

Impact of natural enemies on obligately cooperative breeders

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Courchamp, F., Grenfell, B. T. and Clutton-Brock, T. H. 2000. Impact of natural enemies on obligately cooperative breeders. – *Oikos* 91: 311–322.

Obligately cooperative breeders (cooperators) display a negative growth rate once they fall below a minimum density. Constraints imposed by natural enemies, such as predators or competitors, may push cooperator groups closer to this threshold, thus increasing the risk that stochastic fluctuations will drive them below it. This may indirectly drive these groups to extinction, thereby increasing the risk of population extinction. In this paper, we construct mathematical models of the dynamics of groups of cooperators and non-cooperators in the presence of two types of enemies: enemies whose dynamics do not depend on the dynamics of their victim (e.g., amensal competitor, generalist predator) and those whose dynamics do. In the latter case, we distinguish positive (e.g., specialist predator) and negative (e.g., bilateral competitor) reciprocal effects. These models correspond to the classical amensal, predation and competition models, in the presence of an Allee effect. We then develop the models to study consequences at the population level. By comparing models with or without an Allee effect, we show that enemies decrease the group size of cooperators more than that of non-cooperators, and this increases their group extinction risk. We also demonstrate how an Allee effect at a lower dynamical level can have consequences at a higher level: inverse density dependence at the group level generated lower population sizes and higher risks of population extinction. Our results also suggest that demographic compensation can be achieved by cooperators through an increased intrinsic growth rate, or by decreasing the enemy constraint. Both of these types of compensation have been observed in empirical studies of cooperators.

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Across ecological disciplines, the last few years have witnessed an upsurge of interest in the Allee effect (see recent reviews in Courchamp et al. 1999a, Stephens and Sutherland 1999, Stephens et al. 1999). Not only is the Allee effect considered to have a potentially profound impact where it occurs, but it is also emerging as a widespread phenomenon, being common in animal and plant species and pervading virtually all areas of population biology (Dennis 1989, Fowler and Baker 1991, Sæther et al. 1996, Kuussaari et al. 1998, Lande 1998). It has recently been concluded that most living species are subject, either directly or indirectly, to some extent to the dynamical consequences of the Allee effect: species that do not display inverse density dependence

may interact with one or several which do (Courchamp et al. 1999a). With this growing realisation, it has become apparent that the current theoretical background is generally inadequate to describe specifically the dynamics of populations at low densities (Dennis 1989, Sæther et al. 1996). In particular, the framework of classical interspecific interactions, such as predator-prey, host-parasite and interactions with amensal or bilateral competitors, needs to be redefined to take into account the effects of inverse density dependence at low density.

There is a long and distinguished body of work on the Allee effect, upon which our work (i.e., Courchamp et al. 1999b and the present paper) is built (e.g.,

Accepted 3 June 2000

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ISSN 0030-1299

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Volterra 1938, Odum and Allee 1954, Philip 1957, Wilson and Bossert 1971, Dennis 1989). However, with the notable exception of recent studies on the competitive dynamics of two species subject to an Allee effect (Wang et al. 1999; see also Hopf and Hopf 1985), theoretical studies of the Allee effect have historically considered individual species in isolation. It is this gap that we begin to address with the present study, focusing on the general example of obligately cooperative breeding species and their dynamical relationships with several types of natural enemies.

In most social animals, direct (negative) density dependence is likely to prevent or limit the risk of group extinction. In these species, decreases in group size are generally associated with a decrease in intraspecific competition, and therefore with increased survival and breeding success (Clutton-Brock et al. 1982). In obligately cooperative breeders, however, the need for helpers is likely to induce an inverse density dependence to recruitment and survival at low density, with the result that small groups will have a lower breeding success and/or survival (e.g., Florida scrub jays, *Aphelocoma coerulescens*: Mumme 1992; acorn woodpecker, *Melanerpes formicivorus*: Mumme and DeQueiroz 1985; black-backed jackals *Canis mesomelas*: Moehlman 1979; dwarf mongooses, *Helogale parvula*: Waser et al. 1995; Damaraland mole-rats, *Cryptomys damarensis*, Jarvis et al. 1998; suricates, *Suricata suricatta*: Clutton-Brock et al. 1999a, b). As a consequence, small groups have an increased risk of continuing decline, and thus an accelerating extinction risk (Clutton-Brock et al. 1999a, b). A high rate of group extinction has indeed been observed in several obligately cooperative breeders, including naked mole-rats, *Heterocephalus glaber* (Jarvis et al. 1994), African wild dogs, *Lycaon pictus* (Burrow 1995), and suricates (Clutton-Brock et al. 1999a, b). In particular, the long-term study on suricates provides one of the few demonstrations of a positive relationship between group size and survival (Clutton-Brock et al. 1999a, b). Recent work on reproductive success and survival of African wild dogs has also demonstrated such a relationship (Creel, Courchamp and Clutton-Brock unpubl.).

Because of their critical need for helpers, two consecutive processes may cause the extinction of groups of obligately cooperative breeding species (hereafter, “cooperators”). First, any externally initiated decline in group size can draw the group below its extinction threshold, the minimal viable group size. Below this threshold, a negative growth rate due to inverse density dependence can lead the group towards complete extinction. This inverse density dependence at low densities, or Allee effect, has been addressed in a previous paper for obligately cooperative breeding species considered individually (Courchamp et al. 1999b). The initial decline in group size can take one of two forms. It can be entirely caused by stochastic events that are

dramatic in amplitude (this affects even species close to the ecological carrying capacity). This case is illustrated by exceptional environmental conditions, such as droughts and floods (e.g., treecreepers (Climacteridae): Noske 1991; suricates: Clutton-Brock et al. 1999b), or by epidemics (e.g., wild dogs, Alexander and Appel 1994). Alternatively, the initial decline can be caused by a combination of a group reduction owing to deterministic mechanisms, such as the action of natural enemies, followed by stochastic fluctuations. These fluctuations can be of smaller amplitude (or higher frequency) than catastrophic events, but nevertheless sufficient to draw the group below the critical threshold.

