

Group size, energy budgets, and population dynamic complexity

Karen E. Trainor and Thomas Caraco*

Department of Biological Sciences, University at Albany, Albany, NY 12222, USA

ABSTRACT

Question: If the size of foraging groups directly influences the probability that individuals starve before reproduction, how does increasing group size affect the consumer population's dynamic complexity?

Key assumptions: We partition a population into foraging groups that must search for food. Food per individual forager varies inversely with population density; social interaction within groups amplifies or attenuates the degree of density-dependent starvation. Mortality from predation increases with forager population density. Individuals surviving both predation and starvation go on to breed. Combining mortality and reproduction yields a generalized Ricker map for the population dynamics.

Ranges of key variables: The rate at which an individual finds food clumps decreases with, does not depend on, and then increases with group size. The variance in the food energy per clump is less than, equal to, and then exceeds mean clump size. We also vary the total energy intake required to avert starvation.

Conclusions: (1) When foragers interfere with each other's search for food, and/or when the energy intake required to avoid starving is sufficiently large, increasing foraging group size induces dynamic overcompensation. Consequently, the population dynamics follows the period-doubling route to chaos as group size increases. The cause of overcompensation lies in the inverse relationship between group size and the variance of an individual's total energy consumption. (2) When foragers enhance each other's food discovery, larger groups stabilize the population dynamics. Depending on the particular energy requirement, increasing group size generates a period-halving bifurcation, or the dynamics equilibrates at a stable node for each group size evaluated.

Keywords: chaos, dynamic complexity, group size, starvation probability.

INTRODUCTION

When animals live in persistent social groups, a group's size may directly regulate individual demographic performance (Avilés, 1999; Sumpter and Broomhead, 2001; Krause and Ruxton, 2002). Therefore, social group size may indirectly govern population dynamic complexity (Sutherland, 1996; Giraldeau and Caraco, 2000; Lett *et al.*, 2004). To explore this hypothesis, we model a population partitioned

* Author to whom all correspondence should be addressed. e-mail: caraco@albany.edu
Consult the copyright statement on the inside front cover for non-commercial copying policies.

into groups, and let group size modulate the impact of resource competition on mortality. Specifically, we assume that both density-dependent food availability and foraging group size influence the likelihood an individual consumes enough energy to avoid starvation before breeding. As a result, we find that population density may equilibrate stably or fluctuate chaotically, depending on group size.

We analyse combinations of (1) group-size-dependent food-encounter rate, (2) variance in the amount of food discovered per encounter, and (3) total food intake required to avoid starvation. Within-group behavioural interactions determine whether each individual discovers food at an accelerating or decelerating rate as group size increases. Following a seasonal foraging period, the fraction of the population surviving the hazards of starvation and predation reproduces, and so completes the annual cycle. Hence, non-breeding survival limits the breeding population (Jansson *et al.*, 1981). Our assumptions concerning population dynamics produce a modified Ricker map (Ricker, 1954) with more general properties (Stone, 1993). We quantify the map's dynamic complexity with the Lyapunov exponent (Alligood *et al.*, 1997), and demonstrate computationally that the degree of complexity can depend on group size and behavioural interactions within groups.

Our study roughly parallels Avilés's (1999) analysis of a discrete-time growth model for deme size. She demonstrates that behavioural cooperation can stabilize or destabilize the dynamics, depending on external parameters. At one extreme, cooperation and group living allow colonization of habitats or ecological niches where solitary individuals cannot persist. Consequently, cooperation promotes dynamic stability and helps avoid population extinction. At the other extreme, cooperation may cause a deme to fluctuate in size and so be subject to high turnover; in this case cooperation destabilizes the dynamics. Both Avilés's (1999; Avilés *et al.*, 2002) work and our results suggest that social interactions, processes at the among-individual level, may interact with non-linear population growth to produce patterned variation in dynamic complexity.

GENERAL ASSUMPTIONS

We structure a non-breeding population solely by the size of feeding groups. We fix total food availability; consequently, the expected energy intake per forager declines as global population density increases. Both group size and global population density affect the chance of starvation. Mortality due to predation depends on population density, but not on group size.

Starvation and predation occur independently, and their effects are realized at different scales. Predation acts at the level of individuals; foragers encounter predators mutually independently. Each member of a given group consumes the same amount of food during the non-breeding season; this level of energy intake, a realization of a random process, either meets the individual's energy requirement or does not. Hence all members of that particular group either starve or avert starvation. Individuals in other (identical) groups, foraging in the same environment, experience different outcomes; variation in survival due to starvation occurs among groups. This assumption simplifies translation of random processes into a deterministic population dynamics. In the Discussion, we address a more general partitioning of variation in starvation among and within groups.

Let n_t represent global population density during the non-breeding season of year t . The map $n_{t+1} = F(n_t)n_t$ links densities of consecutive non-breeding seasons. The time-dependent population growth rate, $F(n_t)$, is the product of the proportion of the population whose

energy consumption meets the level required to avert starvation, the proportion of non-breeders surviving predation, and the reproduction parameter R . Below we fix the value of the reproduction parameter R (see Neubert, 1997). Note that we equate two population-level survival proportions with survival probabilities for groups (of equal size) and individuals. We can question the validity of this assumption at low population density, where extinction becomes a concern (Thrall *et al.*, 1995; Caraco *et al.*, 2001; O'Malley *et al.*, in press). Therefore, our computations include an analysis of population extinction risk, as a function of group size.

GROUP SIZE AND MORTALITY HAZARDS

Discovering resources

Each group has G members. We fix G within and among generations to compare population-dynamic consequences of different group sizes.

During the non-breeding season, groups encounter divisible food clumps (Clark and Mangel, 1984, 1986; Caraco and Giraldeau, 1991; Ruxton *et al.*, 1995) at a constant probabilistic rate λG^α ($\lambda, \alpha > 0$). A solitary's ($G = 1$) encounter rate λ should increase with the environment's total resource density ρ , and should decline as the density of consumers exploiting the resource increases. For simplicity, we assume that $\lambda = \rho/n_t$ in year t .

Within-group social interaction, modelled by the G^α term, also affects the rate of food discovery. If $\alpha < 1$, the average rate at which food is discovered *per group member* decreases with group size. $\alpha < 1$ implies either inefficiency [e.g. groups alert their prey (Goss-Custard, 1976)] or competitive interference among foragers (Goss-Custard and Durrell, 1987). If $\alpha > 1$, the average rate at which food is discovered per group member increases with group size. $\alpha > 1$ suggests mutualism: complementary skills enhance searching efficiency (Giraldeau and Caraco, 2000), or group members forage cooperatively (Pusey and Packer, 1997). [For a discussion of social effects on resource discovery, see Clark and Mangel (1986), Mangel (1990), Koops and Giraldeau (1996), or Krause and Ruxton (2002).]

For $\alpha < 1$, the inverse relationship between an individual's rate of clump discovery and group size need not always imply a greater chance of starvation in larger groups. The variance in food consumption also may be reduced as group size increases (Caraco, 1987; Ekman and Rosander, 1987), and the starvation probability depends on both mean and variance.

Given that a group locates food clumps at a constant probabilistic rate $\lambda G^\alpha = \rho G^\alpha/n_t$, let β_G represent the total number of clumps discovered by a group of G during the non-breeding season. β_G varies randomly, since food discovery is a Poisson process. Therefore, both the mean $\langle \beta_G \rangle$ and variance $V[\beta_G]$ equal $\rho G^\alpha/n_t$.

Next, consider the energy within a food clump. The total energy value of a single clump is c , a random variable. For $i = 1, 2, \dots, \beta_G$, the clump sizes c_i are independent and identically distributed; $\langle c \rangle = 1$, and V_c is the clump-size variance. Setting mean clump size equal to unity scales measurement of energy without losing generality (Ekman and Rosander, 1987). We assume that group members divide each clump discovered equally.

