

# Dynamics of a small re-introduced population of wild dogs over 25 years: Allee effects and the implications of sociality for endangered species' recovery

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**Abstract** We analysed 25 years (1980–2004) of demographic data on a small re-introduced population of endangered African wild dogs (*Lycaon pictus*) in Hluhluwe-iMfolozi Park (HiP), South Africa, to describe population and pack dynamics. As small populations of cooperative breeders may be particularly prone to Allee effects, this extensive data set was used to test the prediction that, if Allee effects occur, aspects of reproductive success, individual survival and population growth should increase with pack and population size. The results suggest that behavioural aspects of wild dogs rather than ecological

factors (i.e. competitors, prey and rainfall) primarily have been limiting the HiP wild dog population, particularly a low probability of finding suitable mates upon dispersal at low pack number (i.e. a mate-finding Allee effect). Wild dogs in HiP were not subject to component Allee effects at the pack level, most likely due to low interspecific competition and high prey availability. This suggests that aspects of the environment can mediate the strength of Allee effects. There was also no demographic Allee effect in the HiP wild dog population, as the population growth rate was significantly negatively related to population size, despite no apparent ecological resource limitation. Such negative density dependence at low numbers indicates that behavioural studies of the causal mechanisms potentially generating Allee effects in small populations can provide a key to understanding their dynamics. This study demonstrates how aspects of a species' social behaviour can influence the vulnerability of small populations to extinction and illustrates the profound implications of sociality for endangered species' recovery.

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## Introduction

It is well recognised that individuals of many species may benefit from the presence of conspecifics, a concept broadly referred to as the Allee effect after the pioneering work of W. C. Allee (Allee 1931), who brought attention to the possibility of a positive relationship between aspects of individual fitness and either population size or density. This definition requires that some measurable component of individual fitness is higher in a larger aggregation unit (e.g.

population or social group) and Allee effects then manifest as reductions in fitness as aggregation units become smaller. Whether all direct and indirect components of fitness combine to produce an overall increase or decrease with increasing abundance, however, will depend on the relative strength of negative density dependence (Stephens et al. 1999). Stephens et al. (1999) therefore suggested that it is important to differentiate between component Allee effects (Allee effects manifested by a component of fitness, e.g. benefits of a larger group size in terms of increased individual survival rates) and demographic Allee effects (Allee effects manifested at the level of total fitness by a lower population growth rate at lower density). The overall relationship between fitness and abundance may thus be seen as the cumulative effects of all component Allee effects and all negative density-dependent effects.

Until recently, the concept of Allee effects was generally regarded as an intriguing but relatively unimportant aspect of population ecology. However, it has become the focus of increased attention in the light of concerns over conservation and the problems associated with rarity. This, together with an increased emphasis on the relevance of behavioural ecology to conservation biology, has heightened interest in the implications of sociality for the viability of populations (Courchamp et al. 1999a; Stephens and Sutherland 1999; Berec et al. 2007). As an Allee effect can be generated by a shortage of interactions among conspecifics at low density, the degree of sociality of a species might reflect the degree of severity of the Allee effect to which it is subject. Allee effects thus potentially have particularly serious impacts on the population dynamics of obligately cooperative breeding species, which rely on the presence of a minimum group size (or number of helpers) for raising their young (Creel 1998; Courchamp et al. 1999b). In addition, constraints imposed by natural enemies, such as predators or kleptoparasites, have the potential to push cooperator groups closer to or below this critical group size threshold (Courchamp et al. 2000a; Creel et al. 2001). If this lower threshold is reached, it becomes increasingly difficult for a group to increase or even maintain its size. It has thus been suggested (Clutton-Brock et al. 1999) that the tendency for frequent group extinction witnessed for cooperative breeding species is due to the existence of this lower threshold, the minimum viable group size (Courchamp et al. 1999a; Stephens and Sutherland 1999). As a result, cooperator groups may be substantially more likely to undergo extinction, and small populations of cooperative breeders suffering from competition consequently pose profound problems regarding their recovery.

