations' being at "optimal carrying capacity" (a level far below carrying capacity) but being sensitive to minor as well as major changes in carrying capacity so that even slight changes are enough to bring about demographic changes that keep the population near its supposedly optimal level. Just how this state of affairs could work is not explicated. Although this mechanism may work under some circumstances, without an explicit model showing the circumstances under which stabilization will occur such claims are more realistically seen as being based on a decoupled model.

Not all writers accept or use the standard model. Counter arguments to it are that growth and population stress must have been common in the past and are relevant to change in human cultural systems. This or a similar position is taken by Belovsky (1988), Bronson (1972), Brookfield and Brown (1963), Cohen (1972, 1977), Harner (1970), Harris (1984), Keeley (1988), Lee (1987), Redding (1988), and Sanders and Price (1968). The "growth and stress model" is implicit in work by Glassow (1996) and various cultural ecologists such as Carneiro (1970, 1981) and Rappaport (1967) and is taken as a given by McNeil (1976). Keeley (1988) argues, for example, that the various forms of the standard model are speculative and not

founded on theory or empirical evidence and that population growth followed by population stress was common in the past. He seems to favor the view that occasional population crashes due to famine, disease, etc., were the extrinsic controlling factor for population growth. Whereas the standard model errs by assuming that the default case is a density-independent population in equilibrium with carrying capacity, the counterargument errs by assuming that populations are always subject to growth and hence to constant stress because of population size's reaching carrying capacity under all conditions.

In sum, we believe that an uncritically held model of population growth and its relationship to carrying capacity has obscured important factors in human behavior. Rather than simply rejecting the standard model (or the counterargument), though, we put forth in its stead a multitrajectory model that we believe is far more realistic and better accounts for variation in patterns of population growth and stasis.

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Appendix B: Decision Model for Interbirth Spacing

Assume that each female has some set of activities or tasks, *{A₁, A₂, ..., Aₙ}*, that are done on a regular basis. Some subset of these tasks, say *{S₁, S₂ ..., Sₘ}*, has costs (e.g., energy and/or time) per unit time the activity is performed that vary positively with population size and relate to resource procurement and processing (*subsistence activities*). Another subset of these tasks, say, *{P₁, P₂..., Pₖ}*, has costs per unit time that vary positively with current family structure (age and number of offspring) and relate to parenting activities (*parenting activities*). Finally, the remaining, *other tasks*, *{O₁, O₂ ..., Oⱼ}*, have costs per unit time that are essentially independent of family structure and/or population size. A females's total costs, on a given day, will be the sum of the costs for the activities done that day: $TC = \mathbf{S}a_iA_i$, where a_i is a coefficient that takes into account the amount of time allotted to activity A_i on that day.

Let T_{max} be the maximum value for *TC*. If $TC > T_{max}$ for the activities to be performed on a given day, then for at least one activity, A_j, the coefficient a_j will be set to (or close to) 0 for that day. The activity so selected must be consistent with constraints such as the quantity of food resources the female must procure daily. For simplicity, assume that the set of *subsistence activities* represents the minimal food procurement and processing tasks she must perform daily, and consequently the value of a_i cannot be set to 0 for these tasks. Changing the value of a_i to 0 for the *other tasks* (these are largely independent of family structure and population size) will have only a short-term effect on reduction of the value of *TC*. Consequently, reduction of the value of *TC* derives from altering the *parenting activities*. In particular, by deferring the next pregnancy, parenting costs will decrease through time as children become old enough that they do not need to be carried or brought along while foraging.

For the multiagent simulation of !Kung San population dynamics (Read 1998) the food procurement and processing activities were given a proxy, summary measure based on the current population size. *Other activities* were not included since, on average, they are approximately constant. The *parenting activities* were given a proxy measure based on the age of current offspring. The following decision rule was used in accordance with assumptions 1 - 3: For a given female agent, if her value of $TC < T_{max}$ for the current unit of time (e.g., a year), then do not modify the intrinsic age-specific fertility rate, if $TC \geq T_{max}$ then set her current fertility rate to 0. This decision rule implies that a female will become pregnant in accordance with the intrinsic fertility rate so long as her total costs are within the bounds she perceives as acceptable; she will have as many children as possible (assumption 3) as long as her parenting costs are acceptable to her. When the (potential) parenting costs in conjunction with the food procurement and processing costs would be excessive were she to have another offspring, she defers pregnancy until $TC < T_{max}$, in accordance with assumption 2. Read (1998) demonstrates that this decision rule accounts for (1) the empirical evidence regarding birth spacing among the !Kung San and (2) population stabilization as a consequence of this decision model.

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Appendix C: Test of Predictions Regarding *K* and *K** Due to Change in Foraging Costs with Decrease in Resource Density

Two data sources are used to test the model: one relates the area used by a hunter-gatherer group in Australia to rainfall and the other relates rainfall to net above-ground biomass productivity (NAGP). The NAGP measure, rather than total biomass, can be related to carrying capacity, since "the majority of the food resources taken from the plant community are technically the product of net annual production and not components of the plant community's standing biomass" (Binford 2001: 175). Hence $K \sim$ NAGP. Binford provides tables (tables 4.01 and 4.07) that give the rainfall value and the NAGP value in the region utilized by each Australian hunter-gatherer group. The other data source is Birdsell's (1953, 1973) work relating hunter-gatherer group catchment area to rainfall in Australia and establishing a modal value (of about 500 persons) for the population size of a dialect group. Birdsell found that the equation area $= 7122.8$ (rainfall) $^{-1.58}$ fit his data, and this equation is used here to convert the rainfall in an area used by a hunter-gatherer group to the area used by that group. The modal value permits converting the area data into a proxy measure of population density: $K^* \sim 1/$area. Figure D shows the pattern for the Australian data when comparing K and K^*.

Carrying capacity K is assumed to be proportional to net above-ground biomass productivity. K^* is assumed to be proportional to 1/area based on a fixed, modal value of the population size of Australian hunter-gatherer groups. The curve is a fourth-degree polynomial fit to the data points solely to show the general trend on the assumption that the left group of data points (NAGP < 0.06) connects smoothly with the right group of data points (NAGP > 0.1). The constants in the polynomial have no particular interpretation, and so their values are not shown. Axis scales are relative and not absolute. Data on rainfall, NAGP, and population size are from

Binford (2001: tables 4.01, 4.07, and 5.01); seven data points with population size listed by Binford as questionable have been excluded, and one further data point (Mineng) has been excluded as an outlier. The data have been scaled so that the most extreme point (upper right) has the same K and K^* value on the assumption that a group in the environment with the highest resource density will be close to carrying capacity. The pattern of increasing and then decreasing values for $K - K^*$, however, does not depend upon the scaling choice.

The pattern of the data shows clearly the initial trend, as predicted by the model, of an increase in $K - K^*$ as the resource density decreases and then convergence between K^* and K as resource density reaches low values. The relationship between $(K - K^*)/K^*$ and K is shown in figure E. The trend line was computed excluding the arc of points on the left side of the graph. As predicted, unutilized resources per person vary inversely and approximately linearly with the resource density. Axis scales are relative and not absolute. The vertical axis values are computed from the NAGP ($\sim K$) and the 1/area ($\sim K^*$) values used in figure D. The arc of points is from groups with low NAGP, hence corresponding to a relatively small value for K. The small value of K may constrain variation in K* values. Though the trend for these points may be constrained by low resource density, resource availability per person remains high, as is predicted for an area with low resource density.

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Appendix D: Competition Model

Assume a fixed region for the population so that population density is proportional to population size. The Lotka competition model is a generalization of the Verhulst-Pearl equation for logistic growth. Logistic growth is given by the equation

$$dP/dt = P(a - bP),\tag{1}$$

where $P(t)$ is the population size at time t, a is the intrinsic growth rate for the population, and b is a parameter whose value identifies the effect of an increase in population size on the intrinsic growth rate. When $P(t) = a/b$, $dP/dt = 0$ and the population no longer grows. The differential equation given in equation 1 has the exact solution $P(t) = (a/b)/(1 + exp[-a(t-t_0)])$, where $P(t_0)$ is the initial population size.

