Population Ecology, Nonlinear Dynamics, and Social Evolution. I. Associations among Nonrelatives

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ABSTRACT: Using an individual-based and genetically explicit simulation model, we explore the evolution of sociality within a population-ecology and nonlinear-dynamics framework. Assuming that individual fitness is a unimodal function of group size and that cooperation may carry a relative fitness cost, we consider the evolution of one-generation breeding associations among nonrelatives. We explore how parameters such as the intrinsic rate of growth and group and global carrying capacities may influence social evolution and how social evolution may, in turn, influence and be influenced by emerging group-level and population-wide dynamics. We find that group living and cooperation evolve under a wide range of parameter values, even when cooperation is costly and the interactions can be defined as altruistic. Greater levels of cooperation, however, did evolve when cooperation carried a low or no relative fitness cost. Larger group carrying capacities allowed the evolution of larger groups but also resulted in lower cooperative tendencies. When the intrinsic rate of growth was not too small and control of the global population size was density dependent, the evolution of large cooperative tendencies resulted in dynamically unstable groups and populations. These results are consistent with the existence and typical group sizes of organisms ranging from the pleometrotic ants to the colonial birds and the global population outbreaks and crashes characteristic of organisms such as the migratory locusts and the tree-killing bark beetles.

Keywords: sociality, population dynamics, gregarious behavior, mutualism, altruism, complexity.

Hamilton's (1964) rule provides a simple and powerful paradigm within which the role of relatedness in social evolution can be explored. In contrast, it has proven much more difficult to establish simple rules to subsume the diversity of ecological and demographic factors responsible for social living (Alexander 1974; Wilson 1975; Rubenstein and Wrangham 1986; Slobodchikoff 1988; Choe and Crespi 1997; Queller and Strassmann 1998; Giraldeau and Caraco 2000). However, if social groups are viewed as populations (Brian 1965; Cohen 1969; Wilson 1975; Avilés 1999), the principles of population ecology can be applied to understand their growth and dynamics. In particular, the fitness consequences of complex ecological phenomena, such as predation, competition, or resource acquisition, can be subsumed within a single currency: the per capita rate of growth. The functional relationship between group size and the per capita rate of growth can then be used to make predictions about the origin, growth, and dynamics of social groups. This approach allowed Avilés (1999) to derive relatively simple conditions (a function of ecological and demographic parameters such as the intrinsic rate of growth and the group carrying capacity) under which group living and cooperation become necessary for persistence or under which dynamically unstable groups may emerge. Here, we extend this approach using an individual-based and genetically explicit simulation model to explore the evolution of groups, grouping, and cooperation within a population-ecology and nonlinear-dynamics framework.

In our approach, we assume that the per capita rate of growth (or average individual fitness) of group-living organisms is a unimodal function of group size, a result of enhanced group productivity due to cooperation and unavoidable competition for resources in groups of increasing size. A unimodal fitness function has both broad empirical support (e.g., Bartz and Holldobler 1982; Raffa and Berryman 1987; Cash et al. 1993; Wiklund and Andersson 1994; Avilés and Tufiño 1998) and is the standard assumption in models of sociality (Vehrencamp 1983; Emlen 1984; Pulliam and Caraco 1984; Slobodchikoff 1984; Clark and Mangel 1986; Packer and Ruttan 1988; Avilés 1999; Courchamp et al. 1999*b*; Giraldeau and Caraco 2000).

Avilés (1999) introduced the following relationship to model the average fitness of members of a social group:

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$$f(n) = e^{r}e^{-cn}n^{\gamma}, \quad (1)$$

where n is the number of group members, e is the base of the natural logarithms, r is an intrinsic rate of growth parameter, c is a local negative density-dependent parameter inversely proportional to a group carrying capacity, and γ (taken to range between 0 and 1) represents the synergistic effects of cooperation on individual fitness. "Cooperation" includes any behaviors (joint resource acquisition, information exchange, communal brood care, predator defense, etc.) that, despite any individual costs, have a net beneficial effect on group members (see also Mesterton-Gibbons and Dugatkin 1992). Fitness is a unimodal function of group size when $\gamma > 0$. With this model, Avilés (1999) showed that group living and cooperation either can allow the colonization of harsh or marginal environments in which solitary individuals may not be able to replace themselves (i.e., where $r < 0$) or, under more plentiful conditions, can result in groups that oscillate in size. This model also predicted that a minimum number of cooperators may be necessary for persistence under some environmental conditions (i.e., where $r < c$) and that larger group sizes would arise as γ and r increase and c decreases (Avilés 1999). Courchamp et al. (1999*b*) analyzed a population-growth model with a threshold and reached similar conclusions regarding the existence of a minimum viable group size. The existence of a threshold population density or size below which persistence is not possible was first noted by Allee (1938) and is known in ecological literature as the "Allee effect" (for reviews of Allee effects, see Courchamp et al. 1999*a*; Stephens and Sutherland 1999).

Here, we use equation (1) in a simulation model to explore how parameters such as the intrinsic rate of growth and group carrying capacity may influence social evolution and how social evolution may, in turn, influence and be influenced by the emerging group-level and population-wide dynamics. In addition to explicitly exploring the dynamic consequences of a nonlinear fitness function in a sociality model, ours is, to our knowledge, the first model to consider the simultaneous evolution of grouping and cooperative tendencies, with group size emerging from the interaction of these two traits with each other and with fixed ecological and demographic parameters. In this article, we explore the evolution of a simple social system—one-generation breeding associations among nonrelatives—while allowing for cooperative interactions to range from mutualistic to altruistic. Elsewhere, we will consider the evolution of kin-based social systems and explore the interaction of relatedness and demography in social evolution.

