

Evolution of mammalian social structure

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Social groups may be viewed as collections of individuals exhibiting nonindependent behavior and organized in a cooperative manner. The evolutionary advantage of social behavior to individuals must be measured in its relativity to other potential behaviors, the scale of competitive interactions, and under a variety of environmental and genetic constraints. A primary tenet of social evolution is that coancestry will promote the genes of related individuals. High values of coancestry, however, do not necessarily translate into evolutionary advantage unless the primary competitive interactions occur among the groups. Coancestry is affected by the breeding tactics within and rates of genetic exchange among social groups. Low rates of exchange among groups, regardless of breeding tactics, may result in high values for intragroup coancestry but may lead to inbreeding depression in progeny. Likewise, breeding tactics such as polygyny, may not impart any long-lasting evolutionary advantage if genetic exchange rates are high. The evolution of social organizations typified by different breeding and migration strategies is evaluated to determine the conditions necessary for various tactics to result in genetic contributions by individuals equal to those of monogamous mating systems. The models show that breeding and dispersal tactics have probably evolved in concert and predict that social groups which are characterized by strong gene correlations are likely to exhibit relatively low group advantage for progeny survival and breeding. There is little impetus for high gene correlations to accrue in situations where group advantage is very high relative to monogamous systems.

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Introduction

The concepts of inclusive fitness and altruism (Hamilton 1963, 1964a, b) have lead evolutionary biologists to explore the genetic consequences of social organization. Recently, studies have centered on the ultimate costs or benefits of dispersal and breeding strategies as well as their effects on individual fitness (Bengtsson 1978, Greenwood 1980, Shields 1982, Waser and Jones 1983, Liberg and von Schantz 1986, Chesser and Ryman 1986, Clutton-Brock 1989). Breeding

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and dispersal tactics are primary factors governing the accumulation of gene correlations within, and hence, the partitioning of genetic variance among groups (Chesser 1991a, b). Tactics such as polygyny and sex-biased dispersal may alter genotypic distributions from those expected for panmixia and thereby set the stage for modifying behavioral interactions within and among groups.

Social behavior is defined by interactions among individuals and not by genetic relatedness (cf Wilson 1975). Gene correlations, however, may be viewed as precursors to the maintenance and evolution of social behaviors (Hamilton 1963, 1964a, b, Chesser and Ryman 1986). Evidence of this association is found in the numerous empirical attempts to assess genetic relationships within socially structured populations (Selander 1970, Schwartz and Armitage 1980, Chesser 1983, Foltz and Hoogland 1983, McCullough and Chesser 1987, Melnick 1987). Most studies have considered dispersal, or the lack thereof, as the primary factor influencing coancestry (Cockerham 1969, 1973) within groups (Bengtsson 1978, Moore and Ali 1984, Chesser and Ryman 1986, Keane 1990). Hence, with a paucity of dispersal, inbreeding was seen as the major contributor to gene correlations within groups and much attention centered on the optimal dispersal rate relative to the cost of inbreeding (Bengtsson 1978, Chesser and Ryman 1986).

Chesser (1991a, b) documented that considerable levels of gene correlations (coancestry; Cockerham 1969, 1973) could accrue from polygyny and female philopatry without invoking inbreeding. Coefficients of relationship within breeding groups (lineages in Chesser 1991a, b) between 33 and 40 percent could be maintained even with random male dispersal. These results are particularly relevant to studies of mammalian social evolution because approximately 65 percent of mammalian taxa exhibit some degree of female philopatry and polygyny (Greenwood 1980). The high incidence of these breeding and dispersal tactics indicates that such behaviors may provide selective advantages compared to random admixtures of breeding individuals. However, species vary in the degree of philopatry and polygyny exhibited and many taxa have adopted different breeding and dispersal tactics (Greenwood 1980).

If there are tactics by which species may achieve high genetic relationship within groups without substantial inbreeding costs, relative to other groups, then why have not all taxa evolved to optimize those characteristics? Obviously, there are additional constraints on the individuals and populations, other than genetic relationship, that govern the evolution of behaviors (Moore and Ali 1984). Natural selection acts on the phenotypic expression of the individual, not the breeding group or population. Some behaviors may not allow equitable genetic contributions of all individuals (such as polygyny). In this paper we develop models that determine the conditions necessary for the evolution of various breeding and dispersal behaviors that result in the same individual genetic contributions to progeny as those of monogamy and panmixia. These models do not preclude advantages bestowed on successful individuals, but rather that there is no selective advantage of panmictic mating because the expected genetic contribution by an

individual is the same. The methods employed for development of the models utilize similar parameters and variable definitions as those of Chesser (1991a, b).