In this paper we will focus on this second aspect: the impact of natural enemies on the population dynamics of obligate cooperators. We do so by analysing three main mathematical models accounting for most possible types of detrimental interspecific interactions. These models correspond to classical predator or competitor (Lotka-Volterra) models in the presence of an Allee effect. For the purpose of this paper, we define a “natural enemy” in its broader sense, as another species which reduces the victim’s equilibrium group size; this therefore subsumes the effects of predators, parasites and competitors. Note that, by convention and for the sake of simplicity, we also refer to direct or inverse density dependence, even when it is in fact the size of the group (or population) which is important. Only population dynamic aspects are addressed here: behavioural and evolutionary considerations have already benefited from several recent reviews (e.g., Jennions and Macdonald 1994, Emlen 1997, König 1997). For each interaction, we build a very simple two-species model, the outcomes of which we compare when the victim is a cooperator and a non-cooperator. Comparisons allow an estimation of the impact of the natural enemy, in terms of depletion of the cooperator group size, and increase in extinction risk. We then build an extension of the model to account for the consequences at the population level of an Allee effect at the group level. Our models are general enough to apply to species which are not obligate cooperators, but which still display an Allee effect; in which case our extension describes, as a crude approximation, an expansion from the population to the metapopulation level.

The models

We construct two different models, accounting for a fundamental difference in the dynamics of the relationships between the two species: the Unilateral Effect Model, and the Reciprocal Effect Model. The Unilateral Effect Model concerns pairs of species in which the negative impact of co-occurrence is borne by only one species, and thus the population dynamics of the enemy

are not affected by those of the victim. This case is best illustrated by amensal competition, where one species suffers from the presence of a competitor, but does not affect this competitor in return. This is the case with introduced rabbits, *Oryctolagus cuniculus*, on many islands, which do not seem to be affected by the presence of endemic land birds, but act as serious competitors to the birds, by destroying their nesting sites (Johnstone 1985). Another example concerns generalist predators, kleptoparasites or brood parasites: they have a direct impact on their prey/host population dynamics, but can be considered as relatively unaffected by fluctuations of a single prey/host species because other such species are present. This is the case for several “generalist” brood-parasitic cowbird species (Strausberger and Ashley 1997, Massoni and Reboresda 1998), or for spotted hyenas, *Crocuta crocutta*, which steal prey from wild dogs (Carbone et al. 1997, Gorman et al. 1998) but also hunt and scavenge (Gasaway et al. 1991). A last example may be found in true parasitism. Many parasitic species, whether microparasites (viruses, bacteria and fungi), or macroparasites (helminths and arthropods), do not rely on a single host species: some have one or more reservoir species, whilst others can infect a wide range of host species (Grenfell and Dobson 1995). Avian malaria (Warner 1968, van Riper et al. 1986) and rabies (Bacon 1985), both of which threaten several cooperative breeding species, are among the best known examples of this last case. Other parasitic species are not dependent on population fluctuations of their host because their transmission involves a long external stage in the environment.

The Reciprocal Effect model accounts for relationships in which both the victim species (whether or not it is a cooperator), and its enemy are affected by each other's presence. The simplest case is reciprocal competition, where the instantaneous growth rate of both competitors is lowered by the presence of the other species. Acorn woodpeckers and a variety of acorn-eating competitors illustrate this case (Macroboberts 1970, Mumme and DeQueiroz 1985). The enemy species may also be a predator, whose population dynamics are highly dependent on those of its prey because of a rather specialised diet (as in the classical ecological examples of snowshoe rabbits, *Lepus americanus* and lynx, *Lynx canadensis*; and of arctic lemmings, *Lemmus lemmus*, and foxes, *Alopex lagopus*, e.g., Elton 1927). Finally, many parasitic species have evolved life-history traits that make them highly dependent on the population dynamics of their host, for example because they are restricted to a single host species for all or part of their life cycle. In any parasite taxon, the majority of species tend to be very host-specific (Poulin 1998).

General model

We deliberately keep our models as simple as possible, to allow qualitative and quantitative comparisons. For this reason, the dynamics of non-cooperators will be described by a logistic equation, $dN/dt = rN(1 - N/K)$; the dynamics of cooperators will be described by the same model but with an Allee effect added in a simple way: $dN/dt = rN(1 - N/K_+)(1 - K_-/N)$. We assume that the growth rate of the group of cooperators is negative above an upper threshold (the carrying capacity, K_+) and below a lower threshold (the minimum group size, or extinction threshold, K_-), but positive in between. The derivation and analysis of this general model is given in a previous paper (Courchamp et al. 1999b). For all the following models, we use the following notation: E and V are the number of enemy and victim individuals, respectively; their intrinsic growth rates are r_e and r_v ; and their carrying capacities in the habitat are K_e and K_v . If the victim is an obligate cooperator, then the carrying capacity is denoted by K_{v+} and the lower threshold K_{v-} .