For two populations in competition, each population is assumed to follow the logistic growth curve with the added factor that the growth of one population affects the growth of the other. Competition is modeled via the following pair of differential equations:

$$dP_1/dt = P_1(a_1 - b_{11}\,P_1 - b_{12}P_2) \text{ and}\tag{2}$$

$$dP_2/dt = P_2(a_2 - b_{21}P_1 - b_{22}P_2),\tag{3}$$

where $P_i(t)$ is the population size of population P_i at time t, a_i is the intrinsic growth rate for population P_i, and b_{ij} measures the inhibitory effect of population P_j on population P_i so that b_{11} is the inhibitory effect that growth of population P_1 has on itself, b_{12} is the inhibitory effect that population P_2 has on population P_1, etc., $1 £ i, j £ 2$.

The model assumes a fixed set of relations between P_1 and P_2 and that all individuals are affected equally by population growth in terms of the way in which current net fertility is affected. The pair of differential equations (equations 2 and 3) does not have an exact solution in terms of an explicit form for the functions $P_1(t)$ and $P_2(t)$, hence phase-space diagrams in which

P_1 is plotted against P_2 are used to show population size trajectories as determined by these ewo equations. Equilibrium values for P_1 and P_2 are also plotted in the phase-space diagram.

Equilibrium values are computed from setting $dP_1/dt = 0$ and $dP_2/dt = 0$. If $dP_1/dt = 0$ then $a_1 - b_{11}P_1 - b_{12}P_2 = 0$ and this equation defines a linear relationship between P_1 and P_2 along which P_1 has no growth. If $dP_2/dt = 0$, then $a_2 - b_{22}P_2 - b_{21}P_1 = 0$, and this equation defines a linear relationship between P_1 and P_2 along which P_2 has no growth. Thus in the phase space there will be two lines representing equilibrium values, one determined by the first equation and the second by the second equation.

Appendix E: Four Patterns of Competition

We can graph the way in which one population affects the growth trajectory of the other population by use of a two-dimensional phase-space diagram in which the axes measure the current population size of each of the two populations and arrows indicate the current net growth rates of the two populations for each point in the phase space. We can also indicate the curve along which a population has a net growth rate of zero given its level of competition with the other population. When one of these curves is determined for each of the two populations, the intersection of the two curves, if any, represents the point(s) for which both populations have a net growth rate of zero, that is, in equilibrium with respect to each other.

Depending on the relative magnitudes of the parameters a_i and b_{ij}, there are four qualitative patterns for the two populations (figs. F – I). The curve along which a population has a net growth rate of zero is a straight line (see appendix C). In figure F the two straight lines intersect and divide the upper right quadrant into four subregions. For all four subregions the net growth rate of the two populations (indicated by horizontal and vertical arrows) has the overall effect (indicated by the arrow at an angle) of driving both of the populations in the direction of the intersection of the two lines. Hence for this configuration the two populations have a stable equilibrium represented by the intersection of the two lines, and any perturbation from the equilibrium point will move the population sizes back toward the equilibrium point. For the assumption that the populations have the same intrinsic growth rate, or $a_1 = a_2$, the conditions under which there is a stable equilibrium may be characterized as competition in which one population has a greater inhibitory effect on its own growth than on that of the second population.

Figure G also has an equilibrium point and four subregions, but for two of the subregions

(*bottom left* and *top right*) change in population size moves the populations toward the equilibrium point and for two of the subregions (*middle left* and *middle right*) it moves the populations away from the equilibrium point. The latter property makes the equilibrium point unstable, since perturbation from the equilibrium point could move the populations into any one of the four subregions, and for two of the subregions the perturbed populations would now have growth trajectories that continued to move away from the equilibrium point.

The trajectories of the populations when they move away from the equilibrium point are bounded by one of the populations' becoming extinct (i.e., the trajectory reaches one of the two axes). Which population will become extinct cannot be predicted from the parameters because perturbation from the equilibrium point could move the current configuration of population sizes into the subregion in which population 1 goes extinct or into the subregion in which population 2 goes extinct. If one population becomes extinct, then the remaining population, call it population i, will increase in size until it reaches its equilibrium population size, $K^* = a_i/b_{ii}$. Unstable equilibrium may be characterized, for the case where $a_1 = a_2$, as competition in which population growth in each of the populations has a greater inhibitory effect on the net growth rate of the other population than it does on its own; that is, competition for which $b_{11} < b_{21}$ and $b_{22} < b_{12}$.

Figures H and I have no points of intersection for the two lines representing the configuration in which one or the other of the two populations has zero growth. In figure H, population 1 will win out in competition with population 2, since in the region between the two lines population 1 has a positive net growth rate and population 2 has a negative net growth rate. For figure I the relationship of the two populations is reversed and population 2 will win out in competition with population 1.

Under the assumption that $a_1 = a_2$, population 1 winning out in competition with

population 2 may be characterized as competition in which population 1 has a greater inhibitory effect on the growth of population 2 than it does on itself and population 2 has a greater inhibitory effect on itself than it does on population 1 (i.e. $b_{11} < b_{21}$ and $b_{22} > b_{12}$). In other words, population 1 can grow at the expense of population 2, and therefore population 2 becomes extinct. Conversely, population 2 winning out in competition with population 1 may be characterized as competition in which population 2 has a greater inhibitory effect on the growth of population 1 than it does on itself and population 1 has a greater inhibitory effect on itself than it does on population 2 (i.e. $b_{11} > b_{21}$ and $b_{22} < b_{12}$). This might occur if growth in population 1 had little effect on the resource base for population 2 but growth in population 2 had the effect of removing resources from population 1. An example would be competition between a hunter-gatherer population and an agricultural group in which the two groups overlapped in the use of hunted foods and the expansion of agricultural land reduced the availability of foraged foods.

Of these four sets of competitive relationships, we will primarily be interested in the conditions under which a stable equilibrium can occur and the conditions under which one of the populations will win out in competition with the other.

Parameter Values

For recent human populations we assume that both populations have the same intrinsic growth rate ($a_1 = a_2$). This is reflected in the fact that when correction is made for reduction in the fertility rate due to behavioral practices, the same corrected fertility rate of about 10-15 offspring per reproductive period is obtained, regardless of the population. Assuming that mortality rates for different populations are comparable prior to the introduction of modern medical practices, then the inherent growth rates of recent human populations are about the same. Therefore we will assume throughout the following that $a_1 = a_2 = a$, the populations differing only in the b

parameters.

The parameters b_{11} and b_{22} measure the equilibrium population size of population 1 and population 2, respectively, in terms of the quantities $1/b_{11}$ and $1/b_{22}$. The parameters b_{12} and b_{21} measure the inhibitory effect of one population on the other population. Since we are comparing one group with another, we may assume that the nutritional needs of an individual are independent of the population to which that individual belongs. This assumption allows us to equate the per person use of food resources in one group with the per person use of food resources in the other group. Hence if the food resources used per person in population 1 are all resources that would otherwise be available to population 2, then we may set $b_{21} = b_{11}$ and $b_{12} = b_{22}$. If both populations have the same equilibrium population size, then $b_{11} = b_{22} = b_{12} = b_{22}$. This configuration will arise when the two populations have the same catchment area and use the same resources from that catchment area in comparable ways. An example of such a configuration would be, say, all of the different camps in !Kung San society, since each camp potentially has access to all resources via rights of camp membership through relatives and the *hxaro* system (Wiessner 1982). For culturally distinct groups, however, conditions under which there is complete overlap of catchment areas are rare.

For distinct groups we can relate the parameters b_{12} and b_{21} to the overlap in the catchment areas of the two populations. Initially, we assume that the two populations use the same set of resources and resources are uniformly distributed over the catchment areas. We then relax the first assumption. Let C_1 be the catchment area for population 1 and C_2 the catchment area for population 2. Let c be the zone of overlap of these two catchment areas. The proportion of a group's catchment area in the zone of overlap measures the extent to which one population is using resources otherwise available to the other population and therefore the impact of

population growth of one population on the other population. More precisely, under the specified conditions, after suitable scaling of the parameters, $b_{12} = c/C_1$ and $b_{21} = c/C_2$.

When $C_1 = C_2 = C$, it follows that $b_{12} = b_{21} = c/C$ and the two populations have equivalent effects on each other's growth. If the catchment area for population 1, say, is larger than the catchment area for population 2, then $b_{12} = c/C_1 < b_{21} = c/C_2$ and growth in population 1 has a greater effect on population 2 than does growth in population 2 on population 1.