Gene correlations and parameter definitions

We will investigate the influence of various breeding and dispersal tactics on the gene correlations defined as follows: F – average correlation of genes within individuals (inbreeding coefficient), θ_{mm} – the average coancestry among progeny of the same sex within breeding groups, θ_{mf} – the average coancestry among progeny of different sex within breeding groups, and θ – average correlation of genes between random progeny within breeding groups. The parameters necessary to derive the appropriate variables are:

- n – number of breeding females within breeding groups for a given generation,
- s – number of breeding groups (social groups or subpopulations) within the population,
- d_m and d_f – dispersal rates for males and females, respectively,
- ϕ – probability that random females within a breeding group mate with the same male.

Chesser (1991a) defined the parameter ϕ as

$$(1) \quad \phi = \frac{\sum_{i=1}^m b_i^2 - b_i}{n(n-1)}$$

where m is the number of breeding males per breeding group, and b_i is the number of females mated by the i th male. However, because

$$(2) \quad \sum_{i=1}^m b_i^2 = m(\sigma_b^2 + \bar{b}^2)$$

with σ_b^2 denoting the variance in numbers of females mated by males, the expression for ϕ becomes

$$(3) \quad \phi = \frac{m[\sigma_b^2 + b(b-1)]}{n(n-1)}$$

The expressions above involve several assumptions including steady-state population size, equal size of all breeding groups, and discrete, non-overlapping generations.

Dispersal and breeding tactics

Chesser (1991a, b) concluded that dispersal and breeding tactics probably coevolved. The impetus for particular breeding and dispersal tactics is to increase the coancestry among individuals within breeding groups relative to the coancestry among individuals from different breeding groups. Hence, altruistic behavior dis-

played among individuals within groups enhances the transmittal of genes of group members. Chesser (1991b) used asymptotic values for inbreeding (F), coancestry among progeny of the same sex (θ_{mm}), and coancestry among progeny of different sex (θ_{mf}), to determine the variables necessary for comparison of the resultant gene correlations within breeding groups. Asymptotic values of inbreeding and coancestry are necessary and sufficient because gene correlations among groups (α in Chesser 1991a, b) represent genetic variation that is lost and is therefore unavailable for natural selection as long the groups maintain their integrity. Thus, the variables are asymptotic relative to the amount of *remaining* genetic variation (Chesser 1991b) or to the most distantly related genes (Cockerham 1973). The asymptotic values were defined as

$$(4) \quad \hat{F} = \frac{[1 - (1 - y)(d_m + d_f - d_m d_f)] [\phi(n-1) + 2]}{8n - [8n - \phi(n-1) - 2][1 - (1 - y)(d_m + d_f - d_m d_f)]}$$

(where y denotes $1/s$) for the inbreeding coefficient, and

$$(5) \quad \hat{\theta}_{mm} = \frac{\phi}{4 + 2\phi + 2(1 - y)[d_m(1 - \phi) + d_f]}$$

$$(6) \quad \hat{\theta}_{mf} = \frac{n-1}{n} \hat{\theta}_{mm} + \frac{1}{4n}$$

for coancestry among progeny of the same and different sex, respectively (expression 5 assumes that $(n-1)/(ns-1) \approx 1/s$, see Chesser 1991b). The average coancestry among progeny within breeding groups is

$$(7) \quad \hat{\theta} = \frac{[\hat{\theta}_{mm} + \hat{\theta}_{mf}](1 - \hat{F})}{2} + \hat{F}$$

Finally, the coefficient of relationship (Wright 1922) is

$$(8) \quad r = \frac{\hat{2\theta}}{1 + \hat{F}}$$

which, in this instance, provides a measure of the proportion of genes shared between random members of a breeding group. The value of r attains an equilibrium value for a given breeding and dispersal regime as do the F -statistics (Chesser 1991b). Thus, the coefficient of relationship may be expressed as a differential rate function

$$(9) \quad r = \frac{2\theta}{1 + F} = \frac{2(\theta + \Delta\theta)}{1 + F + \Delta F} = \frac{2\Delta\theta}{\Delta F}$$

Table 1. Expressions for determining the expected asymptotic values of inbreeding (F), coancestry within groups (θ_{mm} – among same sex, θ_{mf} – among different sexes, $\bar{\theta}$ – mean value), and coefficient of relationship (r) within groups for random mating and polygynous mating. Expressions are given for two different breeding and dispersal tactics. Definitions for parameters are provided in the text.