The Unilateral and Reciprocal Effect Models are based on these two equations. We have kept the models general so as to be comparable to most classical two-species models (e.g., May 1981). They account for most detrimental interspecific interactions, including amensalism, competition, kleptoparasitism, predation and brood parasitism. They are also valid as a crude model for true parasitism. Although our examples in this paper concern vertebrates, the models also suit some cooperative insect species and their natural enemies (such as parasitoids) as well as other species displaying an Allee effect for different causes. For both Unilateral and Reciprocal interactions, a model is constructed in which the victim species is not a cooperator (i.e., is density dependent, or DD), and is then compared to a similar model in which the victim species is a cooperator (i.e., is inverse density dependent, or IDD). We first discuss the effects of inverse density dependence at the group level, and then study their consequences at the population level.

Unilateral effect model

The typical example for a Unilateral Effect relationship is amensal competition. In this case, the depletion of the victim V due to the presence of the enemy E , proceeds at a rate η and depends on E . If the victim is not a cooperatively breeding species, we have the following model:

$$\begin{cases} \frac{dV}{dt} = r_v V \left(1 - \frac{V}{K_v}\right) - \eta VE \\ \frac{dE}{dt} = r_e E \left(1 - \frac{E}{K_e}\right) \end{cases} \quad (1)$$

For this model, three equilibrium points are: $\{0, 0\}$, $\{0, K_v\}$ and $\{V_{DD}^*, E_{DD}^*\}$ (where DD stands for Density Dependence and * denotes an equilibrium point). Since the exact solution of the equilibrium points $\{V_{DD}^*, E_{DD}^*\}$ is rather complex in some of the later models, we do not provide them here for the sake of simplicity and brevity (Maple files are available upon request). In this case, however, the enemy population is completely independent of that of the victim, and always reaches $E_{DD}^* = K_e$.

If the victim V is a cooperator, the model becomes:

$$\begin{cases} \frac{dV}{dt} = r_v V \left(1 - \frac{V}{K_v}\right) \left(1 - \frac{K_{v-}}{V}\right) - \eta VE \\ \frac{dE}{dt} = r_e E \left(1 - \frac{E}{K_e}\right) \end{cases} \quad (2)$$

Here again, there are three stable equilibrium points

(although the first one is not mathematically admissible because of a null denominator): $\{0, 0\}$, $\{0, K_{v+}\}$ and $\{V_{IDD}^*, E_{IDD}^*\}$ (where IDD stands for Inverse Density Dependence).

We compared the phase portrait of both Unilateral Effect systems (with DD or with IDD: Fig. 1a and b). This figure illustrates the constraint of IDD on the victim. A phase portrait, or phase plane, is a projection of a tridimensional graph of the numbers of two species against time, onto the two dimensions of the two species numbers. The area of the phase portrait represents all possible combinations of initial numbers of victims and enemies. Our model shows that the part of this area that leads to extinction of the victim (shown in grey on Fig. 1) is larger when victims are cooperators. This area also increases with increasing K_{v-} (not shown), that is, with the constraints of inverse density dependence. The risk of extinction owing to the presence of a natural enemy is thus higher if the victim is a cooperator than if it is not.

Relationship with a natural enemy may not always have such a dramatic outcome as complete extinction. When victim and enemy numbers reach an equilibrium, one can compare the size of the victim group when it is IDD or DD (cooperator or not). The ratio between the

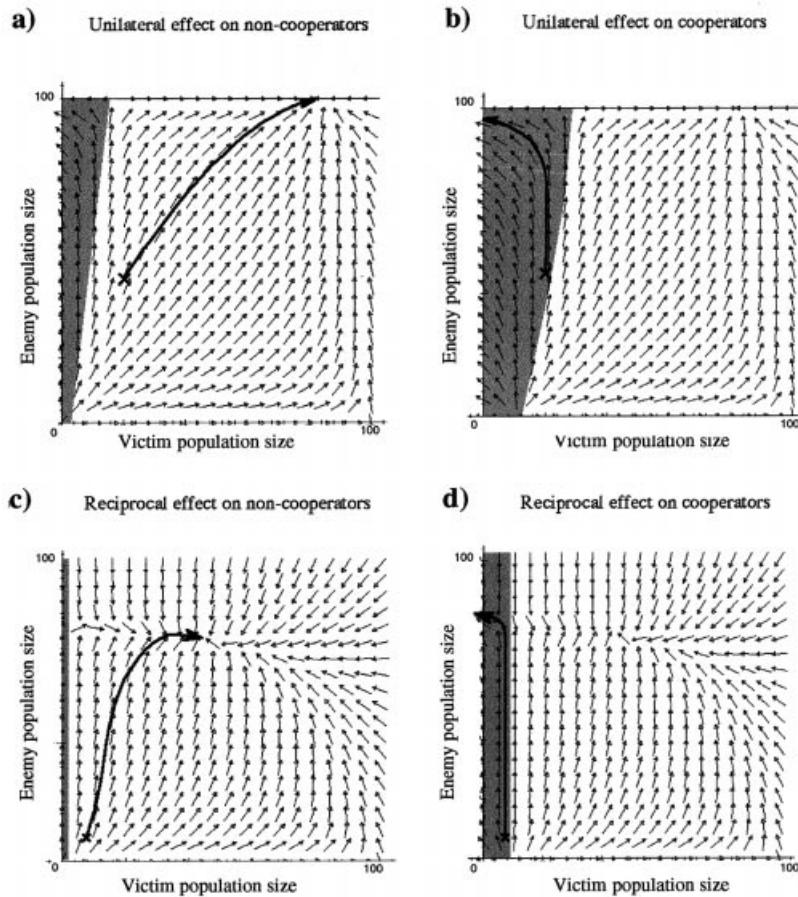


Fig. 1. Phase portraits for the Unilateral Effect Model (a, b) and for the Reciprocal Negative Effect Model (c, d). For each model, we compare the case where the dynamics of the victim are directly density dependent (victim is a non-cooperator, a and c) or are inversely density dependent (victim is a cooperative breeder, b and d). For any given initial condition in the phase portraits, the system will follow the direction given by the arrows (vectors) of the direction field, to an equilibrium point (which can be the extinction of one or both populations). The grey areas cover approximately the values of the populations leading to extinction of the victim. For both models this area is larger for cooperative breeders, reflecting their higher risk of extinction in the presence of an enemy. As illustrated by the black curve, the same initial value of the victim and its enemy can lead to extinction of a cooperative breeding species where other species would survive. All population sizes are given as percentages of the carrying capacity. Results are similar for the Reciprocal Positive Effect Models (not shown).

