
Population dynamics of obligate cooperators

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Obligate cooperative breeding species demonstrate a high rate of group extinction, which may be due to the existence of a critical number of helpers below which the group cannot subsist. Through a simple model, we study the population dynamics of obligate cooperative breeding species, taking into account the existence of a lower threshold below which the instantaneous growth rate becomes negative. The model successively incorporates (i) a distinction between species that need helpers for reproduction, survival or both, (ii) the existence of a migration rate accounting for dispersal, and (iii) stochastic mortality to simulate the effects of random catastrophic events. Our results suggest that the need for a minimum number of helpers increases the risk of extinction for obligate cooperative breeding species. The constraint imposed by this threshold is higher when helpers are needed for reproduction only or for both reproduction and survival. By driving them below this lower threshold, stochastic mortality of lower amplitude and/or lower frequency than for non-cooperative breeders may be sufficient to cause the extinction of obligate cooperative breeding groups. Migration may have a buffering effect only for groups where immigration is higher than emigration; otherwise (when immigrants from nearby groups are not available) it lowers the difference between actual group size and critical threshold, thereby constituting a higher constraint.

Keywords: mathematical model; obligate cooperative breeding species; inverse density dependence; group extinction; population dynamics; Allee effect

1. INTRODUCTION

Obligate cooperative breeding animals are characterized by the presence of non-reproductive individuals which help to raise the offspring of a few breeding individuals. In consequence, reproductive success and/or survival increases with group size in most cooperative breeding species (e.g. white-fronted bee-eaters, *Merops bullockoides* (Emlen & Wrege 1991), Florida scrub jays, *Aphelocoma coerulescens* (Mumme 1992), naked mole-rats, *Heterocephalus glaber* (Jarvis *et al.* 1994), dwarf mongooses, *Helogale parvula* (Rood 1990), suricates, *Suricata suricatta* (Clutton-Brock *et al.* 1999a), jackals, *Canis mesomelas* and *Canis aureus* (Moehlman 1979), coyotes, *Canis latrans* (Bekoff & Wells 1982) and lions, *Panthera leo* (Packer *et al.* 1988)). This can represent an important constraint when the presence of a critical number of helpers is necessary for significant reproductive success or survival (e.g. white-winged choughs, *Corcorax melanorhamphos* (Heinsohn 1992), wild dogs, *Lycan pictus* (Malcom & Martens 1982), banded mongooses, *Mungos mungo* (Cant 1998) and dwarf mongooses (Creel & Creel 1991)). Below this critical group size, the growth rate of these obligate cooperative breeding species (hereafter cooperators) becomes inversely density dependent and their population dynamics display an Allee effect (negative growth rate at low density; Allee *et al.* 1949). As a consequence, if this lower threshold is reached, it becomes increasingly difficult for the group to increase or even maintain its size.

There are several well-documented examples of the existence of such a lower group size threshold, whether helpers are needed for survival or for reproduction. In white-winged choughs, only groups of seven and above produce more than one young on average over the entire year and groups of less than four are incapable of breeding successfully (Heinsohn 1992). Similarly, in banded mongooses, groups of less than six individuals failed to raise pups despite six breeding attempts over three years (Cant 1998) and groups of less than four adult capybaras (*Hydrochaeris hydrochaeris*) were never able to breed successfully (E. Herrera, personal communication). In dwarf mongooses, a minimum group size of five is necessary for their specific cooperative vigilance system (Rasa 1989), under which mortality rapidly exceeds birth, leading to a quick disappearance of the whole group. Groups of less than four adult stripe-backed wrens (*Campylorhynchus nuchalis*) are significantly less successful at mobbing predators and at driving birds from other species to do so (Rabenold 1990). When prey are scarce, groups of less than five adult suricates are not able to both forage and successfully guard the group against predators and, consequently, become extinct (Clutton-Brock *et al.* 1998). Packs of fewer than four African wild dogs rarely manage to raise any pups (Woodroffe *et al.* 1997), mainly because they need to defend them from predation, cooperatively hunt large prey (e.g. Creel & Creel 1995) and need to defend their hills against kleptoparasitism from hyenas (*Crocuta crocuta*) (Carbone *et al.* 1997).

