

Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus*

Franck Courchamp, Tim Clutton-Brock and Bryan Grenfell

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

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Abstract

The current decline of the highly endangered African wild dog (*Lycaon pictus*) may be partly due to the population dynamics induced by their social system. African wild dogs are obligate co-operators, and their need for helpers could generate inverse density dependence at the pack level. We show, through a mathematical model, that this can create an Allee effect, leading to a lower population size and a higher risk of population extinction, compared to populations with direct density dependence. This is due to three different processes. All three processes can increase population extinction individually and probably occur simultaneously in African wild dogs. First, inverse density dependence causes significantly higher rates of pack extinction. Second, it also increases the probability of failure to colonize territories by founders. Third, the Allee effect at the pack level (with a critical number of individuals), generates an Allee effect at the population level (with a critical number of packs). These three processes are likely to apply to other obligate co-operative breeders. Furthermore, our results suggest that habitat fragmentation and destruction, as well as increased human pressure, increase the effects of inverse density dependence. Direct and indirect anthropogenic effects may thus be more detrimental to obligate co-operative breeders than to other species.

INTRODUCTION

The African wild dog, (*Lycaon pictus*), also called the painted hunting dog (Rasmussen, 1999), is one of the most endangered large carnivores in Africa (Ginsberg & Macdonald, 1990). At the beginning of the 20th century, this species was observed in large numbers and was distributed over most of the African continent. Despite current legal protection, its survival is not guaranteed: in the six countries still supporting viable populations, a 'sanguine attitude' caused a further decline of more than 30% during the 1980s (Ginsberg & Macdonald, 1990) and populations have continued to decline during the 1990s (Woodroffe *et al.*, 1997). The past causes of the decline and extinction of their populations are well known: they have historically suffered from a high level of human persecution until recently. It is not yet completely understood why their populations continue to decline when populations of other persecuted animals such as the spotted hyena (*Crocuta crocuta*) seem to have stopped declining (Creel & Creel, 1998; Vucetich & Creel, 1999). Most studies of the continued decline

of wild dog populations have focused on the direct and indirect consequences of human activities and interactions with natural enemies. Direct anthropogenic mortality, caused by shooting, poisoning, snaring and road kills, as well as habitat reduction and degradation are undoubtedly partly responsible (for reviews, see Creel & Creel, 1998; Woodroffe & Ginsberg, 1999). However, this does not explain why sympatric species that suffered from similar anthropogenic pressures are not as endangered as wild dogs (Creel & Creel, 1998). Also, it is generally admitted that natural enemies, such as predators (lions, *Panthera leo*), kleptoparasites (spotted hyenas, lions), competitors (these species and many other carnivores) and parasites (e.g. canine distemper virus, rabies or anthrax) are important limiting factors for this species (for reviews, see Creel & Creel, 1998; Woodroffe & Ginsberg, 1999). However, these factors may not be the only explanation for such declines, since wild dogs have a long history of coevolution with most of them.

Given the good potential for recovery of wild dogs (including very large litters, good juvenile and adult survivorships, long dispersal distances; Fuller *et al.*, 1992), it may appear surprising that their populations are still declining dramatically. While it is clear that natural and anthropogenic factors undoubtedly exert heavy tolls on

All correspondence to: Franck Courchamp. Current address: Ecologie, Systématique & Evolution, Université Paris-Sud XI, Bat 362, F-91405 Orsay Cedex, France. Tel: 00 33 1 69 15 56 85; Fax: 00 33 1 69 15 56 96; E-mail: franck.courchamp@epc.u-psud.fr

wild dogs, we propose that another (non-exclusive) factor plays a crucial role in their decline. The specific features of their social system and life-history traits, which clearly differentiates them from other sympatric carnivore species, could impose a constraint at the population dynamics level, exacerbating their extinction risk in perturbed conditions. Direct and indirect anthropogenic causes of mortality would consequently have a much more dramatic impact on this species.

African wild dogs are obligate co-operative breeders, and their need for helpers is illustrated by many aspects of their life, including most facets of foraging, breeding and surviving natural enemies. Once they have reached reproductive age, individuals may disperse with other members of their packs, typically in single-sex cohorts of 2–8 related individuals (Frame *et al.*, 1979; Fuller *et al.*, 1992; Burrows, 1995; McNutt, 1996). New packs are formed when two such dispersing cohorts of opposite sex meet and fuse.

Using very general models, we have recently suggested that groups of obligate co-operative breeders would suffer inverse density dependence, because of their need for helpers for survival and/or reproduction (Courchamp, Grenfell & Clutton-Brock, 1999b; in press). This could, in some cases, be accompanied by the existence of a critical pack size below which the capacity of the pack to maintain itself is seriously hampered, creating an Allee effect (Courchamp, Clutton-Brock & Grenfell, 1999a; Stephens & Sutherland, 1999), which would increase the risk of pack extinction.

