

Cooperation and non-linear dynamics: An ecological perspective on the evolution of sociality

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ABSTRACT

Using the theory and methods of non-linear dynamics, I explore the consequences of cooperation on the size and dynamics of social groups. I present a model that incorporates into a discrete growth equation a positive density-dependent factor to represent the synergistic effects of cooperation. Analysis of this model shows that, by increasing the net reproductive output of group-living organisms, cooperation could either stabilize or destabilize the dynamics of a social group. At one end of the spectrum, group-living and cooperation could make persistence possible under harsh demographic or ecological conditions. At the other end of the spectrum, in populations already organized in social groups, cooperation could lead to more highly integrated social groups that are subject to a boom-and-bust pattern of growth. When groups last for multiple generations, such a pattern could take the form of periodic or chaotic dynamics. It is suggested that dynamical instability could result in rates of group turnover large enough for selection among the highly integrated social groups to take over as the primary evolutionary force. Consideration of the dynamical effects of cooperation, therefore, may shed light both on the ecological and demographic conditions leading to the origin and maintenance of group-living as well as on the forces responsible for shaping the diversity of animal societies.

Keywords: Allee effect, chaos, complex systems, cooperation, group selection, population dynamics, sociality.

INTRODUCTION

Understanding the evolution of social systems requires explaining, on the one hand, why individuals came together in groups in the first place, and, on the other, why in some instances initially loose aggregations turned into highly integrated and largely autonomous entities. Given the diversity of animal societies, it may appear that not one but a multitude of explanations would be necessary to address these issues. Here, I propose an approach to the study of social systems that explicitly considers the synergistic effect of cooperation on individual fitness and the consequences of such an effect on the size and dynamics of the social groups. This approach makes use of the theory and methods of non-linear dynamics (e.g., May, 1974; Hassell, 1975; May and Oster, 1976; Guckenheimer *et al.*, 1977; Smith and Mead, 1980) and is simple and potentially general enough to give us common tools to

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address these questions in a variety of social systems. Analysing a discrete growth equation to which I have added a positive density-dependent factor to represent the synergistic effects of cooperation, I will show that cooperation can either stabilize or destabilize the dynamics of a social group. At one end of the spectrum, group-living and cooperation may allow the colonization of habitats or ecological niches in which populations consisting entirely of solitary individuals would be unable to persist. At the other end of the spectrum, cooperation may lead to highly cohesive social groups which oscillate in size and may be subject to high rates of turnover. The latter situation could make it possible for selection among groups to take over as the primary evolutionary force. I will argue, therefore, that consideration of the non-linear effects of cooperation on individual fitness can provide new insights into the conditions leading to the origin and maintenance of group-living, as well as on the forces subsequently responsible for shaping the diversity of animal societies.

THE MODEL

Let us envision an organism that forms groups that are long enough lived for their size to be affected by birth and death processes within them. Wilson (1975) labelled such relatively stable groups 'demographic societies', to distinguish them from 'casual societies', which are highly ephemeral aggregations that last for only fractions of the life span of individuals. Examples of demographic societies are primate troops (e.g. Milton, 1982), coati bands (e.g. Gompper, 1997), groups of cooperatively breeding birds (e.g. Heinsohn, 1992), bee hives (e.g. Seeley, 1989), and social spider colonies (e.g. Avilés and Tufiño, 1998). Examples of casual societies are many kinds of bird flocks, feeding groups of monkeys, and groups of playing children (Wilson, 1975). Assume that, in addition to cooperating, individuals within these demographic societies compete for resources, but that those resources cannot be monopolized by one or just a few individuals. The struggle for resources within groups, therefore, takes the form of scramble competition. Finally, assume that reproduction within the groups is either seasonal or occurs in bursts, so that the growth of the groups occurs in discrete generations and can be modelled with a difference equation.

Based on these assumptions, I start with the premise that at least some interactions among members of the social groups will have a synergistic effect on their fitness – that is, they will cause certain components of individual fitness to increase as a function of colony size (Fig. 1a). Mechanistically, such an effect would arise if, for instance, individuals acting as a group could gain access to resources inaccessible to solitary individuals, or if surrogate caregivers would allow the survival of orphaned offspring. I will refer to those interactions as cooperative and will model them with the function $g(N) = N^\gamma$, where N is the number of individuals in the groups and γ , the cooperation parameter, ranges between 0 and 1 (for population growth models that use a similar function to produce a positive density-dependent effect, see Longstaff, 1977; Marotto, 1981; for models with a similar function designed for social insects, see Brian, 1965, pp. 52–53). The synergistic effects of cooperation will be counteracted to some extent by increasing competition within the groups as group size increases. I will model these negative density-dependent effects with the function $h(N) = e^{-cN}$, where the parameter c is inversely proportional to a group 'carrying capacity' (Appendix 1) and reflects the intensity of competition or crowding within groups (e is the base of the natural logarithms). Competition, therefore, will cause certain components of fitness to be a decreasing function of colony size (Fig. 1b). Finally, I will consider that solitary individuals, in the absence of either cooperative or competitive