Random mating	Polygyny
Female philopatry – male dispersal	
$F = \frac{1 - d_m(1 - y)}{4n - (4n - 1)[1 - d_m(1 - y)]}$	$F = \frac{y(n + 1)}{8n - y(7n - 1)}$
$\theta_{mm} = 0, \theta_{mf} = \frac{1}{4n}$	$\theta_{mm} = \frac{1}{6}, \theta_{mf} = \frac{2n + 1}{12n}$
$\bar{\theta} = \frac{2 - d_m(1 - y)}{2[d_m(4n - 4ny + y - 1) + 1]}$	$\bar{\theta} = \frac{4n + 2y + 1 - ny}{3(8n - 7ny + y)}$
$r = \frac{d_m(1 - y) - 2}{2d_m(1 - 2n - y + 2ny) - 2}$	$r = \frac{4n + 2y - ny}{3(4n - 3ny + y)}$
Male philopatry – female dispersal	
$F = \frac{1 - d_f(1 - y)}{4n - (4n - 1)[1 - d_f(1 - y)]}$	$F = \frac{y(n + 1)}{8n - y(7n - 1)}$
$\theta_{mm} = 0, \theta_{mf} = \frac{1}{4n}$	$\theta_{mm} = \frac{1}{6 + 2(1 - y)}$ $\theta_{mf} = \frac{2(n + 1) - y}{4n(4 - y)}$
$\bar{\theta} = \frac{2 - d_f(1 - y)}{2[d_f(4n - 4ny + y - 1) + 1]}$	$\bar{\theta} = \frac{(2 + y)(1 + 2n - ny)}{(4 - y)(8n - 7ny + y)}$
$r = \frac{d_f(1 - y) - 2}{2d_f(1 - 2n - y + 2ny) - 2}$	$r = \frac{(2 + y)(2n + 1 - ny)}{(4 - y)(4n - 3ny + y)}$

which will maintain a constant value until all genetic variation is lost ($\Delta \theta$ and ΔF become zero).

The resultant inbreeding, coancestries, and coefficients of relationship for different breeding and dispersal scenarios are presented in Table 1. Tactics of female philopatry and male dispersal are presented for both randomly mating ($d_f = \phi = 0$) and polygynous ($d_f = 0$; $d_m = \phi = 1$) mating systems. Secondly, male philopatry with female dispersal is depicted for random mating ($d_m = \phi = 0$) and polygyny ($d_m = 0$; $d_f = \phi = 1$). For each tactic, the rate of dispersal from the native area that would be necessary to result in the same genetic correlation within groups can be derived by setting the r for random mating equal to that for polygyny, and solving for the dispersal rate (Chesser 1991b). For male dispersal and female philopatry this solution is

$$(10) \quad d_m = \frac{2(8n-1)}{16n^2 + 8n - 2 - y - ny(4n-1)}$$

If the number of breeding groups is large, then $d_m \approx 1/n$ (cf Chesser 1991b). This relatively low dispersal rate will yield an asymptotic inbreeding coefficient of almost 20%, which will equal the coancestry resultant from philopatry. For female biased dispersal and male philopatry the dispersal rate that would produce equal ultimate coancestry within groups is

$$(11) \quad d_f = \frac{2(12n - 4ny + y - 2)}{16n(n+1) - ny(12 - 5y + 4ny) + 2y - 4 - y^2}$$

which, if the number of groups is large, becomes

$$(12) \quad d_f = \frac{6n-1}{4n(n+1)-1}$$

Thus, the dispersal rate necessary to produce identical relationship within breeding groups for random mating and philopatry is greater when females are the dispersers rather than when males disperse (Fig. 1).

Evolution would not likely favor modification of dispersal rate to increase the gene correlations within breeding groups. Asymptotic inbreeding coefficients of approximately 20% will probably result in decreased viability or fertility (Falconer 1981). Also, it is difficult to conceive how natural selection acting on individuals could maintain a dispersal rate of $1/n$. Similar levels of gene correlations within groups, however, can be achieved with female philopatry, polygyny, and random male dispersal (Chesser 1991a). These traits may be relatively invariant within a sex, and thus represent evolutionary tactics rather than population characteristics such as rates.