One species sharing these characteristics is the African wild dog (*Lycaon pictus*), an endangered carnivore with a nearly obligate cooperative breeding system that is

negatively affected by interspecific competition with other large carnivores (intraguild predation and kleptoparasitism at carcasses; Creel and Creel 2002). Wild dogs throughout their range occur at low population densities compared to other social large carnivores and wild dog populations have been shown to fluctuate widely (Creel and Creel 2002), rendering them especially vulnerable to extinction when deterministic or stochastic fluctuations in numbers reduce population or group size below a critical threshold. Wild dogs have thus been modelled as a prime example where Allee effects might have profound implications on the population dynamics of an endangered species (Courchamp et al. 2000b). The causal mechanisms of the Allee effect proposed to positively affect measurable components of individual fitness in wild dogs include advantages of a large pack size in terms of improved foraging efficiency, breeding success and survivorship (Courchamp and Macdonald 2001).

Here, we used a long-term re-introduction programme to test for evidence of both demographic and component Allee effects in wild dogs, encompassing population, behavioural and conservation ecology. We analysed 25 years (1980–2004) of demographic data on a small population of re-introduced wild dogs in Hluhluwe-iMfolozi Park (HiP), South Africa, to describe population and pack dynamics. We used this extensive data set to test the prediction that, if Allee effects occur, aspects of reproductive success, individual survival and population growth should increase with pack and population size (cf. Malcolm and Marten 1982; Fuller et al. 1992a; Maddock and Mills 1994; Burrows 1995; Creel et al. 1998, 2004; Vucetich and Creel 1999; Courchamp et al. 2002; Creel and Creel 2002; Buettner et al. 2007; McNutt and Silk 2008; Rasmussen et al. 2008). In South Africa, a plan was launched to manage separate sub-populations of wild dogs in several small, geographically isolated conservation areas as a single meta-population (Mills et al. 1998; also see Gusset et al. 2008a). The awareness of Allee effects may thus have direct implications for future conservation management regarding re-introductions of wild dogs into other conservation areas and translocations among them. The findings presented here may apply generally to the dynamics and attempted recovery of small populations of cooperative breeding species.

## Materials and methods

### Study area

The ca. 900-km<sup>2</sup> HiP is located in northern KwaZulu-Natal (KZN) Province, eastern South Africa. HiP lies about 300 km south of Kruger National Park, which has the

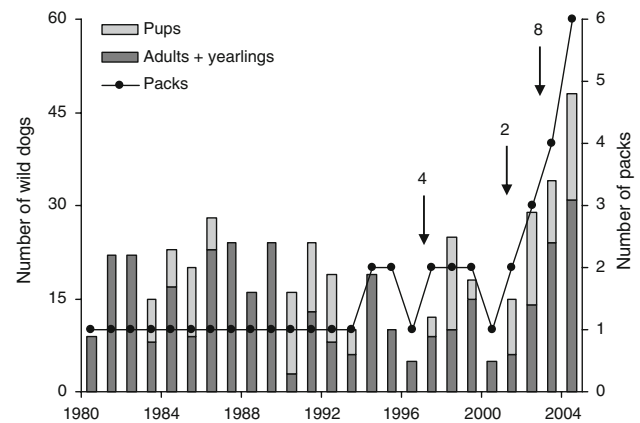
nearest viable population of wild dogs (Maddock and Mills 1994). The park, with its subtropical climate, has a diverse topography and the predominant vegetation is bushveld savannah (for details on the study area, see Andreka et al. 1999; Krüger et al. 1999). HiP supports a large potential prey base and a broad spectrum of large carnivores, including lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) as potential intraguild competitors of wild dogs. Wild dogs in HiP predominantly feed on nyalas (*Tragelaphus angasi*) and impalas (*Aepyceros melampus*). Although the park is enclosed by an electrified fence, wild dogs are notoriously difficult to contain within the perimeter fence that separates HiP from the densely human populated surroundings. There is also a public, frequently used tarmac road bisecting the park.

### Study animals

Twenty-two wild dogs were re-introduced into HiP in four stages in 1980/1981 after an absence of half a century. These animals formed a single pack. Despite an addition of four animals in 1986, wild dog numbers in HiP fluctuated greatly over the years and dwindled to a mere five animals in 1996, without any signs of breeding activities among the remaining individuals (Maddock 1995, 1999). It was then decided to increase the number of wild dogs in an attempt to stimulate breeding through a translocation of a second pack (consisting of two males and two females) to the park in 1997 (Somers and Maddock 1999). This was the first implementation of the meta-population management plan for the conservation of wild dogs in South Africa (Mills et al. 1998; also see Moehrensclager and Somers 2004), in which the previously largely isolated HiP became linked to other conservation areas through translocations (Fig. S1). Another two packs (consisting of five males and five females) were subsequently added to the park in 2001 and 2003 (Graf et al. 2006; Gusset et al. 2006a). At the end of 2004, there were 48 known wild dogs living in six packs (Gusset et al. 2006b; Fig. 1). In addition, an unknown number of wild dogs occur around HiP on private and communal land (also see Lindsey et al. 2004a).