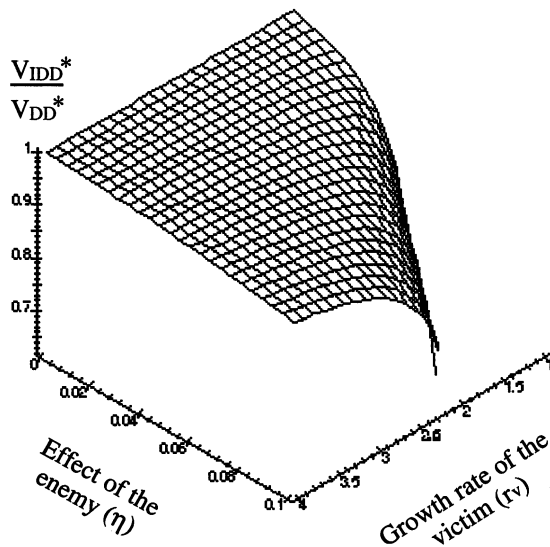


Fig. 2. Value of the ratio between the population size at equilibrium in the presence of a natural enemy when the victim is a cooperator and when it is not (V_{IDD}^*/V_{DD}^*), as a function of its intrinsic growth rate, r_v , and the enemy constraint η , for the Unilateral Effect. Values less than 1 indicate that the cooperator has a lower population size than the non-cooperator. This ratio provides a quantitative estimate of the demographic cost of cooperative breeding in the presence of a natural enemy. At equilibrium, the group size of victims is always lower if they are cooperators (if they display an Allee effect) than if they are not. This difference decreases with increasing values of the cooperator intrinsic growth rate, and with decreasing values of the enemy constraint. Results are similar for the Reciprocal Effect Models (not shown).

victim group size in the two models, (V_{IDD}^*/V_{DD}^*), is given in Fig. 2. This ratio illustrates the extent to which cooperation is an advantage (values above 1) or a disadvantage (below 1) with regards to depletion of the victim group by the enemy. The figure shows that this ratio is always less than 1: cooperative breeding always implies a lower group size at equilibrium in the presence of an enemy. This lower size may be up to ca 40%. As expected, the ratio decreases with the constraints of cooperative breeding (i.e., with increasing values of the critical group size, K_{v-}). In addition, as shown in Fig. 2, this ratio increases with values of the intrinsic growth rate of the cooperator (r_v) and the constraint imposed by the enemy (η). Together the two figures show that the presence of amensal competitors (or natural enemies of a similar type) is more deleterious for cooperators than it is for species without an Allee effect.

Reciprocal effect models

For the Reciprocal Effect Model we distinguish two cases, depending on whether the enemy benefits or suffers from the presence of the victim. We choose to

base our analyses on the classical Lotka-Volterra models for predation in the former case (Reciprocal Positive Effect) and for competition in the latter case (Reciprocal Negative Effect).

Reciprocal Positive Effect model

The typical example for a Reciprocal Positive relationship is predation. We define η as the rate at which the victim suffers from the enemy's presence. The enemy dies at a rate δ and benefits from the victim's presence at a rate γ . For biological realism, as well as for consistency with other models in this paper, we also assume that density dependence in the enemy leads to a logistic growth rate when the victim is present (intraspecific competition for prey or for other resources). The form of density dependence is chosen so that it is similar to the other models of this paper; however, more standard Lotka-Volterra predation models such as $\sigma VE - \alpha E - \beta VE^2$ (May 1981) yield the same results. If the victim is not a cooperatively breeding species (i.e., it shows DD dynamics), we have:

$$\begin{cases} \frac{dV}{dt} = r_v V \left(1 - \frac{V}{K_v}\right) - \eta EV \\ \frac{dE}{dt} = \gamma V \eta E \left(1 - \frac{E}{K_e}\right) - \delta E \end{cases} \quad (3)$$

This gives three stable equilibrium points: $\{0, 0\}$, $\{0, K_{v+}\}$ and $\{V_{DD}^*, E_{DD}^*\}$.

If the victim is a cooperatively breeding species (IDD dynamics), the model becomes:

$$\begin{cases} \frac{dV}{dt} = r_v V \left(1 - \frac{V}{K_{v+}}\right) \left(1 - \frac{K_{v-}}{V}\right) - \eta EV \\ \frac{dE}{dt} = \gamma V \eta E \left(1 - \frac{E}{K_e}\right) - \delta E \end{cases} \quad (4)$$

Here again, three stable equilibrium points are possible: $\{0, 0\}$, $\{0, K_{v+}\}$ and $\{V_{IDD}^*, E_{IDD}^*\}$ (although the first one is not mathematically admissible because of a zero denominator).