The Model

We simulate a simple social system in which individuals associate with each other as a function of their genetically coded grouping tendencies but with no regard to kinship or to their genetically coded cooperative tendencies. Associations endure for one reproductive period following which the offspring produced within the groups join a global population pool from which they disperse to initiate a new cycle of group formation. Groups form by accretion, with the acceptance of new group members being a decreasing function of group size (eq. [A1]; appendix). Once within groups, individuals help one another but also compete for resources. This is modeled by equation (1), where γ now corresponds to the average cooperative tendencies of a group's members (eqq. [A3] and [A4]; appendix). Cooperative and grouping tendencies, coded as separate polygenic traits subject to mutation and recombination (see appendix for details), evolve in the simulations along with the average group size and group and global population dynamics.

We control whether and to what extent cooperation carries a relative fitness cost by introducing an additional factor to calculate the reproductive output of particular individuals as a function of their cooperative tendencies. This factor is controlled by the parameter β, which is the slope of the relationship between individual cooperative tendencies and relative fitness within a group (eq. [A5]; appendix). When $\beta = 0$, cooperators do not suffer a relative fitness cost, and the interactions are said to be mutualistic. As β increases in magnitude (i.e., the slope becomes steeper), individuals that help more suffer a relative fitness cost within their group, and the interactions are said to be altruistic (this definition is in agreement with that of Uyenoyama and Feldman [1980] and, because it refers to relative fitness within a group, corresponds to Wilson's [1990] "weak altruism").

We consider two models of global population control. In the global density-dependence (GDD) model, the size of the global population was controlled by a negative density-dependent function of the total number of individuals in the global population (eq. [A4]; appendix). In the limited nesting-sites (LNS) model, there was a cap on the total number of groups, but the number of individuals was only controlled by local density-dependent effects (eq. [A3]; appendix).

Response Variables, Experimental Design, and Analysis

We initiated the simulations with a population of solitary individuals that, except for new mutations, lacked grouping and cooperative tendencies. We were interested in the evolution of groups, grouping, and cooperation given dif-

ferent combinations of the group carrying capacity, intrinsic rate of growth, and the relative fitness costs of cooperation parameters. For each of the models of global population control, we explored these parameters in a fully factorial design, with three, four, and five levels, respectively (table 1). Using different random number sequences, we ran four replicate simulations for each combination of parameter values, each run for a sufficient number of generations to ensure that equilibrium had been reached. We considered that equilibrium had been reached when a response variable no longer showed an increasing or decreasing trend and had remained at that level for at least 500 generations. Runs of 2,500–3,500 generations were sufficient for this purpose. We calculated global equilibrium values by averaging the response variable values over the last 500 generations for each replicate and then taking the average of the four replicates. The model was developed in the CodeWarrior Pro 4 environment, with the algorithms for random number generation coded in C (Press et al. 1992) and the remainder of the program in Pascal.

We used the ANOVA to test for the effect of the various parameters, their second- and third-order polynomials, and their interactions. We customized the tests for each response variable by dropping all nonsignificant ($P > .05$) polynomial terms and their interactions. The fit of the reduced models was excellent, with r^2 values on the order of 98% (table 2). Cooperative and grouping tendencies were arcsine transformed and group size log transformed before analyses. To calculate the percentage variance explained by each of the parameters, we reran the reduced analyses to obtain the Type I sums of squares (which add up to the model sums of squares). For the Type I sums of squares, the terms were introduced in the following order: main effects (starting with those with the largest sums of squares in the main ANOVA), polynomial terms, two-way interactions, interactions with polynomial terms, and three-way interactions.

Table 1: Factors and levels used in a fully factorial design for both the global density-dependence (GDD) and limited nesting-sites (LNS) models

Factor	Levels
r	.5, 1.0, 1.5, 2.0
c	.1, .06, .02
β	.0, .2, .4, .6, .8

Note: r = intrinsic rate of growth; c = inverse of group carrying capacity; β = relative fitness costs of cooperation. In the GDD model, $w = 0.0005$ was the value used for the global negative density-dependence parameter (eq. [A4]; appendix). The maximum number of groups in the LNS model was set to 200.

Table 2: Percentage variance explained by each of the parameters of the model

	Cooperation		Grouping		Group size	
Parameter	GDD	LNS	GDD	LNS	GDD	LNS
r	.2	.0	36.5	1.4	.3	.1
c	4.7	4.3	27.4	27.1	31.7	30.7
β	88.6	89.8	31.5	66.4	61.7	64.8
Interactions	4.2	4.3	2.6	3.1	4.0	2.8
Total (r^2)	97.7	98.3	97.9	98.0	97.6	98.4

Note: Calculated by dividing the Type I sums of squares corresponding to the respective parameter and its polynomial terms by the total sums of squares of the ANOVA (see text for details).

Results

Groups, grouping, and cooperation evolved in the simulations under all combinations of parameter values investigated, albeit to lower levels when cooperators suffered a relative fitness cost within their groups and, thus, behaved altruistically (fig. 1). The relative fitness costs of cooperation, group carrying capacity, and intrinsic rate of growth parameters all had a significant effect on one or more of our sociality measures (table 2). Cooperation was primarily affected by the relative fitness costs of cooperation, group size by a combination of the group carrying capacity and relative fitness costs of cooperation, and grouping by a combination of the group carrying capacity and relative fitness costs of cooperation in the LNS model and by all three parameters in the GDD model. Interestingly, the two models of global population control resulted in relatively similar patterns of the equilibrium levels of our three sociality measures, even though they resulted in dramatically different dynamics of the local groups and the global population (fig. 2).

The Relative Fitness Costs of Cooperation

In both the GDD and LNS models, consistently lower levels of the three sociality measures evolved as the relative fitness costs of cooperation increased (fig. 1*A*–1*L*). However, even with the steepest relative fitness costs of cooperation investigated, groups formed and some level of cooperation evolved. This result is of particular interest given that the groups consisted of nonrelatives, and, thus, no inclusive fitness benefits accrued to cooperators. The relative fitness costs of cooperation parameter had a significant effect on all three sociality measures ($P < .0001$ in each case), explaining a significant portion of the variance in group size, grouping tendencies, and, in particular, cooperative tendencies (table 2).