### Data collection

Data on the demography of wild dogs for the period of 1980–1996 (extracted from Maddock 1995, 1996, 1999) were collected by non-invasive procedures (photographic records and sightings by HiP staff) and from direct observations using radio telemetry (1992–1995). Demographic data from 1997–2004 were collected from photographic records and direct observations, mainly when following the animals by means of radio tracking. One to three adults or yearlings per pack, including dispersers,



**Fig. 1** Dynamics of the Hluhluwe-iMfolozi Park (HiP) wild dog population from 1980–2004. Arrows (with number of individuals on top) indicate when the population was supplemented with additional packs

were radio-collared after immobilisation with tranquilliser darts. One year after being handled, there were no differences in survival rates between these individuals ( $15/20 = 75\%$  alive) and the population as a whole ( $81\%$  alive;  $G$  test:  $G = 0.18$ ,  $P = 0.67$ ). All wild dogs were identified by their unique coat markings and were individually known from birth or the date of transfer to HiP. Dominance was assessed from behavioural observations on social interactions and scent marking patterns. Pups were first counted and sexed when emerging from the den at about 3 weeks of age. Data on adult lion and spotted hyaena numbers, nyala and impala numbers, and amount of rainfall were sampled consistently and made available by the provincial conservation authorities (Ezemvelo KZN Wildlife).

### Data analysis

The fate of each individual was traced throughout its life. Pack and population characteristics were summarised monthly and for the whole calendar year on 31 December, the midpoint in the annual breeding cycle. This procedure provided demographic data for 41 pack-years that were analysed combining static and cohort life tables. As all translocations were soft releases (i.e. animals were kept in temporary holding facilities before release), only wild dogs released into the park, and only those staying within the park boundary, were considered part of the HiP population. A pack was defined as a potential reproductive unit containing at least one adult of each sex. Pack and population size refers to adults plus yearlings. Pups were less than 1, yearlings between 1 and 2, and adults more than 2 years of age. Reproduction was considered successful when pups emerged from the den.

To test for a demographic Allee effect, the shape of the population growth function was examined by plotting the

number of packs and population size (excluding translocated animals) at year  $t$  (from 1981 onwards) against the population growth rate, calculated as the natural logarithm of the change in population size  $n$  from year  $t$  to year  $t + 1$  [ $\ln(n_{t+1}/n_t)$ ] (Turchin 1990). To test for component Allee effects, linear regression models controlling for pack identity were used to investigate the relationship between pack size and: (1) litter size; (2) number of pups raised to 1 year; (3) annual survival rates (for pups, yearlings and adults); and (4) disperser group size and annual survival rates of dispersers. Using the same statistical procedure, ecological influences (number of adult lions and spotted hyaenas, number of nyalas and impalas, and amount of rainfall) on wild dog demography were tested. All statistical tests were two-tailed, with the significance level set at  $P = 0.05$ , and were run on Systat 10 (2000) following Sokal and Rohlf (1995). Unless otherwise stated, mean values are given  $\pm$ SE. The normal distribution of residuals was confirmed with the Lilliefors test.

## Results

### Population and pack characteristics

From 1980–2004 (Table S1), wild dog population size in HiP was  $14.1 \pm 1.5$  (range 3–31,  $n = 25$  years; Fig. 1), with a density of  $1.6 \pm 0.2$   $100 \text{ km}^{-2}$  (range 0.3–3.4,  $n = 25$  years). Number of packs was  $1.6 \pm 0.2$  (range 1–6,  $n = 25$  years; Fig. 1), with a pack size of  $8.1 \pm 1.1$  (range 2–24,  $n = 41$  pack-years). The annual population growth