It has been suggested that the tendency for frequent group extinction witnessed for these cooperative breeding species (Jarvis *et al.* 1994; Burrow 1995; Clutton-Brock *et al.*

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1998) is due to the existence of this lower threshold (Clutton-Brock *et al.* 1999b). The aim of this paper is to investigate the demographic consequences of obligate cooperative breeding through a simple mathematical model mimicking the population dynamics of these species (mainly the Allee effect). We distinguish three possible cases: a critical number of helpers is needed (i) for survival, (ii) for reproduction, and (iii) for both survival and reproduction. In addition, we examine the effect of migration on the population dynamics of these particular species. Finally, we investigate the differential impact of random catastrophes on species with different breeding systems.

2. THE MODELS

(a) *Cooperators versus non-cooperators*

Although by convention we will often refer to ‘population’ parameters, the basic unit of breeding individuals we model here is the social group. Our study is focused on population dynamics, expressing conclusions from the viewpoint of the persistence of the population only: we do not tackle the evolutionary strategies behind processes. Aiming for simplicity, we chose to describe non-cooperative breeding population dynamics starting from the continuous-time logistic equation, because it is a good compromise between realism and simplicity (e.g. May 1973; Berryman 1992):

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right). \quad (1)$$

Here, r is the per capita intrinsic growth rate of the population and K is the carrying capacity of the habitat.

We next want to study the effect of inverse density dependence on obligate cooperators. The effect of density dependence is, however, not truly inverse: it is inverse at low densities, below a critical threshold, say K_- . Above this threshold, there is a density-dependent constraint, since the population growth has to be limited by an upper threshold, the carrying capacity of the environment, say K_+ . The instantaneous growth rate of the population will be negative below K_- and positive above it: dN/dt will be proportional to a term $(1 - K_-/N)$. Meanwhile, the instantaneous growth rate will be negative above K_+ and positive below it: dN/dt will be proportional to a term $(1 - N/K_+)$. The product of these two terms will provide a positive growth rate between K_- and K_+ and a negative growth rate elsewhere.

This leads to the following model,

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K_+} \right) \left(1 - \frac{K_-}{N} \right). \quad (2)$$

This very simple model displays the Allee effect (Allee *et al.* 1949): once the group falls below the lower threshold, the negative instantaneous growth rate leads to disappearance. The two stable equilibrium points of the density-dependent model (equation (1)), 0 and K , are also found in equation (2), in addition to a third and unstable point, K_- . Whereas in the non-cooperator system any point will reach the stable equilibrium point corresponding to the carrying capacity, only initial conditions above the lower threshold (K_-) will do so in the cooperator system.

(b) *Constraints on reproduction and on survival*

Not all cooperative breeders have a group size constraint on both reproduction and survival: the constraint may be on survival only (helpers increase survival) or on reproduction only (helpers increase reproductive success) and the population dynamics may change accordingly. We thus study the effect of different constraints on cooperative breeding by modifying equation (2). We make a distinction between the effect of density dependence on reproduction only and on survival only. For this, we use $r = b - m$, where b is the intrinsic birth rate and m is the intrinsic death rate of the population. The effect of a density-dependent constraint on mortality is opposite to its effect on birth: the mortality term will increase with N , while the birth term will decrease. We start from the following density-dependence model,

growth rate = birth rate – death rate

$$\frac{dN}{dt} = \left(\overbrace{bN - \frac{bN^2}{K}} \right) - \left(\overbrace{mN - \frac{mN^2}{K}} \right),$$

where bN is the density-independent birth rate, $(bN^2)/K$ is the density-dependent constraint on birth rate, mN is the density-independent mortality rate, and $(mN^2)/K$ is the density-dependent mortality rate.

We adopt the following logistic model,

$$M_{DD} B_{DD}: \frac{dN}{dt} = bN \left(1 - \frac{N}{K} \right) - mN \left(- \left(1 - \frac{N}{K} \right) \right), \quad (3)$$

where DD stands for density dependence.