In African wild dogs, inverse density dependence at the pack level could be generated by their need for helpers for co-operative hunting (Fanshawe & Fitzgibbon, 1993; Creel & Creel, 1995), defense of kills from kleptoparasites (Fanshawe & Fitzgibbon, 1993; Carbone, DuToit & Gordon, 1997; Gorman *et al.*, 1998), pup feeding (Malcom & Marten, 1982) and baby-sitting (Malcom & Marten, 1982). A significant relationship has been shown in several populations between pack size and breeding success (Burrows, 1995; Creel, Creel & Monfort, 1998; G. S. A. Rasmussen, unpublished data) and between pack size and foraging success (Fanshawe & Fitzgibbon, 1993; Creel & Creel, 1995). In fact, the need for helpers seems to pervade virtually all aspects of the life of African wild dogs (F. Courchamp & D. W. Macdonald, unpublished results). It is hypothesized that below a critical number of helpers (typically around five adults, including the breeding pair), the pack cannot successfully raise new pups to independence (F. Courchamp, G. S. A. Rasmussen & D. W. Macdonald, unpublished results; S. Creel, F. Courchamp & T. H. Clutton-Brock, unpublished results). We do not imply that successful reproduction is impossible for a pair, since this has been observed in the wild (Burrows, 1995, but see Estes & Goddard, 1967 for a seemingly more likely fate of the litters from pairs). Rather, we suggest that such occurrences are exceptional and not representative of the species (see S. Creel *et al.*, 1998; unpublished results; for tests of the relationship between pack size and breeding success). Our goal in this work is

twofold. First, we aim to show that inverse density dependence at the pack level both increases the rate of pack extinction and decreases the rate of colonization of new territories. For this we use a stochastic model of the dynamics of several packs linked through dispersal, which we study through simulations. Second, using the same mathematical model, we will investigate the effects of habitat destruction (both quantitatively and qualitatively) and human persecution on the fate of wild dog populations.

METHODS

We considered a total of nine patches, each holding at most one pack of wild dogs. The dynamics of each pack is governed by either a logistic, density dependent (DD, 'classical model') growth rate, based on the classical logistic equation, or by the same model with inverse density dependence (IDD, 'co-operative model'), yielding an Allee effect (see Courchamp *et al.*, 1999a). Each pack is assumed to occupy a distinct patch (although we did not consider here any spatial dimension *per se*), meaning that if one becomes extinct, another pack can take its place. Each patch is indirectly linked to all the others by dispersal. It has been shown that larger packs of African wild dogs will generate larger dispersing cohorts (Creel & Creel, 1995). For each pack in our model, the number of dispersers each year increases with the size of the pack. This assumption leads to an Allee effect – small packs produce fewer juveniles and, thus, fewer dispersers than large packs. For the sake of simplicity, we assume that it follows an exponential relationship (there is a limit to pack size through the logistic growth). In African wild dogs, individuals disperse in single-sexed cohorts that will join an opposite sex cohort to form a new pack. Immigration of individuals into already formed packs is rare (Frame *et al.*, 1979; Fuller *et al.*, 1992; Burrows, 1995; McNutt, 1996). In our model, the dispersers do not immigrate into existing packs, but instead are considered to join the pool of dispersers, until there are enough individuals to form a new pack. The minimum size for a new pack to be formed from the dispersing pool is defined as p , and this new pack can be formed as soon as one of the nine patches is vacant. New packs are formed from a number of individuals, F , set randomly from a value between 2 and p .

A deterministic version of the two models (DD and IDD) was first built, in order to test for the sensitivity to parameterization. Analysis showed that small changes in the value of the model parameters did not result in a large change in the outcome of the models, which is a good indication of robustness. Pack extinction cannot arise in a deterministic model: each pack would build up to carrying capacity and stay at this value. We thus included the possibility of stochastic mortality, in the form of random catastrophes. These catastrophes are supposed to mimic environmental constraints as well as epidemics and human pressure, which are believed to be among the greatest mortality factors of wild dogs (Woodroffe & Ginsberg, 1999). Indeed, ranchers can