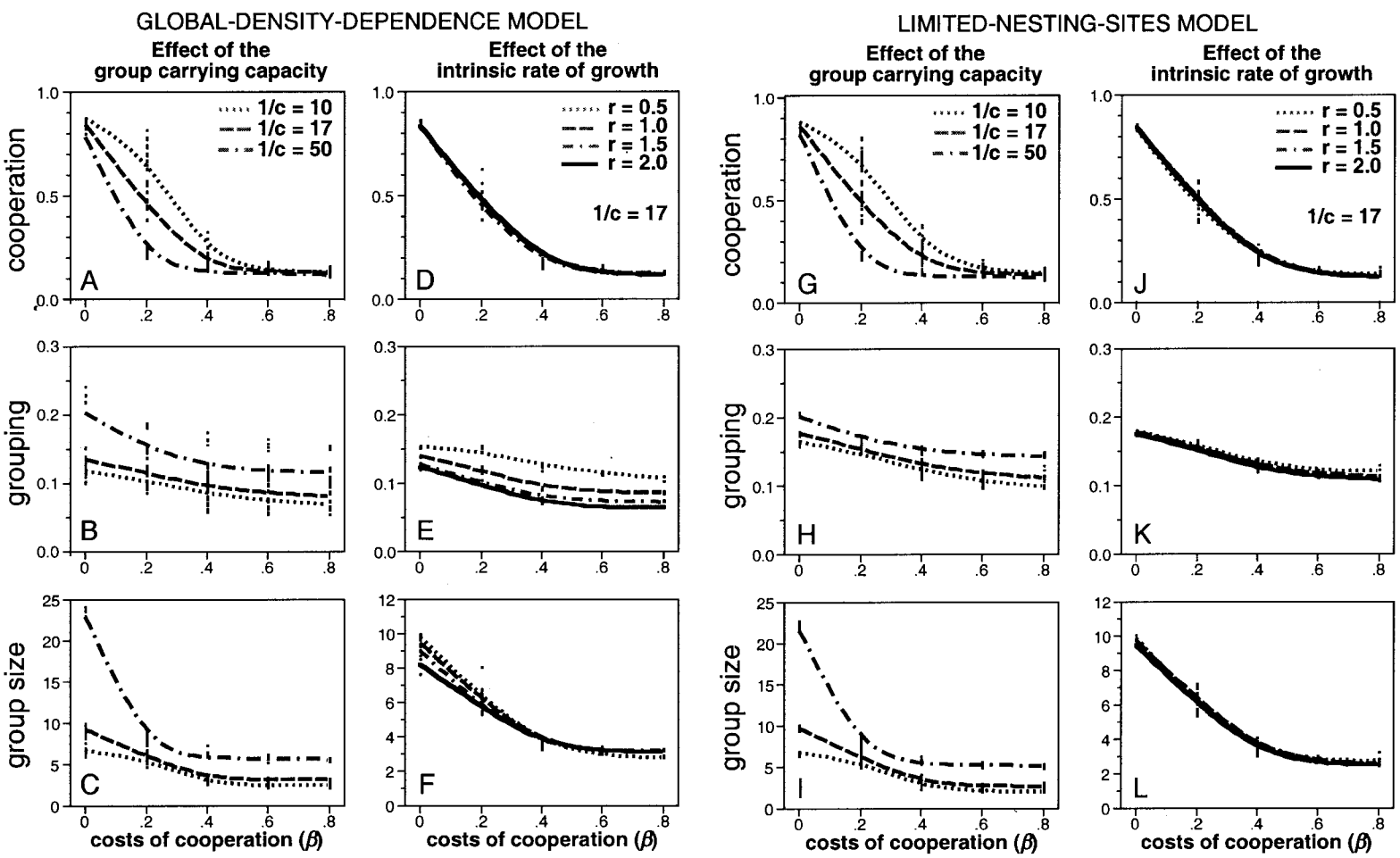

Figure 1: Equilibrium levels of cooperation, grouping tendencies, and group size as a function of the relative fitness costs of cooperation for the two models of global population control. *A–C*, *G–I*, Effect of the group carrying capacity. *D–F*, *J–L*, Effect of the intrinsic rate of growth. Graphs for the group carrying capacity include all data; graphs for the intrinsic rate of growth are for $1/c = 17$ only. The lines shown are cubic spline fits ($\lambda = 0.01$) of four replicates for each combination of parameter values. In the global density-dependence (GDD) model, all linear effects are significant at $P < .0001$, except for r on cooperation (NS) and r on groups size ($P = .007$). In the limited nesting-sites (LNS) model, all linear effects are significant at $P < .0001$, except for r on cooperation (NS). For all three variables in both the GDD and LNS models, β^2 was highly significant ($P < .0001$). For all three variables in the LNS model and only for cooperation in the GDD model, β^3 was significant ($P < .001$). In both the GDD and LNS models, c^2 was highly significant for grouping and groups size but not for cooperation; r^2 was significant only for grouping. The percentage variance explained by each of the parameters is shown in table 2.

The Group Carrying Capacity

The group carrying capacity parameter also had a significant effect on all three sociality measures ($P < .0001$ in each case). As might have been expected, with greater group carrying capacities, larger groups evolved (fig. 1*C*, 1*I*). Interestingly, however, grouping and cooperative tendencies evolved in opposite directions; as the group carrying capacity increased, greater grouping but lower cooperative tendencies evolved (fig. 1). The group carrying capacity explained about one-third of the variance in group size and grouping tendencies in both the GDD and LNS models (table 2).

The Intrinsic Rate of Growth

The intrinsic rate of growth had no or only a minor effect on equilibrium levels of most response variables (table 2; fig. 1). Notable exceptions were the grouping tendencies in the GDD model and group size at low relative fitness costs of cooperation, also in the GDD model (fig. 1*D* and 1*F*). When an effect was present, lower cooperative and grouping tendencies and smaller groups evolved for larger intrinsic rates of growth. As we describe below, some of these effects appear to have resulted from the intrinsic dynamic instability that arose as cooperation increased the per capita rate of growth beyond a base level set by the intrinsic rate of growth that was not too small.