Here, the effect of density dependence acts in opposite ways for reproduction and survival. Similarly, we have for the inverse density-dependent model $r = b - m$, which gives the following model,

$$\frac{dN}{dt} = bN \left(1 - \frac{N}{K_+} \right) \left(1 - \frac{K_-}{N} \right) - mN \left(- \left(1 - \frac{N}{K_+} \right) \left(1 - \frac{K_-}{N} \right) \right). \quad (4)$$

The birth term can be either density dependent [$B_{DD} = bN(1 - N/K_+)$] or inverse density dependent [$B_{IDD} = bN(1 - N/K_+)(1 - K_-/N)$] and the mortality term can be either density dependent [$M_{DD} = mN(- (1 - N/K_+))$] or inverse density dependent [$M_{IDD} = mN(- (1 - N/K_+)(1 - K_-/N))$]. By adding the effects of birth and mortality, we obtain four possible instantaneous growth rates of the population. They are given in figure 1, with the corresponding curve of the instantaneous growth rate of the population as a function of the population size and for arbitrary values of the parameters (the point here being comparison of the lower equilibrium for the different models). The points at which these curves cross the x -axis are the equilibrium points: minimum group size (except for the model with strict density dependence) and carrying capacity. The growth rate is always negative above the carrying capacity and below the minimum group size. The carrying capacity is the same for all models. It is not the case for the minimum group size: as shown by the curves in figure 1, $(b + m)K_-/(b + m) > bK_-/(b + m) > mK_-/(b + m)$ for any population with a positive intrinsic growth rate