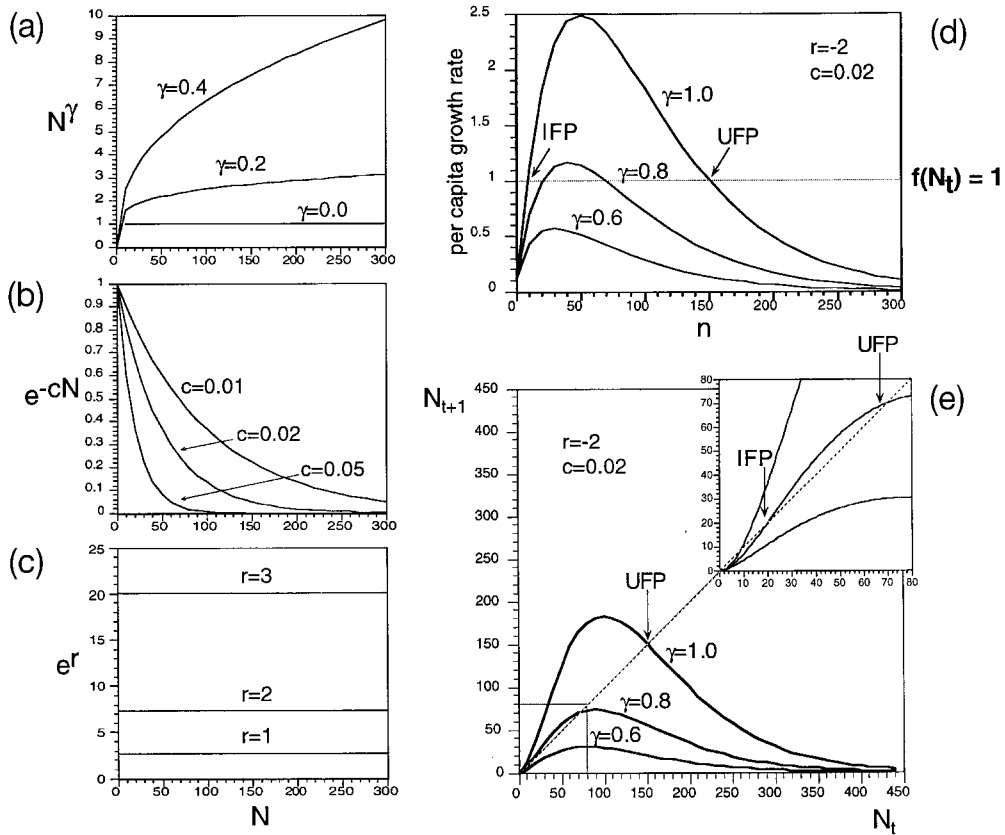


Fig. 1. Factors, fitness function and return map of equation (2) used to predict the growth of a social group. (a) Cooperation, (b) crowding and (c) intrinsic rate of growth factors forming part of the fitness function. (d) Fitness function showing the effects of varying the cooperation parameter; note that when $\gamma > 0$, the per capita reproductive output is maximum at intermediate colony sizes. (e) Return map showing that increasing the value of γ has the effect of ‘pulling’ the graph of the function from below to above the 45° line. As the function crosses the 45° line, two new equilibria are created (insert in e). An intermediate unstable equilibrium (IFP) determines the boundary between the basins of attraction of $N = 0$ and the upper fixed point (UFP), which are both stable.

interactions, will have a fitness of R or e^r , where r is an intrinsic rate of growth parameter (Fig. 1c).

These three components of fitness can be multiplied together to produce an overall fitness function of the form (see also Appendix 1):

$$f(N) = N^\gamma e^r e^{-cN} \quad (1)$$

Equation (1) represents the *average* per capita reproductive output of group members as a function of colony size and is a unimodal function when $\gamma > 0$ (Fig. 1d). Note that equation (1) allows for, but is not explicit about, fitness heterogeneity within social groups. To the extent that such heterogeneity could result from different individual tendencies to

cooperate, within-group selection could limit the extent to which cooperation evolves. Elsewhere (L. Avilés and P. Abbot, in prep.), I consider the interplay between various individual costs of cooperation and group-level population dynamics. Here, I assume that different overall levels of cooperation have evolved and consider their impact on the size and dynamics of social groups given a variety of ecological settings in which the groups could live.

I should note that the assumption of a unimodal fitness function is standard in models that consider the effects of group size on individual fitness (e.g. Vehrencamp, 1983; Pulliam and Caraco, 1984; Slobodchikoff, 1984; Giraldeau, 1988; Emlen, 1991). For empirical examples which show that as a result of cooperation some components of individual fitness may increase as a function of colony size, see Caraco and Wolf (1975), Nudds (1978), Buss (1981), Itô (1987), Raffa and Berryman (1987), Heinsohn (1992), Cash *et al.* (1993), Komdeur (1994), Wiklund and Andersson (1994), Booth (1995), Jeanne and Nordheim (1996) and Avilés and Tufiño (1998). These and other studies (e.g. Michener, 1964) also show that other components of individual fitness may decrease as a function of colony size.

Equation (1) can be used to predict the size of the groups in the next generation, as follows:

$$N_{t+1} = N_t f(N)_t = N_t^{1+\gamma} e^r e^{-cN_t} \quad (2)$$

Note that the last two factors of the right-hand side of equation (2) are elements of the Ricker equation (Ricker, 1954), which has been used extensively to model the discrete growth dynamics of populations that are subject to negative density-dependent effects (e.g. Gatto, 1993). Equation (2), therefore, can also be taken to represent the growth of a population that is subject to both positive and negative density dependence. The presence of a positive density-dependent factor in equation (2) creates what in the ecological literature is known as an 'Allee effect' (Allee, 1938; Hutchinson, 1947; Odum and Allee, 1954; see Marotto, 1981, for a partial analysis of an equation with an Allee effect). In addition to equation (2), I also studied the consequences of adding a cooperation factor to an alternative version of the Ricker equation and to two versions of the discrete logistic equation (Table 1).