If the resource bases of the two groups are not identical, then we can introduce a term, r_i, representing the proportion of the resources used by population i that are also used by population j. With this notation, $b_{21} = (r_1 c)/C_2$ and $b_{12} = (r_2 c)/C_1$, since growth in population 1 reduces the resource base for population 2 in the overlap region, c, only by the proportion of the resources used by population 1 that otherwise would be used by population 2 (and similarly for the effect of population 2 on population 1). One implication is that when one group expands its resource base and the other group does not, the former group will have a greater impact on the latter group than the latter group has on the former.

Baseline Competition: Two Groups with Identical Parameters

Assume that we start out with, say, two hunter-gatherer populations having the same internal population dynamics (i.e., $a_1 = a_2 = a$ and $b_{11} = b_{22}$), and using the same mix of resources. The parameters b_{12} and b_{21}, as discussed above, measure the impact of one population on the growth of the other population due to, for example, resources utilized by one population thereby being made unavailable to the other population. The size of the overlap of the catchment areas, C_1 and C_2 (fig. J) for groups 1 and 2, respectively, measures the relative magnitude of the parameters b_{12} and b_{21}.

If $C_1 = C_2$, then the two populations use exactly the same resources and both the same

effect on each other as on themselves; hence $b_{12} = b_{22} = b_{21} = b_{11}$ (fig. K, A), and the two population sizes at equilibrium will be $K^* = a/b_{11} = a/b_{22}$. All points along the common line for the two groups are quasi-stable equilibrium values for the population size of each group. At the other extreme, if the regions C_1 and C_2 do not overlap, then the two populations are independent of each other and $b_{12} = b_{21} = 0$ (fig. K, B). Each group now independently increases to the carrying capacity of the area from which it obtains resources, and the point representing the carrying capacity of the area for each of the two groups is a stable equilibrium value. If the catchment areas only partially overlap and the two populations use the same resource base, then $b_{12} = b_{21} < b_{11} = b_{22}$ (fig. K, C). The latter corresponds to the configuration shown in figure F, namely, stable equilibrium between the two populations. In all cases, the parameters drive the populations to a stable equilibrium configuration. We now consider in more detail the third and first possibilities with regard to stability of the configuration. For the third possibility, namely, incomplete overlap of catchment areas, we consider two subcases: territorial exclusion and lack of territorial exclusion. For all possibilities we arrive at the same conclusion, namely, that the only stable configuration is the second one, with non-overlapping catchment areas.[i]

Partial overlap Although a stable configuration with partial overlap is theoretically possible, this configuration unrealistically assumes that each population responds only to the reduction in resources available to it due to the use of resources by the other group as if this were a feature of its environment over which it had no control. If, however, the members of one population, say, population 1, begin to practice territorial exclusion, then the parameters b_{21} and b_{12} will be affected. The parameters b_{11} and b_{22} will not change, since they measure the equilibrium population size when only a single population is present. The parameter b_{12} will decrease to b_{12}^* (i.e., $a/b_{12} < a/b_{12}^*$), since population 1 is isolating itself from population 2 via

territorial exclusion. The parameter b_{21} will increase to $b_{21}*$ (i.e. $a/b_{21}* < a/b_{21}$) since population 2 is affected not only by population 1's use of resources but also by its reduction of access to resources. The effect is to shift the stable equilibrium of figure F in the direction of a configuration in which population 1 will win out in competition with population 2.

Realistically, population 2 may not become extinct; the ability of population 1 to practice territorial exclusion may be limited as its catchment area increases in size, or population 2 may be able to find a catchment area in which it can also practice territorial exclusion. In either case, stability will reemerge only when the overlap in catchment areas between populations 1 and 2 is small, thereby making the population dynamics of the two populations essentially independent.

Where neither group is defending its catchment area against the other, partial overlap of catchment areas assumes that catchment area is bounded for reasons other than the presence of the other group. Partial overlap may occur, for example, when the two groups exploit different resources that only partially overlap in their geographical distribution. If, however, the two groups are utilizing the same resource base and not practicing territorial exclusion, then partial overlap is not a stable arrangement, since one group can grow by expanding its catchment area without opposition from the other. Population growth will be expected because the model implies that both populations are stabilized at a population level below the equilibrium population size of each group were there no competition. Hence expansion of the catchment area would reduce the cost of foraging, thereby obviating the need for decisions to increase spacing of offspring. Consequently, we would expect that in the absence of territorial exclusion, groups utilizing the same resource base would eventually either completely overlap, be reduced to one by the extinction of the other, or be geographically isolated with no overlap of their catchment areas. Complete overlap will be equivalent to neutral equilibrium along the line of overlap of

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equilibrium values in the phase-space diagram. Any stochastic variation along this line simply moves the two populations from one equilibrium value to another, and so the two populations will not return to their previous equilibrium value. Thus by stochastic drift one population may go to extinction along the line of intersection. The only alternative will be geographic isolation.

!Kung San camps are an example of complete overlap. The rules of camp membership effectively allow access to resources throughout the territory. This is a stable configuration that does not lead to intercamp conflict over resources, although the membership of an individual camp may die out because of drift effects were it not for cultural means through which new camp members are recruited

Complete Overlap. While the theoretical case of complete overlap of catchment areas would be a stable arrangement in a fixed, deterministic universe (fig. L, A), change in any one of the parameters for the two populations will shift the arrangement to a configuration in which one population will win out in competition with the other (figure L, B). Thus complete overlap is unstable in the face of long-term change in parameter values, and so we can assume that for there to be a stable configuration with complete overlap in the catchment areas, any change in parameter value by one group must be matched by an equivalent change in parameter value by the other group.

For groups that are part of the same society (e.g., the !Kung San camps), equivalence of parameter values in all subgroups could arise out of a common cultural context, such as a shared valuation placed on the well-being of a family. If the two groups are part of different societies, however, then differences in their cultural contexts make possible long-term differences in parameter values between the two groups. Hence we would expect that the theoretical pattern of a stable arrangement with complete overlap in catchment areas would be more likely to occur

when the groups are part of the same society.[ii]

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Appendix F: Warfare Fatalities in Small-Scale Societies

Although it is commonly assumed that warfare in the past, especially nonstate warfare, was insignificant from a cultural or biological point of view (Braun and Plog 1982, Hassan 1981, Knauft 1991, Reyna 1994, Service 1975, Turney-High 1949). Keeley's and others' (e.g., Ember and Ember 1992) careful assessment of a large body of evidence shows this assumption to be false. (Other useful considerations of prehistoric or early ethnographic cases of warfare include Bamforth 1994; Berndt 1964; Bovee and Owsley 1994; Burch 1974, 1988; Chagnon 1988; Feil 1987; Haas 1990; LeBlanc 1999; Manson and Wrangham 1991; Maschner and Maschner 1997; Meggitt 1977; Milner, Anderson, and Smith 1991; Moss and Erlandson 1992; Owsley 1994; Rappaport 1967; Redmond 1994; Strathern 1971; Tuck 1978; Vayda 1960). Keeley makes the very convincing case that "primitive" warfare is neither ritualistic nor nonfatal. He shows that when warfare is endemic, the cumulative effect of warfare on mortality rates in societies from bands to chiefdoms is significant. While formal battles in places such as New Guinea may have resulted in only one casualty in a single battle, such battles were sufficiently common that the cumulative effect was large. Moreover, formal battles were accompanied by raiding and ambush, which were much more deadly for women and children and further increased the death rate. Where the information is relatively good (Berndt 1964, Chagnon 1988, Meggitt 1977, Morren 1984, Shankman 1991, Sillitoe 1977), death rates of adult males (lifetime cause of death) due to warfare range from 20 to 32%, with 25% probably a reasonable generalization. Death rates for women due to warfare were from 3 to 16% for reproductive-aged women, with a reasonable generalization of 4-5%.

Figures for the Ache are instructive: "Death at the hands of another human being was by far the most common cause of death to forest-dwelling Ache" (Hill and Hurtado 1995:168).

Among adult Ache males, external warfare accounted for 35% of all deaths, and more than 40% of reproductive-aged females died or were captured (removed from the reproductive group) because of warfare.