As for the previous case, the comparison of the phase portrait for the two Reciprocal Positive Effect models indicates that in the presence of a natural enemy, the extinction area is larger for cooperators than for non-cooperators. Thus, extinction risk is higher for cooperators. This risk increases with increasing values of K_{v-} . When the victim is not eradicated by the enemy, we can study the ratio (V_{IDD}^*/V_{DD}^*) between the points of the two models where both species are present in stable equilibrium. This ratio is always less than 1, meaning that cooperative breeding implies a lower size at equilibrium in the presence of an enemy. Again, this lower value may be close to 40%. The ratio varies with

parameters in a similar fashion to the previous model. This shows that the presence of predators (or natural enemies of a similar type) is more deleterious for cooperators than it is for species without an Allee effect.

How do predator-prey oscillations affect cooperative prey? We explore this for the Reciprocal Positive Effect Model in Fig. 3. In such cases, the victim may

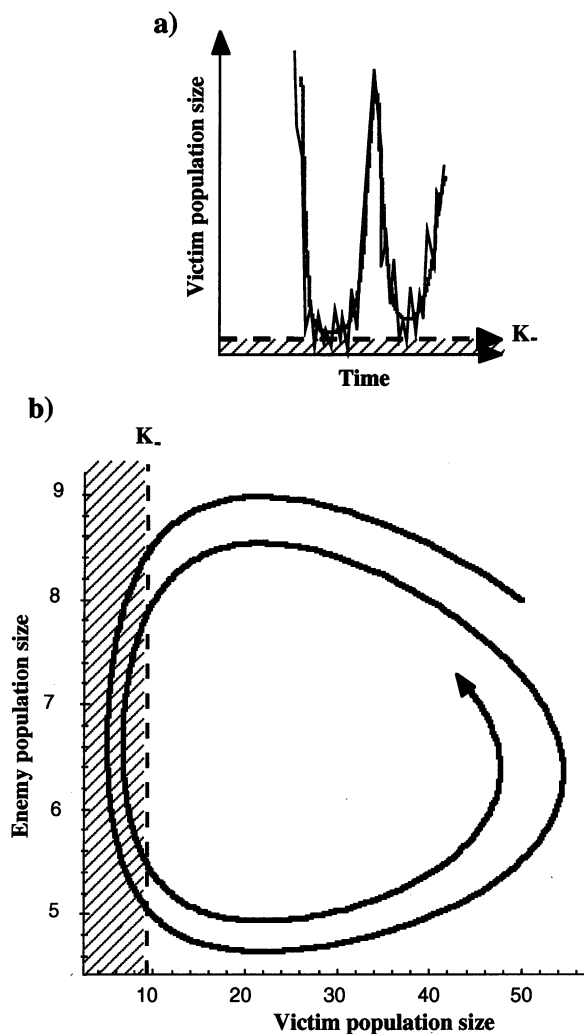


Fig. 3. a) Simulation of the victim population size as a function of time, for the Reciprocal Positive Effect Model (grey line), with parameter values set to generate damped oscillations (first 30 time steps). The black line represents potential fluctuations around the average deterministic model, to illustrate how stochastic variability puts cooperative victims at risk of reaching the critical group size (K_- , hatched area) during the low phases of the cycle. b) Phase portrait for the same model (different parameter values). Here again, the non-cooperator victim avoids extinction, whereas a cooperator victim is unable to cope with such oscillations because part of them drive its population below the critical group size.

be dangerously close to the critical group size during the lower part of the cycle, especially when stochastic fluctuations are taken into account (Fig. 3a), increasing its extinction risk. This result implies that cycles may not be observed for cooperative species because for some systems, as shown in Fig. 3b, part of the cycle would imply a group size below the critical threshold for cooperators. It is also worth noting that this also holds when it is the predator that displays an Allee effect: in this case, specialist predators would undergo cycles that would put them at a high risk of extinction.

Reciprocal Negative Effect model

The typical example for a Reciprocal Negative relationship is competition. In this case, the victim suffers from the constraint of the enemy (λ), but imposes its own constraint (μ) on this enemy. We have the classical Lotka-Volterra competition model if the victim is not a cooperative breeder:

$$\begin{cases} \frac{dV}{dt} = r_v V \left(1 - \frac{V + \lambda E}{K_v} \right) \\ \frac{dE}{dt} = r_e E \left(1 - \frac{E + \mu V}{K_e} \right) \end{cases} \quad (5)$$

If the victim is a cooperative breeder, this model becomes:

$$\begin{cases} \frac{dV}{dt} = r_v V \left(1 - \frac{V + \lambda E}{K_{v+}} \right) \left(1 - \frac{K_{v-}}{V} \right) \\ \frac{dE}{dt} = r_e E \left(1 - \frac{E + \mu V}{K_e} \right) \end{cases} \quad (6)$$

Results of these models are similar to the results of models (3) and (4). They show that for bilateral competition, the extinction risk of the cooperator is heightened: in the presence of a competitor, the extinction area is larger if the victim is a cooperator than if it is not (Fig. 1c and d). Similarly, when the victim avoids extinction, the constraint imposed by the enemy (λ) results in a decrease of the equilibrium size of the victim, attenuated only for the highest values of the constraint imposed by the victim on the enemy (μ). This shows that the presence of bilateral competitors (or natural enemies of a similar type) is more deleterious for cooperators than it is for species without an Allee effect.

For each of the three sets of models presented so far, the effect of cooperation of the victim is also summarised through the change of the null clines (or isoclines) on a phase portrait (Fig. 4).