shoot the greater part of a pack in a single event (Rasmussen, 1999) and poachers can snare most of a pack at the den (Rasmussen, 1997). Both of these events can be considered here as catastrophes at the pack level. If the shooting of packs is considered to be a random catastrophic event (as assumed in our model), then the data of Burrows (1995) suggest a frequency of documented catastrophic events of approximately 0.14 (three packs shot in 22 years; packs that disappeared following handling are not considered here to be victims of a catastrophic event because of the controversy on the causality of these events). In our simulations, the random catastrophic regime has been set to one catastrophic mortality event per pack every 5–10 years on average (i.e. 0.1 to 0.2). This regime (and frequencies of a similar level) minimized the differential effect of catastrophes on classical and co-operative species. In contrast, much more frequent catastrophes (e.g. every year) would cause systematic extinction of co-operative species, and much less frequent ones (e.g. every 20 years) would prevent extinction of classical species. We feel that the frequencies used here avoid overestimation of the difference of sensitivity between these two types of species. Other investigators have used similar frequencies of up to one every third year (Ginsberg, Mace & Albon, 1995; Woodroffe *et al.*, 1997). As a second step, we then studied the effect of decreasing the frequency of such catastrophic events (see Results, below). We also set the amplitude of the random catastrophes so that they could not wipe out a complete pack: for each event, from one to four-fifths of the population are removed. These approximations should tend to underestimate the real effect of environmental stochasticity on wild dog populations. We built our model with the following structure:

[dynamics of a pack] = [intrinsic dynamics] – [dispersal] – [random mortality]
 [dynamics of the pool of dispersers] = [sum of dispersers from the i packs] – [mortality during dispersal] – [eventual colonization of empty patch]

The size of the i th pack at time t is noted N_i and the size of the pool of dispersers is N_d . K is the carrying capacity for each pack (i.e. the maximum number of individuals in a pack), $f(\alpha)$ is a function setting both the frequency of random catastrophes (one every 5–10 years) and their amplitude (one to four-fifths of the pack size), δ is the dispersal rate and μ the rate of mortality during dispersal (which may be different from natural mortality of pack members: see Vucetich & Creel, 1999).

The two models can thus be described by the following set of differential equations:

$$\begin{cases} \frac{dN_i}{dt} = G(N_i) - \frac{\delta}{K} N_i^2 - f(\alpha)N_i \\ \frac{dN_d}{dt} = \frac{\delta}{K} \sum_{i=1}^{i=9} N_i^2 - \mu N_d - C(F_{[2,p]}, p) \end{cases}$$

The intrinsic dynamics of the packs is given by $G(N_i) = rN_i (1 - \frac{N_i}{K})$ in the case of the density dependent model and by $G(N_i) = rN_i (1 - \frac{N_i}{K}) (1 - \frac{K_-}{N_i})$ in the case of the inverse density dependent model. The intrinsic growth rate is r ; K_- is the critical pack size (below which the instantaneous reproductive rate is negative) In this paper, K_- is set to five following F. Courchamp *et al.*, unpublished results.

The colonization of an empty patch is described by the term $C(F_{[2,p]}, p)$, which means that a group of F dispersers, taken at random between 2 and p , will colonize an empty patch, if one exists, when the pool of dispersers is larger than or equal to p . In the study of the model, the value for p is set at 8.

Both models (with and without IDD) were run 1000 times. Each simulation was run for a period of 100 years, starting with four existing packs, of 12, 10, six and four individuals, and two individuals in the dispersal pool. For each simulation, we recorded four variables: number of packs, average size of the packs, number of pack extinctions and number of pack colonizations. We were, therefore, able to calculate two further variables: total population size and percentage of the carrying capacity. Colonization occurred frequently in the IDD model, due to increased extinction events. This increase in colonization events was not a sign of vigorous population growth, because many of the colonization events failed within 1 to 4 years without reaching full pack size (typically not increasing beyond F , the number of founder individuals). Thus, we also recorded the number of failed colonization events for both models. These are defined as colonization resulting in an extinction within 4 years without previous increase. We then compared the distribution of these variables for the two models (with and without IDD). When these distributions were not normal, we used Mann–Whitney tests; otherwise we used t -tests.

In addition, we studied the effect of habitat destruction ('quantitative reduction') and habitat degradation ('qualitative reduction'), both of which are major factors affecting wild dog population survival. We first simulated the effect of a quantitative reduction of the wild dog habitat, by reducing the number of available territories. An example of this would be the transformation of natural habitat into agricultural areas. We compared the results obtained for nine patches to those obtained for six and for three patches. We also considered the case of qualitative reduction, by studying the situation where the territories are not completely unsuitable for wild dogs, but where their prey abundance is depleted (i.e. lower carrying capacity, K). An example of this would be the transformation of natural habitat into ranches, with or without persecution of passing packs or individuals by ranchers. Furthermore, we studied the effect of human persecution by increasing both the mortality during dispersal (μ) and the severity of the random mortality events on the nine patches (β). Finally, we added a preliminary exploration of the effects of a decrease in the human persecution. We chose to simulate this effect through an increase in the average time

separating two random mortality events, but without decreasing the strength of such events. Such a pattern is likely to occur if, for example following campaigns of information, fewer ranchers shot dogs on sight. We chose to double, then to triple the length between two such events.