Table 1. Ricker-type (Ricker, 1954) and logistic-type (Guckenheimer *et al.*, 1977) difference equations to which a positive density-dependent factor (N^γ) has been added to represent the synergistic effects of cooperation. The equations for the fixed points and for the surfaces separating regions of different dynamical behaviours (absence from point equilibria and point equilibria from stable limit cycles) are given for each function

Model: $N_{t+1} =$	Fixed points	Absence $\rightarrow$ persistence	Point equilibria $\rightarrow$ cycles
$N_t^{1+\gamma} e^r e^{-cN_t}$	$r = cN^* - \gamma \ln N^*$	$r - \gamma + \gamma \ln \left(\frac{\gamma}{c} \right) = 0$	$r - \gamma + \gamma \ln \left(\frac{\gamma + 2}{c} \right) = 2$
$N_t^{1+\gamma} r \left(1 - \frac{N_t}{K} \right)$	$r = \frac{1}{N^\gamma \left(1 - \frac{N}{K} \right)}$	$\gamma - \frac{r}{K} \left(\frac{\gamma + 1}{r} \right)^{(\gamma+1)/\gamma} = 0$	$\gamma - \frac{r}{K} \left(\frac{\gamma + 3}{r} \right)^{(\gamma+1)/\gamma} = -2$
for $N < K$; $0 < r < 4$			

Note that equation (2) is concerned only with density-dependent interactions within local groups. In a social species, however, individuals often interact with members of other groups or whole groups interact with one another. Such higher level interactions could be accounted for by the parameters of the model if their effect on local fitness remained constant through time, as would be the case if the total number of groups or of individuals in the overall population remained fixed. In such a case, r would account for effects that are independent of the size of the groups, γ for effects for which larger groups are at an advantage, and c for effects for which larger groups are at a disadvantage. However, if the number of groups or the total number of individuals in the overall population changes – and the intensity of interactions decreases when fewer groups or fewer individuals are involved – then a hierarchical model that accounts for density dependence at two levels would become necessary. Such a model (L. Avilés and P. Abbot, in prep.), although a desirable extension to the present model, is beyond the scope of this paper. I will assume, therefore, the absence of interactions with members of other groups or a fixed number of total groups or of members of such groups in the overall population.

Finally, note that equation (2) can be applied to groups that last any number of generations, as it can be interpreted as predicting the expected size at time $t + 1$ of groups of a range of sizes or, when applied iteratively, the expected growth trajectory of a single group that lasts for multiple generations (Fig. 1e). In either case, the shape of the fitness function (Fig. 1d) or of its return map (Figs 1e, 2a,c,e) can be used to make predictions regarding the size and dynamics of the social groups given particular values of the parameters r , γ and c . This is done in the following sections.

RESULTS

The size of social groups

The expected minimum and equilibrium size of social groups can be predicted from the points at which the return map of equation (2) intersect the 45° line (Fig. 1e) or, alternatively, the points at which equation (1) intersect the $f(N_t) = 1$ line (Fig. 1d). When $\gamma > 0$, the return map intersects the 45° line at three points: at $N = 0$ and at intermediate and upper points which are the solutions to the equation

$$r = cN^* - \gamma \ln N^* \quad (3)$$

These points of intersection, which are the fixed points of equation (2), occur when $f(N_t) = 1$ (i.e. when individuals in the groups exactly replace themselves), so that the groups neither grow nor decrease in size. Two of these points, $N = 0$ and the upper fixed point, are stable equilibria, while the intermediate fixed point is an unstable equilibrium. I will refer to the latter two points as UFP and IFP, respectively (Fig. 1). In the absence of cooperation, on the other hand (i.e. when $\gamma = 0$), there are only two equilibria: at $N = 0$, which is unstable, and at a $N > 0$ value, which is stable. Finally, when $\gamma = 0$ and $r < 0$ (or $R < 1$), the return map lies entirely below the 45° line and $N = 0$ is the only equilibrium.

The UFP is equivalent to the stable group size that has been described in the literature (Giraldeau, 1988; Giraldeau and Caraco, 1993; Higashi and Yamamura, 1993; Rannala and Brown, 1994) as the point at which it is no longer profitable for individuals to join a group, with two important differences: (1) While in existing models of group size evolution this is the point at which the fitness of group members is equal to the fitness of solitary

individuals, in the present case it is the point at which the fitness of group members is equal to the fitness of individuals in groups of the minimum size (Fig. 1d). (2) In the group size literature, the groups are expected to be regulated at the stable size by a more or less instantaneous flow of individuals in and out of the groups. By contrast, in the present model, the groups may oscillate around the stable size because precise regulation may not be possible given feedback mechanisms that require the birth or death of individuals. This is essentially the contrast between models designed for casual versus demographic societies. I will discuss the dynamical consequences of this difference in the following section.

The IFP, which is an unstable equilibrium, corresponds to the minimum viable size of the social groups: groups that drop below this size will go extinct, while groups that remain above this size will go to the UFP or oscillate around it. Finally, the distance between the IFP and UFP corresponds to the range of colony sizes at which growth is positive, while the hump of the map corresponds to the expected maximum size of the groups (Fig. 1e).

The effects of varying the parameters of equation (2) on the expected minimum, maximum and stable group sizes are shown in Table 2 and the left-hand panels of Fig. 2. Note that as r decreases or c increases, the minimum group size (the IFP) increases. This implies that, as the match between the organisms and their environment worsens, a larger number of cooperators becomes necessary for group persistence. Alternatively, more effective social interactions may be needed for group persistence under worsening demographic or environmental conditions: when $r < c$, the IFP decreases as γ increases. The expected stable (UFP) and maximum size of the social groups, on the other hand, increase as environmental conditions improve, r increases, or cooperation becomes more effective (Table 2 and Figs 2 and 1e). The model, therefore, predicts that not only the stable size, but also the range of expected group sizes, will change as a function of the parameter values.