An individual's total energy intake, and hence its probability of starvation, depends on the number of clumps found (β_G) and the energy per clump (c). E_G represents the total energy consumed by each individual in a group of G during the non-breeding season:

$$E_G = \sum_{i=1}^{\beta_G} c_i / G \quad (1)$$

E_G is a ‘randomly stopped sum of random variables’ (Boswell *et al.*, 1979; Giraldeau and Caraco, 2000). The mean and variance of E_G are, respectively, $\mu_G(n_t)$ and $V_G(n_t)$. From Ekman and Rosander (1987), we have:

$$\mu_G(n_t) = \langle \beta_G \rangle / G = \rho G^{\alpha-1} / n_t \quad (2)$$

since $\langle c \rangle = 1$, and

$$\begin{aligned} V_G(n_t) &= (\langle \beta_G \rangle V_c + V[\beta_G]) / G^2 = \rho G^{\alpha-2} (V_c + 1) / n_t \\ &= \mu_G(n_t) (V_c + 1) / G \end{aligned} \quad (3)$$

The mean and variance of an individual’s energy intake decline as population density increases, but both the mean and variance increase as α increases. The mean intake declines with G when $\alpha < 1$, while the variance declines with G when $\alpha < 2$. Not surprisingly, an individual’s energy-intake variance increases as the amount of food per clump becomes more variable. As long as the number of food clumps discovered is sufficiently large, the central limit theorem allows us to approximate E_G with a normal random variable.

To model the starvation probability, suppose that any forager failing to consume more than Q energy units starves before breeding successfully (Stephens, 1981; Caraco and Brown, 1986; Caraco and Gillespie, 1986; Stephens and Krebs, 1986; Houston *et al.*, 1988). Then the individual’s probability of starvation is:

$$\Pr[E_G \leq Q] \approx \Phi[z_G(Q, n_t)] = \Pr\left[z_G \leq \frac{Q - \mu_G(n_t)}{[V_G(n_t)]^{1/2}}\right] \quad (4)$$

where $\Phi[z_G]$ is the standard normal distribution. We take $(1 - \Phi[z_G])$ as the fraction of the non-breeding population averting starvation, but still subject to predation.

Starvation probability and model parameters

Since $\Phi[z_G]$, expression (4), increases strictly monotonically in its argument, an increase in z_G implies that a greater fraction of the population starves. After substitution, we have:

$$z_G(Q, n_t) = \left[\left(\frac{n_t}{\rho} \right)^{1/2} Q G - \left(\frac{\rho}{n_t} \right)^{1/2} G^\alpha \right] / G^{\alpha/2} (V_c + 1)^{1/2} \quad (5)$$

By inspection, we see that starvation becomes more likely (z_G increases) as either population density n_t or required energy intake Q increases. Just as clearly, an increase in food density ρ reduces the probability of starvation for any given n_t . For $G > 1$, increasing α (lowering the ‘cost of flocking’) reduces z_G , and so reduces the probability of starvation. Each observation matches intuition.

In equation (5), the sign of the numerator determines how z_G varies with V_c , the variance in the amount of food per clump. Therefore:

$$Q > \left(\frac{\rho}{n_t} \right) G^{\alpha-1} \Rightarrow \partial z_G / \partial V_c < 0 \quad \text{and} \quad Q < \left(\frac{\rho}{n_t} \right) G^{\alpha-1} \Rightarrow \partial z_G / \partial V_c > 0 \quad (6)$$

Starvation becomes less likely as V_c increases if the energetic requirement Q exceeds the forager’s expected energy consumption $\mu_G(n_t)$, defined by equation (2). However, starvation

becomes more likely as clump-size variance increases if the forager requires less energy than it expects to consume. That is, increasing the variance of the energy obtained per food clump can reduce the probability of starvation, if population density is large enough to drive expected *per capita* energy consumption below the requirement. However, the same increase in clump-size variance can increase the probability of starvation if the forager can expect to find more than enough food to meet its physiological requirement. Consequently, random variation in clump size affects starvation probabilities in a manner recalling a behavioural ‘energy budget rule’ (Caraco *et al.*, 1980; Stephens and Charnov, 1982; Houston and McNamara, 1986; Ekman and Rosander, 1987; Lovegrove and Wissel, 1988; Mangel, 1990). Given a mean energy-intake level, effects of clump-size variance directly translate to effects of energy-intake variance $V_G(n_t)$, by equation (3), and we emphasize the latter variance below.

The probability of starvation also varies with group size. $\partial z_G / \partial G$ has the sign of:

$$(1 - \alpha/2)Q - (\alpha\rho/2n_t)G^{\alpha-1} = (1 - \alpha/2)Q - (\alpha/2)\mu_G(n_t) \quad (7)$$

For $\alpha \geq 2$, the likelihood of starvation decreases as group size increases, since an individual’s clump-discovery rate and expected energy intake increase so rapidly with G . If $0 < \alpha < 2$, the probability of starvation *may* decrease as group size increases, depending on parameter values. Suppose $\alpha = 1$, so that the individual’s clump-discovery rate is independent of group size. For this case, the chance of starvation increases with group size if $Q > \mu_G(n_t)$; that is, when the requirement exceeds expected intake. But the probability of starvation declines as group size increases if mean intake exceeds the requirement. Now suppose that $Q = \mu_G(n_t)$, a ‘neutral energy budget’ (Caraco *et al.*, 1990). For this case, the chance of starvation declines with group size if $\alpha > 1$. But starvation increases with group size if $\alpha < 1$, where inefficiency or aggressive interference among foragers imposes a cost of flocking. Combining specifics, we see that if $\mu_G(n_t) \geq Q$, then:

$$\alpha \geq 1 \Rightarrow \partial z_G / \partial G \leq 0 \quad (8)$$

Below we use this relationship to link dynamic complexity and group size.

Predation hazard

We assume that predator density P_t scales with consumer density, so that each forager independently encounters a fatal predatory attack at a constant probabilistic rate kP_t . Since $P_t \sim n_t$, let $kP_t = \zeta n_t$. Then, the *per capita* hazard of predation increases with population density, and the probability that an individual forager survives the non-breeding season (of unit duration) without suffering a fatal attack is $\exp[-\zeta n_t]$. We take this probability as the proportion of the non-breeding population surviving predation, but not necessarily avoiding starvation.

THE RETURN MAP

As indicated above, the map between consecutive non-breeding densities depends on the product of the probability of averting both starvation and predation and the reproduction parameter R . Since mortality hazards are independent, we have:

$$n_{t+1} = R(1 - \Phi[z_G])e^{-\zeta n_t} n_t \quad (9)$$

Equation (9) resembles the well-known Ricker map (May, 1976; Sumpter and Broomhead, 2001) and can be termed ‘Ricker-type’ (Avilés, 1999). The unique feature is that z_G depends on global density n_t through the distribution of individual energy consumption.

Given parameters (R, α, V_c, Q) , the continuous return map possesses a single maximum, and the map’s shape is governed solely by group size G . These simple properties imply that equation (9) could belong to the class of one-dimensional maps exhibiting a bifurcation-structure universality (Feigenbaum, 1978) where increasing the governing parameter G produces the period-doubling route to chaos (Kaplan and Glass, 1995). That is, the number of stable periodic points doubles at consecutive bifurcations, until the governing parameter reaches a critical value and the dynamics enters the chaotic regime, where bounded, aperiodic trajectories (chaotic orbits) emerge. Further increases in the governing parameter reveal that the chaotic regime also contains windows of stable periodic behaviour (May, 1976). Both the Ricker map and the familiar logistic map (May and Oster, 1976; Kot and Schaffer, 1984) are members of this universality class.

Below we report that increasing group size can produce the period-doubling route to chaos, but some parameter combinations result in period-halving bifurcations [termed antimonotonicity (Alligood *et al.*, 1997)]. Stone (1993) shows that minor changes to chaotic return maps, alterations consistent with reasonable ecological assumptions, may reverse the march towards chaos. That is, altering the return map may produce transitions in the dynamics where increasing the governing parameter (G) halves the number of stable periodic points. Stone (1993) adds immigration to the logistic map, and the resulting dynamics maintains simple population cycles of low period; Ruxton and Rohani (1998) extend the analysis. Our results link combinations of within-group interaction and energy-intake variance to the way dynamic complexity varies with group size.