RESULTS

Extinction/recolonization

A set of typical simulation outcomes for both models is shown in Fig. 1. These simulations show the opposing forces of growth rate and stochastic mortality. Comparisons of the outputs of the two models show that, after a period of 100 years, there are significantly fewer pack extinction events in populations with the DD model

than in the IDD model (on average 6.34 versus 44.19, respectively: $Z = -36.90$; $P < 10^{-4}$). This is accompanied by a significantly higher percentage of failed colonization of empty patches in the IDD model (1.6% in the DD model versus 54% in the IDD model: $Z = -38.68$; $P < 10^{-4}$). The higher rate of extinctions in the IDD model remains even after removing extinctions coming from failed colonization attempts (6.18 versus 19.19: $Z = -37.19$; $P < 10^{-4}$). As a result, there are fewer packs in populations with IDD (8.86 versus 6.04 on average: $Z = -31.17$; $P < 10^{-4}$). Because of the Allee effect, these populations are also made up of smaller packs (15.04 versus 8.82: $Z = -34.26$; $P < 10^{-4}$). This results in a lower total population size (135.36 versus 79.38: $Z = -34.26$; $P < 10^{-4}$), and therefore a lower percentage of the carrying capacity is used (75.2(± 0.3)% versus 50.6(± 0.5)%). Furthermore, the percentage of total extinction, that is