On the existence and dynamics of social groups

In addition to determining the size of social groups, the shape of the return map of equation (2) determines whether groups of any size exist at all and, if so, the dynamical pattern with which they grow. To visualize this, consider the effect on the return map of varying the cooperation parameter. Figures 1e and 2a show that, as the synergistic effect of cooperation increases, a return map originally lying entirely below the 45° line can be ‘pulled’ above this line and progressively made taller as its slope around the UFP becomes steeper. As discussed below (see also Fig. 3), the consequences of this ‘pulling’ property of cooperation

Table 2. Effect of the model parameters on the expected minimum (IFP), stable (UFP) and maximum size of the social groups, as predicted from equation (3)

Parameter	Predicted minimum group size (IFP)	Predicted stable size (UFP)	Predicted maximum size
as γ increases	decreases for $r < c$ (IFP > 1) for $r = c$, IFP = 1 increases for $r > c$ (IFP < 1)	increases	increases
as r increases	decreases	increases	increases
as c decreases (or K increases)	decreases	increases	increases

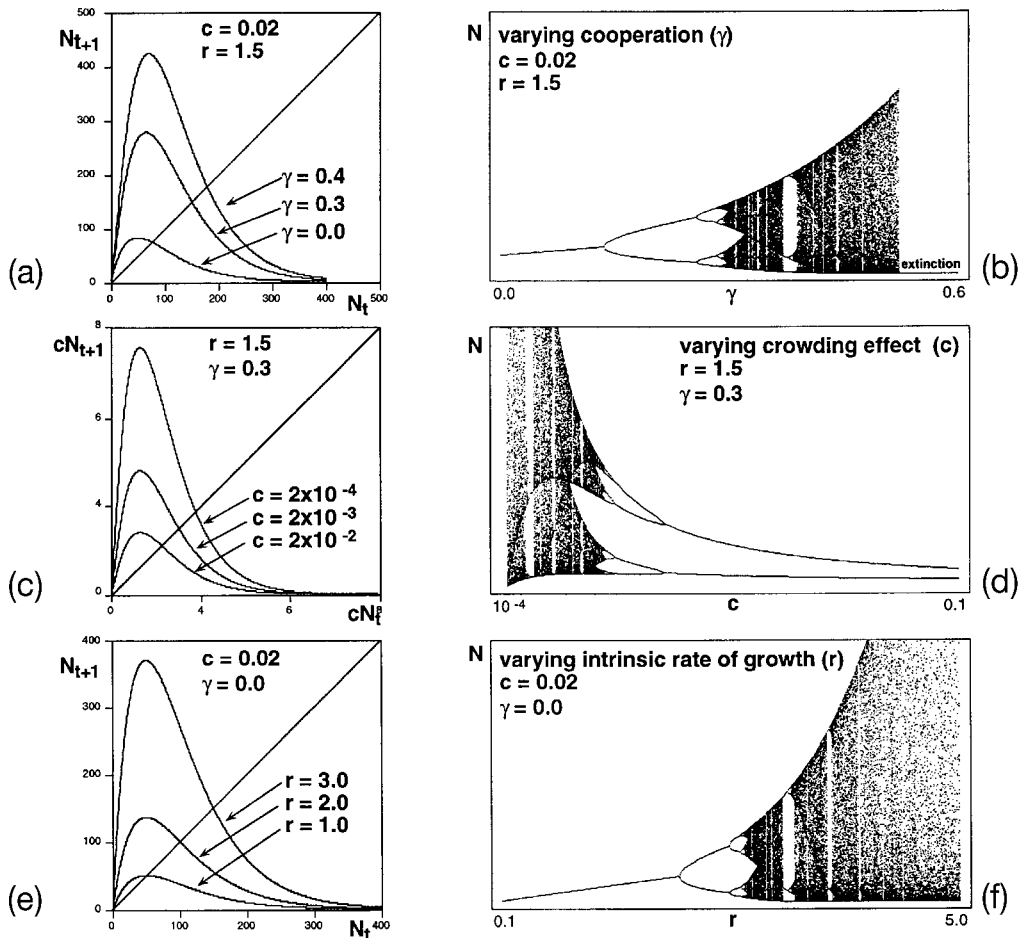


Fig. 2. The effect of varying the cooperation (γ), crowding (c) and intrinsic rate of growth (r) parameters on the return map (a, c, e) and dynamics (b, d, f) of equation (2). Note that as the value of γ increases, both the maximum height of the map as well as its slope around the upper stable equilibrium increases. Decreasing the magnitude of c has a similar effect on the height and, as long as $\gamma > 0$, the slope of the map (c). Changes in the slope of the function (see text) result in a period-doubling (or halving) bifurcation cascade shown in the final state diagrams (right-hand panels) as each of the three parameters is varied (b, d, f). Note that, at large values of γ , there is a sudden drop to $N = 0$ (b) that occurs when mappings from the hump of the function fall below the intermediate unstable equilibrium. (e) and (f) correspond to the traditional Ricker equation without cooperation.

include: (a) a transition from absence to persistence in habitats in which populations of solitary individuals would be unable to replace themselves; (b) a transition from groups that grow to a stable size to groups that oscillate in size either periodically or chaotically (Figs 2a,b); and (c) a transition to a second region of deterministic extinction when oscillations are steep enough that extremely large colonies crash to below the minimum viable group size (i.e. below the IFP). I will consider each of these transitions in turn.

A transition from absence to persistence

Envision an asocial species that is unable to colonize an area where solitary individuals cannot reproduce successfully. Populations of that species in this marginal environment would be doomed to extinction: their growth functions would lie entirely below the 45° line, so that N_{t+1} would always be smaller than N_t and $N = 0$ would be the only equilibrium. In the ecological literature, such populations are referred to as ‘sink’ populations. Assume that a mutation arises that causes some colonizers to cooperate with each other in acquiring food, caring for their offspring, or avoiding predators. Individuals that receive sufficient help can leave descendants, so that groups within a certain size range may occupy this marginal environment and have positive growth. Reproductive isolation from the source population would then complete the colonization process. Figure 1e illustrates this situation by showing that, as the synergistic effect of cooperation increases, a growth function can be pulled from below to above the 45° line so that equilibria other than zero can exist.

I show analytically (Appendix 2) that this transition from absence to persistence takes place when

$$r - \gamma + \gamma \ln \left(\frac{\gamma}{c} \right) = 0 \quad (4)$$

where r can be negative whenever

$$\gamma > c e \quad (5)$$

(and e is the base of the natural logarithms).