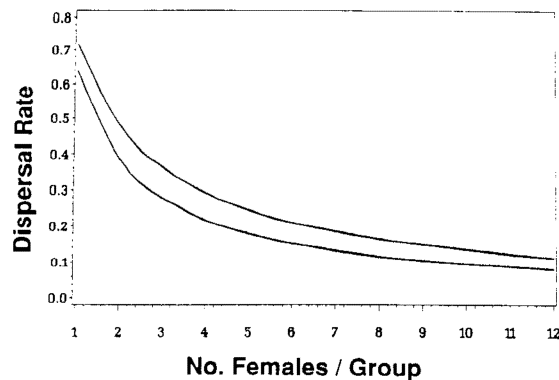


Fig. 1. The dispersal rate, as a function of the number of females per group, necessary to produce identical coefficients of relationship within breeding groups for random mating and philopatry for both males and females.

Individual fitness and the evolution of social groups

Tactics that result in high coancestry within breeding groups may not necessarily infer an advantage to individuals. Similarly, homogeneity of gene frequencies within a population will not provide any advantage for altruistic behavior. Therefore, the formation of groups, which provides a means to partition gene frequencies within the population, provides an impetus for cooperative behavior. If social groups are to be the foci for cooperation and altruism, then there must be some advantage for individuals to be affiliated with the groups. In the following procedures we will develop the conditions necessary for the equivalence of fitnesses for individuals in either monogamous or polygamous mating systems in which groups may or may not be present.

One major difference between monogamous and polygynous mating systems is that the probability of mating for polygynous males may be considerably lower than that for monogamy. For example, if there is but one breeding male for each group of n females, the probability that a male will breed is $1/n$; with monogamy, however, the probability of a male mating may be near unity. With monogamy, the coancestry of a breeder to his progeny is $1/4$ and is $1/8$ to his sibling's progeny. Thus, in a monogamous mating system, the expected coancestry of an adult to progeny is

$$(13) \quad \theta_M = \frac{\omega}{4} + \frac{\omega}{8} = \frac{3\omega}{8}$$

where ω is the probability of survival of the progeny. In a monogamous mating system there is no expected coancestry to other individuals outside of the direct family. In polygynous mating systems, however, the genes of progeny produced by different females within groups are expected to be correlated (by θ). The value of θ is dependent upon the value of ϕ (mean and variance of male mating success) and the number of females per breeding group as is shown in equation (5). Using p to reference the probability of a male mating and g as a scalar by which group membership increases or decreases the probability of progeny survival (probability of survival of progeny is $g\omega$), the expected coancestry of an adult male to progeny born within a polygynous mating group is

$$(14) \quad \theta_p = \frac{gp\omega}{4} + \frac{gp\omega}{2} \theta + \frac{g\omega}{2} \theta = \frac{g\omega [p(1 + 2\theta) + 2\theta]}{4}$$

By setting $\theta_M = \theta_p$ we can determine the conditions at which the expected gene contributions of a breeding male are equivalent regardless of the male breeding tactic. These boundary conditions are

$$(15) \quad \theta = \frac{3 - 2pg}{4g(1 + p)}$$

$$\text{or (16)} \quad g = \frac{3}{2[p(1 + 2\theta) + 2\theta]}$$

For adult females the coancestry to the progeny is

$$(17) \quad \theta_M = \frac{g\omega}{4} + \frac{gp\omega}{2} \theta + \frac{g\omega}{2} \theta = \frac{g\omega [1 + 2\theta (1 + p)]}{4}$$

which yield the same boundary conditions for coancestry (equation 14). However, the solution for group advantage is slightly different, giving

$$(18) \quad g_{females} = \frac{3}{2 + 4\theta (1 + p)}$$

Equation 14 gives the coancestry within polygynous breeding groups that would be necessary for adults to have the same gene contributions as they would have if there was a monogamous mating system. A portion of the gene contributions may be provided by their relatives because not all of the males breed. Figure 2

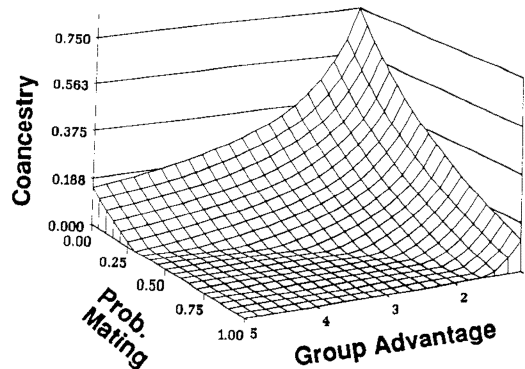


Fig. 2. Three-dimensional surface diagram depicting the boundary conditions for coancestry within groups as a function of group advantage (g) and probability of mating (p) which yield the genetic equivalence of monogamy and polygynous mating systems for individual adults.