Group size is highly significant for success in endemic warfare. Because much of the warfare is attritional, the larger groups (larger value for *a/b*) prevailed. Moreover, skill at warfare cannot be easily turned on and off. Typically, boys are taught techniques of fighting from a young age, and good war leaders are discovered because of the frequency of fighting. Any group that avoids warfare, does not train its boys, and does not allow military leadership to be developed, discovered, and recognized is greatly disadvantaged if attacked. Thus, it is simply impossible, except on small islands or in other conditions of isolation, for a group to "refuse to play." A group cannot simply lower its birth rate so that it does not need more land and then stop fighting. Unless all the neighboring groups do likewise, it will be at a great disadvantage and an easy and likely target for another group that is expanding through aggression.

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Fig. A. *Population density and average foraging cost per unit of resource per female forager, keeping fixed the resource base and the catchment area (schematic).*

Fig. B. *Total parenting costs and interbirth spacing (schematic).*

Fig. C. *Population size and net growth rate (schematic).*

Fig. D. K *and* K* *values for Australian hunter-gatherer.*

Fig. E. *Unutilized resources per person and resource density.*

Fig. F. *Stable equilibrium. Area where population 2 grows, shown by a vertical arrow pointing upward (horizontal shading). Area where population 1 grows, shown by horizontal arrow pointing to the right (vertical shading). Area where both populations grow (double shading).   In all three shaded areas and the unshaded area the increase or decrease in the sizes of the two populations pushes them to the point of intersection of the two lines (diagonal arrows).*

Fig. G. *Unstable equilibrium. Population 1 wins out when the populations are in the region at the lower right; population 2 wins out when the populations are in the region at the upper left.*

Fig. H. *Population 1 wins out as the populations move in the direction of the vertical axis when the pair of populations is in the middle region.*

Fig. I. *Population 2 wins out as the populations move in the direction of the vertical axis when the pair of populations is in the middle region.*

Fig. J. *Catchment areas for two populations.   The extent of the area of intersection for the two catchment regions (gray) measures the degree to which each population inhibits the growth of the other.*