A first result, therefore, suggests that cooperation can allow the colonization of environments or ecological niches in which solitary individuals would have negative values of r (or $e^r < 1$) (Fig. 3). The degree of synergism required for persistence increases as the value of r decreases (Fig. 3) and is inversely proportional to the carrying capacity of the environment (since c is inversely proportional to K ; Appendix 1). A function with similar properties to (4) describes the boundary between absence and persistence in the logistic version of equation (2) (Table 1), where persistence in the absence of cooperation is not possible when $r < 1$ (Guckenheimer *et al.*, 1977).

A transition from simple to complex dynamics

Once the persistence threshold has been crossed, the shape of the map will determine the growth dynamics of the social groups. In particular, the dynamics will depend on the slope of the map around the UFP: if the slope lies between +1 and -1, we expect that the groups will grow to a stable equilibrium; if, on the other hand, the slope is steeper than -1, we expect that the groups will oscillate around this equilibrium. The dynamical effects of changing the shape of a unimodal map have been studied extensively in discrete population growth models involving negative density dependence (e.g. May, 1974; May and Oster, 1976; Guckenheimer *et al.*, 1977; Smith and Mead, 1980). In the Ricker and discrete logistic equations, in particular, it has been shown that increasing the value of r , which steepens the slope around the UFP, results in a period doubling bifurcation cascade that leads to transitions from simple to complex dynamics (Fig. 2, bottom panels). In the present model, transitions from point equilibria to stable periodic cycles or chaos also occur as (a) the

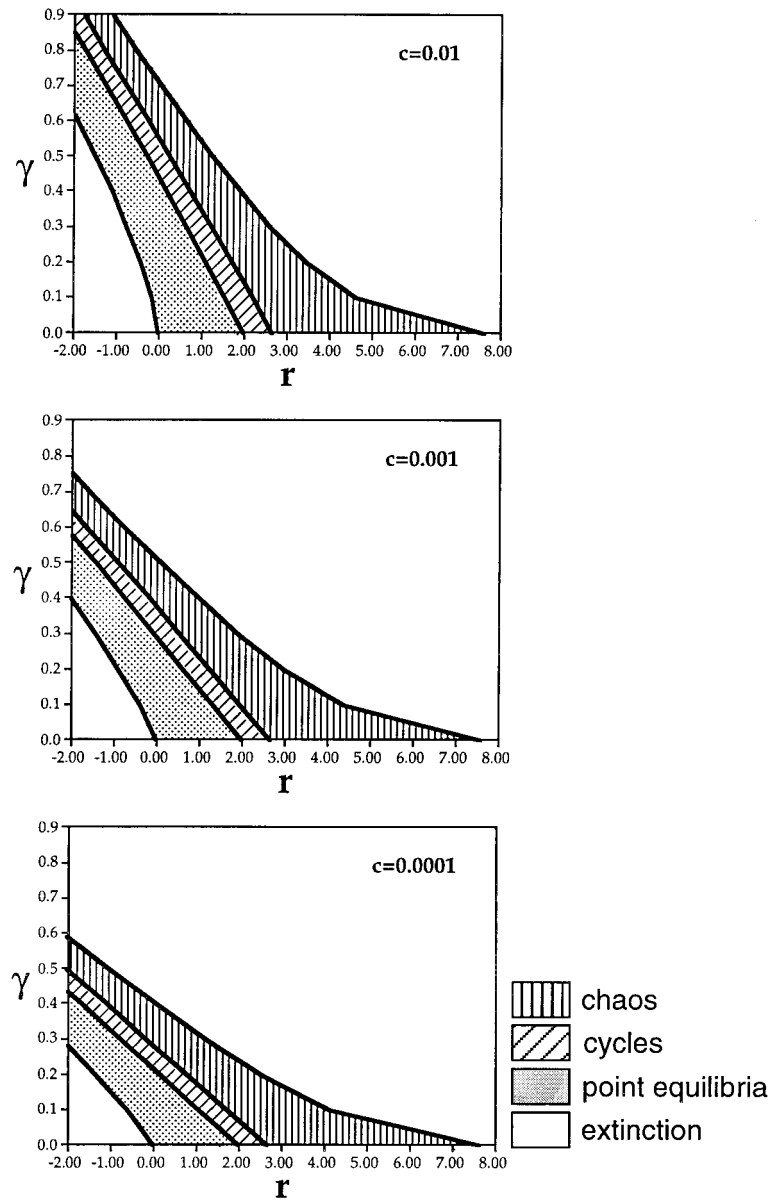


Fig. 3. Regions of different dynamical behaviours in the r - γ parameter space for three values of c . The boundaries between absence and point equilibria and point equilibria and cycles were obtained analytically (Appendix 2), while those between stable periodic cycles and chaos and chaos and the upper extinction region were obtained numerically using the Dynamical Systems software (Schaffer *et al.*, 1988), with 500 convergence iterations, 200 asymptotic iterations, and a trapping radius of 10,000. Note that at $\gamma = 0$ (i.e. the Ricker equation without cooperation), all three figures are identical.

magnitude of γ , the cooperation parameter, increases, or (b), perhaps surprisingly, the magnitude of c , the crowding parameter, decreases (Figs 2 and 3). Increasing γ leads to a left to right period doubling bifurcation cascade (forward bifurcations), while increasing c results in backward or period halving bifurcations (Fig. 2) (for other examples of period halving bifurcations, see Gatto, 1993; Stone 1993). The dynamical effect of the crowding parameter (or its inverse, the carrying capacity) is of special interest because, in the traditional Ricker or logistic equations (i.e. without a cooperation term), the negative density-dependence parameter only has a scaling effect (i.e. only the height, but not the shape, of the function is varied) (Gatto, 1993).

In Appendix 2, I show that the transition from point equilibria to stable periodic cycles takes place when

$$r - \gamma + \gamma \ln\left(\frac{\gamma + 2}{c}\right) = 2 \quad (5)$$

which depends on all three parameters, r , γ and c , whenever $\gamma > 0$. When $\gamma = 0$, (5) reduces to $r = 2.0$, the well-known result for this transition for the Ricker equation (May, 1974; May and Oster, 1976). In the logistic version of the model, the boundary between simple and complex dynamics is also a function of all three parameters (Table 1), which, when $\gamma = 0$, reduces to $r = 3$ (Guckenheimer *et al.*, 1977).