The Mode of Global Population Control

Under some combinations of the parameter values, global population dynamics of a periodic or chaotic nature evolved in the GDD simulations as cooperative tendencies increased through time (fig. 2). Global dynamic instability, which was reflected in oscillations of the average group size, the number of groups, and the size of the global population, arose through period-doubling bifurcations when the intrinsic rate of growth was not too small and the relative fitness costs of cooperation were small or nonexistent. Under these circumstances, increasing levels of cooperation raised the average per capita rate of growth beyond the critical value (a function of r, c, γ, and w) at which a transition from simple to complex dynamics is expected (Avilés 1999). It should be noted that, in the absence of cooperation, all levels of r considered (i.e., $r \leq 2.0$) would lead to point equilibria (May and Oster 1976; Avilés 1999). Bifurcations leading to global population oscillations, however, did not occur in the LNS model (fig. 2) because density-dependent effects were restricted to the local groups.

The extreme dynamic instability that arose as cooperative tendencies increased in frequency in the GDD model led to global extinction in eight out of the eight simulations with the largest group carrying capacity ($1/c = 50$), the two largest intrinsic rates of growth ($r = 1.5$, $r = 2.0$), and no relative fitness cost of cooperation (fig. 1*D*–1*F*). Because in the LNS model the dynamics of the groups were independent of one another, global extinction did not occur with this model. Global extinction in the GDD model did not occur when the presence of relative fitness costs of cooperation prevented the evolution of high cooperative tendencies.

Discussion

Table 3 lists a number of social systems, ranging from colonial breeding birds to social bacteria, that bear resemblance to our model. These are all systems in which individuals that may not be related to one another come together in breeding associations. The benefits derived from such associations include increased feeding success, access to resources that are unavailable to solitary individuals, increased predator protection, ability to outcompete conspecifics, or ability to escape harsh environmental conditions. Information exchange and group foraging, for instance, are thought to allow the exploitation of patchy and ephemeral resources in colonial breeding birds (e.g., Berg et al. 1992; Wiklund and Andersson 1994; Brown and Brown 1996; reviewed in Brown et al. 1990; Rolland et al. 1998). Mass attacks allow the tree-killing bark beetles to overcome the defenses of live trees and to gain access to a resource that is not available to solitary beetles (Raffa and Berryman 1987). Communal nesting in fish (Tyler 1995) and bees (Kukuk and Sage 1994; Kukuk et al. 1998) apparently reduces loss of offspring due to predation. Cooperation among queens in pleometrotic ant species (e.g., Bartz and Holldobler 1982; Rissing and Pollock 1987; Rissing et al. 1989; Tschinkel 1992; reviewed in Bernasconi and Strassmann 1999) or among males in lion coalitions (Packer et al. 1991) allows the successful takeover of other conspecific associations. Aggregation and the formation of stalks for spore dispersal make it possible for cellular slime molds and social bacteria to escape deteriorating local conditions (Bonner 1982; Velicer et al. 2000). These benefits are expected to be large enough to compensate for inevitable costs of group living, such as competition for local resources or increased parasite loads (Alexander 1974).

The results of our model allow us to place this diversity of social forms within a common framework in which complex ecological phenomena are subsumed within a single currency: the per capita rate of growth. We have shown that in the presence of synergistic effects of cooperation (i.e., a unimodal relationship between group size and average individual fitness), groups form and sociality develops even when the groups consist of nonrelatives and

Please, note that the lines for cooperation in figures A and D are too faint to be visible. See complete figure at the end of this pdf file.