Group size and dynamic complexity

Suppose that $n^* > 0$ is a positive equilibrium node, so that $n_{t+1} = n_t = n^*$ in equation (9). Of course, n^* depends on group size and parameter values. Let D_n represent the derivative of the population growth function, $F(n_t)$, with respect to global density. Local stability of the positive equilibrium node n^* requires $|D_n(n^*)| < 1$; equivalently,

$$-2 < n^* \left(\frac{dF}{dn_t} \right)_{n^*} < 0 \quad (10)$$

where

$$\left(\frac{dF}{dn_t} \right)_{n^*} = R e^{-\xi n^*} \left(\zeta [\Phi[z_G] - 1]_{n^*} - \left[\frac{\partial}{\partial n_t} \Phi[z_G] \right]_{n^*} \right) \quad (11)$$

is the derivative of the *per capita* growth function evaluated at n^* . $\Phi[z_G]$, a probability, < 1 , and $(\partial \Phi[z_G] / \partial n_t)_{n^*} > 0$, since starvation probability increases as population density increases. Therefore, $(dF/dn_t)_{n^*}$, hence D_n , must be negative at a positive equilibrium node.

For return maps generating period-doubling bifurcations, an increase (decrease) in dynamic complexity requires an increase (decrease) in $|D_n(n^*)|$ (May and Oster, 1976; Kaplan and Glass, 1995). We address this topic, particularly entry into the chaotic regime, more carefully below. But we can anticipate that different group sizes, both through direct effects on $\Phi[z_G]$

and through the starvation probability's sensitivity to global density (i.e. through $(\partial\Phi[z_G]/\partial n_t)_{n^*}$), influence dynamic complexity. From expressions (7) and (8), we expect increasing group size to reduce the chance of density-dependent starvation only when $\alpha \geq 1$ and Q is not too large. But increased group size will amplify density-dependent starvation when $\alpha < 1$, especially if the energy requirement Q is large. So, when a larger group enhances an individual's rate of food discovery, complexity of the population dynamics should not increase (and may decrease) as group size increases. Equivalently, if (α/Q) is sufficiently large, increasing group size may cause $|D_n(n^*)|$ to decline. Consequently, population growth just exceeding n^* need not be followed by a 'crash', caused by an abrupt increase in starvation. On the other hand, when a larger group diminishes an individual's rate of food discovery, density dependence gains strength with group size. That is, a smaller (α/Q) can imply stronger overcompensation, so that larger groups might induce more complex population dynamics.

Increasing dynamic complexity implies that the temporal variance in population densities should also increase. Generally, greater variability in population density increases the likelihood that additional, random effects could induce local extinction (Allen *et al.*, 1993). Below we report the frequency of visits to various population-density bins (Peitgen *et al.*, 1992; Roughgarden, 1998) and find patterns linking group size, population dynamics, and exposure to chance extinction.

The Lyapunov exponent

The hallmark of chaos is sensitivity to initial conditions (Hastings *et al.*, 1993; see Neubert, 1997). That is, nearby trajectories diverge; similar initial population densities lead to different temporal records. Sensitivity to initial conditions distinguishes chaos from dynamics exhibiting stable nodes or stable cycles, and we detect this difference with the Lyapunov exponent.

Consider any initial density $n_0 > 0$. We repeatedly apply equation (9), and calculate a series of points to obtain the orbit of n_0 . That is, we obtain the temporal sequence of population densities $\{n_0, n_1, n_2, \dots, n_m\}$. For the orbit beginning at n_0 , the Lyapunov exponent $h(n_0)$ is defined as (Alligood *et al.*, 1997)

$$h(n_0) = \lim_{m \rightarrow \infty} \left(\frac{1}{m} \right) \sum_{t=0}^{m-1} \ln |D_n(n_t)| \quad (12)$$

provided this limit exists; $h(n_0)$ is undefined if any $D_n(n_t) = 0$. D_n , the derivative of the growth function with respect to n_t (see expression 10), is evaluated at each point of the orbit. Given our deterministic computations, we can estimate the Lyapunov exponent $h(n_0)$ from a finite (but lengthy) sequence of m consecutive values of the growth function (Peitgen *et al.*, 1992). Short time-series and/or noise make the problem far more challenging (e.g. Godfray and Blythe, 1990; Olsen and Schaffer, 1990; Sugihara *et al.*, 1990; Ellner and Turchin, 1995; Hunt *et al.*, 2003).

The Lyapunov exponent depends on the average per-iteration divergence of nearby points on the orbit. For stable nodes and stable cycles, $h(n_0) < 0$, since different trajectories ultimately must converge. A chaotic orbit, in contrast, forever exhibits the instability of dynamics near a repeller. At any point of a chaotic orbit, there are points arbitrarily near that move away upon further iteration of the map (Hastings *et al.*, 1993; Alligood *et al.*, 1997). That is, nearby trajectories diverge, and $h(n_0) > 0$ for chaotic dynamics. Finally, the Lyapunov exponent is zero at a bifurcation. Therefore, $h(n_0)$ increases as dynamic complexity increases.

The Appendix provides details about computing orbits of the return map, and our calculation of the Lyapunov exponent.

RESULTS

We studied the return map's behaviour by varying each of three parameters over three levels. We let the behavioural-interaction parameter $\alpha = 0.8, 1.0,$ and 1.2 to model non-cooperative, independent, and mutually enhanced clump-discovery respectively. We set clump-size variance V_c at $0.5, 1.0,$ and 1.5 ; recall that mean clump size was always 1.0 . We let the energy requirement $Q = 8, 10,$ and 12 . We fixed the reproductive parameter $R = 4$, and kept the *per capita* predation rate $\xi = 0.03$. We let the initial population density $n_0 = 5$ throughout.

For each of the 27 different combinations of (α, V_c, Q) , we iterated the return map for group sizes 1 through 32, advancing in units of 0.1; this graining of G nicely reveals patterns in the dynamics. We discarded the first 200 returns of each orbit to avoid effects of transient population dynamics, and analysed the next 1000 n_t values. We associated an 'extinction risk' with an orbit's parameters whenever n_t fell below 0.01, an arbitrary choice. To organize our results, we first report population dynamics, and then interpret the observed complexity in terms of each group member's energy intake and the associated starvation probability.

Pattern in the dynamics

Given values for α and Q , the dynamics exhibited only minor variation across the three levels of clump-size variance V_c . Therefore, we categorize the dynamics by the different (α, Q) -combinations. Table 1 shows that for $\alpha = 0.8$ (where foragers hamper each other's search), increasing group size produced a bifurcation cascade to chaos at each level of the required energy intake Q .

When we increased α to 1.0 (where foragers search independently), dynamic complexity increased as the requirement Q increased. That is, population density equilibrated at a stable node for $Q = 8$, and cycled stably with a period ≤ 4 (depending on group size) when $Q = 10$. However, when we increased Q to 12, the dynamics again followed the period-doubling route to chaos as group size increased.

Table 1. Behaviour of return map as group size increases from 1 to 32

α	Q		
	8	10	12
0.8	BC	BC	BC
1.0	SN	SC	BC
1.2	SN	PH	PH

Note: α is the within-group interaction parameter, and Q is intake required to avert starvation. Dynamics varies quantitatively, but not qualitatively, with clump size variance V_c . Results include bifurcation cascades and chaos (BC), stable cycles of low period (SC), period-halving bifurcations leading to a stable node (PH), and stable nodes (SN).

Finally, we increased α to 1.2 (where foragers enhance each other's search). The dynamics equilibrated at a stable node for $Q = 8$, and decreased in complexity as group size increased, via period-halving bifurcations (a two-cycle became a stable node), at both $Q = 10$ and 12.