A couple of points need to be made with respect to the applicability of the latter results to biological systems. Recall that the return map can be interpreted as representing the growth of groups that last for one or for multiple generations. The prediction of dynamical instability should apply in either case: For a certain range of the parameter values, groups that grow to or are founded below but close to the UFP would overshoot the stable size, while those that grow to or are founded above the UFP would crash in the next generation. The qualifiers 'chaotic' or 'periodic', on the other hand, require relatively long time series and would, therefore, be restricted to groups that last for multiple generations. Potential examples of either kind are given in the Discussion.

Beyond chaos

The third potential effect of cooperation concerns a transition from chaos (or a region of extreme dynamical instability) to extinction at the other extreme of the r , γ and c parameter space (Figs 2b and 3). When γ and r are relatively large and c is relatively small (or, conversely, the carrying capacity is relatively large), the colony size oscillations become so steep that mappings from the hump of the function may come within the basin of attraction of $N = 0$ (i.e. below the unstable equilibrium). Thus, deterministic colony extinction, and not just demographic stochasticity, which is thought to increase the extinction probability of chaotic populations (May and Oster, 1976; Thomas *et al.*, 1980; Berryman and Millstein, 1989; but see Nisbet *et al.*, 1989; Allen *et al.*, 1993), may prevent the evolution of social species with extreme parameter values (Fig. 3).

Other models investigated

In addition to the Ricker and logistic versions of the model discussed above, I also investigated alternative versions of these equations in which the negative density-dependent and intrinsic rate of growth factors are combined into one, as follows:

$$N_{t+1} = N_t^{1+\gamma} e^{r(1-(N_t/K))} \text{ (Ricker-type)}$$

and

$$N_{t+1} = N_t \left[N_t^\gamma + r \left(1 - \frac{N_t}{K} \right) \right]$$

Interestingly, in both of these models, the final state diagram for the parameter r is a combination of period-halving bifurcations at small values of r coalescing with period-doubling bifurcations as the value of r increases. This result, which is probably mostly of mathematical interest, apparently arises because the coupling of the crowding and intrinsic rate of growth factors causes the crowding factor to decrease as the growth parameter decreases. The final state diagram for the parameter r would thus combine the right-left and left-right bifurcations (Fig. 2) that arise in equation (2) when varying c and r , respectively. The dynamical transitions in the system, therefore, apparently reflect the balance between the negative and positive density-dependent terms.

DISCUSSION

Cooperation, by definition, has a positive effect on the fitness of the interactors. As a result, some components of individual fitness should increase as a function of the number of cooperators in the groups. The net effect, given unavoidable competition within the groups, should be an individual fitness function which is highest at intermediate group sizes (Alexander, 1974; Wilson, 1975; Rubenstein and Wrangham, 1986; Emlen, 1991; Heinsohn, 1992; Cash *et al.*, 1993; Booth, 1995; Avilés and Tufiño, 1998). The results of this study suggest that consideration of such synergistic effects of cooperation on individual fitness can provide new insights into the forces behind the origin and evolution of animal sociality. At one end of the spectrum, cooperation could allow the colonization of environments or ecological niches where populations consisting entirely of solitary individuals would not be able to persist. At the other end of the spectrum, in populations already organized in social groups, a large synergistic effect of cooperation could lead to a boom-and-bust pattern of colony growth and potentially high rates of colony turnover. As I will argue next, taking into account this stabilizing or destabilizing effect of cooperation may be critical when trying to understand the forces leading to the origin and maintenance of sociality as well as the forces subsequently responsible for shaping the diversity of animal societies.

The first question to be addressed in the study of animal sociality is why individuals came together in groups in the first place. A variety of conditions have been suggested to select for social-living, including constraints on independent breeding (Emlen, 1991), intense predator pressure (Alexander, 1974; Wilson, 1975; Caraco and Pulliam, 1984; Stern and Foster, 1996), strong intra- or inter-specific competition (Wilson, 1975; Buss, 1981; Hogendoorn and Velthuis, 1993), harsh or unpredictable environments (e.g. Emlen and Wrege, 1991; Jarvis *et al.*, 1994), or resources that are difficult to acquire except as a group (Slobodchikoff, 1984). These various conditions, which have been collectively referred to as the 'ecological constraints hypothesis' (Emlen, 1991; Brockmann, 1997), would result in deaths outpacing births and, thus, in unsustainable rates of growth for populations of solitary individuals attempting to colonize such adverse environments. The results of this study suggest that groups of cooperators could colonize such environments if the groups were sufficiently large (larger than the unstable IFP) and the effectiveness of their

cooperative interactions sufficiently strong to overcome particular levels of demographic or environmental hardship (as determined by the parameters r and c) (equations 4 and 5 and Fig. 3).

The naked mole rats are a dramatic example of this situation, as these organisms are only able to inhabit the inhospitable deserts of eastern Africa by cooperatively searching for new food patches during the short windows of time that unpredictable rains permit digging (Jarvis *et al.*, 1994). Among the cooperative breeding birds, the white-fronted bee-eaters (Emlen and Wrege, 1991) and the white-winged choughs (Heinsohn, 1992) are examples in which sparse and unreliable food resources make the presence of helpers indispensable to prevent nestling starvation. Several other examples could be used to illustrate this situation, as colonization of ecologically or demographically adverse environments may have been the most common cause behind social evolution (for a recent review covering vertebrates and wasps, see Brockmann, 1997).