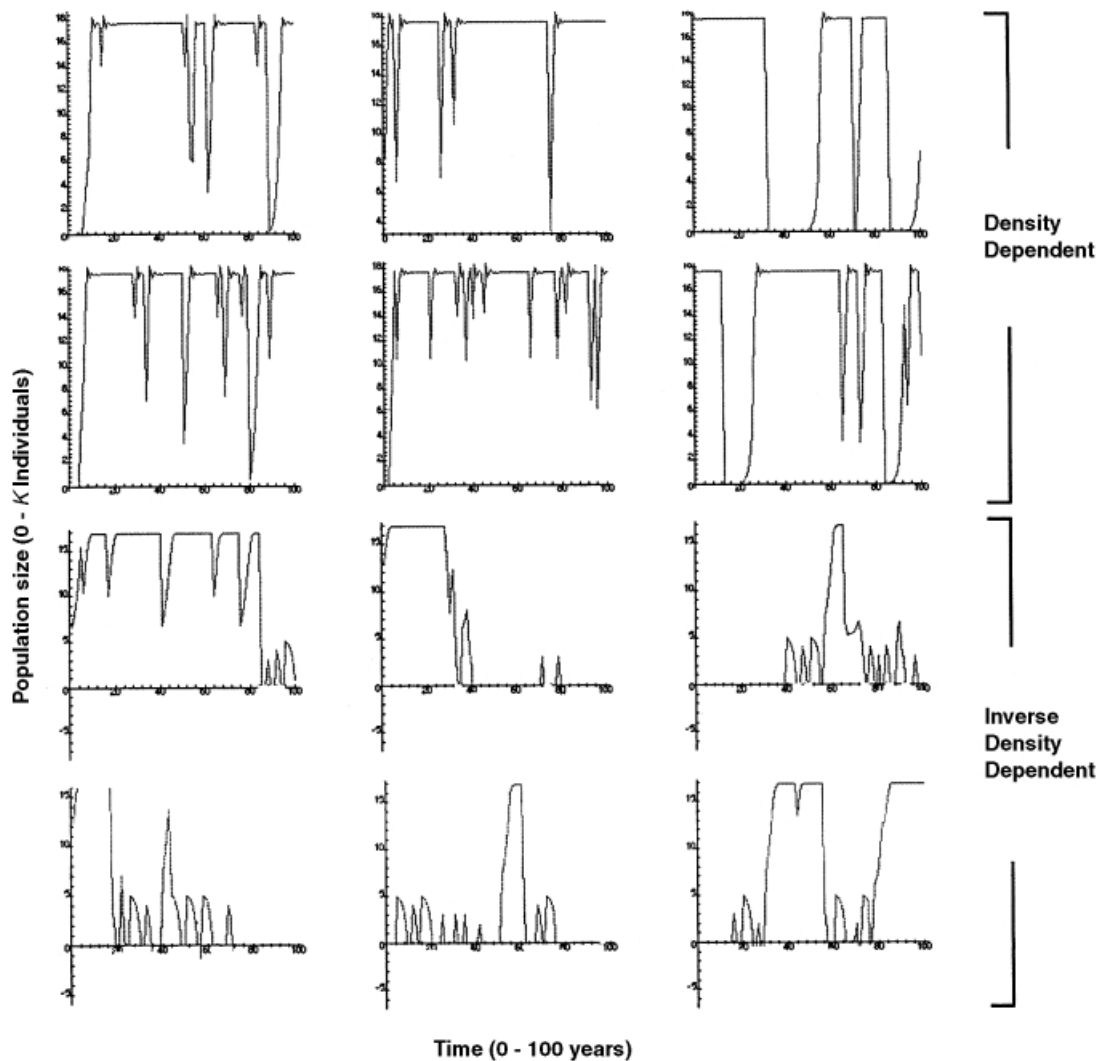


Fig. 1. Typical examples of the simulation obtained from both density dependent and inverse density dependent populations in the presence of random catastrophes. Each simulation represents the dynamics of one pack during 100 years, a population being constituted of nine such packs linked together by dispersal. Not only do the perturbations lead more often to pack extinction in the inverse density dependent population, but they are often followed by a failed colonization (short narrow peaks), resulting in a higher probability that the population as a whole goes extinct. The values used here are $K = 20$, $r = 1.5$, $\delta = 0.2$, $\mu = 0.3$, $p = 8$ (see the text for explanation of parameters) and one random mortality event every 5 years on average.

the extinction of all nine packs plus the pool of dispersers, is significantly higher when there is an Allee effect (0% versus 12.8%, $\chi^2 = 136.75$, $P < 10^{-4}$). The higher percentage of failed colonizations presumably arises from the smaller and fewer packs, generating smaller and fewer dispersing cohorts (after 100 years, the number of dispersers available for colonization was significantly smaller in the IDD model 61.36 versus 26.03: $t = -19.56$, $P < 10^{-4}$), which results in smaller founding packs that are more likely to fall below the critical threshold. In summary, the populations following IDD dynamics suffer more pack extinctions and failed colonization events, leading to fewer packs, which on average are also smaller, than the populations with classical density dependence. The risk of total population extinction is also higher.

Lastly, the distribution of the number of packs in the 1000 populations after 100 years provides an important and unexpected result. As shown in Fig. 2, there is a lack of populations with few packs, compared to populations with more packs or with zero packs (total extinction). This indicates that populations reaching a small number of packs (around five) are likely to go completely extinct. This is typical of an Allee effect at the population level.

Reduction in quantity or quality of habitat

For the purpose of comparison between models (with different dynamics and with varying parameter values), the average size of the total population is best summarized by the fraction of the carrying capacity occupied after 100 years. This variable is obtained by dividing the total population size by the product of the number of patches and the maximum pack size. As shown in Fig. 3, decreasing the number of suitable patches does not change this fraction in either model. On the other hand, decreasing the number of suitable patches does dramatically change the number of total extinctions after 100 years in the IDD model, with more than half of the populations going extinct. The DD populations never go extinct in our model over the time period studied, regardless of the number of patches. The effect of habitat quantity reduction is thus an increased probability of population extinction when there is an Allee effect.

Reduction of the carrying capacity of the territories (for example because of a lower abundance of game) results, in the case of IDD, in an increase of the extinction risk of populations (up to 100% when the packs have a maximum of ten individuals) and in a decrease of the average population size of those which do not go extinct. In contrast, density dependent populations, whatever the value of the carrying capacity, have a high average population size despite random catastrophes, and have a null extinction risk (Fig. 3).

Human persecution

The increase of the mortality rates of both territorial packs and dispersers show results that are qualitatively