The computed dynamics indicates that cooperative search for shared food and a lower energy requirement lead to a stable equilibrium density n^* or to stable cycles at all group sizes analysed. When the dynamics produced a stable node for all group sizes, the equilibrium density increased, though only slightly, as G increased. Behavioural interference (lower values of α) and/or a greater energy requirement increased dynamic complexity. In this case, increasing group size quickly led to chaos at the population level.

Figures 1 and 2 plot bifurcation cascades, and the associated Lyapunov exponents, for two ($\alpha \leq 1$, Q) combinations. In each, the chaotic regime commences before G exceeds 7; the figures show that further increases of group size reveal periodic windows. Note the structural similarity of the two bifurcation plots. Figure 3 has the Q and V_c values of Fig. 2,

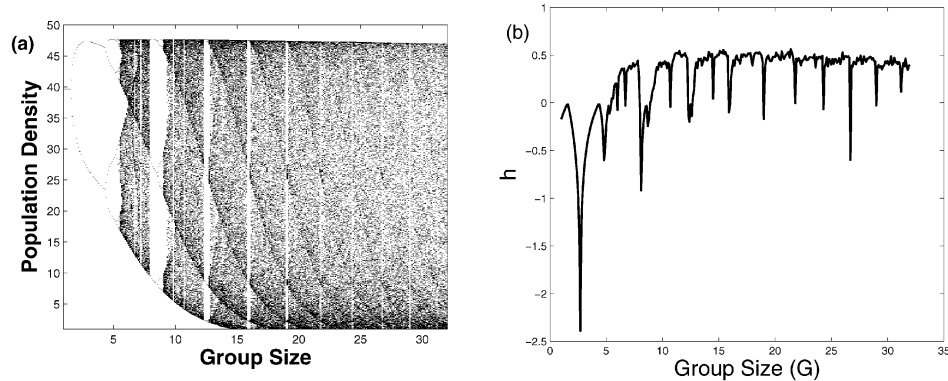


Fig. 1. (a) Bifurcation diagram. $\alpha = 0.8$, $Q = 8$, and $V_c = 1.0$. Ordinate is population density $n(t)$; abscissa is group size G . Note periodic windows in the chaotic region. (b) Lyapunov exponent (h) for orbits generating the bifurcation diagram. Lyapunov exponent is negative for stable dynamics (node or cycle), zero at a bifurcation, and positive for chaotic dynamics.

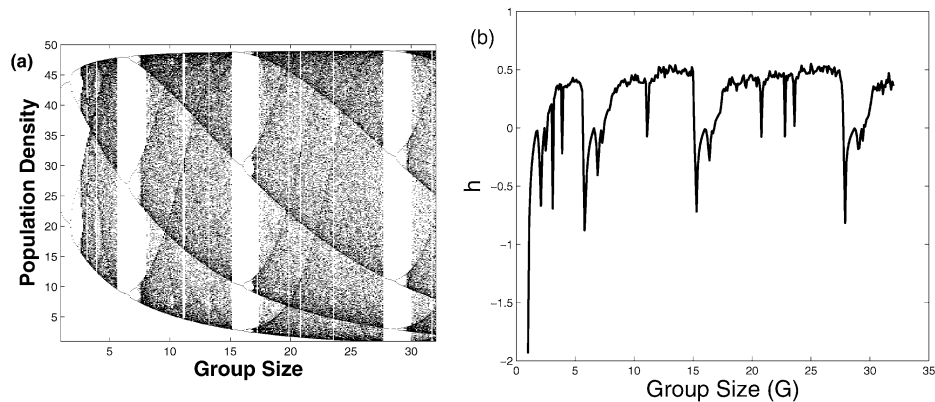


Fig. 2. (a) Bifurcation diagram. $\alpha = 1.0$, $Q = 12$, and $V_c = 1.0$. Note structural similarity to Fig. 1a. (b) Lyapunov exponent for orbits generating the bifurcation diagram.

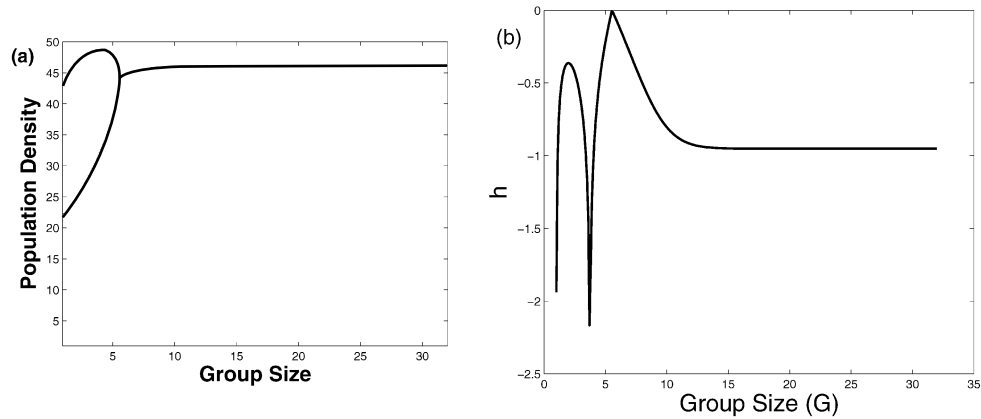


Fig. 3. (a) Bifurcation diagram. $\alpha = 1.2$, $Q = 12$, and $V_c = 1.0$. Note period-halving transition. (b) Lyapunov exponent for dynamics. Lyapunov exponent is negative everywhere except for period-halving bifurcation, where it is zero.

but α is increased to 1.2. The larger α (cooperative search) produces a plot with a single, period-halving bifurcation; a two-cycle becomes a stable node at $G \approx 6$.

Extinction risk

Recall that we associated an extinction risk with a trajectory if the population density fell below 0.01 at any time. For our parameter values, only some chaotic fluctuations reached such low densities. Any trajectory with $\alpha = 1.2$ averted extinction risk, since the dynamics was stable. For $\alpha = 1.0$, the largest energy requirement produced a bifurcation cascade and chaos, but population density never fell below 0.01, for any group size, over the 1000 iterations of the return map.

For $\alpha = 0.8$, increasing group size generated a bifurcation cascade at each level of required energy intake (Table 1), and the trajectories commonly generated extinction risk. So, for each ($\alpha = 0.8$, Q , V_c) combination, we identified G_{ex} as the smallest integer group size where population density fell below 0.01. Table 2 shows the G_{ex} results. The smallest group incurring an extinction risk decreased as the required energy intake increased, and G_{ex}

Table 2. Extinction risk, where entries are G_{ex} , the smallest (integer) group size where dynamics took global density below 0.01

V_c	Q		
	8	10	12
0.5	21	12	8
1.0	25	14	9
1.5	28	16	11

Note: Results based on computations with $\alpha = 0.8$.

increased as clump-size variance increased. Of course, groups larger than G_{ex} also risked extinction, except for group sizes where periodic windows emerged.

Energy-intake variance and population dynamics

Next we address relationships between foraging processes at the level of groups and dynamical patterns at the population level. The link between the starvation probabilities and population dynamics depends, in part, on the variance of an individual's total energy consumption, $V_G(n_t)$ (see equation 3). To motivate the results discussed below, consider a simplification.

Suppose $V_G(n_t) \rightarrow 0$. Then all individuals (hence groups) have essentially the same energy intake. If intake exceeds the requirement, most individuals/groups survive, and the population can grow. But should the requirement exceed the intake, most individuals and groups starve, given the lack of intake variability. A smaller energy-intake variance can first delay, and then sharpen, the onset of density-dependent starvation, and so contribute to overcompensation. In contrast, a greater energy-intake variance blunts the transition from population increase to decline as global density increases. Some groups starve when mean intake exceeds the requirement, and some groups avoid starvation when the requirement exceeds expected energy consumption. Hence a greater energy-intake variance moderates transitions between population growth and decline, and so diminishes the likelihood of overcompensation.