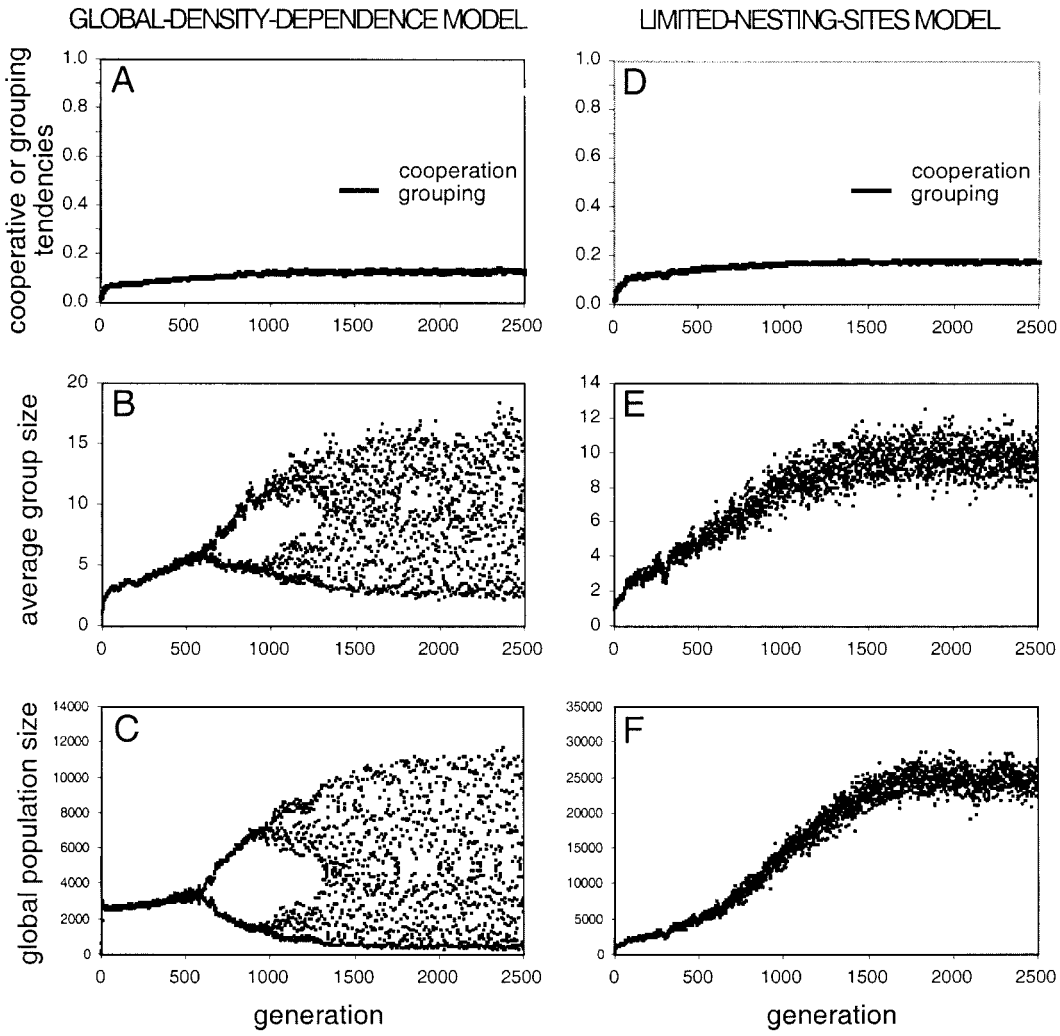

Figure 2: Time series of the evolution of cooperation, grouping tendencies, average group size, and global population size in the global density-dependence (GDD) and limited nesting-sites (LNS) models for mutualistic ($\beta = 0.0$) interactions. *A–C*, Run for $r = 1.5$, $c = 0.06$, and $w = 0.0005$ (eq. [A4]). *D–F*, Run for $r = 1.5$, $c = 0.06$ (eq. [A3]), and a maximum of 200 groups.

cooperation carries relatively steep fitness costs. Simple ecological and demographic parameters, such as the intrinsic rate of growth, group carrying capacity, and relative fitness costs of cooperation, then set the stage for the evolution of groups of a wide range of sizes, varied dynamics, and different strengths of social interactions (figs. 1, 2). These are properties that naturally emerge out of our model since grouping and cooperation are treated as separate traits capable of influencing each other's evolution, in contrast with earlier models in which these traits have been considered in isolation (see Axelrod and Hamilton 1981; Boyd and Richerson 1988; Crowley et al. 1996; Wilson and Dugatkin 1997 for models in which cooperation arises in groups of a fixed size; Clark and Mangel 1986 and Giraldeau and Caraco 2000 for models in which groups form given a fixed fitness function).

Associations among Nonrelatives and the Relative Fitness Costs of Cooperation

The finding that cooperation among nonrelatives emerges even in the presence of relatively steep fitness costs of cooperation, although surprising from a theoretical perspective, is consistent with the existence of organisms such as the pleometrotic ants, social bacteria, or cellular slime molds in which only a subset of individuals achieves reproductive status within groups that have formed by aggregation (table 3). In our model, cooperation may evolve

Table 3: Examples of social systems that resemble our model

Organism	Group size (range, mean)	Reproductive skew[a]	Wide-amplitude population size fluctuations	References
Colonial-breeding birds:				
Cliff swallows	1–3, 700, 393 (nests)	No	No	Brown and Brown 1996
Fieldfares	1–32	No	No	Wiklund and Andersson 1994
Lapwings	2–28	No	No	Berg et al. 1992
Colonial-nesting fish:				
Coral-reef fish	1–15+	No?	No	Tyler 1995
Male coalitions:				
Lions	2–9	Increases with coalition size	No	Packer et al. 1991
Galápagos hawks	2–8	No	No	Faaborg et al. 1995
Long-tailed manakins	2–13, α and β display	Yes ($\alpha > \beta >$ others)	No	McDonald and Potts 1994
Communal-nesting bees:				
Lasioglossum hemichalceum	2–20	No	No	Kukuk and Sage 1994; Kukuk et al. 1998
Pleometrotic ants				Bernasconi and Strassmann 1999
Messor pergandei	1–6, 1.6; 1–28, 1.0–7.4	Yes	?	Pfennig 1995; Rissing and Pollock 1987
Acromyrmex versicolor	1–16, 2.5	Yes	?	Rissing et al. 1989
Solenopsis invicta	1–17, 1.1–3.4	Yes	?	Tschinkel 1992
Myrmecocystus mimicus	1–9, 2–4 most common	Yes	?	Bartz and Holldobler 1982
Tree-killing bark beetles:				
Mountain pine beetle	40–130/m^2	Increases with group size	Yes	Berryman 1973; Raffa and Berryman 1987
Fir engraver	20–160/m^2	No	Not as wide	Berryman 1973; Raffa and Berryman 1987
Migratory locusts:				
Schistocerca gregaria	Millions (10^4–10^{10})	No?	Yes	Uvarov 1977; Roffey et al. 1968
Locusta migratoria	Millions	No	Yes	Uvarov 1977
Cellular slime molds:				
Dictyostelium	10^2–10^5	Yes	?	Bonner 1982
Social bacteria:				
Myxobacteria	$>10^7$	Yes	?	Velicer et al. 2000

[a] Excludes reductions in reproductive output due to crowding.

even when costly because grouping and group size coevolve with it. Thus, for a given group carrying capacity increasing relative fitness costs of cooperation are associated with smaller group sizes (fig. 1). With smaller groups, the lower within-group and greater among-group genetic variances that emerged in the simulations (data not shown) may have been responsible for a balance of selection at these two levels still favorable to the group level (Price 1972; Hamilton 1975; Wade 1985; Wilson and Dugatkin 1997; Pepper and Smuts 2000; see also Goodnight et al. 1992).