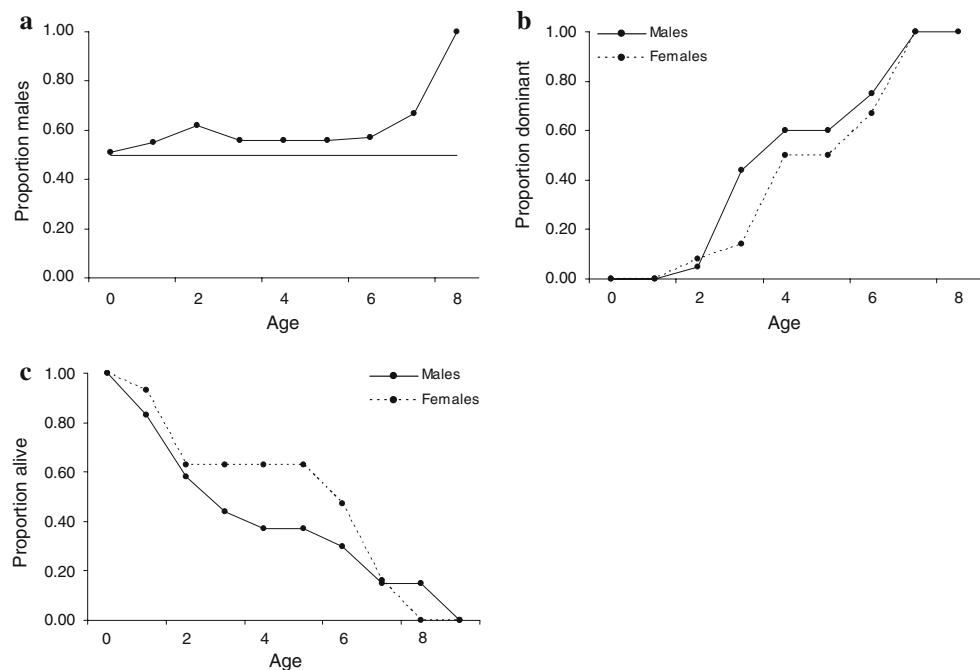
rate was  $0.01 \pm 0.18$  (range  $-2.08$ – $1.47$ ,  $n = 23$  years), indicating on average a 1% annual increase in population size. The overall sex ratio (56% males) was not skewed ( $G$  test:  $G = 2.29$ ,  $P = 0.13$ ; Fig. 2a).

### Reproduction

The number of helpers (subordinate adults plus yearlings) at birth of the pups was  $5.2 \pm 1.3$  (range 0–15,  $n = 13$  litters), with two litters being successfully raised by the breeding pair alone. The number of potential breeding packs per year was  $1.5 \pm 0.2$  (range 0–4,  $n = 25$  years), which annually produced  $1.0 \pm 0.2$  litters (range 0–3,  $n = 24$  years). The annual proportion of potential breeding packs reproducing thus was  $0.64 \pm 0.10$  (range 0.00–1.00,  $n = 24$  years). Twenty-four litters were born in 37 pack-years and 166 pups emerged (including 40 males and 38 females;  $G$  test:  $G = 0.05$ ,  $P = 0.81$ ), with  $6.9 \pm 1.5$  pups emerging per year (range 0–27,  $n = 24$  years; Fig. 1). Litter size at emergence was  $7.9 \pm 0.8$  (range 2–13,  $n = 21$  litters). At least since 1997, no pack had more than one breeding female. Range in age of breeding females was between 3 and 7 years. All pups were born from May to July, the driest months in HiP (Fig. S2). The inter-birth interval was  $11.7 \pm 0.3$  months (range 11–13,  $n = 7$  intervals), independent of whether pups emerged or not.

No evidence for a sex bias with respect to litter size was found. Litter size, number of pups raised to 1 year and pup survival rate were not related to the age of the breeding female. Whether a female has given birth before or not (parity status) did not influence pack size at birth of the

**Fig. 2** Age- and sex-specific demographic characteristics of the HiP wild dog population: **a** sex ratio across age classes, **b** proportion of males and females dominant across age classes, **c** survivorship curves for males and females



pups or the pups' sex ratio. The proportion of successfully produced litters in newly formed packs was 0.33 (2/6 breeding attempts), compared to a proportion of 0.66 (19/29 breeding attempts) in established packs (Fisher's exact test:  $P = 0.19$ ).