Our results suggest that increasing group size destabilizes population dynamics, and increases extinction risk when individuals interfere with each other's search for food. But larger groups stabilize the dynamics when mutualism enhances resource-encounter rates. The value of α directly affects changes in energy-intake mean and variance with increasing group size, and so indirectly affects changes in density-dependent starvation probabilities.

For $\alpha < 1$, both the mean and variance of an individual's energy intake decline as group size increases; at the same time, larger groups produce period-doubling bifurcations and chaotic dynamics at each required-energy level. As global density n_t increases, expected energy budgets must eventually shift from positive ($\mu_G(n_t) > Q$) to negative ($\mu_G(n_t) < Q$) for groups of any size. In *small* foraging groups, the greater mean intake implies that this energy-budget shift will occur at a greater global density, where predation plays a stronger regulatory role (see below). The greater intake variance in small groups induces a relatively gradual increase in the chance of starvation as density increases. The increased effect of mortality from predation and the variance-mediated response of starvation probabilities avoid dynamic overcompensation when group size is small enough.

Now consider *large* groups when $\alpha < 1$. The reduced mean intake implies that the shift from a positive to a negative energy budget will occur at a lower global density, where predation plays a lesser role in population regulation. The lower energy-intake variance, as indicated above, tends to homogenize individuals, and groups, and so generates an abrupt transition from most individuals meeting their energy requirement to starvation of most individuals. Large groups consequently can induce dynamic overcompensation when $\alpha < 1$.

Small groups (large intake variance) do not delay the onset of density-dependent starvation until the population nears n^* . As a consequence, $(\partial\Phi[z_G]/\partial n_t)_{n^*}$ does not take too large a value (see expression 11), implying lower values for $|D_n(n^*)|$ and consequently less dynamic complexity for smaller G when $\alpha < 1$.

For large groups, negative energy budgets and low energy-intake variance imply that the return map declines steeply in the neighbourhood of n^* when $\alpha < 1$. The abrupt increase in density-dependent starvation increments $(\partial\Phi[z_G]/\partial n_t)_{n^*}$, so that the lower intake variance in larger groups can generate complex population dynamics.

To summarize the preceding point graphically, we plotted starvation probability, as a function of population density, for a small group ($G = 2$) and a large group ($G = 32$). We let $\alpha = 0.8$, $Q = 10$, and $V_c = 1.5$, a parameter combination where large groups induced chaotic dynamics. Figure 4 shows the density-dependent starvation frequencies for the two group sizes. Since $\alpha < 1$ in this example, energy intake for members of large groups has the lesser mean and variance at any global density.

At low population density, $n < 20$, starvation probabilities are negligible for members of both small and large groups (Fig. 4). Since predation responds to global density only, the two group sizes will therefore generate essentially the same per capita growth rate $F(n)$, and the differently structured populations will grow similarly. Consider the *large* group. At some point, a small increase in population density transforms the outcome of foraging; most individuals avert starvation until a slightly greater density implies that most individuals will starve. As energy budgets shift from positive to negative among large groups, the small energy-intake variance produces the abrupt increase in the frequency of starvation, and consequently ensures a population crash.

For the *small* groups, the picture differs considerably (Fig. 4). As a consequence of the greater energy-intake variance (hence more variability among groups), starvation slows population growth at densities below equilibrium and so averts overcompensation and a crash at higher densities. The greater intake variance of small groups (for $\alpha < 1$) ‘flattens’ the return map’s peak, density effects are not delayed, and the return map descends more gently at the group-size-dependent equilibrium n^* .

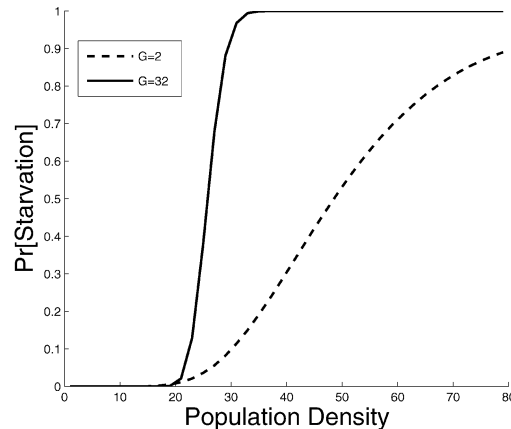


Fig. 4. Starvation probability, as a function of population density, for paired foragers and for members of a large group. $\alpha = 0.8$, $Q = 10$, and $V_c = 1.5$. Since $\alpha < 1$, both the mean and variance of a forager’s total energy intake in a large group ($G = 32$) are less than the corresponding quantities for members of a small group ($G = 2$). These differences hold across population densities. As density increases, frequency of starvation for the large group (solid curve) rapidly changes from low to high since each member’s energy-intake variance $V_c(n_t)$ is small. Increase in starvation frequency is gradual for the small group (dashed curve).

Figure 5a shows mortality fractions as functions of global density, n_t , for $G=2$ (for $\alpha = 0.8$ and $Q = 8$). The plots show the fraction of the non-breeding population that starves, the fraction of the population taken by predators, and their sum (proportion of n_t dying before breeding). Figure 5b plots corresponding proportions for a population with $G = 32$.

For *small* groups (Fig. 5a), starvation appears at densities less than the level where mortality due to predation begins to decline (starvation leaves fewer total candidates for predation). The starvation fraction increases smoothly, and never exceeds mortality from predation. Total mortality increases as population density increases, but in a decelerating manner.

For *large* groups (Fig. 5b), mortality from predation begins to decline at the onset of starvation. Proportional starvation increases abruptly, and quickly exceeds mortality from predation. The rapid increase in starvation accelerates total mortality in this example. Dynamic complexity increases where starvation contributes more to density-dependent population regulation than do losses to predators.

To complete our results, we consider dynamics with a period-halving transition. The ($\alpha = 1.2$, $Q = 10$) parameter combination exhibited a stable two-cycle at small group size, and equilibrated at a stable node for $G \geq 6$. Recall that when $\alpha > 1$, expected energy intake increases with group size, but intake variance still declines as group size increases.

Figure 6a shows mortality fractions, as functions of global density, for $G = 2$, $\alpha = 1.2$, and $Q = 10$. Figure 6b shows corresponding plots for $G = 32$. *Small* groups suffer more predation than starvation, but mortality from starvation is sufficient to induce a two-cycle in the population dynamics. *Large* groups suffer essentially no starvation until population density far exceeds the equilibrium node n^* (from the bifurcation plot). That is, the population equilibrating at a stable node is regulated by predation, and not by starvation. The same is true for the dynamics with $\alpha = 1.2$ and $Q = 8$, where the dynamics produced a stable node for every group size computed.

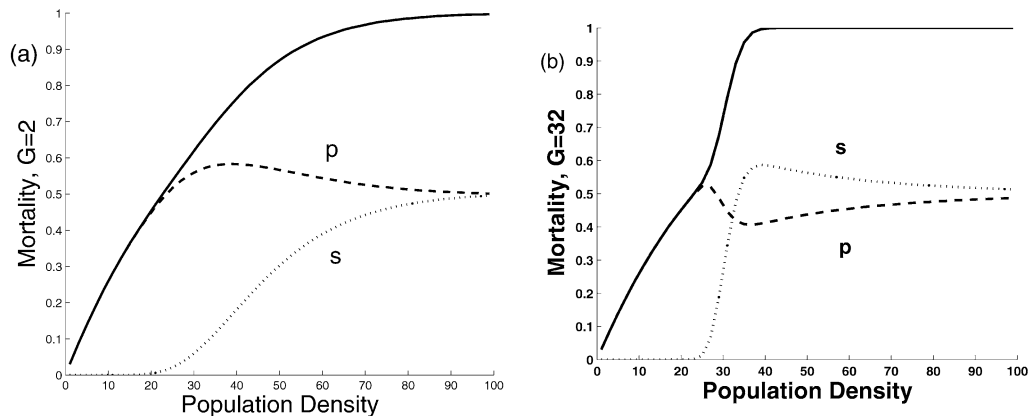


Fig. 5. Mortality proportions as a function of population density. If $s_n = \Phi[z_G(Q, n_t)]$ is the probability of starvation, and $p_n = 1 - \exp[-\xi n_t]$ is the probability of suffering predation, then the fraction of the population starving is $s_n [1 - (s_n p_n / [s_n + p_n])]$, the fraction of the population killed by predators is $p_n [1 - (s_n p_n / [s_n + p_n])]$, and total mortality is $s_n + p_n - s_n p_n$. (a) $G = 2$; $\alpha = 0.8$, $Q = 8$, and $V_c = 1.5$. The fraction starving is plotted as a dotted line (indicated by s), the fraction lost to predation as a dash-dot line (indicated by p), and total mortality as a solid line. (b) As in (a), but $G = 32$. Note that starvation increases abruptly, and soon exceeds the fraction lost to predation.