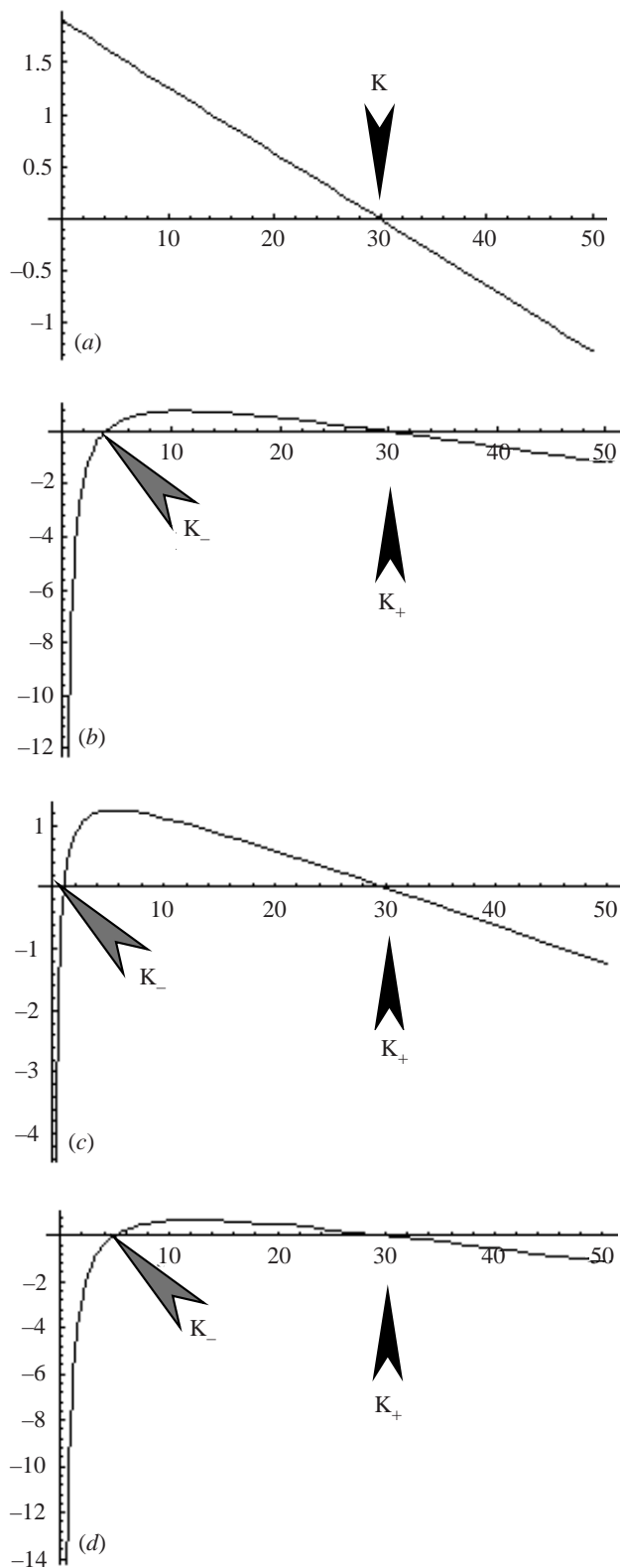


Figure 1. Equilibrium points for the four different models with reproduction and survival taken as density dependent or inverse density dependent. The instantaneous growth rate of the four models is given as a function of the number of individuals. The higher equilibrium point (black arrows) is the carrying capacity. The lower equilibrium point (grey arrow) is the minimum population size (lower threshold). The former is the same for all models; the latter is lower (lower constraint) when inverse density dependence is on mortality only and higher (higher constraint) when it is on both reproduction

(i.e. where $b > m$). In other words, the minimum group size threshold is higher when the cooperative breeding is due to reproduction only and even higher when it is due to both reproduction and survival. The higher the equilibrium point, the higher the constraint on the group (because this threshold is more likely to be reached). This shows that if cooperative breeding is needed for reproduction only (e.g. babysitting or offspring feeding), the constraint is more severe than if it is needed for survival only (e.g. guarding or defence).

So far, we have assumed that the constraint on survival and on reproduction was either absent or present, but that it was the same, provided that it existed. This may not always be the case, as some species may need helpers for both survival and reproduction aspects (e.g. helpers are needed for cooperative hunting without which both survival and reproduction are compromised), but with a higher constraint on one aspect. We now consider the case where the constraint of cooperative breeding is present for both survival and for reproduction, but is not the same. We do so by setting a different value for the lower threshold (K_-) for survival and for reproduction. We also complete this analysis by considering that the upper threshold value (K_+) may also be different for survival and for reproduction.

If the lower threshold has a different value for mortality (K_{-m}) and for birth (K_{-b}), the equilibrium points are 0, $(bK_{-b} + mK_{-m}) / (b + m)$ and K_+ , whereas if the upper threshold has a different value for mortality (K_{+m}) and for birth (K_{+b}), the equilibrium points are 0, K_- and $(K_{+b}K_{+m}) / (b + m) / (bK_{+m} + mK_{+b})$. If both $K_{-b} \neq K_{-m}$ and $K_{+b} \neq K_{+m}$, the equilibrium points are 0 and $-B \pm \sqrt{B^2 - 4AC} / (2A)$, with $B = (b + m)(K_{+b}K_{+m}) + bK_{-b}K_{+m} + mK_{-m}K_{+b}$, $A = bK_{+m} + mK_{+b}$, and $C = (K_{+b}K_{+m})(bK_{-b} + mK_{-m})$.

This shows that if the lower threshold (K_-) is not the same for reproduction and for survival, then the equilibrium point will be between these two values (K_{-b} and K_{-m}). However, the equilibrium point will be closer to the value for birth, since the intrinsic birth rate is always higher than the intrinsic death rate. The higher the intrinsic birth rate, the closer the equilibrium point to the birth thresholds (K_{-b}). The same applies to the upper threshold (K_+). Similarly, if both the minimum and the maximum group sizes are simultaneously different for birth and mortality, then the two equilibrium points will take a value intermediate to K_{-b} and K_{-m} for the lower threshold and to K_{+b} and K_{+m} for the upper threshold. However, as shown in figure 2 for the lower threshold,

Figure 1. (Cont.) and survival. The graphs are obtained with the following parameter values: $b = 2$, $m = 0.5$, $K = K_+ = 30$ and $K_- = 10$. Values are given only to allow model comparison. (a) Complete density-dependence model (abbreviation $B_{DD} - M_{DD}$) with equilibrium points 0 and K_+ . (b) Density dependence on survival only model (abbreviation $B_{IDD} - M_{DD}$) with equilibrium points 0, $bK_- / (b + m)$ and K_+ . (c) Density dependence on reproduction only model (abbreviation $B_{DD} - M_{IDD}$) with equilibrium points 0, $mK_- / (b + m)$ and K_+ . (d) Complete inverse density-dependence model (abbreviation $B_{IDD} - M_{IDD}$) with equilibrium points 0, $(b + m)K_- / (b + m)$ and K_+ .