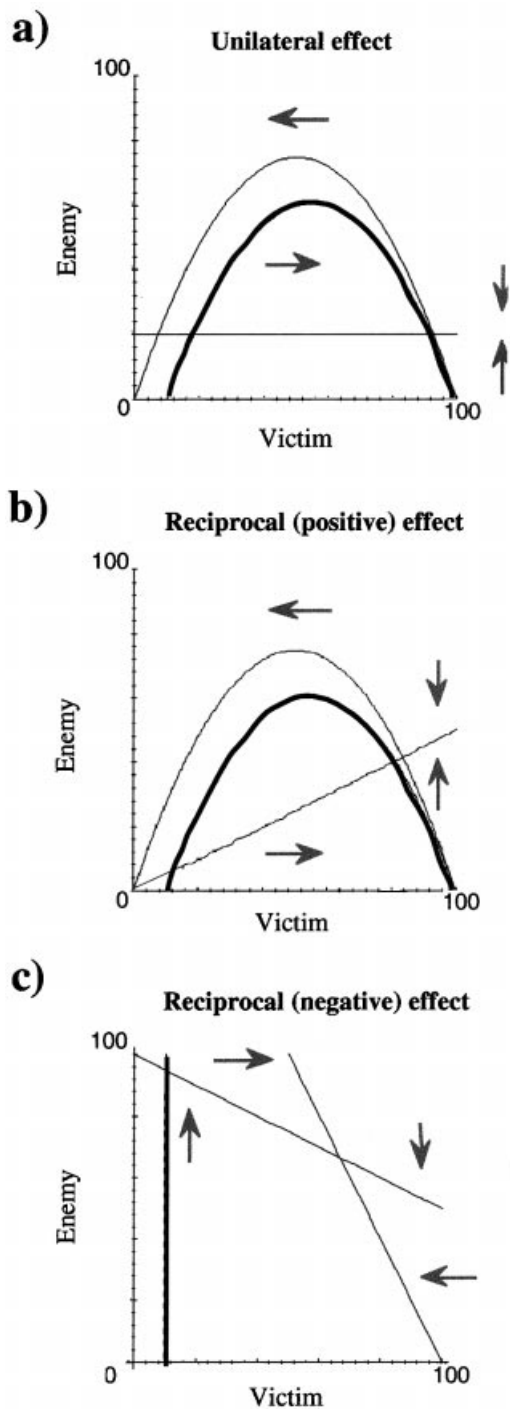


Fig. 4. Isoclines (or nullclines) for the three models: a) Unilateral Effect, b) Reciprocal Positive Effect and c) Reciprocal Negative Effect. For each model, the change in the victim's isocline due to cooperative breeding is indicated by a new isocline in bold. The presence of an Allee effect, such as that seen in cooperators, decreases the area for which the victim's growth is positive. Parameter values are as follow: $r_v = 1.5$; $\eta = \gamma = \mu = \lambda = 0.5$; $K_{v-} = 10$; $K_{v+} = K_e = 100$ (except for (c) where $K_e = 20$).

From cooperator groups to populations

In the models just described, our approach focused on the group level, because we were concerned with obligate cooperators (for which inverse density dependence is generated at the group level). We are now in a position to briefly study the consequences of this social system at the population level. We thus describe how an Allee effect at the group level can have dynamical consequences at the population level, if the groups are interconnected through dispersal. However, since the previous models can also describe the dynamics of populations of other types of species subject to an Allee effect, this extension can also be considered in terms of its consequences for these species at the metapopulation level.

For each of the previous models, we have constructed an extension in which the victim species is no longer represented by a single equation for its group, but by several equations, one for each of the groups forming its population, all connected through dispersal. All groups show the same interspecific relationship with the enemy as previously described. Dispersal is such that individuals emigrate from large groups and immigrate into small groups. After carrying out complete analytical studies with two groups, we then modified the models for three groups, which we present here. Numerical studies show that the same conclusions can be drawn when populations comprise more than three groups. We provide an example below with the Reciprocal Positive Effect Model (predator-prey), when the victim is an obligate cooperator (i.e. shows inverse density dependence) and its population comprises three groups of size V_a , V_b and V_c :

$$\begin{cases} \frac{dV_a}{dt} = r_v V_a \left(1 - \frac{V_a}{K_{v+}}\right) \left(1 - \frac{K_{v-}}{V_a}\right) - \eta E V_a - \beta \frac{(2V_a - V_b - V_c)}{3} \\ \frac{dV_b}{dt} = r_v V_b \left(1 - \frac{V_b}{K_{v+}}\right) \left(1 - \frac{K_{v-}}{V_b}\right) - \eta E V_b - \beta \frac{(2V_b - V_a - V_c)}{3} \\ \frac{dV_c}{dt} = r_v V_c \left(1 - \frac{V_c}{K_{v+}}\right) \left(1 - \frac{K_{v-}}{V_c}\right) - \eta E V_c - \beta \frac{(2V_c - V_b - V_a)}{3} \\ \frac{dE}{dt} = \alpha \mu E (V_a + V_b + V_c) \left(1 - \frac{E}{K_e}\right) - \delta E \end{cases} \quad (7)$$

For the sake of space, we do not provide the corresponding modifications for the DD and IDD versions of the other models (Unilateral and Reciprocal Negative), but their analysis is available upon request. Analytical study of eqs (7) shows that the conclusions are the same as for the model without group subdivisions (eqs (3) and (4)). As shown in Fig. 5, populations with IDD are more likely to go extinct than populations with DD, and when they survive, populations with IDD are smaller on average. Because this is a deterministic model, no further properties emerge from partitioning a population into spatially distinct fragments. However, a stochastic version of a similar model shows

that inverse density dependence at the group level can create an Allee effect at the population level, further enhancing the dynamical constraints of this process (Courchamp et al. in press).