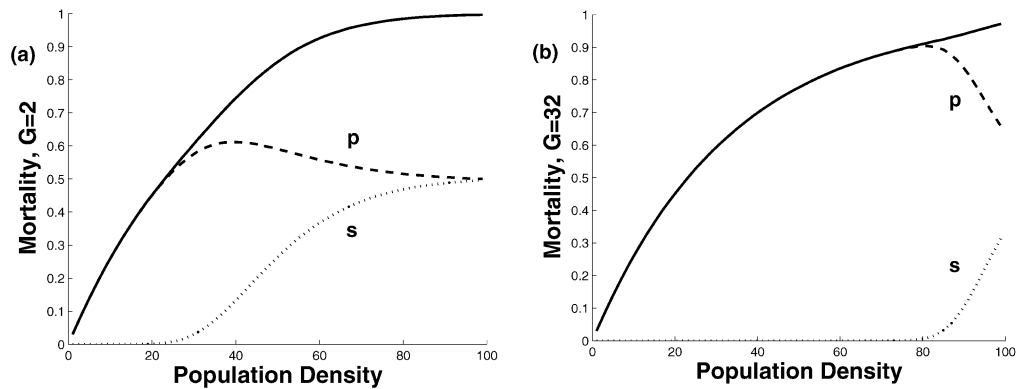


Fig. 6. Mortality proportions as a function of population density; see legend for Fig. 5. (a) $G = 2$, $\alpha = 1.2$, and $Q = 10$. (b) As in (a), but $G = 32$. For $n_i < 75$, the large group's regulation is due almost entirely to predation.

The comparatively simple return-map dynamics for $\alpha = 1.2$, given $Q \leq 12$, results from the relatively large expected energy intake at every group size. The difference in intake variance across group size, which contributed to the complexity for $\alpha < 1$, matters little when mean intake is sufficiently large (since $\alpha > 1$). The increased expected intake diminishes the role of starvation, and predation regulates the population of social foragers.

DISCUSSION

The influence of group size on our model's population dynamics depends on within-group behavioural interaction. When larger groups diminish each member's efficiency in discovering or capturing food, the model suggests an increasing likelihood of erratically fluctuating population density, driven by frequencies of starvation. However, when larger groups enhance each member's rate of encountering food, the likelihood of starvation declines with group size and the model predicts that larger groups promote dynamic stability.

Our model includes mortality from predation and starvation. The first mortality hazard acts at all densities, gradually increasing in strength as population density increases. The model imposes mortality from starvation more abruptly as density increases. We found that increased population regulation via predation stabilized the dynamics, and greater regulation through starvation increased dynamic complexity. We return to this topic below.

Chaotic dynamics includes excursions near population extinction. Our model indicates that in the chaotic regime, the smallest group size producing an extinction risk decreases as the energetic requirement increases, and increases as the variance of the amount of food per clump increases. For $\alpha < 1$ in our model, factors increasing dynamic complexity necessarily increased the risk of local extinction. However, our model's population dynamics advances deterministically, so that our extinction-risk analysis is somewhat arbitrary.

Evaluating the model's assumptions

We fixed group size among generations to compute any particular trajectory; group size governed the dynamics by translating global density into a mortality frequency. A more

complex analysis would allow group size to vary economically according to game-theoretical 'rules of entry' (Giraldeau and Caraco, 1993; Higashi and Yamamura, 1993). Individuals might seek different group sizes as they try to maximize the probability of surviving to breed. Group size in any particular generation might then be realized through free entry of solitaries, group-controlled entry, or a combination of entry rules (Giraldeau and Caraco, 2000). The different rules produce different equilibrium group sizes in the same density-dependent foraging economy, and the consequences of either entry rule for consumer dynamics are unclear. A further complication would allow total food abundance to vary dynamically, modelling either temporal variation in the environment or a resource–consumer biotic interaction (see Lett *et al.*, 2004).

Given global population density, our model assumes that a group encounters food at a constant probabilistic rate. The number of clumps encountered, β_G , therefore follows a Poisson probability function. The assumed process simplifies analysis of starvation probabilities, by equality of mean and variance. Alternative processes, where the rate at which an individual/group encounters the next clump depends on the number already found (e.g. due to resource depletion), would generalize this aspect of the model. The result would either increase or decrease the variance of an individual's energy intake, relative to the mean (see Caraco, 1987). Such changes would affect the starvation probability's increase with global density, and so could influence population dynamics. Furthermore, the spatial distribution of both mobile consumers/exploiters and their resources can influence the rate at which an individual consumer acquires energy (Cosner *et al.*, 1999; Duryea *et al.*, 1999).

We invoke a threshold energy requirement to discriminate starvation from successful foraging, and treat forces of mortality as independent. In nature, either or both assumptions may often fail; reduced food intake may increment an individual's susceptibility to predation or parasitism.

We assumed an equal division of resource clumps among group members. This particular averaging, however, appears somewhat artificial when coupled to population dynamics. As we noted above, equal energy consumption within groups restricts variation in starvation to the among-group level. Caraco and Giraldeau (1991) offer an alternative. Food clumps consist of an integer number of indivisible 'items'. The separate items are allocated among group members according to a multinomial probability function. The multinomial produces energy-intake variation among members of the same group; the associated population dynamics would include consequences of both within-group and among-group variation in starvation. This difference presumably could leave the population dynamics less sensitive to increasing group size.

Within-group variation in survival follows when foraging groups are structured by social dominance, so that higher ranking individuals consume more food, forage in sites offering protection from predators, or enjoy both benefits (e.g. Janson, 1985; Ekman, 1987). These advantages of dominance can imply enhanced survival and reproduction (e.g. Blanckenhorn *et al.*, 1998). The economic consequences of dominance condition the distribution of individual energy intake on rank. Rank-based differences inflate the variance of the unconditional distribution of energy intake, so that mortality from starvation responds less abruptly to increasing population density. Within the context of our model, the tendency for sudden increases in mortality with small increments in density should decline, so that social dominance will simplify population dynamics. Strong dominance hierarchies might have the same effect as a 'floor', a positive lower bound on population density that can limit dynamic

complexity (Ruxton and Rohani, 1998). [Gurney and Nisbet (1979) and Łomnicki (1988) offer further discussion of population-level effects of stratified access to resources.]

Our model takes the probability of surviving predation as an exponentially decaying function of population density. The model's probability of averting starvation is (the equivalent of) an error function, which declines in a concave, then convex manner as density increases. When the energy-intake variance is small, mortality from starvation can increase rapidly if the individual's expected energy budget shifts from positive to negative. For the parameter ranges we investigated, dynamic complexity increased as the relative contribution of the latter mortality process to total mortality increased, since its functional form could permit overcompensation. However, we cannot conclude that predation stabilizes a population where starvation depends on a threshold energy requirement. The same exponential function we use to model avoiding predation can model general competitive crowding (Stone, 1993; Neubert, 1997), scramble competition within a resource patch (Ives and May, 1985), offspring survival (Henson *et al.*, 2001), or an effect of disease (May, 1976). In general, decreasing survival as an exponential function of density increases dynamic stability; Avilés (1999) generates period-halving bifurcations this way. [For a general technical discussion, see Cull (1988).]