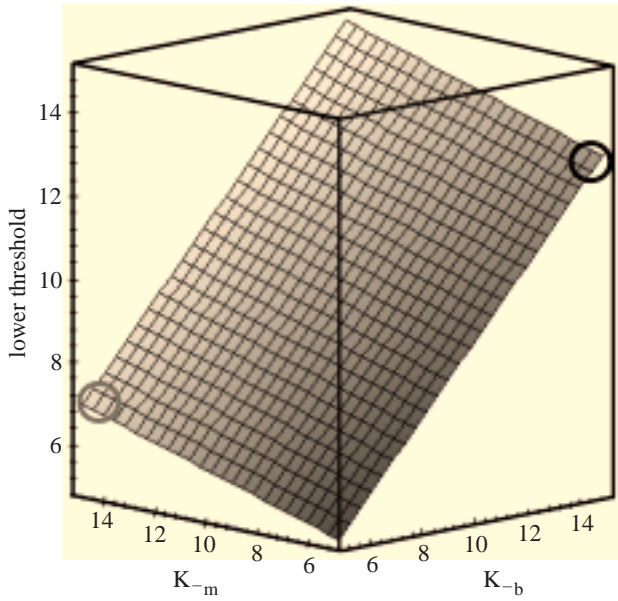


Figure 2. Value of the minimum population size according to the minimum number of helpers needed for survival (K_m) and for reproduction (K_b). If the constraint is on survival (high K_m and low K_b , grey circle), then the minimum population size will be lower (the constraint of cooperative breeding will be lower) than if the constraint is more on reproduction (high K_b and low K_m , black circle).

these points will depend more closely on the threshold for reproduction (steeper slope). Other things being equal, the constraint caused by cooperative breeding is more severe when owing to reproduction than when owing to survival: the larger the number of helpers needed for reproduction, the higher final constraint on the group.

(c) Migration

To test the effect of migration in cooperative breeders, we incorporate a rate of migration of individuals between groups. We assume that migration is density dependent (e.g. Janosi & Scheuring 1997): provided a sufficient source, immigration decreases proportionally to group size, up to the upper threshold, after which it stops. Emigration follows the opposite pattern. We set $d = e - i$, where the migration rate d is the difference between the emigration rate e and the immigration rate i . We thus have a positive migration rate when $i > e$. For the sake of simplicity, we assume that e and i have the same variation according to group size and, therefore, only take d into account. Since d is density dependent, we now have the following model,

$$\frac{dN}{dt} = bN \left(1 - \frac{N}{K_+}\right) \left(1 - \frac{K_-}{N}\right) - mN \left(-\left(1 - \frac{N}{K_+}\right) \times \left(1 - \frac{K_-}{N}\right)\right) - dN \left(1 - \frac{N}{K_+}\right), \tag{5}$$

with the following equilibrium point, $[0, (b + m)K_- / (b + m - d), K_+]$, with only 0 and K_+ being stable. If cooperative breeding is based on reproduction only or on survival only, the equilibrium point becomes $(0, bK_- / (b + m - d), K_+)$ or $(0, mK_- / (b + m - d), K_+)$, respectively. When migration is taken into account, the upper (stable) equi-