If eqs (1) to (6) represent the dynamics of a group of obligate cooperators, then eq. (7) represents a set of such groups, forming a population. Alternatively, eqs (1) to (6) can represent populations of other types of species showing an Allee effect, in which case eq. (7) describes its consequences at the metapopulation level. Both scenarios show that inverse density dependence at the lower level (group or population) has dynamical consequences at the higher level (population or metapopulation).

Discussion

In a previous paper, we showed how obligately cooperative breeding species undergo a demographic cost due to the existence of an Allee effect below a critical group size threshold (Courchamp et al. 1999b). This is due to cooperators' need for helpers to enhance survival and/or reproduction, which makes it increasingly difficult to restore the group size once it is below a critical threshold. In addition, the closer the group to this critical size, the more important the risk of being drawn below it by stochastic (e.g., environmental) fluctuations. We provide here a modification of the classical (Lotka-Volterra) models of interspecific relationships by including a component for the Allee effect. We illustrate our points with examples of obligately cooperative breeding species. Through this modelling exercise, we show that natural enemies increase the demographic cost incurred by species displaying an Allee effect, sometimes driving them below a critical threshold, and thus to extinction (Fig. 1). Even when the enemy has a weaker effect, it can drive these species closer to the extinction threshold, so that stochastic variability of smaller amplitude and/or frequency may be sufficient to drive them below it (Fig. 3). In addition, we show that the risk experienced by cooperators increases with the constraint imposed by cooperative breeding (the number of helpers needed) and with the constraint imposed by the natural enemy. These conclusions are valid for interactions involving unilateral as well as reciprocal effects. However, reciprocal effects can act in two possible directions: to the enemy, the presence of the victim can either be a benefit (e.g., predators) or a nuisance (e.g., competitors). The impact of the enemy will be higher in the case of a nuisance: at low cooperator density, reciprocal competitors will be freed from competitive constraints, and their resulting population increase will add to the threat for the cooperators. Moreover, when both are at low density, the greater increase potential of non-cooperators makes them better competitors when confronted with cooperators.

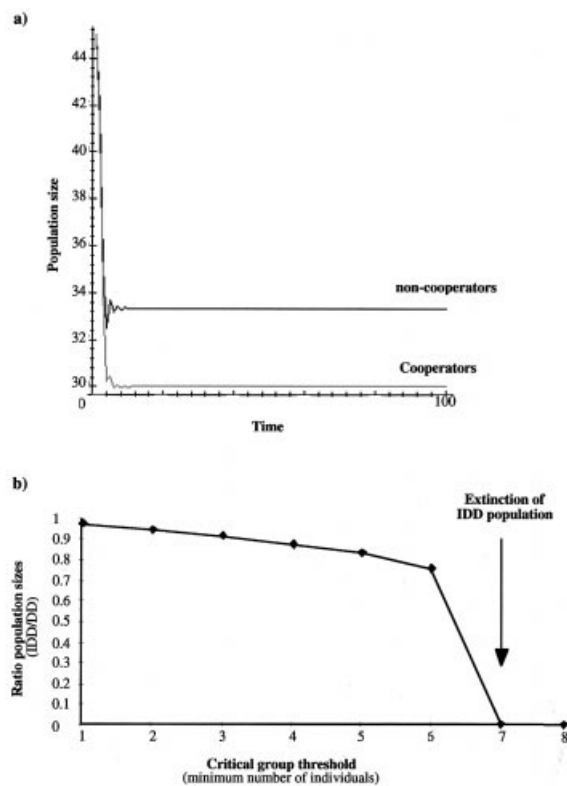


Fig. 5. a) Simulation of the size, with time, of populations comprising groups with (cooperators) or without (non-cooperators) inverse density dependence, in the presence of a natural enemy (model 7). Populations in which groups show inverse density dependence are smaller. b) Ratio of the size of the two types of populations, as a function of the size of the critical threshold. As this threshold (which illustrates the strength of inverse density dependence) increases, the difference between the two types of population increases, reflecting the dynamical constraints of cooperative breeding. The ratio is always lower than one, indicating that populations in which groups show inverse density dependence are always smaller than those showing no inverse density dependence; it reaches zero when the population with inverse density dependent groups goes extinct, for a critical threshold of seven individuals per group.

The aim of this exercise was to contribute to a theoretical framework for the dynamics of interacting populations in the presence of an Allee effect. Obviously, further refinements of the models are needed to enhance biological realism. For example, including demographic and/or environmental stochasticity is crucial, and taking into account individual, spatial and temporal heterogeneities would be useful regarding the population and metapopulation levels. Furthermore, in these models, we did not account for disadvantages conferred by small group size regarding defence against natural enemies. However, as emphasised by Sæther et al. (1996), there is now much evidence that group size is important for the efficiency of the defence against both predators and parasites. Using an increasing function

Table 1. Mechanisms providing dynamical advantages to cooperatively breeding species.