In general, our results suggest that a combination of steep relative fitness costs of cooperation and large aggregate groups is unlikely. Consistent with this prediction, organisms with very large aggregations, such as the tree-killing bark beetles or the cliff swallows (table 3), lack reproductive specialization within their groups while organisms with reproductive specialization, such as the pleometrotic ants, form relatively small aggregations (table 3). Apparent exceptions to this trend are the cellular slime molds and the social bacteria that may form associations of dozens, hundreds, or thousands of cells but still exhibit extreme reproductive altruism (Bonner 1982; Rosenberg 1984; Gadagkar and Bonner 1994; Velicer et al. 2000). In these cases, however, the relevant unit is not the number of cells but the number and proportional representation of clones forming part of the assemblages. With a viscous population structure, just a few clones may dominate the

assemblages. Alternatively, reproductive altruism in these organisms (or in the pleometrotic ants) could involve dissociation between genes and behavior, so that a lottery system decides who becomes a spore (or the sole reproductive) and who does not (Gadagkar and Bonner 1994). "Cheater" genotypes, however, have been identified in both cellular slime molds and social bacteria (Ennis et al. 2000; Velicer et al. 2000).

Associations among Nonrelatives and the Group Carrying Capacity

We have shown that when a greater amount of resources (i.e., larger group carrying capacities, $1/c$) allows the formation of larger groups, greater grouping tendencies and larger groups evolve, but group members tend to be less cooperative (fig. 1). The latter result is in agreement with findings of N-player prisoner dilemma games (e.g., Boyd and Richerson 1988) or game-theoretic models of cooperative hunting (Packer and Ruttan 1988) that have shown that larger groups are less stable and more susceptible to cheating. In our simulations, the decrease in cooperative tendencies with increasing group size was associated with a concomitant increase in the within-group and a decrease in the among-group genetic variances (data not shown) and thus probably reflects a change in the balance of selection at these two levels (Boyd and Richerson 1988; Packer and Ruttan 1988).

The relationship between group size and cooperation, however, is likely to be a complex one since larger group sizes could also be a consequence of greater and more efficient cooperation (Avilés 1999). In fact, a positive association between greater social complexity and larger group sizes is well documented in a number of social systems, particularly in kin-based systems such as those of bees and wasps (Brian 1965; Michener 1974; Ross and Matthews 1991).

Noting the association between group size and complexity, Bourke (1999) suggested that larger group sizes would lead to the evolution of more complex social systems. We would argue for the reverse direction of causality; more efficient cooperation would lead to the evolution of larger groups (Avilés 1999). Not only would more efficient cooperation increase group productivity by increasing the fecundity and/or survival of group members and their offspring, but it could also facilitate access to new resources, thus expanding the groups' carrying capacity. The utilization of live trees by the tree-killing bark beetles, for instance, might have followed the development of better communication systems (pheromones) to attract conspecifics during group attack (Raffa and Berryman 1987). Also, some form of colonial living was apparently a prerequisite for the occupation of the marine environment by the phylogenetic lineages of marine birds (Rolland et al. 1998). The ability of social systems to access new resources could then initiate a positive feedback loop that, in kin-based systems in particular, could have led to the evolution of large and complex societies.

Associations among Nonrelatives and the Intrinsic Rate of Growth

The fact that grouping tendencies consistently decreased with increasing r in the GDD model (fig. 1*E*) probably reflects a greater ease of group formation when greater fecundity increases the number of individuals seeking to join groups. We have found that the intrinsic rate of growth becomes increasingly important as the groups become more exclusively kin based. In the limit, when only kin are admitted in the groups, the intrinsic rate of growth has a decisive effect on the equilibrium levels of our three sociality measures (L. Avilés and A. Cutter, unpublished observation), in contrast with the results reported here.

From Individual Behavior to Population Dynamics

Giraldeau and Caraco (2000) note in the preface of their excellent monograph on social foraging theory that "scaling up" from individual behavior to population dynamics has remained a significant but elusive objective of behavioral ecology. Analyzing equation (1), Avilés (1999) suggested that cooperation is a behavior that may profoundly influence population dynamics. Our results support this suggestion, showing how individual behaviors such as grouping and cooperation may have a dramatic effect not only on the structure but also the dynamics of populations. In particular, within the range of parameter values investigated in this study, outbreaks and crashes of the groups and the global population are predicted for organisms in which group living and cooperation would enhance reproductive output above and beyond an intrinsic rate of growth that is not too small (fig. 2).

In fact, dynamically unstable global populations are characteristic of a variety of social systems. Most notable among these are the tree-killing bark beetles (Berryman 1973; Raffa and Berryman 1987) and the migratory locusts (Roffey et al. 1968; Uvarov 1977) among nonkin-based systems and the tent caterpillars (Myers 1993), prairie voles (Getz et al. 1987; Getz and McGuire 1997), and red grouse (Matthiopoulos et al. 2000) among kin-based systems. The tree-killing bark beetles, in particular, closely match the assumptions of our model (Berryman 1973; Raffa and Berryman 1987). These beetles use an attractant pheromone to aggregate on the surface of live conifer trees, which they are able to kill and colonize by attacking en masse. Fitness is highest in groups of intermediate size.

Groups that are too small are unable to overcome the tree defenses; groups that are too large suffer the effects of competition for resources among their developing offspring (Raffa and Berryman 1987). Following their development within the trees, the beetles disperse to restart the cycle. Group members, therefore, are not related to one another. As predicted by our model, outbreaks and crashes are characteristic of these beetle populations (Berryman 1973), presumably reflecting the enhanced reproductive output that results from their cooperative behavior.

It should be noted that the prediction of dynamic instability would only hold in systems in which, in addition to density dependence and a large reproductive output, growth is discrete rather than continuous (e.g., May and Oster 1976). The social systems listed in table 3 meet this requirement, with those known to be the most dynamically unstable (mountain pine beetles, locusts, and voles) having the most clearly discrete generations (Uvarov 1977; Getz et al. 1987; Raffa and Berryman 1987; Getz and McGuire 1997).