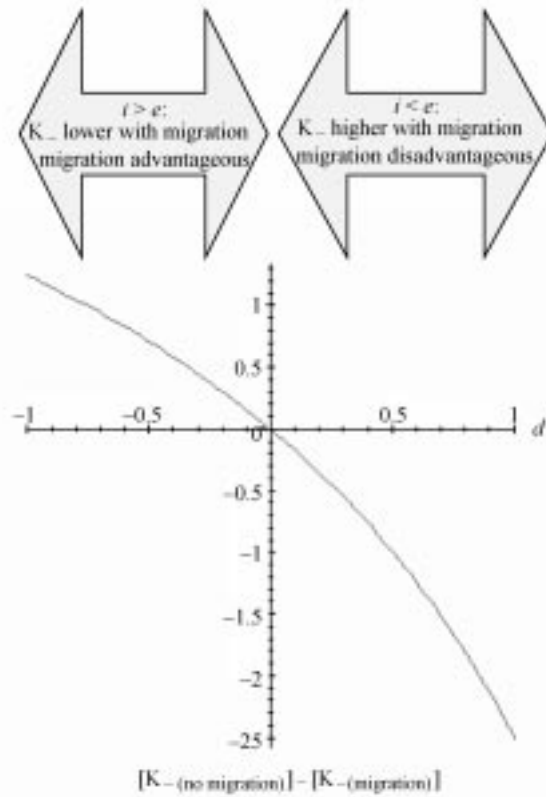


Figure 3. Difference between the value of the minimum group size when there is no migration and when there is migration, as a function of the migration rate (taken as emigration minus immigration). When this difference is positive, then migration lowers the constraint of cooperative breeding by lowering the minimum group size (and thereby the risk that it will be reached). This is the case when immigration is higher than emigration, which does not occur on a large scale because of mortality due to dispersal.

rium point remains the same. The lower (unstable) equilibrium point, however, becomes higher (proportionally to the migration rate) than K_- . The difference between the new equilibrium point and the one without migration (K_-) is a function of the migration rate d . As seen in figure 3, if $d < 0$ (immigration is higher than emigration), taking migration into account decreases the value of the lower threshold, which means a less severe constraint of cooperative breeding on the group. If $d > 0$, migration increases the lower threshold, which means a more severe constraint of cooperative breeding on the group. As could be expected, given a constant emigration rate, immigration can be viewed as acting as a buffer: the higher the immigration rate, the less likely the group is to reach K_- . It is thus advantageous for a group to have migration in obligate cooperator species only if immigration is higher than emigration.

(d) Effects of random catastrophes

Once the carrying capacity is reached, changes can only occur from perturbations external to the population dynamics, for both non-cooperators and cooperators, with the current models. We thus simulated random catastrophic events, which are usually more important than environmental and demographic stochasticity in determining the persistence times of populations (Shaffer

1987; Lande 1993). We did so by adding a stochastic mortality term to the basic models (equations 3 and 4). This new mortality term varies randomly in both magnitude and frequency and allows comparisons of the impact of random catastrophes on populations with different breeding systems. Figure 4*a* shows the stochastic mortality term alone and figure 4*b* and 4*c* the dynamics of both non-cooperators and cooperators, respectively, in the presence of this additional mortality term. Figure 4 shows that both population types can recover from catastrophic events. However, non-cooperative breeding populations can recover even from important or frequent perturbations, because density dependence stimulates survival and reproduction at low density. On the contrary, the existence of a lower threshold in obligate cooperators renders them vulnerable to catastrophic events of lower magnitude and/or frequency. It is also clear from figure 4 that the smaller the difference between the actual population size and the lower the threshold, the smaller (or less frequent) stochastic perturbations need to be, to drive the population below this threshold and therefore to extinction. In addition, the buffer effect of immigration may be smaller if catastrophic events are taken into account, because these events (climate and epidemics) often affect equally nearby groups, thereby limiting immigration from them.