#### Dispersal and dominance

A confirmed 36 animals dispersed from their natal packs in 14 dispersal events (19 males and 17 females;  $G$  test:  $G = 0.11$ ,  $P = 0.74$ ). All dispersal events involved groups of same-sexed animals and dispersal mainly occurred from September to December (10/11 = 91% of dispersal events with known date). Wild dogs started leaving HiP in 1984 and occasionally returned or were chased back, while a confirmed 44 animals emigrated and mostly disappeared. The maximum confirmed linear dispersal distance outside the park was 150 km.

Following dispersal, three cases of pack formation were documented. In all three events, one or two dispersing females of the same cohort met up with one to three dispersing male litter mates from a different pack. There were also two cases of pack fission. In 1994, two males and a female (probably all related) split from the Hluhluwe Pack to become the only other pack occurring in HiP between 1980 and 1997. They failed to breed for 2 consecutive years and dissolved. In 2002, two males and a female split from the New iMfolozi Pack to form the Makhamsa Pack, with all three animals probably being related. This pack also did not reproduce during the rest of the study period (Fig. S1).

In three cases of dominance change, an adult male took over the dominant position from his brother, another adult male from his father and a yearling male from the unrelated adult male that adopted him as a pup. In the second case, the new dominant pair probably was mother and son. For a male, the annual probability of being displaced as a dominant was 0.20 (3/15 pack-years). All displaced males remained in the pack. In two cases where the dominant animals died, an adult female took over the dominant position immediately after her mother was killed and an adult male immigrated into a pack 4 months after the presumed death of the previous dominant male. In the latter case, six sons (from three cohorts) of the dominant female were present; they did not take over the dominant position but left the pack after the immigration event. In total, animals becoming dominant in an established pack originated from the natal pack in four cases (three males and one female) and one male became dominant after joining an existing pack, the only documented immigration event of an unrelated animal at least since 1997. The proportion of animals dominant increased with age in both sexes (Fig. 2b).

#### Survival and mortality

One year after being released into HiP, there were no differences in survival rates between these translocated individuals (12/14 = 86% alive) and the population as a whole (81% alive;  $G$  test:  $G = 1.68$ ,  $P = 0.20$ ). There were 15 confirmed mortalities, nine inside and six outside HiP. The known causes of mortality were: three killed by humans, three killed in vehicle accidents, three killed by lions and one killed by a conspecific. Since 1997, sixty-two animals disappeared and probably died, 57 inside and five outside the park. Maximum life span recorded was 8 years (Fig. 2c).

A population crash occurred between 1998 and 2000, when over a 2-year period 83% (33/40) of wild dogs across all age classes disappeared and probably died, including four dominant animals and three complete litters before emergence (Fig. 1). The peak of the crash, with the probable death of 20 wild dogs, was between August 1999 and May 2000. As a consequence of this catastrophic event, two of the three existing packs at that stage dissolved and the only remaining pack was reduced to two animals. Descendants of this group, the Hluhluwe Pack, have persisted over the whole 25-year study period.

#### Ecological influences

Adult lion number in HiP was  $38.7 \pm 1.4$  (range 29–52,  $n = 25$  years; Fig. S3), with a density of  $4.3 \pm 0.2$   $100 \text{ km}^{-2}$  (range 3.2–5.8,  $n = 25$  years). Adult spotted hyaena number in HiP was  $292.0 \pm 3.3$  (range 265–319,  $n = 25$  years), with a density of  $32.4 \pm 0.4$   $100 \text{ km}^{-2}$  (range 29.4–35.4,  $n = 25$  years). Wild dog number, litter size, number of pups raised to 1 year or annual survival rates (for pups, yearlings and adults) were not related to either adult lion or spotted hyaena numbers ( $P > 0.05$  for all tests). The wild dog:lion:spotted hyaena ratio on average was 1.0:2.7:20.7.

Nyala number in HiP was  $7,371.2 \pm 273.7$  (range 4,730–9,543,  $n = 22$  years; Fig. S4), with a density of  $819.0 \pm 30.4$   $100 \text{ km}^{-2}$  (range 525.6–1,060.3,  $n = 22$  years). Impala number in HiP was  $14,502.0 \pm 1,600.3$  (range 5,745–26,731,  $n = 22$  years; Fig. S4), with a density of  $1,611.3 \pm 177.8$   $100 \text{ km}^{-2}$  (range 638.3–2,970.1,  $n = 22$  years). Wild dog number, litter size, number of pups raised to 1 year or annual survival rates (for pups, yearlings and adults) were not related to either nyala or impala numbers in the same or the following year ( $P > 0.05$  for all tests).