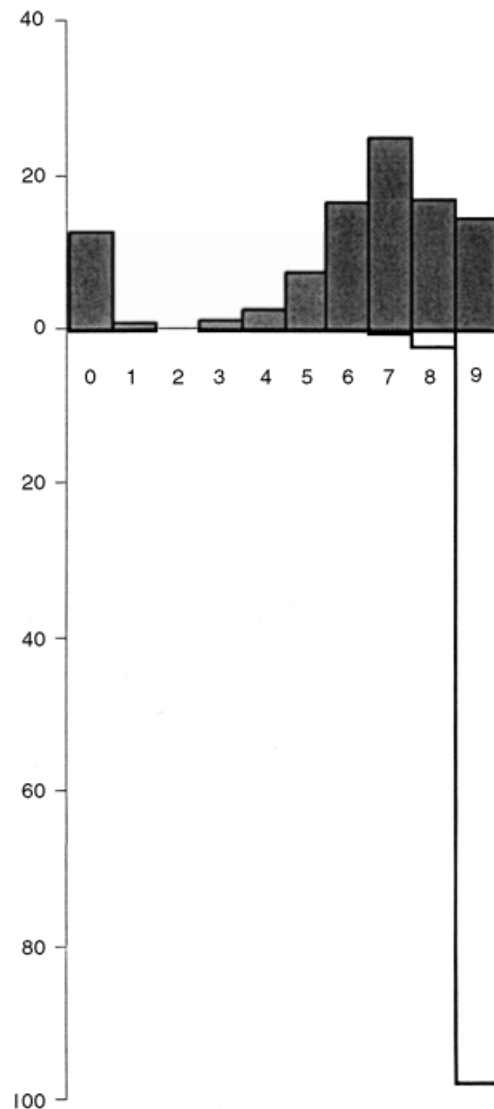


Fig. 2. Distribution of the number of packs for 1000 populations after 100 years of either inverse density dependence (IDD: shaded bars) or direct density dependence (DD: open bars). For the IDD populations, the relative lack of populations with few groups (five and below) and the abundance of extinct populations suggest that small populations are likely to completely disappear once below a critical pack number. Because fewer packs generate fewer dispersers, which are thus less likely to successfully colonize a territory, natural erosion of the population by pack extinction is not balanced by new colonization below a certain threshold. It results in a higher probability of IDD population extinction.

similar to the case of decreased carrying capacity (Fig. 3). The proportion of extinct populations increases dramatically with increasing mortality, and the surviving populations have an increasingly lower average size than the populations with the DD model.

A decrease in the human persecution, simulated through a decrease in the frequency of random mortality events, dramatically reduces the difference between