3. DISCUSSION

In a previous paper, Clutton-Brock *et al.* (1999*b*) hypothesized that the high frequency of group disappearance in obligate cooperatively breeding species (Jarvis *et al.* 1994; Burrow 1995; Clutton-Brock *et al.* 1999*a*) could be due to the existence of a minimum number of helpers needed to maintain a positive population growth rate. We tested this hypothesis with a simple mathematical model. Our results show that the existence of this lower threshold increases the extinction risk of cooperative breeding groups. In addition, we show that reproduction imposes a higher constraint than survival for cooperative breeders. This is simply because all species have a positive intrinsic growth rate, implying that the intrinsic birth rate is higher than the intrinsic death rate. Cooperative breeders which need helpers mostly for reproduction (e.g. baby-sitting, offspring and breeding-female feeding) will have a larger minimal sustainable group size than species needing helpers mostly for survival (e.g. guarding, defence of territory and/or group members, and hunting), provided all other things are equal. Similarly, species needing cooperative breeding for both survival and reproduction (i.e. most cooperative species) are under a higher constraint if the number of helpers needed for reproduction is higher than that needed for survival.

Our results also suggest that at low densities migration may be a regulatory mechanism in the population dynamics of obligate cooperators. At the group level, being density dependent while the growth rate is inverse density dependent, migration through dispersal may act as a buffer, limiting the erosion of the group. It has been shown, for example, that in stripe-backed wrens there is more immigration than emigration in small groups, with all immigration into small groups (Rabenold 1990). However, immigration may prevent the group from

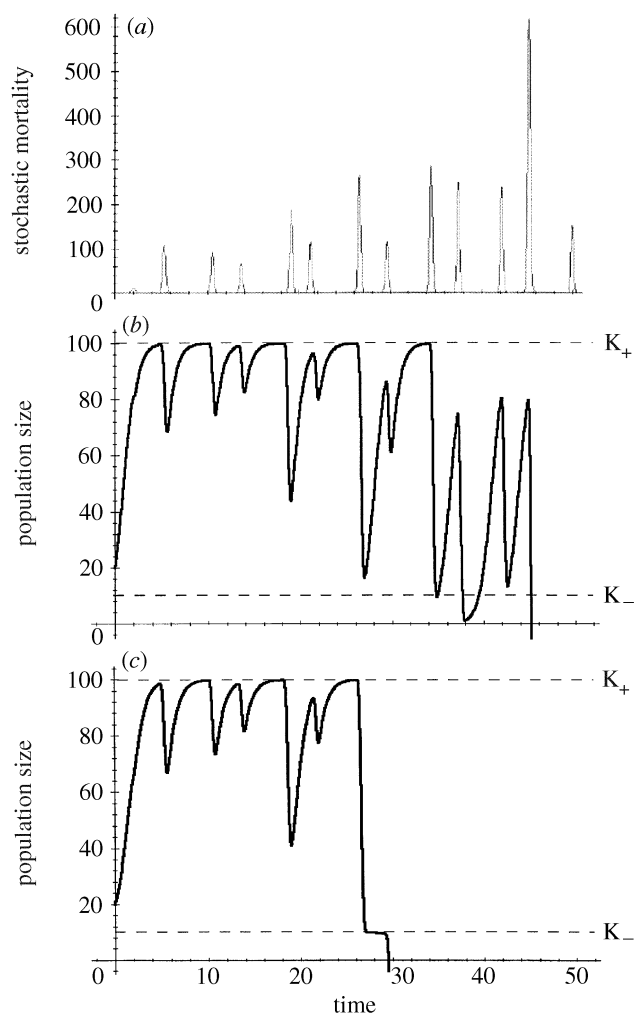


Figure 4. (a) Stochastic model accounting for mortality due to random catastrophic events. The model is set so that mortality peaks occur at random frequency and with random amplitude. (b) Population growth with time of non-cooperators when stochastic mortality is taken into account. The population becomes extinct only in extreme catastrophic events and it recovers even from a decrease down to below the minimum population size of cooperators (lower dashed line). (c) Population growth with time of obligate cooperators when stochastic mortality is taken into account. Cooperators may not recover from large catastrophic events or from frequent ones, since either would drive them below the minimum population size.