Annual rainfall in HiP was  $802 \pm 41$  mm (range 458–1,185,  $n = 25$  years; Fig. S5). Wild dog number, litter size, number of pups raised to 1 year or annual survival rates (for pups, yearlings and adults) were not related to the

amount of rainfall in the same or the following year ( $P > 0.05$  for all tests).

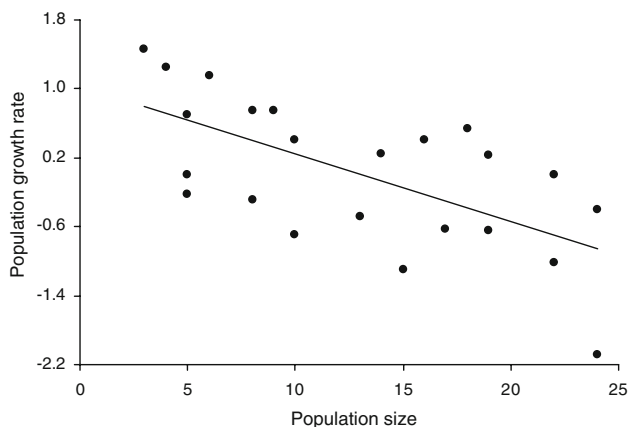
### Allee effects

The annual population growth rate was not related to the number of packs but decreased with population size ( $n = 23$  years,  $F = 14.48$ ,  $P = 0.001$ ,  $R^2 = 0.41$ ; Fig. 3). Pack size did not influence litter size, number of pups raised to 1 year or annual survival rates (for pups, yearlings and adults;  $P > 0.05$  for all tests). Population size was more positively related to the number of packs ( $n = 25$  years,  $F = 5.83$ ,  $P = 0.02$ ,  $R^2 = 0.20$ ) than to pack size ( $n = 27$  pack-years,  $F = 3.66$ ,  $P = 0.07$ ,  $R^2 = 0.13$ ; excluding those years in which the whole population consisted of one pack). Pack size did not influence disperser group size or annual survival rates of dispersers ( $P > 0.05$  for both tests). The annual number of dispersers was not related to population size but increased with the number of packs ( $n = 7$  years with dispersal events,  $F = 6.27$ ,  $P = 0.05$ ,  $R^2 = 0.56$ ; Fig. 4). The annual number of pack formation events was positively related to the number of existing packs ( $n = 25$  years,  $F = 19.06$ ,  $P < 0.001$ ,  $R^2 = 0.45$ ).

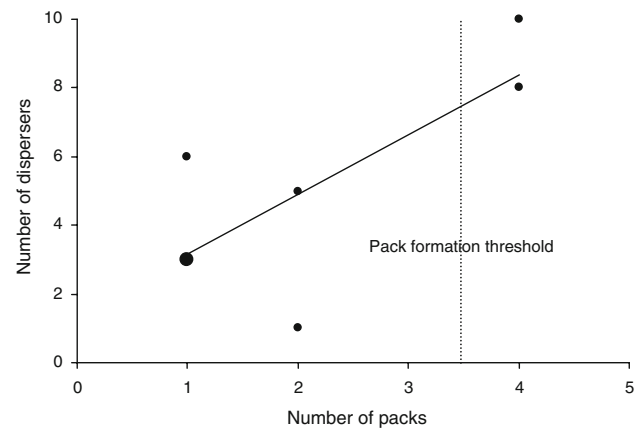
## Discussion

### Demographic and component Allee effects

The lack of a demographic Allee effect in the absence of component Allee effects is not surprising, as an Allee effect at the level of the population implies that inverse density dependence results from the effects of density on the fates of, and interactions between, individuals within



**Fig. 3** The growth rate of the HiP wild dog population was negatively related to its size ( $n = 23$  years,  $F = 14.48$ ,  $P = 0.001$ ,  $R^2 = 0.41$ )