Fig. K. *Phase-space diagram for three patterns of catchment overlap.*

Fig. L. *Equilibrium with complete overlap of catchment areas (top) and shift in configuration with change in parameter value (decrease in* b_{12}*) to one in which population 1 wins out.*
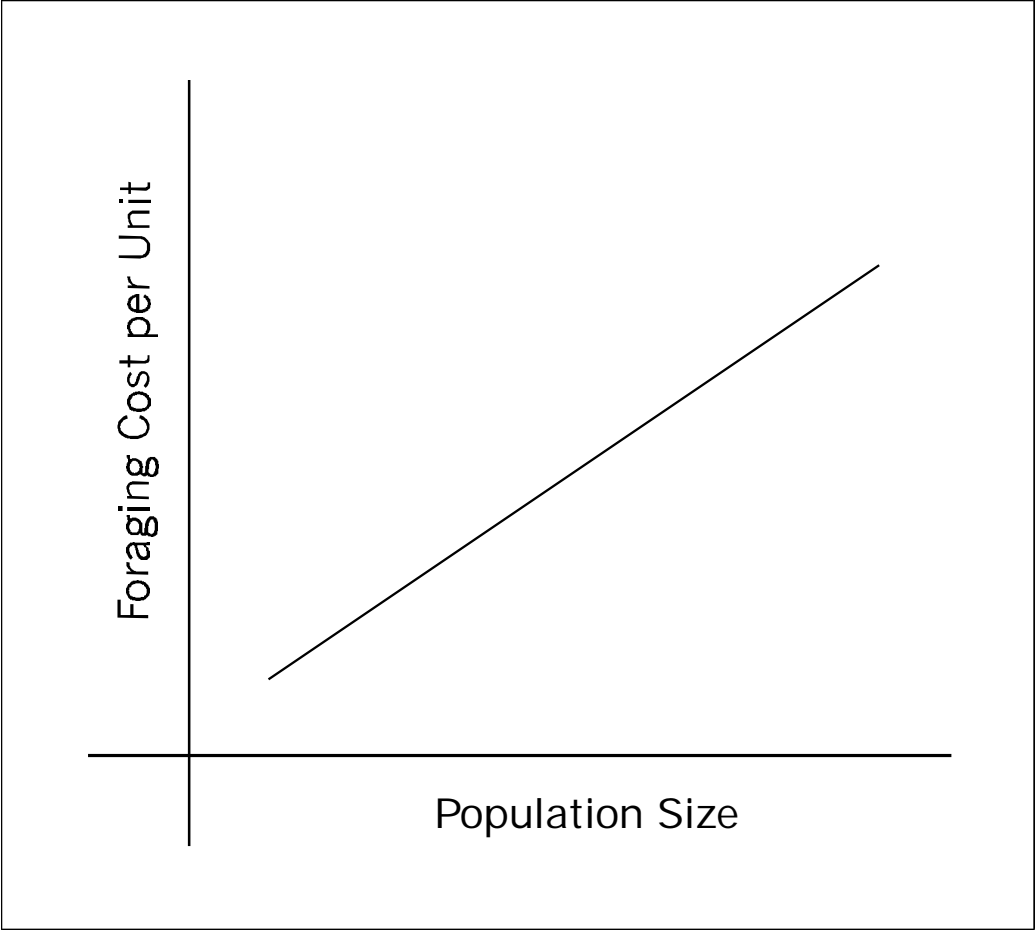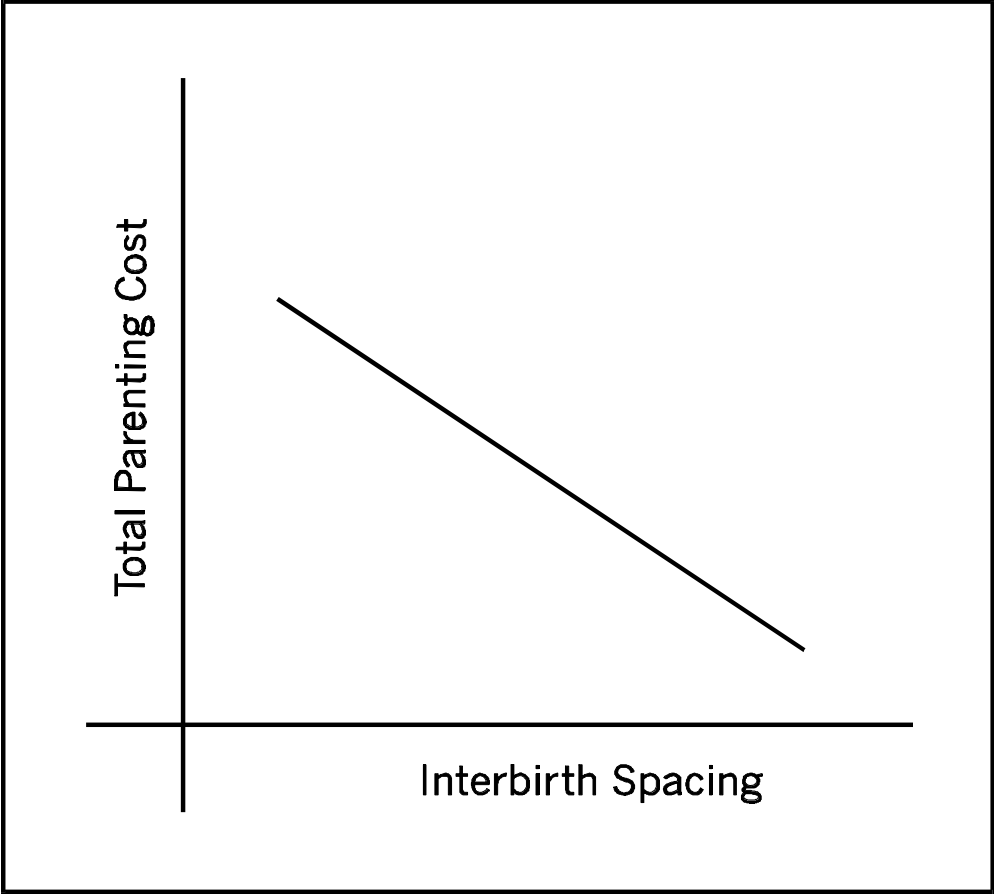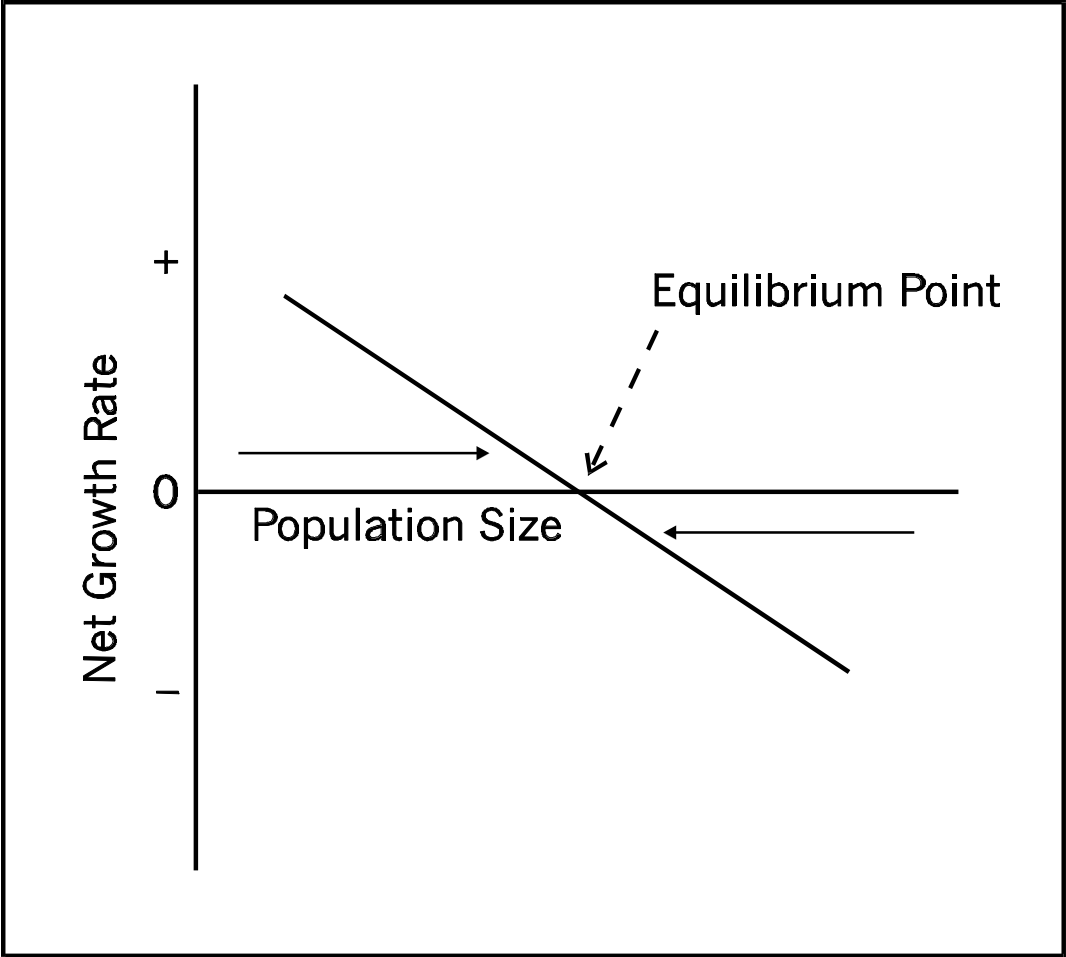
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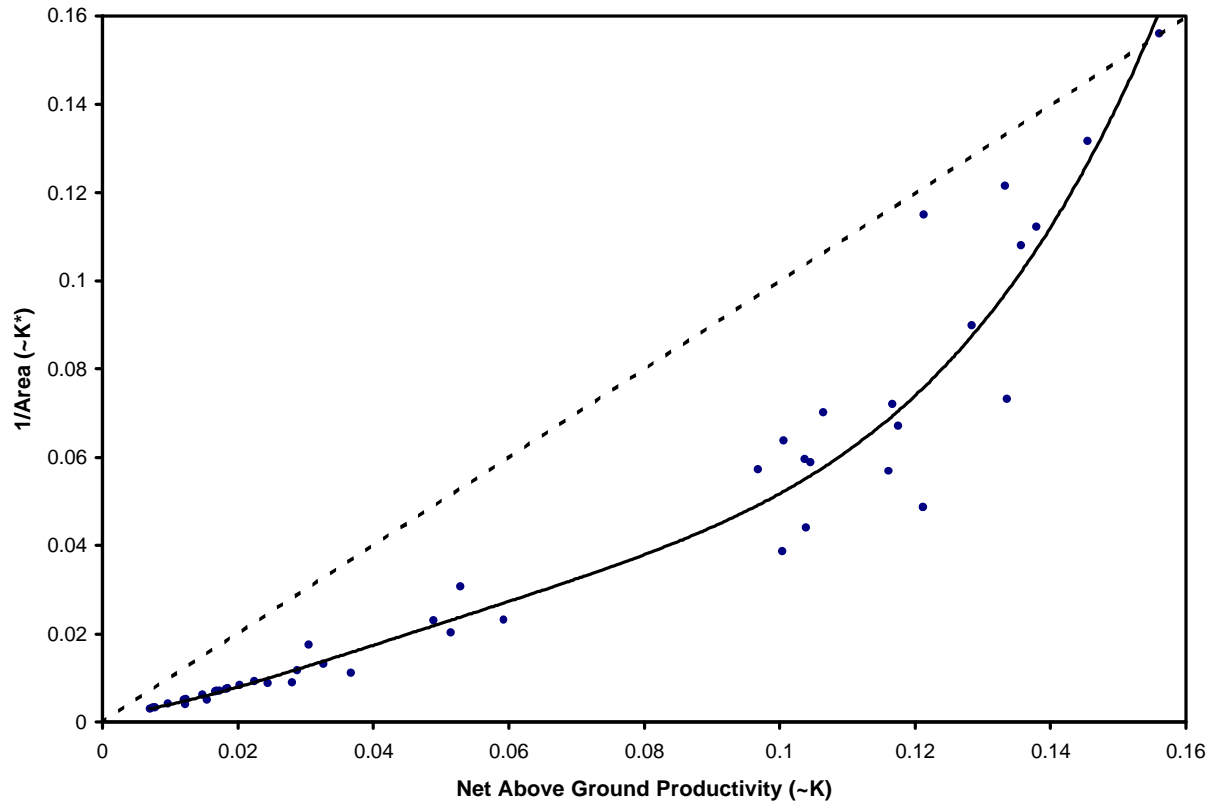
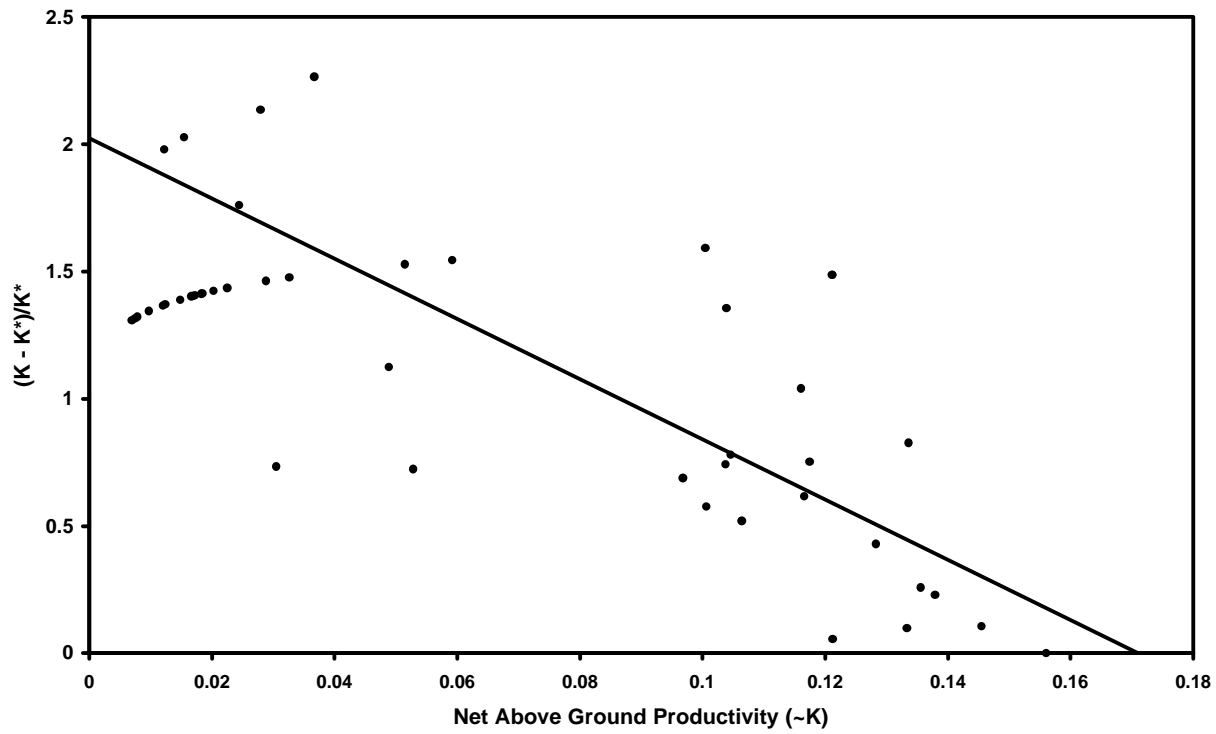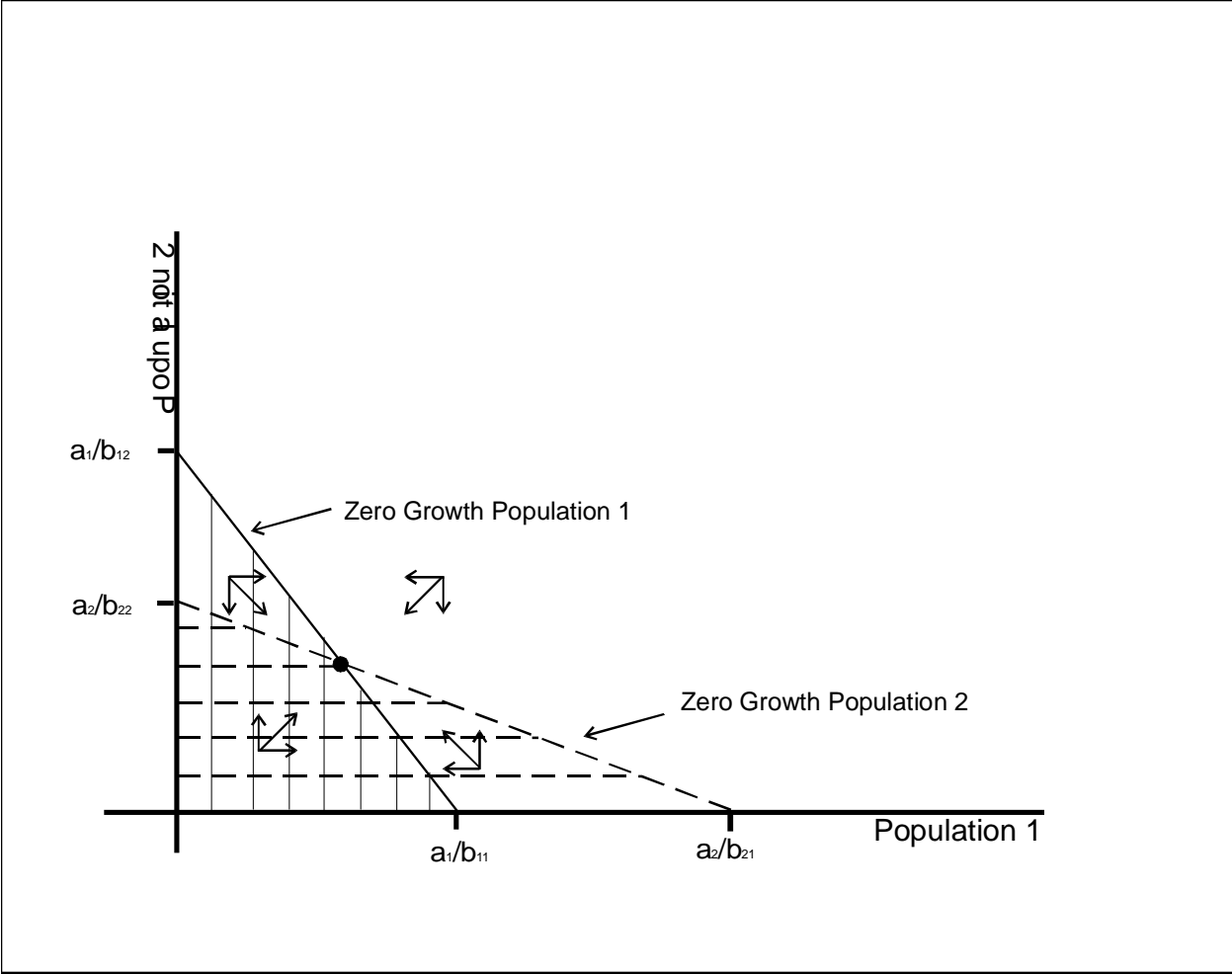Figure B -- Read/Leblanc