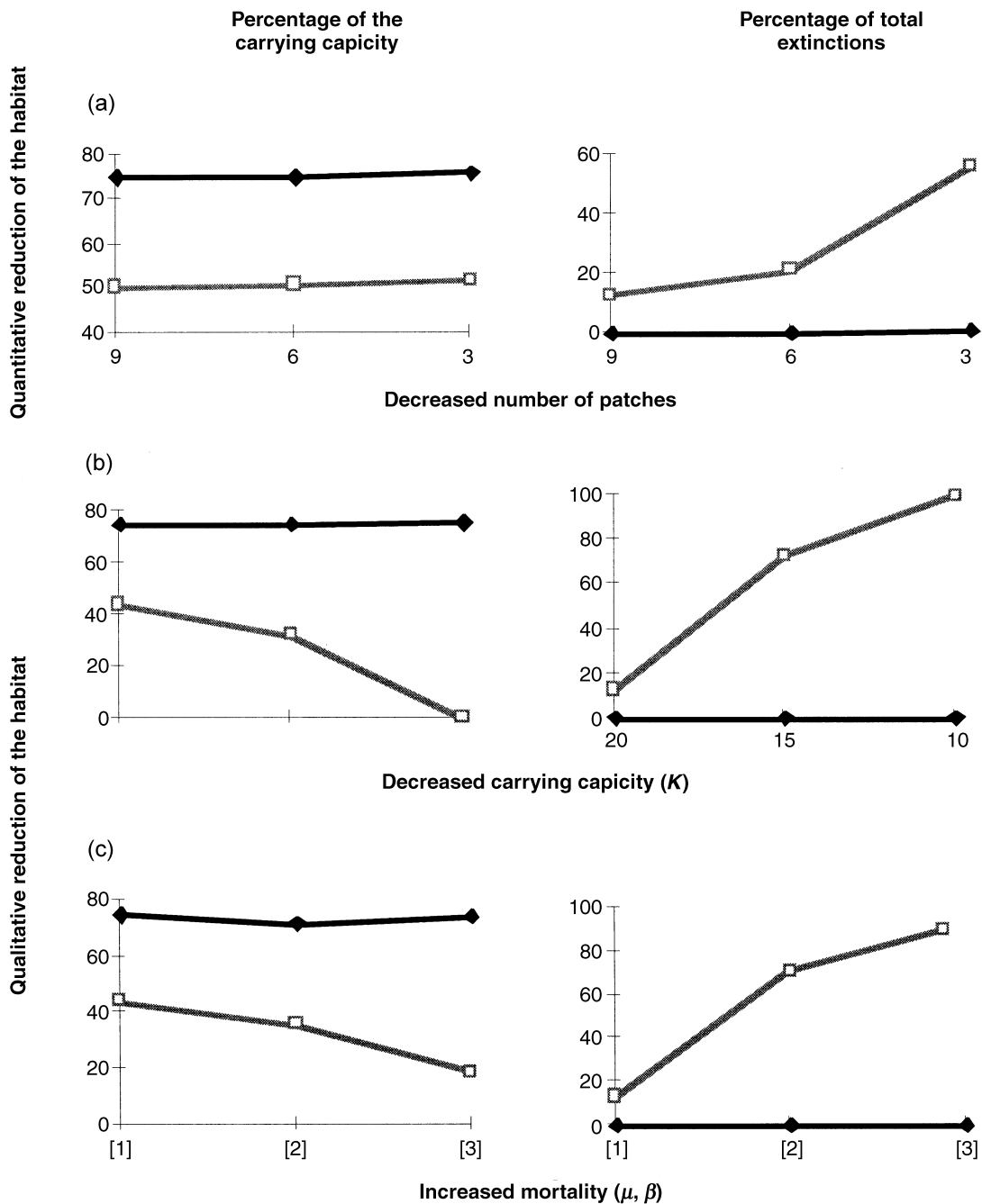


Fig. 3. Effect on populations with density dependence (DD: \blacklozenge) and inverse density dependence (IDD: \square) of (a) a decrease in the habitat quantity (i.e. the number of available patches, where packs can establish a territory); (b) a decrease in the habitat quality (i.e. the maximum size of the pack on the patch) and (c) an increase in human persecution (i.e. three increasing levels of the mortality during dispersal, μ , and of the amplitude of random catastrophic events, β). The three levels of mortality are given the following values: [1], $\mu = 0.3$, $\beta = 0.2$; [2], $\mu = 0.5$, $\beta = 0.25$; [3], $\mu = 0.7$, $\beta = 0.3$. These effects are each time illustrated as the average population size (omitting extinct populations) expressed as a percentage of the carrying capacity (first column), as well as the percentage of total population extinction (second column). Each dot represents 1000 simulations run over a period of 100 years. Variance is not shown because it is too low. In all three cases, the population with DD is not sensitive to the changes, whereas the population with IDD decreases dramatically in its average population size (except in the case of quantitative reduction of the habitat), as well as drastically increasing its probability of total extinction.

the DD and the IDD models. As shown in Fig. 4 for both average population sizes (of surviving populations only) and percentage of population extinction, a lowering of this mortality pressure is sufficient to decrease the dynamical disadvantage induced by inverse density dependence in the conditions used here.

In the different steps of the study, we checked that the values of the variables used had little influence on the outcome of the model (see Methods). This suggests the present pattern is generated by the structure of the model and, therefore, that the results are relevant to other co-operative breeding species.

DISCUSSION

Through a mathematical model, we have shown that inverse density dependence in the African wild dog was likely to increase the risk of population extinction through three different processes. First, this increases the risk of pack extinction, which results in a higher risk of the whole population going extinct. Second, packs are on average smaller in the presence of an Allee effect. Smaller packs produce smaller dispersing cohorts (if any), which may have a lower survival rate until they find an opposite-sex dispersing cohort with which to establish a new pack (Creel & Creel, 1995). This results in the creation of a smaller founder pack which, because of the inverse density dependence, is much less likely to successfully establish itself in an empty patch (our results show that dispersers are fewer in the presence of IDD). This leads to an increase of what we refer to as failed colonization events. As a consequence, a lower colonization rate of empty patches cannot balance the natural erosion of the population, resulting in a higher likelihood of its total extinction, even if the pack extinction rate is not enhanced. In populations with direct density dependence, the rare pack extinctions were balanced by a higher percentage of successful colonization, result-

ing in a lower probability of total population extinction. Third, as more patches are simultaneously empty, less colonization from other packs is likely to occur because fewer packs produce fewer dispersers. The resulting erosion leads to a higher likelihood of total population extinction. This is, to our knowledge, the first demonstration that a local Allee effect, with individuals as a basic unit at a pack level, can generate a global Allee effect with packs as a basic unit at a population level. This could have major implications for the population dynamics of obligately co-operative breeding species. Since the strength of the Allee effect will be related to the extent to which species rely on co-operation, we would predict that it will be the strongest in obligate co-operatively breeding species, but its impact may also be important in facultative co-operatively breeding species. From a theoretical study of the causes of extinction of the Serengeti wild dog population, Ginsberg *et al.* (1995) concluded that 'extinction is not unlikely from chance events alone in a small and declining population of wild dogs with rapid fluctuation in population number.' We agree with this conclusion and suggest that taking inverse density dependence into account would have greatly enhanced their estimates of population extinction risk.