**Fig. 4** For wild dogs in HiP, the probability of finding suitable mates only substantially improved after the population was artificially increased to a critical number of four packs, which simultaneously produced enough unrelated dispersers for successful pack formation events to occur ( $n = 7$  years with dispersal events,  $F = 6.27$ ,  $P = 0.05$ ,  $R^2 = 0.56$ ). Accordingly, the number of pack formation events was positively related to the number of existing packs ( $n = 25$  years,  $F = 19.06$ ,  $P < 0.001$ ,  $R^2 = 0.45$ )

the population (Stephens et al. 1999). What is striking is the negative relationship between population size and population growth rate (Fig. 3). Plausible explanations consistent with our data are that: (1) pack size increased with population size whereas reproductive success, survival rates and number of breeding females (due to reproductive suppression by older animals; Fig. 2b) were not related to pack size; and (2) an increasing number of packs at larger population size produced more dispersers, which suffered from higher mortality, especially after emigration (see below). An almost identical form of negative density dependence was discovered by Ginsberg et al. (1995) for the equally small Serengeti wild dog population (also see Creel and Creel 2002 for density-dependent adult survival). This remarkable phenomenon of negative density dependence at such low population size in the absence of any apparent ecological resource limitation indicates that behavioural studies of the causal mechanisms potentially generating Allee effects in small populations can provide a key to understanding their dynamics.

The unexpected absence of component Allee effects might be explained by low density and a restricted spatial distribution of lions, small feeding groups in spotted hyenas and dense vegetation in most parts of the park (Andreka et al. 1999; Krüger et al. 1999), which is likely to have reduced the negative impact of these competitors on wild dogs (Creel and Creel 2002). In this regard, two different breeding pairs successfully raising a litter without helpers is a highly unusual phenomenon in wild dogs (Creel and Creel 2002). Together with a high prey density that could sustain even more wild dogs (Lindsey et al.

2004b; Hayward et al. 2007), this indicates that wild dogs in HiP have not been limited primarily by ecological factors (i.e. interspecific competition and prey availability; Fig. 5). Our results thus suggest that aspects of the environment can mediate both the effects of interspecific competition among carnivores and the strength of Allee effects. Given this apparent lack of ecological constraints and correspondingly high survival rates (Fig. 2c; cf. Creel and Creel 2002), why did the wild dog population in HiP not flourish but crashed repeatedly, 3 times to near extinction?

Disease

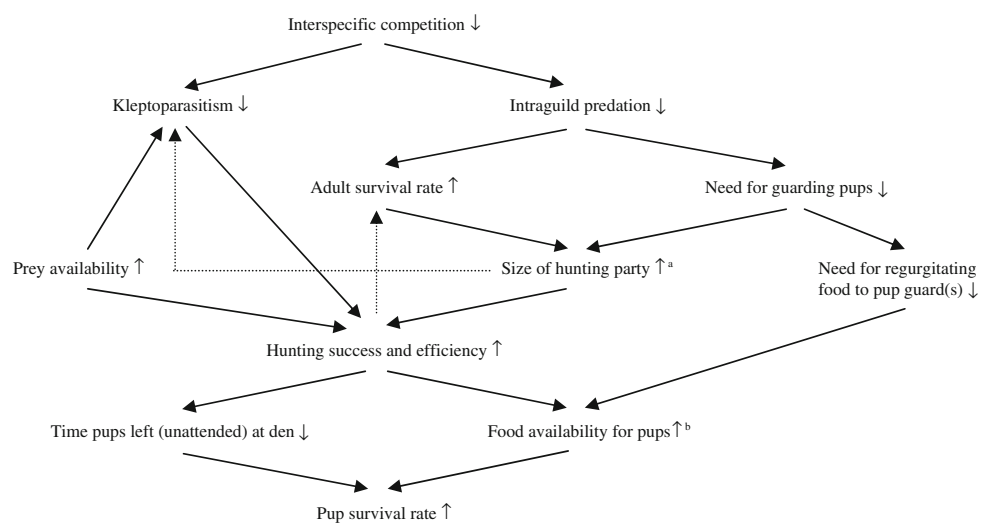
Wild dogs in HiP showed seroprevalence of antibodies to canine distemper virus (3/3 animals tested) and canine parvovirus (2/3 animals tested), with one animal showing symptoms of canine distemper in 1994 (J. van Heerden, unpublished data). This, together with the occurrence of several other pathogens also found in Kruger National Park (van Heerden et al. 1995), might explain the disappearance of three complete litters before emergence (Creel and Creel 2002) and the population crash peaking in 1999/2000 (Fig. 1). The small size of HiP together with the wide ranging behaviour of wild dogs increases contact with domestic dogs (*Canis familiaris*) outside HiP, which can act as reservoirs for infectious diseases, as the vast majority of domestic dogs carried antibodies against canine distemper (47/48 animals tested; J. van Heerden, unpublished data). Although speculative without further investigation, this provides indirect evidence that disease could have played a role as a limiting factor in the HiP wild dog population, with the rate of disease transmission directly being related to the wild dogs' inter- and intraspecific behaviour.