Figure C -- Read/Leblanc

Figure D

Figure E

Population 2

a_1/b_{12}

Zero Growth Population 1

a_2/b_{22}

Zero Growth Population 2

Population 1

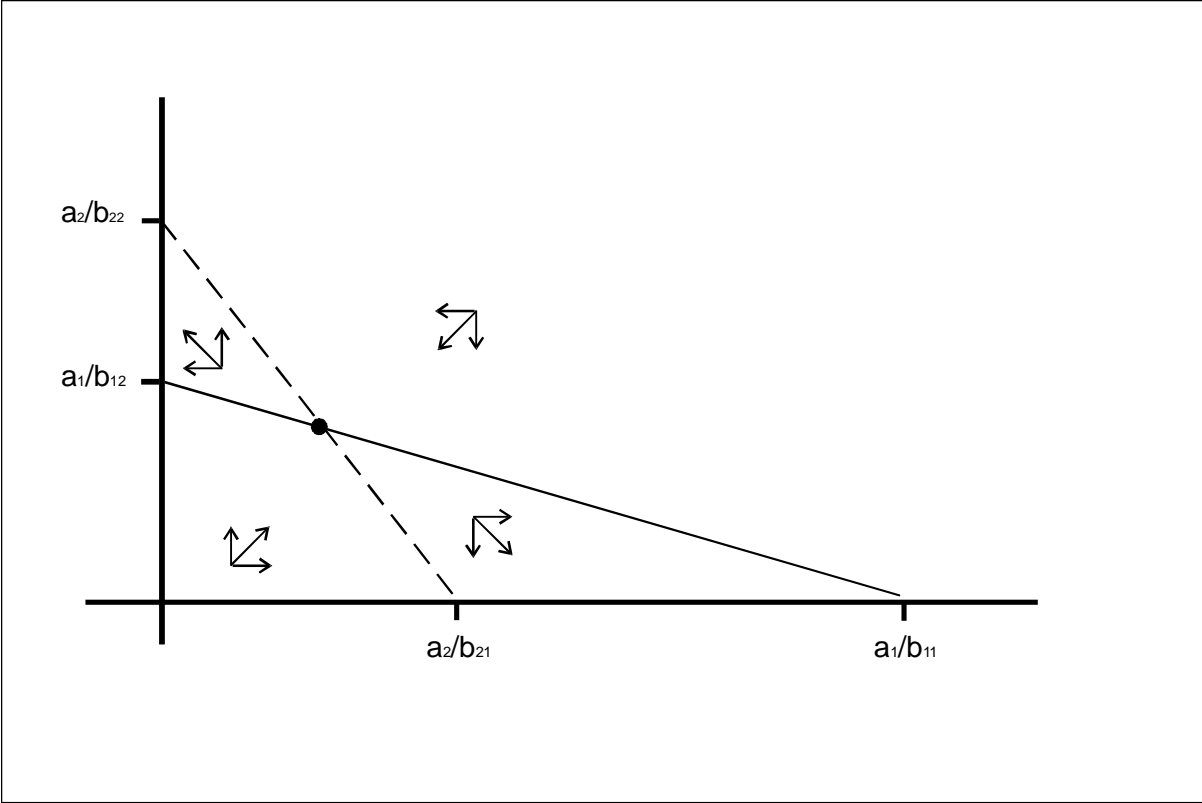a_1/b_{11} a_2/b_{21}
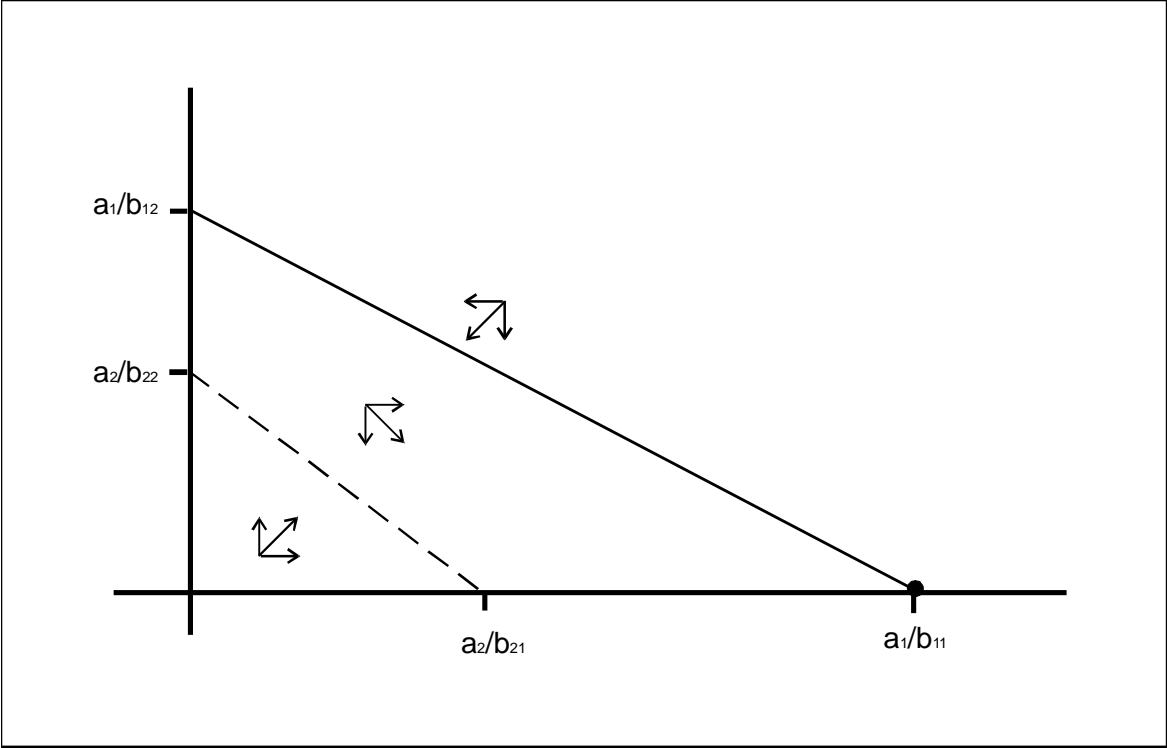
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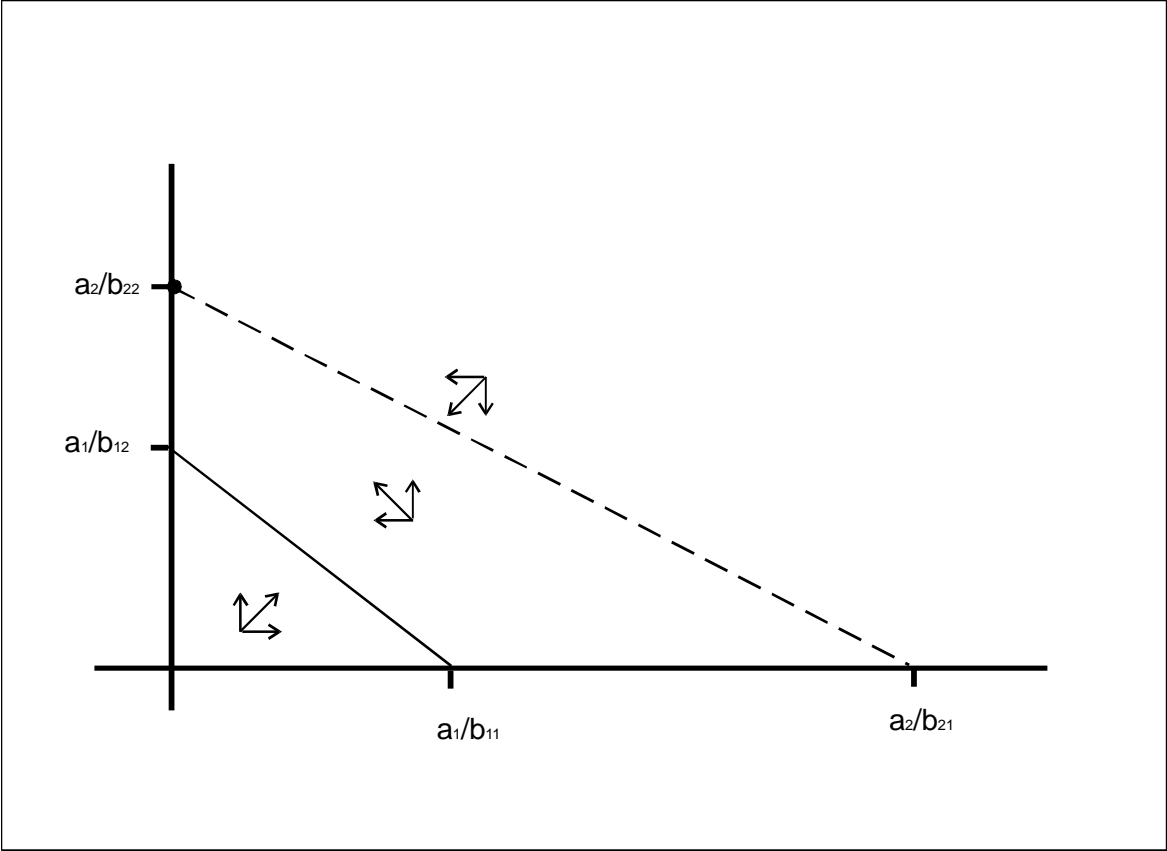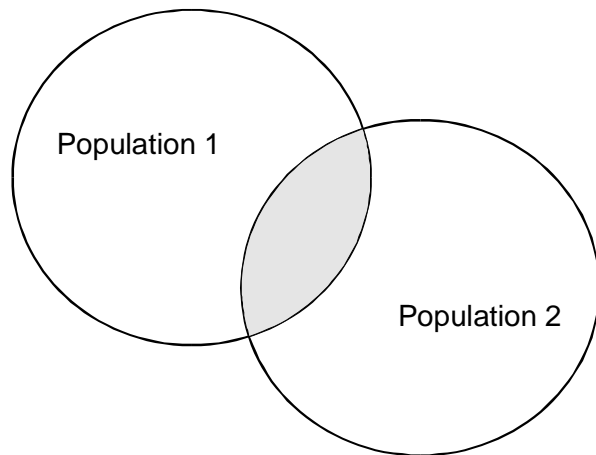
Figure G -- Read/Leblanc

Figure H -- Read/Leblanc

Figure I -- Read/Leblanc

Two Identical Populations: $b_{11} = b_{22}$, $b_{12} = b_{21}$ and $a_1 = a_2$.