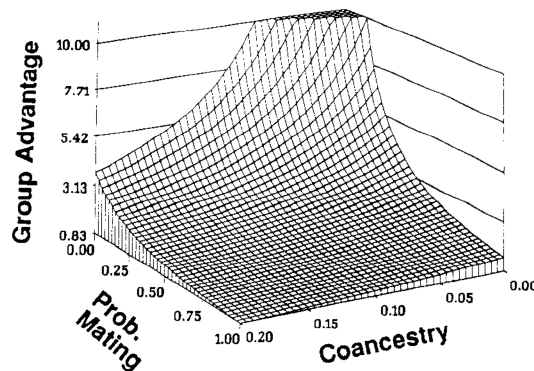


Fig. 3. Three-dimensional surface diagram depicting the boundary conditions for group advantage (g) as a function of coancestry within groups (θ) and probability of mating (p) which yield the genetic equivalence of monogamy and polygynous mating systems for individual adult males.

depicts the surface of this genetic equivalence wherein the effects of monogamy and polygyny are equal for individuals. Equations 15 and 17 give the group advantage scalar as a function of the coancestry within groups and the probability of male mating (Fig. 3). Clearly, as the group advantage becomes large ($g \gg 1$) small values of coancestry within breeding groups are necessary to convey equivalence to a monogamous breeding system.

The variables for coancestry (θ) and probability of mating (p) are not necessarily independent. Without inbreeding, the highest possible coancestry within groups ranges from 0.167 (very large groups) to approximately 0.194 (small groups; Chesser 1991a) in completely polygynous systems exhibiting female philopatry. However, in such systems the probability of a particular male mating is $1/n$. Thus, $\theta \approx 0.175$ and $p \approx 0.20$ appear to be reasonable values for many polygynous mammals, values which require relatively low values for group advantage ($g \approx 2.4$) to insure the same genetic contributions for adult males as monogamy. Without female philopatry, polygynous mating systems can produce coancestry values between 0.125 and 0.167 depending on the size of the groups. Using $p = 0.2$ as above, the required value of group advantage would range between 2.5 and 3. However, because of the female dispersal the groups would necessarily be re-formed each generation.

Discussion

The above models were designed to explore boundary conditions for particular behaviors. As such, they provide the functional equivalence for different breeding and dispersal tactics in producing intragroup gene correlations and contributions of adult individuals to the subsequent generation whether they actually breed or not. The models define the conditions for which the tactics are equivalent in producing a result; thus, they represent the lower bounds of the evolutionary process. The values necessary to result in equality are therefore minimum values.

Dispersal tactics for mammalian populations have received considerable attention in ecology, evolution, sociobiology, and conservation biology. Although dispersal strategies vary among sex and age categories (Lidicker 1975, Lidicker and Caldwell 1982, Stenseth 1983), it is more common among male than female mammals (Greenwood 1980, Clutton-Brock 1989). Hypotheses for causation of age- and sex-biased dispersal fall into two general models: (1) philopatry by both sexes is preferred and subordinates are forced to leave their natal area or social group because of resource competition (Dobson 1982, Moore and Ali 1984, Dobson and Jones 1985, Waser 1985, Anderson 1989); (2) juveniles disperse voluntarily to search for mates and avoid inbreeding with close relatives (Packer 1979, Greenwood 1980, Chesser and Ryman 1986, Harvey and Ralls 1986, Clutton-Brock 1989). Because the cost of inbreeding in mammals may be higher for females than males, females may evolve mechanisms to avoid mating with male relatives (Chesser and Ryman 1986). Male-biased dispersal and female philopatry are tactics which effectively avoid close inbreeding (Cockburn *et al.* 1985, Chesser

1991a). However, if polygyny persists, only a relatively small fraction of males may mate regardless of the cost of dispersal. For mammals such as the black-tailed prairie dog (Hoogland 1982) breeding groups comprise a single breeding male and 5 – 8 breeding females. In such cases, the probability at birth of a male mating is approximately $1/n$. Other species exhibit polygamy wherein a male may breed with several females, yet over the lifetime of the males the probability of mating may be relatively high; thus, the variance in reproductive success of males is low; these breeding tactics will result in relatively low coancestry values and probably little group integrity.