The pattern of bifurcations that lead to dynamic instability in the GDD model (fig. 2) parallels the expectations derived from the analysis of Avilés (1999), even though the latter model was concerned with the dynamics of single groups. Our results suggest that periodic or chaotic oscillations of the average size of the social groups, the number of groups, and the size of the global population are expected even when groups break and reform every generation. This result holds as long as there is density-dependent control of the total number of individuals in the global population, as in the GDD simulations (appendix; eq. [A4]). In the LNS simulations, in contrast, local but not global instability is expected because density-dependent effects are restricted to the local groups (appendix; eq. [A3]). Local instability in the form of periodic or chaotic dynamics, however, would only be detectable in systems in which groups last for multiple generations (Avilés 1999). In practice, the distinction between the GDD and LNS models is somewhat artificial because most systems probably lie somewhere in between these two extremes. Honeybees, for instance, might be subject to global density-dependent control because individual bees compete for a limited number of flowers, as in the GDD model. Honeybees, however, would also be limited by the number of sites that their nests might occupy, as in the LNS model. Local and global dynamics, therefore, should in practice reflect the combined effects of these two modes of global population control.

Finally, our results predict that global extinction may be an outcome of extreme dynamic instability in models with GDD control. In pure LNS models, global extinction is not expected since the dynamics of the local groups are independent of one another.

Summary of Predictions

To summarize, other things being equal, our model predicts that in associations among nonrelatives:

First, with greater relative fitness costs of cooperation (i.e., more altruistic interactions), smaller groups should form. The contrast in typical group sizes between the pleometrotic ants and the tree-killing bark beetles, for instance, supports this prediction.

Second, whenever cooperation carries a relative fitness cost, lower levels of cooperation should characterize systems in which large resource patches allow the formation of larger groups. In testing this prediction, care should be taken to distinguish cases in which access to more abundant resources was made possible by greater and more efficient cooperation.

Third, outbreaks and crashes of the groups and global population should characterize systems in which cooperation significantly increases reproductive output relative to a base level that is not too small. Because greater cooperative tendencies among nonrelatives are more likely to evolve when the within-group relative fitness costs of cooperation are small or nonexistent, systems that exhibit oscillations should be mutualistic rather than altruistic. The tree-killing bark beetles, among others, support this prediction.

Extensions of the Model

The model we have presented here could be labeled the "conifer bark beetle," the "cliff swallow," the "pleometrotic ants," or the "communal bees" model because of its resemblance to those systems. Extensions along several axes are possible, including the formation of kin-based social systems, systems in which groups last for multiple generations, or systems in which altruistic interactions involve complete sterility rather than simply a reduced contribution to the group's offspring pool. These are directions in which we are extending the current model and the framework introduced by Avilés (1999).

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APPENDIX

An Agent-Based Model for the Evolution of Grouping and Cooperation within a Population-Ecology Framework

Genetic System

Individuals are assumed to be diploid with a 30-locus genome coding for grouping and cooperative tendencies, 15 loci per trait. Two alleles (1 or 0) can occur at each locus, so that raw phenotypic values range from 0 to 30. The proportion of 1's in the diploid complement corresponding to each trait represent, respectively, the tendency of individuals to form groups (g_i) and to cooperate once within groups (γ_i). To prevent mutation pressure, which is biased against the most common allele, we introduce mutations primarily in the form of inversions and translocations (see Avilés 1993) at a rate of 10^{-2} per locus. Individuals produce gametes through processes that mimic meiosis and recombination. For simplicity, no separate sexes are assumed. Mating occurs during a global-mixing phase (see below) during which individuals randomly draw a partner whose gametes they use to fertilize their eggs.

Group Formation

At the start of a cycle, individuals occur in a global population pool. One at a time and in random order individuals leave this pool to either initiate new groups or to join already-formed groups. Individuals join a group with probability equal to

$$g_m \times \bar{g}\left(1 - \frac{n}{n^*}\right), \tag{A1}$$

where g_m represents the grouping tendencies of the potential immigrant m, n and $\bar{g}$ represent, respectively, the number and average grouping tendencies of the group's existing members, and n^* is the expected stable group size at the time of group formation (see eq. [A2]). Whenever $n \geq n^*$, the group acceptance probability is 0.

Individuals with no grouping tendencies or individuals that fail to find an accepting group become established on their own (when the total number of groups is not limited) or are removed from the simulation (when the total number of groups is limited and all available sites are occupied).

The stable group size used in equation (A1) corresponds to the size beyond which the per capita rate of growth drops below 1 as a result of overcrowding (Avilés 1999). Avilés (1999) showed that this stable group size, which corresponds to the upper fixed point of equation (1), can be obtained from the implicit relationship

$$r = cn^* - \bar{\bar{\gamma}} \ln n^*, \tag{A2}$$

where $\bar{\bar{\gamma}}$ is calculated as the average cooperative tendencies in the global population at the time of group formation, and r and c are fixed parameters of a run (see table 1).

In calculating n^*, only local negative density-dependent effects (c, from eqq. [A3] and [A4]) are considered, under the assumption that individuals can assess the size of their group but not of the global population. Note that because n^* is a function of evolving global cooperative tendencies, it also evolves in the simulations.

Local and Global Density Dependence

We consider two models of global population control. In the LNS model, the total number of groups is limited, but there is no effect of the total number of individuals in the global population on local rates of growth. In the GDD model, there is no limit to the number of groups, but the total number of individuals in the global population is limited and affects local interactions. The local per capita rate of growth functions for each of the models are as follows:

$$\text{LNS}: \ f(n, \bar{\gamma}) = e^r e^{-cn} n^{\bar{\gamma}}; \tag{A3}$$

$$\text{GDD}: \ f(n, \bar{\gamma}, N) = e^r e^{-cn} n^{\bar{\gamma}} e^{-w(N-n)}, \tag{A4}$$

where n is the local group size, $\bar{\gamma}$ is the average cooperative tendencies of the group's members, w is a global negative density-dependence parameter inversely proportional to a global carrying capacity, N is the total number of individuals in the global population, and r and c are as in equation (1). Equations (A3) and (A4) are unimodal functions of group size when $\bar{\gamma} > 0$.