Allee effects and dispersal

It has been suggested that at low densities, migration may be a regulatory mechanism in the population dynamics of cooperative breeders, as migration between groups through dispersal may act as a buffer, limiting the erosion of the group (Courchamp et al. 1999b). However, immigration may prevent the group from falling below the critical threshold size only when individuals are always available from other groups nearby, particularly as inverse density dependence in wild dogs was demonstrated to result in fewer dispersers and a lower colonisation rate of empty patches (Courchamp et al. 2000b). This may not be realistic given the low success rate of dispersing wild dogs in HiP (cf. Creel and Creel 2002), manifested in the disappearance of a large number of dispersing animals from the park, although wild dogs can disperse over considerable distances (Fuller et al. 1992b).

Moreover, Courchamp et al. (1999b) showed that when emigration exceeds immigration, migration is a disadvantageous process for groups of cooperators, making it more probable for groups to drop below the critical threshold size. In the HiP wild dog population, young adults were the most common dispersers and dispersal was most likely following the recruitment of sexually mature individuals, suggesting a role of dispersal in avoiding reproductive suppression (Creel and Creel 2002). However, the probability of finding suitable mates only substantially improved after the sub-population was artificially increased to a critical number of four packs, which simultaneously produced enough unrelated dispersers for successful pack formation events to occur (Fig. 4). More packs have been formed since crossing this pack formation threshold (M. J. Somers et al., unpublished data). Inbreeding avoidance within packs might thus explain the repeated periods

**Fig. 5** The absence of component Allee effects in the HiP wild dog population might be explained by low interspecific competition and high prey availability. These factors, mediated by reduced kleptoparasitism, decreased intraguild predation and increased hunting success and efficiency, may result in high survival rates across age classes. *a* Including hunting-experienced breeding female. *b* Including likelihood that pack members regurgitate food to pups



without pups born, followed by population crashes in 1990 and 1996 (Fig. 1). Larger numbers of occupied patches can increase the number of successful migrants in a metapopulation, thus reducing the rate of local extinction. This leads to a meta-population analogue of the Allee effect, where there can be a lower threshold of patch occupancy, below which all sub-populations will be highly likely to go extinct (Amarasekare 1998).

Therefore, unsuccessful dispersal due to a mate-finding Allee effect and subsequent emigration of animals, followed by their likely death, might have been an important factor that has kept wild dog numbers low in HiP. Mortalities were probably more often than not human-caused (60% of known-cause mortalities; also see Woodroffe et al. 2007; Gusset et al. 2008b). Particularly in a small conservation area like HiP, the wide ranging behaviour of wild dogs increases contact with people at park boundaries and their conspicuous pack-living social structure together with diurnal activity makes them especially prone to human persecution (Woodroffe 2003).

#### Implications of sociality for endangered species' recovery

Behavioural mechanisms can cause effects that considerably increase the vulnerability of small populations to extinction, particularly those characterised by cooperative breeding and reproductive suppression (Stephens and Sutherland 2000). By using a re-introduction programme as a real-scale experiment to link individual behaviour to population dynamics and conservation (Sarrazin and Barbault 1996), our study demonstrates how aspects of a species' social behaviour (particularly dispersal and pack formation behaviour) can limit population growth and thus a population's recovery. Our considerations of sociality suggest a minimum number of packs to be necessary for maintaining population viability (i.e. the continued formation of new packs), which may apply generally to the persistence of small populations of group-living species. We acknowledge that these conclusions are based on the findings of one study only, but without investigating the potential manifestations of the Allee effect in our study population, this key aspect probably would have been missed. In the light of such profound implications of sociality for endangered species' recovery, we conclude that practical management of small populations can be strongly affected by behavioural considerations and that an appreciation of their importance may be critical for future conservation efforts.

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