Previous inequality models emphasized the constraining costs of dispersal and inbreeding on the inclusive fitness of individuals (Bengtsson 1978, Chesser and Ryman 1986). While these papers elucidate the limits to inbreeding and dispersal strategies, they require that individuals have some means to accurately assess the risks of inbreeding and dispersal as well as the relatedness of group members (Chesser and Ryman 1986). The efficacy of such assessment as an evolutionary tactic is complicated by the fact that the relatedness within groups may be constantly changing. Concomitant evolution of particular breeding and dispersal tactics may make assessment of vicissitudinal conditions unnecessary because the results are based on expectations of parameters that remain relatively constant. Therefore, these behaviors become fixed tactics rather than varying strategies.

Breeding behaviors may have evolved to take advantage of particular dispersal tactics (or vice versa). Polygyny will contribute little to group integrity for adults unless it is accompanied by male-biased dispersal. Likewise, female philopatry and male dispersal result in minimal values of group coancestry when monogamy prevails. In all of the models presented it is assumed that all females breed. Females may be readily accepted as mates whereas the competition among males may be substantial (Clutton-Brock 1989).

Membership in social groups may bestow an advantage via predator avoidance, rearing of progeny, and cooperative attainment of resources (e.g. prey). Interestingly, our models predict that social groups which are characterized by relatively strong gene correlations are likely to exhibit low to moderate group advantage (Figs 2 and 3). If the scalar for group advantage is below 2, then only inbreeding or groups comprised of full siblings may ensure an individual the same genetic contribution to the next generation as that of monogamy. There is little impetus for high gene correlations to accrue in situations where the group advantage is very high ($g \gg 5$) relative to monogamous systems. Such may be the case in large herding mammals and predators which rely on cooperative hunting to capture large, mobile prey, especially where the prey may be scarce or difficult to kill (e.g. wolf packs in some environments).

Group advantage is not solely dependent on environmental factors, but may also be a function of the gene correlations themselves. Competition among relatives is $1 - r$ (Hamilton 1964a, b, Chesser and Ryman 1986); thus, g , the scalar for group advantage, may become $g = g' + r$, where g' is the scalar independent of

genetic effects, solely by coancestry within breeding groups. In the instance where male polygyny and female philopatry persist, $g \approx 2.4$, and $r \approx 0.35$, leaving about 2 to 2.1 for the group advantage independent of gene correlations (g'). Clearly, even for the most robust social organizations the advantages for group membership must exceed those due to inclusive fitness.

The asymptotic nature of relationship and coancestry within socially structured populations (Chesser 1991a, b) clearly indicates that genetic variance within groups accrues at the expense of genetic variance among groups. The partitioning of genetic variance likewise infers that the decrease in competition within groups may be accompanied by a concomitant increase in competition among groups. Competition is produced by a limited supply or availability of resources and a primary objective of social groups may be to partition and protect limiting resources, ultimately to increase supply within at the expense of the among groups. Partitioning of any resource (genetic, sustenance, nesting sites, etc.) infers variance of the resource either over space or time. The logical sequence leads us to the conclusion that maintenance of robust social organizations whose primary purpose is the attainment of resources are dependent more upon the variance of resource distributions than upon the mean value of the resources. It follows from our models that if the resource variance is high relative to the mean, then group advantage may also be high, and groups may be characterized by relatively low genetic relationship. Intermediate values of resource variance may facilitate high gene correlations within groups and no variation may invoke little or no group advantage or coancestry within.

Obviously, there are numerous causes for the persistence of social groups. We have focused on but a few and our account of the possible factors is in no way complete. The solutions to the models herein do, however, present valuable insight into boundary conditions that would lead to a variety of social systems and prediction for the genetic characterization of social groups. The evolutionary consequences of social organization must follow from the fitnesses of individuals. We have shown that there exists a functional equivalence of individual contributions in socially organized systems wherein breeding success is highly variable relative to that of homogeneous monogamous systems. Furthermore, this functional equivalence may be attained by relatively invariant breeding and dispersal tactics.

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