Our study addresses dynamic complexity of a single population, and we conclude that chaos increases the likelihood of (local) extinction. However, when demes coupled by migration fluctuate chaotically and asynchronously, the likelihood of metapopulation extinction may decline (Allen *et al.*, 1993; Earn *et al.*, 2000).

Closing comment

Growth or decline of populations and, more generally, patterns in biotic communities emerge from the behavioural ensemble of their component individuals (Rosenzweig and Abramsky, 1986; McNamara and Houston, 1987; Bernstein *et al.*, 1991; Nakamura *et al.*, 1997; Korniss and Caraco, 2005). Our analyses admittedly simplify behaviour to couple the time scales of social interaction and population dynamics. But the results do suggest that readily observable behavioural interaction of social foragers may exert significant effects on population growth.

ACKNOWLEDGEMENTS

We dedicate the paper to Dr. George Martin, who recently retired from the Department of Mathematics and Statistics at UAlbany. This material is based upon work supported by the National Science Foundation under Grant No. DEB 0342689. We appreciate comments by L.-A. Giraldeau, G. Korniss, and G. Belovsky, and we thank James Basham for technical assistance.

REFERENCES

- Allen, J.C., Schaffer, W.M. and Rosko, D. 1993. Chaos reduces species extinction by amplifying local population noise. *Nature*, **364**: 229–232.
- Alligood, K.T., Sauer, T.D. and Yorke, J.A. 1997. *Chaos: An Introduction to Dynamic Systems*. Berlin: Springer-Verlag.
- Avilés, L. 1999. Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. *Evol. Ecol. Res.*, **1**: 459–477.
- Avilés, L., Abbot, P. and Cutter, A.D. 2002. Population ecology, nonlinear dynamics, and social evolution. I. Associations among nonrelatives. *Am. Nat.*, **159**: 115–127.

- Bernstein, C., Kacelnik, A. and Krebs, J.R. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *J. Anim. Ecol.*, **60**: 205–225.
- Blanckenhorn, W.U., Grant, J.W.A. and Fairbairn, D.J. 1998. Monopolization in a resource queue: water striders competing for food and mates. *Behav. Ecol. Sociobiol.*, **42**: 63–70.
- Boswell, M.T., Ord, J.K. and Patil, G.P. 1979. Chance mechanisms underlying univariate distributions. In *Statistical Distributions in Ecological Work* (J.K. Ord, G.P. Patil and C. Taille, eds.), pp. 3–156. Burtonsville, MD: International Cooperative Publishing House.
- Caraco, T. 1987. Foraging games in a random environment. In *Foraging Behavior* (A.C. Kamil, J.R. Krebs and H.R. Pulliam, eds.), pp. 389–414. New York: Plenum Press.
- Caraco, T. and Brown, J.L. 1986. A game between communal breeders: when is food-sharing stable? *J. Theor. Biol.*, **118**: 379–393.
- Caraco, T. and Gillespie, R.G. 1986. Risk-sensitivity: foraging mode in an ambush predator. *Ecology*, **67**: 1180–1185.
- Caraco, T. and Giraldeau, L.-A. 1991. Social foraging: producing and scrounging in a stochastic environment. *J. Theor. Biol.*, **153**: 559–583.
- Caraco, T., Martindale, S. and Whittam, T.S. 1980. An empirical demonstration of risk sensitive foraging preferences. *Anim. Behav.*, **28**: 820–830.
- Caraco, T., Blanckenhorn, W.U., Gregory, G.M., Newman, J.A., Recer, G.M. and Zwicker, S.M. 1990. Risk-sensitivity: ambient temperature affects foraging choice. *Anim. Behav.*, **39**: 338–345.
- Caraco, T., Duryea, M.C., Glavanakov, S., Maniatty, W. and Szymanski, B.K. 2001. Host spatial heterogeneity and the spread of vector-borne infection. *Theor. Pop. Biol.*, **59**: 185–206.
- Clark, C.W. and Mangel, M. 1984. Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.*, **123**: 626–641.
- Clark, C.W. and Mangel, M. 1986. The evolutionary advantages of group foraging. *Theor. Pop. Biol.*, **30**: 45–75.
- Cosner, C., DeAngelis, D.L., Ault, J.S. and Olson, D.B. 1999. Effect of spatial grouping on the functional response of predators. *Theor. Pop. Biol.*, **56**: 65–75.
- Cull, P. 1988. Stability of discrete one-dimensional population models. *Bull. Math. Biol.*, **50**: 67–75.
- Duryea, M., Caraco, T., Gardner, G., Maniatty, W. and Szymanski, B.K. 1999. Population dispersion and equilibrium infection frequency in a spatial epidemic. *Physica D*, **132**: 511–519.
- Earn, D.J.D., Levin, S.A. and Rohani, P. 2000. Coherence and conservation. *Science*, **290**: 1360–1364.
- Ekman, J. 1987. Exposure and time use in willow tit flocks: the cost of subordination. *Anim. Behav.*, **35**: 445–452.
- Ekman, J. and Rosander, B. 1987. Starvation risk and flock size of the social forager: when there is a flocking cost. *Theor. Pop. Biol.*, **31**: 166–177.
- Ellner, S. and Turchin, P. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. *Am. Nat.*, **145**: 343–375.
- Feigenbaum, M.J. 1978. Quantitative universality for a class of nonlinear transformations. *J. Stat. Physics*, **19**: 25–52.
- Giraldeau, L.-A. and Caraco, T. 1993. Genetic relatedness and group size in an aggregation economy. *Evol. Ecol.*, **7**: 429–438.
- Giraldeau, L.-A. and Caraco, T. 2000. *Social Foraging Theory*. Princeton, NJ: Princeton University Press.
- Godfray, H.C.J. and Blythe, P. 1990. Complex dynamics in multispecies communities. *Phil. Trans. R. Soc. Lond. B*, **330**: 221–233.
- Goss-Custard, J.D. 1976. Variation in the dispersion of redshank *Tringa totanus* on their winter feeding grounds. *Ibis*, **118**: 257–263.