A question that remains, however, is whether harsh demographic or ecological conditions are *necessary* for sociality to evolve. It is possible that sociality may also have arisen in species sitting comfortably in a region of sustainable growth, if, by cooperating, individuals could gain access to rich and otherwise inaccessible resources (Slobodchikoff, 1984; Packer and Ruttan, 1988). Potential examples of this second alternative are the conifer-bark beetles, which, by attacking *en masse*, are able to overcome the defences of live trees (Raffa and Berryman, 1987) and some of the cooperative hunters such as wolves (Moehlman, 1986) and social spiders (Buskirk, 1981; Avilés, 1997), which by hunting in groups are able to gain access to a range of prey sizes unavailable to non-social species of a similar body size (Macdonald, 1983; Packer and Ruttan, 1988; Uetz, 1992).

Once groups of cooperators have formed, the next question to be addressed concerns the forces responsible for shaping those societies into loosely connected or highly cohesive entities. Again, consideration of the non-linear effects of cooperation on individual fitness may suggest some answers. A unimodal fitness function, for instance, suggests that individuals would tend to remain affiliated with groups that have not yet reached their stable size. More humped fitness functions could, then, produce more tightly knit social groups. Likewise, fitness functions that cover a wide range of colony sizes may lead to groups that last for multiple generations, if the groups are small when founded. For sufficiently humped fitness functions, however, stability considerations become critical, as such functions predict that groups should exhibit a boom-and-bust pattern of growth, becoming overcrowded and then either crashing or dispersing in the next generation.

It is important to emphasize that the prediction of dynamical instability, unlike the persistence results discussed above, requires that the assumptions of discrete generations and lack of resource monopolization within the groups are met. If growth were continuous, for instance, the groups could readily modulate their size around the stable equilibrium, so that overshoots and crashes would not occur. Likewise, if some individuals within the groups were able to monopolize resources through contest competition, then dynamical instability could be prevented (Lomnicki, 1978; Lomnicki and Sedziwy, 1989). With continuous growth, however, overshoots and crashes could still occur if there were sufficiently large time delays in the feedback mechanisms controlling colony growth (see Smith and Mead, 1980). Also, an uneven distribution of resources, without resource monopolization, is expected to be insufficient to stabilize the dynamics (Lomnicki and Sedziwy, 1989).

Whether and how frequently intrinsically driven unstable dynamics are characteristic of animal social systems is a question that needs to be addressed empirically. A potential

example in a system in which groups last for multiple generations are the above-mentioned cooperative spiders. The colonies of some of these species have been observed to exhibit abrupt changes in size and to be subject to relatively high rates of turnover (for a recent review, see Avilés, 1997). Locally unstable dynamics in these systems may have arisen as a consequence of the inherent proliferation advantage of faster growing colonies (e.g. Avilés, 1993). A balance between colony extinction and proliferation could then have been reached at the metapopulation level (Avilés, 1997). An interesting possibility is that the dynamics of these groups may not only be unstable, but also chaotic, since, as suggested by Allen *et al.* (1993), chaotic dynamics of the subunits in a metapopulation would enhance global persistence despite the inherent instability at the local population level. In systems that last one or very few generations, the qualifiers 'periodic' and 'chaotic' would not apply, although dynamical instability might still play a significant role. Unstable dynamics, for instance, may underlie the abrupt switch to the production of alates, followed by colony death, which is characteristic of certain social insect species (e.g. Brian, 1965, p. 54).

Even in those social systems in which the conditions leading to unstable dynamics are not currently met, dynamical instability might have been a factor in their past evolutionary history. In particular, the existence of a second region of deterministic extinction at large values of r and γ and small values of c (Fig. 3) suggests strong selection to prevent the evolution of extreme parameter values. An interesting possibility that requires further exploration is that, near the boundary between chaos and extinction, selection against dynamical instability will occur primarily at the level of colonies. The necessary genetic structure of small within-group and large between-group variance may be present in this region because, owing to the strong synergistic effects of cooperation, individuals would tend to be bound to their colonies. Simultaneously, the opportunity for inter-colony selection to take place would be heightened because dynamical instability would result in large rates of group turnover. Inter-colony selection against extreme dynamical instability might explain, for instance, the reduction in brood size, relative to solitary related species, that has been documented in some of the cooperative spiders discussed above (Kullmann, 1972; Buskirk, 1981; Avilés, 1997), or the monopolization of resources and reproduction that may have contributed, in some instances, to the evolution of eusociality. In more highly integrated societies, such as those of ants or termites, unstable dynamics could have been suppressed, without a reduction in the rate of increase, by improving the feedback mechanisms responsible for the control of colony growth. This could be accomplished by reducing the time delay in the feedback response to changes in colony size and, effectively, violating the assumption of discrete generations of the model.

The finding that in the presence of cooperation, and only then (see Results), a decrease in the crowding parameter (or an increase in the group carrying capacity) leads to transitions from simple to complex dynamics also has implications for social evolution. Because sociality may expand the pool of resources available to a species (e.g. making live trees available for colonization by bark beetles; Raffa and Berryman, 1987) or increase individual tolerance to crowding (Wilson, 1975), this result suggests that cooperation, in addition to having a direct dynamical effect, may further increase the opportunity for unstable dynamics by releasing the limits to maximum colony size. This effect may lead to a positive feedback loop by which groups of cooperators may be swept into increasingly more complex social systems (see below).

Another set of predictions emerges from considering the effects of the model parameters, and cooperation in particular, on the typical sizes of the social groups (Table 2). At the

lower end of the range, a minimum – and under some conditions a sizeable – number of cooperating individuals (corresponding to the intermediate unstable equilibrium) might be required for persistence in species occurring near the lower extinction region. An example of this minimum size requirement are the white-winged choughs of south-eastern Australia, which require the participation of at least four individuals to successfully raise one chick a year (Heinsohn, 1992). At the high end of the range, the size of social groups is expected to be larger in species in which cooperation has a stronger synergistic effect (Table 2). The latter prediction is consistent with observations that, within certain clades of bees and wasps, for instance, larger colony sizes are typical of species with more complex social systems (Brian, 1965; Ross and Matthews, 1991). These results further suggest that the characteristic size and range of animal societies could be used as indicators of where in the r , γ and c parameter space a particular species sits: species whose social groups never drop below at least a few individuals (unless they are headed for extinction) probably occur near the lower boundary between absence and persistence, whereas species whose colonies can be successfully established by a single individual, and that may attain very large sizes, probably occur deeper within the range of dynamical regimes depicted in Fig. 3.