Mutualistic versus Altruistic Interactions and the Relative Fitness Costs of Cooperation

Equations (A3) and (A4) represent the average per capita rate of growth in a group. Individuals within groups, however, may differ in their relative contributions to the group's offspring pool. We assume an inverse relationship between an individual i's probability of helping (γ_i) and its relative fitness within its group. Individuals that contribute less than average to communal activities, but still profit from group-level benefits, have a relative fitness >1;

individuals that contribute more than average suffer a fitness cost and have a relative fitness of <1. The reproductive output of an individual is then calculated by multiplying the expected reproductive output of its group (eq. [A3] or eq. [A4]) times the following function:

$$\text{relfitness}_i = a - \beta\gamma_i, \tag{A5}$$

where $a = 1 + \beta\bar{\gamma}$ is the intercept of the function calculated so that the average cooperator will have a relative fitness of 1 (i.e., when $\gamma_i = \bar{\gamma}$). Here, γ_i and $\bar{\gamma}$ are, respectively, the individual and group cooperative tendencies, and β (the slope of the function and a fixed parameter of a run) represents the extent to which cooperation exerts a relative fitness cost. When $\beta = 0$, there are no relative fitness costs of cooperation and the interactions are said to be mutualistic. As β increases in magnitude, cooperation becomes costly and the interactions are said to be altruistic because individuals increase the fitness of other group members while diminishing their relative contribution to the group's offspring pool. Actual clutch sizes were then obtained stochastically by drawing from a Poisson distribution with mean equal to the newly calculated expected reproductive output of individual *i*.

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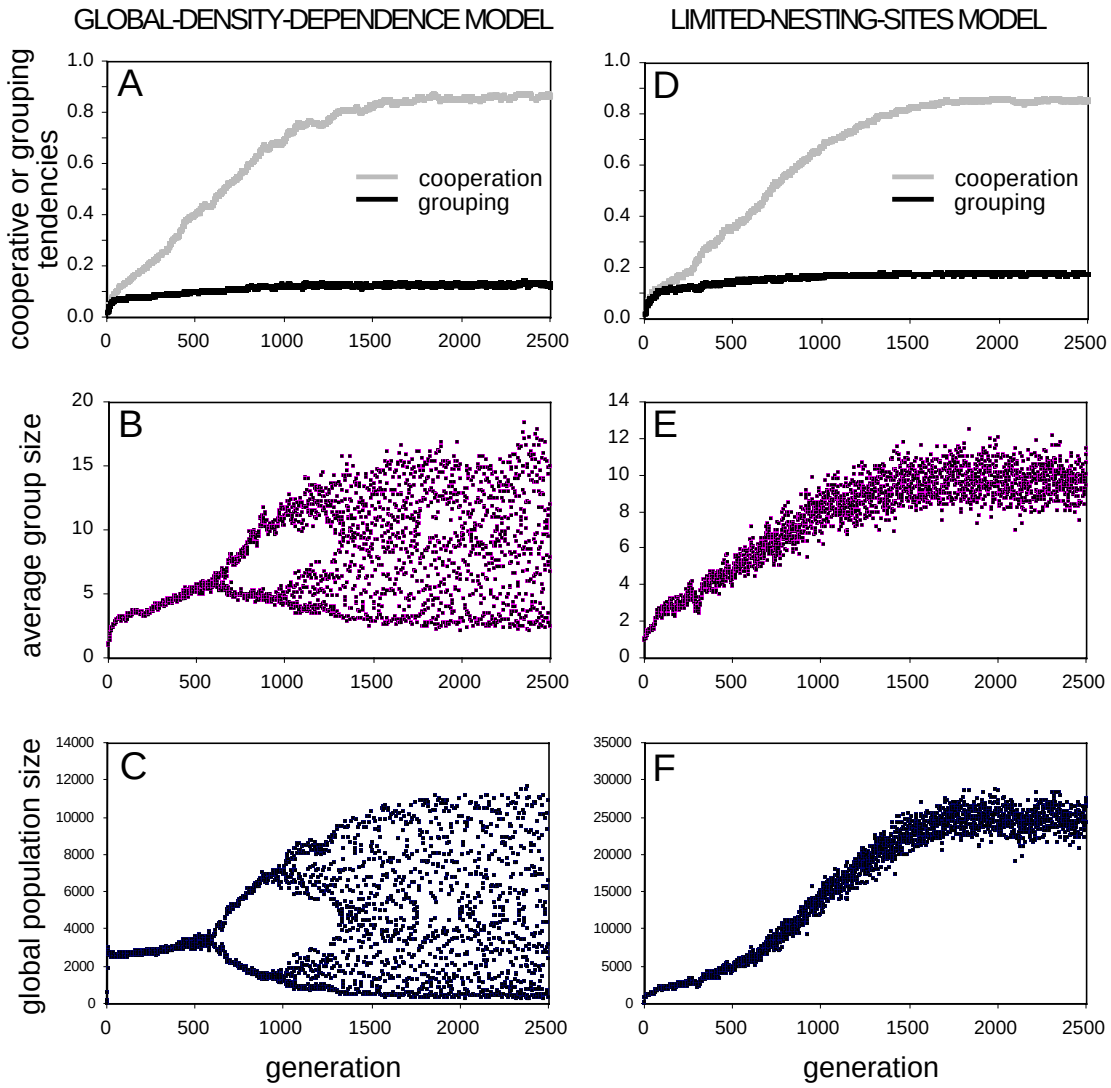

Figure 2: Time series of the evolution of cooperation, grouping tendencies, average group size, and global population size in the Global Density Dependence (GDD) and Limited Nesting Sites (LNS) models for mutualistic ($\beta = 0.0$) interactions. *A-C*, run for $r = 1.5$, $c = 0.06$, and $w = 0.0005$ (eq. [A4]), *D-F*, run for $r = 1.5$, $c = 0.06$ (eq. [A3]), and a maximum of 200 groups.