- Goss-Custard, J.D. and Durell, S.E.A. 1987. Age-related effects in Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. III: The effect of interference on overall foraging efficiency. *J. Anim. Ecol.*, **56**: 549–558.
- Gurney, W.S.C. and Nisbet, R.M. 1979. Ecological stability and social hierarchy. *Theor. Pop. Biol.*, **16**: 48–80.
- Hastings, A., Hom, C.L., Ellner, S., Turchin, P. and Godfray, H.C.J. 1993. Chaos in ecology: is mother nature a strange attractor? *Annu. Rev. Ecol. Syst.*, **24**: 1–33.
- Henson, S.M., Costantino, R.F., Cushing, J.M., Desharnais, R.A., Dennis, B. and King, A.A. 2001. Lattice effects observed in chaotic dynamics of experimental populations. *Science*, **294**: 602–605.
- Higashi, M. and Yamamura, N. 1993. What determines the animal group size? Insider–outsider conflict and its resolution. *Am. Nat.*, **142**: 553–563.
- Houston, A.I. and McNamara, J.M. 1986. Evaluating the selection pressure on foraging decisions. In *Relevance of Models and Theories in Ethology* (R. Campan and R. Zayan, eds.), pp. 61–75. Toulouse: Privat.
- Houston, A.I., Clark, C.W., McNamara, J.M. and Mangel, M. 1988. Dynamic models in behavioural and evolutionary ecology. *Nature*, **332**: 29–34.
- Hunt, H.W., Antle, J.M. and Paustian, K. 2003. False determinations of chaos in short noisy time series. *Physica D*, **180**: 115–127.
- Ives, A.R. and May, R.M. 1985. Competition within and between species in a patchy environment: relations between microscopic and macroscopic models. *J. Theor. Biol.*, **115**: 65–92.
- Janson, C. 1985. Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebu apella*). *Behav. Ecol. Sociobiol.*, **18**: 125–138.
- Jansson, C., Ekman, J. and von Brömssen, A. 1981. Winter mortality and food supply in tits *Parus* spp. *Oikos*, **37**: 313–322.
- Kaplan, D. and Glass, L. 1995. *Understanding Nonlinear Dynamics*. New York: Springer-Verlag.
- Koops, M.A. and Giraldeau, L.-A. 1996. Producer–scrounger foraging games in starlings: a test of rate-maximizing and risk-sensitive models. *Anim. Behav.*, **51**: 773–783.
- Korniss, G. and Caraco, T. 2005. Spatial dynamics of invasion: the geometry of introduced species. *J. Theor. Biol.*, **233**: 137–150.
- Kot, M. and Schaffer, W.M. 1984. The effects of seasonality on discrete models of population growth. *Theor. Pop. Biol.*, **26**: 340–360.
- Krause, J. and Ruxton, G.D. 2002. *Living in Groups*. New York: Oxford University Press.
- Lett, C., Auger, P. and Gaillard, J.-M. 2004. Continuous cycling of grouped vs. solitary frequencies in a predator–prey model. *Theor. Pop. Biol.*, **65**: 263–270.
- Łomnicki, A. 1988. *Population Ecology of Individuals*. Princeton, NJ: Princeton University Press.
- Lovegrove, B.G. and Wissel, C. 1988. Sociality in molarats: metabolic scaling and the role of risk sensitivity. *Oecologia*, **74**: 600–606.
- Mangel, M. 1990. Resource divisibility, predation and group formation. *Anim. Behav.*, **39**: 1163–1172.
- May, R.M. 1976. Simple mathematical models with very complicated dynamics. *Nature*, **261**: 459–467.
- May, R.M. and Oster, G.F. 1976. Bifurcations and dynamic complexity in simple ecological models. *Am. Nat.*, **110**: 573–599.
- McNamara, J.M. and Houston, A.I. 1987. Starvation and predation as factors limiting population size. *Ecology*, **68**: 1515–1519.
- Nakamura, M., Matsuda, H. and Iwasa, Y. 1997. The evolution of cooperation in a lattice-structured population. *J. Theor. Biol.*, **184**: 65–81.
- Neubert, M.G. 1997. A simple population model with qualitatively uncertain dynamics. *J. Theor. Biol.*, **189**: 399–411.

- Olsen, L.F. and Schaffer, W.M. 1990. Chaos versus noisy periodicity: alternative hypotheses for childhood epidemics. *Science*, **249**: 499–504.
- O'Malley, L., Basham, J., Yasi, J.A., Korniss, G. Allstadt, A. and Caraco, T. in press. Invasive advance of an advantageous mutation: nucleation theory. *Theor. Pop. Biol.*
- Peitgen, H.-O., Jürgens, H. and Saupe, D. 1992. *Chaos and Fractals: New Frontiers of Science*. New York: Springer-Verlag.
- Pusey, A.E. and Packer, C. 1997. The ecology of relationships. In *Behavioral Ecology: An Evolutionary Approach*, 4th edn. (J.R. Krebs and N. Davies, eds.), pp. 254–283. Oxford: Blackwell.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.*, **11**: 559–623.
- Rosenzweig, M.L. and Abramsky, Z. 1986. Centrifugal community organization. *Oikos*, **46**: 339–348.
- Roughgarden, J. 1998. *Primer of Ecological Theory*. Upper Saddle River, NJ: Prentice-Hall.
- Ruxton, G.D. and Rohani, P. 1998. Population floors and the persistence of chaos in ecological models. *Theor. Pop. Biol.*, **53**: 175–183.
- Ruxton, G.D., Hall, S.J. and Gurney, W.S.C. 1995. Attraction toward feeding conspecifics when food patches are exhaustible. *Am. Nat.*, **145**: 653–660.
- Stephens, D.W. 1981. The logic of risk-sensitive foraging preferences. *Anim. Behav.*, **29**: 628–629.
- Stephens, D.W. and Charnov, E.L. 1982. Optimal foraging: some simple stochastic models. *Behav. Ecol. Sociobiol.*, **10**: 251–263.
- Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.
- Stone, L. 1993. Period-doubling reversals and chaos in simple ecological models. *Nature*, **365**: 617–620.
- Sugihara, G., Grenfell, B. and May, R.M. 1990. Distinguishing error from chaos in ecological time series. *Phil. Trans. R. Soc. Lond. B*, **330**: 235–251.
- Sumpter, D.J.T. and Broomhead, D.S. 2001. Relating individual behavior to population dynamics. *Phil. Trans. R. Soc. Lond. B*, **268**: 925–932.
- Sutherland, W.J. 1996. *From Individual Behaviour to Population Ecology*. Oxford: Oxford University Press.
- Thrall, P.H., Biere, A. and Uyenoyama, M.K. 1995. Frequency-dependent disease transmission and the dynamics of the *Silene-Ustilago* host–pathogen system. *Am. Nat.*, **145**: 43–62.

APPENDIX

Our objectives required computing the return map repeatedly, deleting initial values to avoid transients, and then employing some standard tools.

Return map: computational simplification

We rewrite the dynamics, equation (9), in a more computationally convenient form. We replace the (cumulative) normal probability with an error function according to the equality

$$\Phi[z_G] = \frac{1}{2} \left[1 + \operatorname{erf} \left(\frac{z_G}{2^{1/2}} \right) \right] \quad (\text{A1})$$

where

$$\operatorname{erf}(z) = \frac{2}{\pi^{1/2}} \int_0^z \exp[-x^2] dx \quad (\text{A2})$$

We replace the term for the fraction of the non-breeding population averting starvation, i.e. $(1 - \Phi[z_G])$, with the appropriate error-function term, and the difference equation for population dynamics becomes

$$n_{t+1} = \left(\frac{R}{2}\right) \left[1 - \operatorname{erf}\left(\frac{z_G}{2^{1/2}}\right)\right] e^{-\xi n_t} n_t \quad (\text{A3})$$

Equation (A3) has dynamical behaviour identical to the behaviour of equation (9).

To compute a Lyapunov exponent for a given orbit, we require the derivative of the return map, equation (A3), with respect to n_t , evaluated at each population density n_t on the orbit. We have the derivative of a product:

$$\begin{aligned} D_n(n_t) &= (R/2) \frac{d}{dn_t} \left\{ \exp[-\xi n_t] \left[1 - \operatorname{erf}\left(\frac{z(Q, n_t)}{2^{1/2}}\right)\right] n_t \right\}_{n_t} \\ &= (R/2) \left\{ \begin{aligned} &-\xi e^{-\xi n_t} \left[1 - \operatorname{erf}\left(\frac{z(Q, n_t)}{2^{1/2}}\right)\right] n_t + e^{-\xi n_t} \left[1 - \operatorname{erf}\left(\frac{z(Q, n_t)}{2^{1/2}}\right)\right] \\ &+ e^{-\xi n_t} n_t \frac{d}{dn_t} \left[1 - \operatorname{erf}\left(\frac{z(Q, n_t)}{2^{1/2}}\right)\right]_{n_t} \end{aligned} \right\} \quad (\text{A4}) \end{aligned}$$

where $\frac{d}{dn_t} \left[1 - \operatorname{erf}\left(\frac{z(Q, n_t)}{2^{1/2}}\right)\right]_{n_t}$ equals

$$-\frac{\sqrt{2}}{\sqrt{\pi} \sqrt{V_c + 1}} \left[\frac{Q G^{1-a/2}}{2(\rho n_t)^{1/2}} + \frac{\rho^{1/2} G^{a/2}}{2(n_t)^{3/2}} \right] \exp[-\xi_G(n_t)] < 0 \quad (\text{A5})$$

and

$$\xi_G(n_t) = \frac{\left[\left(\frac{n_t}{\rho}\right)^{1/2} Q G^{1-a/2} - \left(\rho/n_t\right)^{1/2} G^{a/2} \right]^2}{2(V_c + 1)} \quad (\text{A6})$$