The present results suggest the following scenario for the evolution of highly complex social systems from asocial ancestral species: Populations consisting initially of solitary individuals may have coalesced into groups as a result of selection to colonize harsh or unpredictable environments or to gain access to previously inaccessible resources. Once formed, the groups may in some cases have moved into richer environments or become increasingly efficient in accessing those resources. This effect would have further ‘pulled’ upwards the individual fitness function, increasing the interdependency of group members, increasing group cohesiveness, and making unstable dynamics more likely. Dynamical instability may then have led to a relatively high rate of group turnover owing to higher rates of group extinction and proliferation. Rapid turnover of increasingly more cohesive social groups could then have made inter-colony selection the primary evolutionary force. At that point, the stage would have been set for the evolution of traits that could give the social groups superorganismic qualities (Wheeler, 1911; Seeley, 1989; Wilson and Sober, 1989) and, I would argue, for the origin of a new level of organization. Cooperation, therefore, may not have provided simply the glue that brought together individuals into social groups, but also the fuel by which such groups could, in some instances, spiral up through a positive feedback loop into more highly integrated and autonomous entities.

In conclusion, the model presented here expresses in simple and general terms the demographic and ecological conditions that, on the one hand, would select for social living, and, on the other, might lead to colonies that are cohesive enough and subject to a large enough rate of turnover to become units on which selection could act. Consideration of the dynamical effects of cooperation may thus shed light both on the forces leading to, and those resulting from, social living. Finally, the results presented here bring the discussion of social evolution back into the realm of ecology, an area that, as pointed out by Slobodchikoff and Shields (1988; see also Strassmann and Queller, 1989), has been temporarily overshadowed by the emphasis on genetics and relatedness that followed Hamilton’s seminal paper on inclusive fitness (Hamilton, 1964). A synthesis now seems warranted as, in my opinion, and using Wilson’s terminology (Wilson, 1975), the prime movers of social evolution lie in the ecological conditions that can make cooperation either necessary ($r < 0$) or enticing (e.g. tapping into richer resources). I argue, therefore, that only by fully incorporating ecological and population dynamical considerations in the study of

animal sociality will we be able to gain an understanding of the forces that brought together individuals into loosely connected or highly cohesive social groups. Because the processes that have given rise to the diversity of life have often involved the association of lower level units into higher levels of organization (Maynard Smith and Szathmáry, 1995), an appreciation of the forces behind social evolution may also shed light on other fundamental processes in the history of life.

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APPENDIX 1

Equation (1) can be shown to be dimensionless by introducing a fourth parameter, n_0 , which represents the threshold number of individuals above which cooperative efforts have a synergistic effect. With this new parameter, and expressing the crowding parameter as the inverse of a carrying capacity parameter, K , we have:

$$f(n) = \left(\frac{n}{n_0} \right)^{\gamma} e^r e^{-(1/K)n} \quad (\text{A1})$$

Rescaling by n_0 we recover equation (1), where $N = n/n_0$ and $c = n_0/K$. The dimensionless N can now be taken to represent any type of measure of group size, including number of individuals, biomass, density, etc.

APPENDIX 2

The equations of the surfaces marking the transitions from absence to persistence and from point equilibria to cycles can be obtained by evaluating the derivative (i.e. the slope) of equation (2) (see text) at the points at which (a) a non-trivial stable fixed point is born via a tangent bifurcation and (b) when this stable fixed point first becomes destabilized and bifurcates into a 2-point cycle via a period-doubling bifurcation. Using standard techniques, it can be shown that the derivative of equation (2) is:

$$\frac{dF(N_i)}{dN} = e^r e^{-cN_i} N_i^{\gamma} (1 + \gamma - cN_i) = f(N_i)(1 + \gamma - cN_i)$$

Evaluated at the tangent bifurcation (where $f(N_i) = 1$ and the slope of the map is equal to +1), this reduces to:

$$cN^* - \gamma = 0 \quad (\text{A2})$$

Similarly, evaluated at the first period-doubling bifurcation (where $dF(N_i)/dN = -1$ and $f(N_i) = 1$) gives:

$$cN^* - \gamma = 2 \quad (\text{A3})$$

The fixed points, obtained by setting $f(N_i)$ from equation (2) to 1, can be evaluated from the following implicit relationship:

$$r = cN^* - \gamma \ln N^* \quad (\text{A4})$$

Solving for the fixed point at the tangent and first period-doubling bifurcation using equations (A2) and (A4), or (A3) and (A4), yields the following explicit solutions, with the restriction that $\gamma > 0$:

$$N^* = e^{(\gamma-r)/\gamma}, \text{ at the tangent bifurcation} \quad (\text{A5})$$

$$N^* = e^{(\gamma-r+2)/\gamma}, \text{ at the period-doubling bifurcation} \quad (\text{A6})$$

Substituting (A5) into (A2), still with the restriction that $\gamma > 0$, yields the following solution for the surface in the three-parameter space separating absence from persistence (i.e. extinction from point equilibria):

$$c e^{(\gamma-r)/\gamma} - \gamma = 0 \quad (\text{A7})$$

And substituting (A6) into (A3), again with the restriction that $\gamma > 0$, gives the following solution for the surface separating point equilibria from complex population dynamics:

$$c e^{(\gamma-r+2)/\gamma} - \gamma = 2 \quad (\text{A8})$$

When $\gamma = 0$, $N^* = r/c$ (from (A4)), and the transitions between absence and persistence and point equilibria and complex dynamics occur at $r = 0$ and $r = 2$, respectively.