In addition, we studied the effects of two different causes of mortality that are believed to be among the major threats to wild dogs: degradation of the habitat and persecution by humans (Creel & Creel, 1998; Woodroffe & Ginsberg, 1999). The first category was studied both quantitatively (by reducing the number of available patches to be colonized by packs) and qualitatively (by reducing the maximum pack size on each patch). The second was simulated by increasing the amplitude of stochastic mortality events, as is the case when ranchers increase the persecution pressure on this species: the larger part of a pack can be shot, poisoned or snared in a single event, and these may be considered

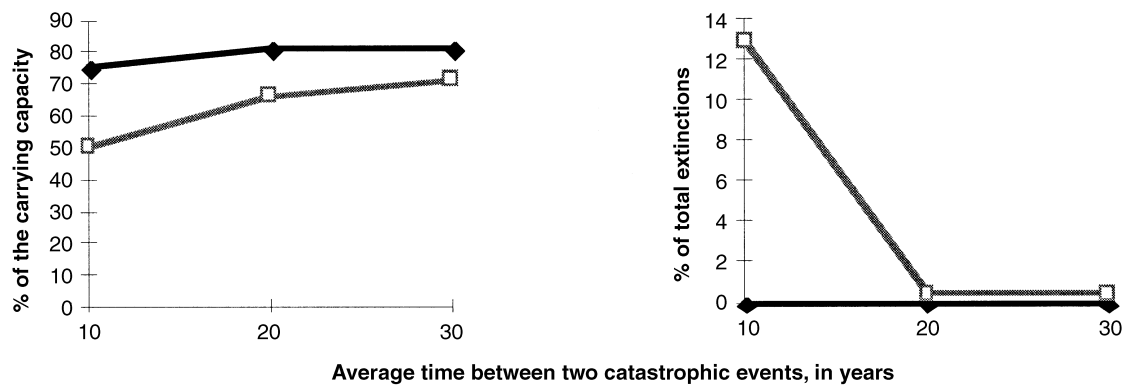


Fig. 4. Effect on populations with density dependence (DD: —◆—) and inverse density dependence (IDD: -□-) of a release of the human pressure, in terms of frequency of random mortality events. As these decrease, the difference between the two types of population decreases, illustrating the importance of human pressure on inverse density dependent populations. A near-absence of population extinction can be obtained by decreasing persecution on IDD species.

as occurring randomly in time. While populations with direct density dependence do not suffer overly from any of these disturbances, populations with inverse density dependence have decreased average population size and increased risk of total population extinction with each type of disturbance. A decrease in the frequency of human persecution decreases the differences between the two population types. It is to be expected that a combination of these factors, which is what wild dog populations face in the wild, would compound their problems for survival.

These results should be considered in the light of the empirical evidence for inverse density dependent dynamics of wild dogs that have been reviewed elsewhere (F. Courchamp & D. W. Macdonald, unpublished results). It is noteworthy here that although we focused on dynamic processes, a similar reasoning holds at the evolutionary scale (Aviles, 1999). The positive feedback loop that we described here with population dynamics has an equivalence in the evolution of co-operation: group size cannot be decreased once success of the species depends on it. As co-operators increase their reliance on helpers, life-history variables become adapted to the presence of co-operators, which leads to an increase of dependence on helpers, up to the point where it becomes a constraint, generating an Allee effect. When groups compete with each other and success of groups is size related, strong selection may favour large groups. This is particularly relevant to wild dogs, for which it has been shown that intraspecific competition is important, with large groups having an advantage over small ones (Creel & Creel, 1995).

It is worth emphasizing that our results do not merely demonstrate that these factors are detrimental to populations, or that decreasing human persecution is beneficial to threatened species. Our results highlight the fact that the mortality factors considered here are far more detrimental to co-operative breeders than to species with classical social system and population dynamics. We believe that this may be a key point in understanding the problems of population dynamics faced by wild dogs.

We have shown elsewhere that other mortality factors that were not taken into account in our model (such as those due to interactions with natural enemies) are likely to increase the risk of pack extinction (Courchamp *et al.*, in press). Our present results are, thus, likely to underestimate the real magnitude of the Allee effect in wild dogs. Although it was sufficient for our present purpose (to show the importance of pack size in wild dogs), this model is highly simplified. Some assumptions, such as the function used for dispersion, will require more attention in future versions of the model. Indeed, it would be interesting to increase the biological realism of this study by more closely tailoring a model to the population biology of wild dogs, for example using age and sex structures of actual populations, together with the corresponding rates of reproduction, mortality and dispersal. On the research front, probably the most urgent need concerning the dynamics of this species is to collect unambiguous data that reveals whether or not the

Allee effect occurs at the population level. Although logistically challenging, such a programme would be helpful with regard to conservation plans for the African wild dog.

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