Area of overlap is a measure of b_{12} and b_{21}

(A) With 100% overlap, $b_{12} = b_{11} = b_{22} = b_{21}$
(B) With 0% overlap, $b_{12} = 0 = b_{21}$, the two populations are decoupled
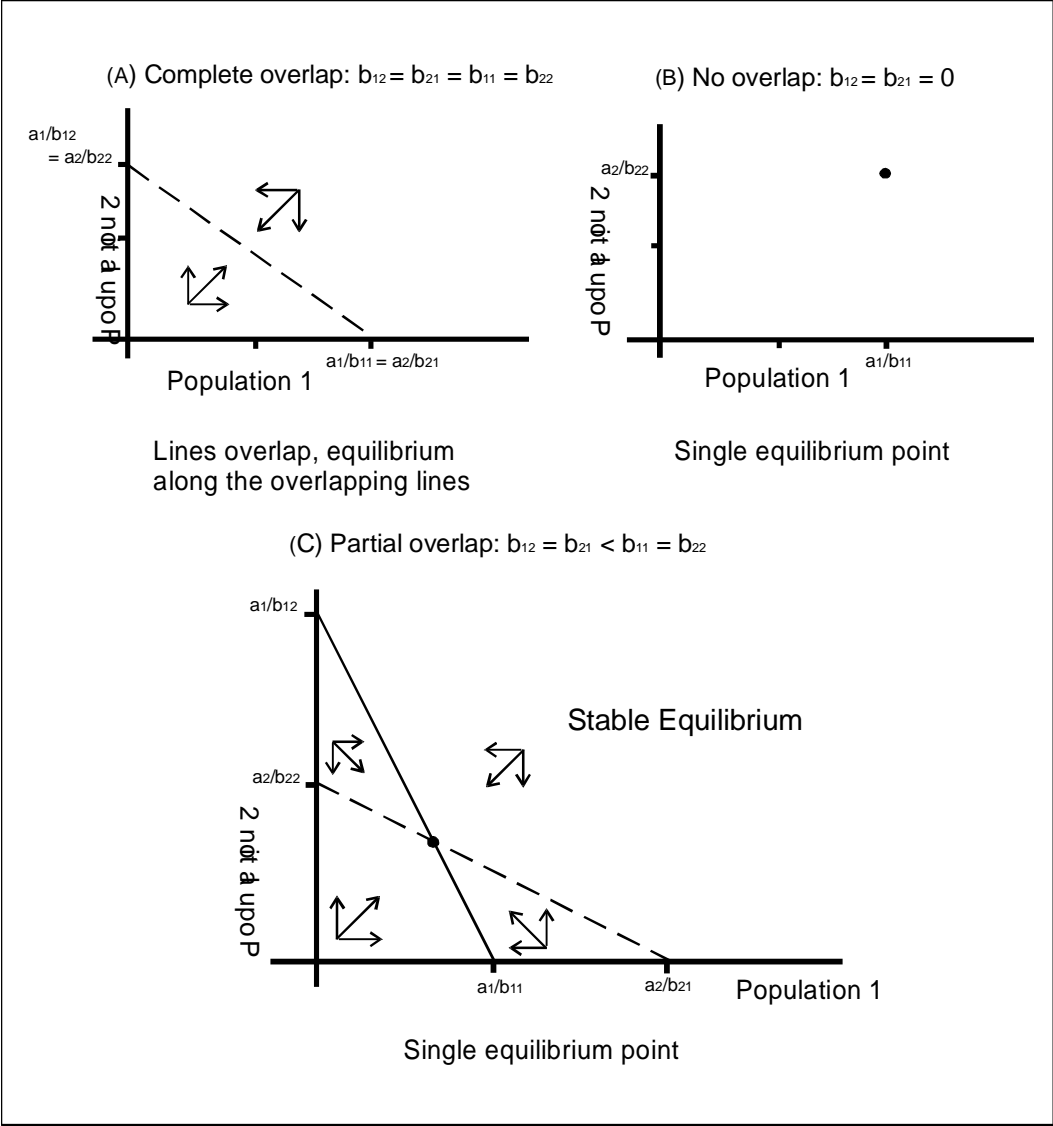(C) With partial overlap, $b_{12} = b_{21} < b_{11} = b_{22}$

Figure J -- Read/Leblanc

(A) Complete overlap: $b_{12} = b_{21} = b_{11} = b_{22}$

a_1/b_{12}
$= a_2/b_{22}$

Population 2

Population 1

$a_1/b_{11} = a_2/b_{21}$

Lines overlap, equilibrium
along the overlapping lines

(B) No overlap: $b_{12} = b_{21} = 0$

a_2/b_{22}

Population 2

Population 1

a_1/b_{11}

Single equilibrium point

(C) Partial overlap: $b_{12} = b_{21} < b_{11} = b_{22}$

a_1/b_{12}

Stable Equilibrium

a_2/b_{22}

Population 2

a_1/b_{11} a_2/b_{21} Population 1

Single equilibrium point

Figure K-- Read/LeBlanc

a_1/b_{12}
$= a_2/b_{22}$

Population 2

Population 1 $a_2/b_{21} = a_1/b_{11}$

a_1/b_{12}

Population 2

a_2/b_{22}

equilibrium value
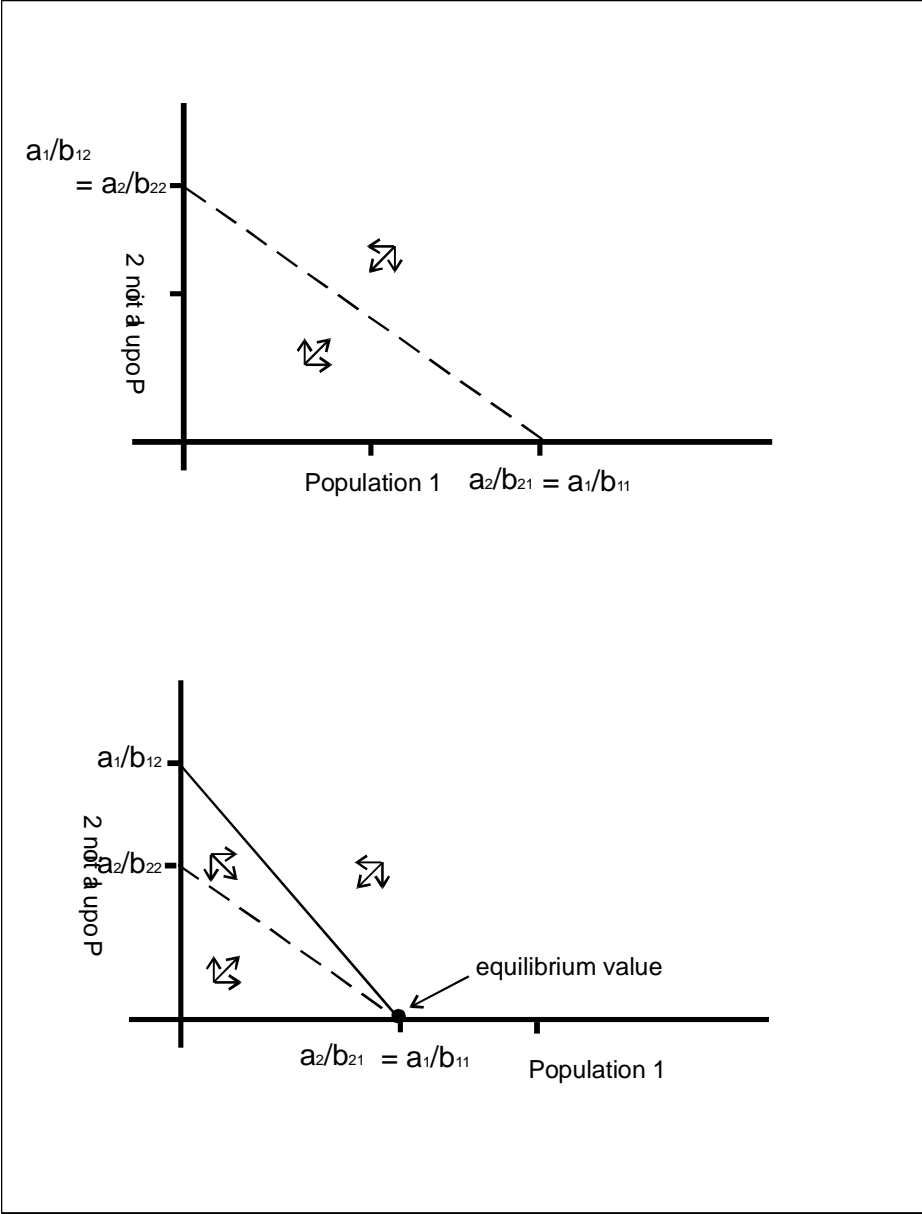
a_2/b_{21} $= a_1/b_{11}$ Population 1

Figure L--Read/LeBlanc

[i] We include under nonoverlapping catchment areas a configuration in which there might be limited overlap in the respective regions for which the impact of one group on the other is within the range of "noise" or stochastic variation in the population dynamics within a single population. Our concern here is with effects of one group upon a second group that are more pronounced than background fluctuations within a single group in isolation.

[ii] Pielou (1969:64) observes that the theoretical possibility of a stable configuration between different species in competition contradicts the "competitive exclusion principle," hence "no 'proof' of the principle will ever be had" (p. 64). She does not consider, though, that the theoretical model of stable equilibrium between two species that are ecological homologues assumes fixed parameters for each of the two species. Since the pattern of complete overlap is an unstable configuration in the face of parameter variation, it follows that two species that are ecological homologues can arrive at a stable configuration only when each species precisely tracks changes in the other's parameter values. The latter is not likely and so with changes in parameter values a possibility for one or the other of the two species it follows that the "competitive exclusion principle" is consistent with a model of competition between two species.