Advantage	Improved intrinsic growth rate		Reference
	Cooperative process	Example of species	
Improved survival	Enhanced efficiency in localising feeding sites	Varied sittella, <i>Daphoenositta chrysoptera</i> Evening bats, <i>Nycticeius humeralis</i>	Noske 1998 Wilkinson 1992
	Enhanced efficiency in capturing prey	Harris' hawks, <i>Parabuteo unicinctus</i> Lions Spotted hyenas Wild dogs	Faaborg and Bednarz 1990 Stander 1992 Kruuk 1972 Creel and Creel 1995
Increased reproduction (through reduced parental effort)	Increased reproductive lifespan of breeders	Chimpanzees, <i>Pan troglodytes</i> Pied kingfisher, <i>Ceryle rudis</i>	Boesch 1994 Reyer and Westerterp 1985
	Shortened inter-clutch/litter intervals	Splendid fairy-wren, <i>Malurus splendens</i> Dwarf mongooses Splendid fairy-wrens	Russell and Rowley 1988 Rood 1990 Rowley and Russell, 1990 Solomon 1991
(through increased offspring survival)	Increased clutch/litter size	Prairie voles, <i>Microtus ochrogaster</i> House mice, <i>Mus domesticus</i>	König 1994 Moehlman 1979
	Offspring feeding	Black-backed jackals White-fronted bee-eaters, <i>Merops bullockoides</i> Arabian babblers, <i>Turdoides squamiceps</i>	Emlen and Wrege 1991 Wright 1998
	Offspring defence	Suricates Wild dogs	Manser 1999 Malcolm and Marten 1982
	Offspring grooming and warming	Red-billed woodhoopoes, <i>Phoeniculus purpureus</i> Pine voles, <i>Microtus pinetorum</i>	BoixHinzen and Lovegrove 1998 Powell and Fried 1992
	Increased breeding experience	Splendid fairy-wrens Seychelles warbler, <i>Acrocephalus sechellensis</i> Several primate species	Russell and Rowley 1988 Komdeur 1996 Hrdy 1976
Advantage	Defence against natural enemies		Reference
	Cooperative process	Example of species	
Defence against predators	Communal guarding	Florida scrub jays Stripe-backed wrens, <i>Campylorhynchus nuchalis</i> Dwarf mongooses Suricates	MacGowan and Woolfenden 1989 Rabenold 1984 Rasa 1989 Clutton-Brock et al. 1999c
	Cooperative mobbing and defence of attacked individuals	White-winged choughs, <i>Corcorax melanorhamphos</i> Florida scrub jays Banded mongooses, <i>Mungo mungo</i> Geoffroys marmosets, <i>Callithrix geoffroyi</i>	Heinsohn 1992 Francis et al. 1989 Rood 1975 Passamani 1995
Defence of resources against competitors, kleptoparasites or brood parasite	Communal mobbing	Banded mongooses Spotted hyenas	Rood 1975 Kruuk 1972
	Coercion through group size	Splendid fairy-wrens Acorn woodpeckers Wild dogs	Payne et al. 1985 Mumme and DeQueiroz 1985 Fanshawe and FitzGibbon 1993
Prevention of offspring predation and brood parasitism	Nest/den attendance (baby-sitting)	Florida scrub jay	Woolfenden and Fitzpatrick 1990
		Bay-winged cowbird, <i>Molothrus badius</i>	Fraga 1992

Table 1. (Continued)

Advantage	Improved intrinsic growth rate		Reference
	Cooperative process	Example of species	
Care against parasites	Feeding or defence of infected individuals Allogrooming and wound-licking	Coyotes, <i>Canis latrans</i> Wild dogs	Bekoff and Wells 1982 Malcolm and Marten 1982
		Suricates	Clutton-Brock et al. 1998
		Wild dogs	Kruuk 1972
			Loehle 1995

of the efficiency of defence with victim group size would serve to strengthen our conclusions that inverse density dependence is likely to increase extinction risks in the presence of natural enemies. Our models also show that if group size is to remain constant in the presence of a natural enemy, two different factors may dynamically compensate for the effects of inverse density dependence. As shown qualitatively in Fig. 2, the first one is an improved intrinsic growth rate, the other a decreased constraint from the enemy. Indeed, without implying any adaptive process, there are several advantages of cooperation that could possibly result in either an increased intrinsic growth rate or a decreased enemy constraint, emphasising the robustness of our models. Examples of mechanisms enhancing breeding success and/or survival in cooperating species are presented in Table 1.

Through mathematical models, we have identified one potential reason for the high risk of group extinction observed in obligate cooperators: they have a minimum group size under which the growth rate becomes negative, and are pushed closer to this critical threshold by their natural enemies. This analysis suggests that the Allee effect exerts a massive pressure on species to lower their sensitivity to natural enemies, as shown by several empirical studies. In the light of growing interest in conservation biology, it appears paradoxical that the population dynamics of obligately cooperative breeding species, which are often at high risk of local extinction, have not been investigated theoretically. The need for such studies is well illustrated by the case of the African wild dog. As an obligate cooperator, this highly endangered canid is likely to display an Allee effect (Courchamp et al. 1999a, in press). Since the main causes of mortality are believed to include natural enemies such as predators (lions), kleptoparasites (hyenas) and parasites (e.g., rabies and Canine Distemper Virus; see reviews in Creel and Creel 1998, Woodroffe and Ginsberg 1999), an awareness of the importance of group size in this species could be critical for its survival. Furthermore, although we have focused here on obligate cooperators, the results hold for other species displaying an Allee effect. As an example, the case of host – parasite

metapopulation interactions (Grenfell and Harwood 1997) where both species may exhibit Allee effects could be a particularly fruitful area for future study.

In conclusion, many other species could benefit from increased awareness of the dynamical processes occurring in the presence of an Allee effect, particularly concerning relationships with natural enemies. We hope that, as well as constituting a useful step towards a stronger theoretical framework for this ecological process, the present work will stimulate further studies in this critical area of conservation biology.

Acknowledgements – This work was supported by a TMR 30 Marie Curie Fellowship from the European Community, and BBSRC grants. We thank Rosie Cooney, Tim Fawcett, Hanna Kokko, Naomie Langmore and Sue McRae for critical reading of the manuscript, and Pej Rohani and Nigel Yoccoz for helpful discussions about the models. We also thank Peter Hudson for reviewing the paper.

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