falling below the lower threshold only when individuals are always available from other groups nearby, which may not be realistic. Indeed, catastrophic events, such as droughts, are likely to affect nearby groups in a similar way, reducing immigration when it is most needed. Moreover, we show that when immigration is not higher than emigration, then migration is a disadvantageous process for groups of obligate cooperators, because it increases the value of the lower threshold, making it more probable for groups to drop below it. On a (meta)population level, emigration is always higher than immigration, because of mortality due to dispersal. This is especially true in the harsh environments typical of many cooperative breeding species (Jarvis *et al.* 1994; Waser *et al.* 1994; Doolan & Macdonald 1996). As a consequence, migration (taken here as the difference between emigration and

immigration) can prevent smaller groups from reaching the critical group size when nearby large groups exist, but, at the population level, migration is a disadvantage for obligate cooperators from a dynamic point of view. Gruntfest *et al.* (1997) recently demonstrated that, under the Allee effect, an increase in the migration rate is not always profitable for the persistence of populations. Although other satisfying explanations have been proposed, our model shows that dynamics alone can justify the evolution of the low migration rate observed in cooperative breeding species (e.g. Koenig *et al.* 1992; Jarvis *et al.* 1994).

We finally demonstrate that obligate cooperators are more sensitive to stochastic mortality. When catastrophic events are taken into account, populations can be driven to very low densities by a single event of large amplitude or by a succession of events of smaller amplitude and/or higher frequency. Where reproduction and survival would be stimulated in non-cooperative breeding species by a low density, on the contrary the existence of the lower threshold in obligate cooperators leads them to extinction. In the southern Kalahari, a severe drought in 1994–1995 resulted in the cessation of breeding in the ten groups of suricates studied. The resulting erosion in all these groups led to the extinction of all five groups below nine individuals but of only one of the five groups above nine individuals (Clutton-Brock *et al.* 1998). This illustrates how similar stochastic catastrophic events can drive small-sized groups to extinction, while groups with initially more helpers are not driven below the threshold and will survive the decrease. From a model simulating the risks of wild dog populations' extinction, Ginsberg & Woodroffe (1997) concluded that catastrophes affect the persistence of the smallest populations, particularly if they are not supplied by migration from other populations. Since, for different reasons, cooperative breeding populations are not very large *in natura*, stochastic events of small amplitude and/or low frequency may be sufficient to drive relatively large groups to extinction. It is noteworthy that we did not take into account demographic stochasticity in the model. Even though it is said to be less important than environmental stochasticity and random catastrophes (Shaffer 1987), it is not to be neglected (Kokko & Ebenhard 1996), meaning that this simplification underestimates the risk that a group of a given size will be driven below the lower threshold. The results here can therefore be considered as optimistic, since environmental and demographic stochasticity will increase the risk of extinction and, therefore, the constraint of cooperative breeding. In an associated paper (Courchamp *et al.* 1999), we show how interactions with natural enemies, such as predators or competitors, increase the extinction risk of obligate cooperative breeding populations, mainly by decreasing their size, thereby rendering them more susceptible to stochastic events.

The Allee effect is a basic manifestation of multiple equilibria much discussed by modellers, in particular in the context of fisheries (e.g. Roughgarden & Smith 1996) or pest management (e.g. Royama 1984). However, examples of biological causes of the Allee effect are generally restricted to plant–pollinator interactions (e.g. Groom 1998), genetic diversity (e.g. Asmussen 1979) and, most of

the time, difficulty in finding a mate at low densities (Hopper & Roush 1993; Myers *et al.* 1995; Veit & Lewis 1996; see Fowler & Baker (1991) for more examples). As a consequence, the Allee effect has mostly been considered for plants, invertebrates or fishes; birds and mammals have seldom been considered, mainly because their high mobility and communication abilities increase their chance of finding mates even at low densities. Consequently, population dynamics studies on birds and mammals have focused only on density dependence and density independence. We show here that inverse density dependence at low density, yielding an Allee effect, is however of major importance for the large number of vertebrate species with obligate cooperative breeding systems. Even though adding more realism (e.g. metapopulation and spatial heterogeneity) would be important, our present results show that the population dynamics of these species imposes on them a higher risk of extinction than non-cooperative breeding species. Since many of them are currently endangered, this aspect is likely to be of major importance for the conservation of cooperative breeding species.

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