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How important is the role that social behaviour of African Wild Dogs (*Lycoan pictus*) plays in their conservation and extinction risk?

Only recently has behavioural ecology been incorporated into conservation biology to aid the understanding and protection of threatened species. Here African wild dogs (*Lycoan pictus*) are used to illustrate the need for the inclusion of complex social behaviour in conservation and extinction risks. From examining the effects of sociality and predictions made by population viability analyses it can be seen that social species have a greater risk of extinction due to 'inverse density dependence' and reproductive suppression. Thus, including social behaviour in both population viability analyses and conservation biology is essential. Improvements to population viability analyses, the direction of future work, and possible management options are suggested.

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May 2004

Introduction

Conservation biology aims to protect biodiversity through management, understanding threats and documenting the present extent of biodiversity (Spellerberg, 1996; Caro, 1998; Primack, 2002). Anthropogenic impact has lead to a dramatic increase in the extinction rate of species (Ulfstrand, 1996). One method of predicting the probability of extinction or survival of a species is by taking into consideration extinction risks. Certain mutually exclusive characteristics of species can make them particularly vulnerable to extinction, such as narrow geographical range, few populations, small population size, little genetic variability, declining population size, low population densities, large home ranges, and economic value to humans (Primack, 1995). African wild dogs (*Lycoan pictus*), the focus of this study, are only remaining in small, declining populations and inevitably are under very high risk of extinction (IUCN, 2003). Small, declining populations are particularly at risk from stochastic extinctions. Demographic stochasticity, the random variation in a population's dynamics, and environmental stochasticity, the random series of environmental changes, are threatening to small populations but would have little impact to large stable populations as they have the ability to recover. To successfully assess extinction risks and protect biodiversity, conservation biology is a multidisciplinary study, which integrates aspects of taxonomy, genetics, ecology, biogeography, politics, economics and education (Spellerberg, 1996). Only recently has behavioural ecology been included in this multidisciplinary science (Clemmons & Buchholz, 1997; Caro, 1998; Gosling & Sutherland, 2000; Festa-Bianchet & Apollonio, 2003).

Behavioural ecology attempts to discover and understand how the behaviour and morphology of a species affects its reproduction and survival (Caro, 1998). Individual behaviour, such as reproductive success, foraging efficiency, and dispersal has implications for a population's reproduction and survival, thus affecting population dynamics (Sutherland, 1996). Each individual species behaves differently and has different roles in their ecological environment, which can directly affect their survival and reproduction (Ulfstrand, 1996). To achieve an understanding of the population dynamics of a species for successful conservation, behaviour must be taken into account. Behavioural studies could provide essential knowledge and understanding inorder to aid the protection of biodiversity.

Sociality, as exhibited in the wild dog, is one aspect of animal behaviour that can have important implications for conservation issues. Animal societies are groups of individuals of the same species that are formed for mutual benefit and act cooperatively (Drickamer *et al*., 1996). The most convincing theory for cooperative behaviour is Kin selection (Hamilton, 1964), which involves an individual (altruist) conducting an action which appears to be costly to its fitness, but is actually increasing its inclusive fitness by promoting its own genes within the closely related recipient. The cost to the altruist must be smaller than the benefit to the recipient for kin selection and cooperation to occur, so the recipient must be closely related (Hamilton's Rule; (Hamilton, 1964)).

Group-living and complex social behaviour has a dramatic effect on the population dynamics a species and consequently may affect their conservation and extinction risk. Factors of group-living affecting survival include enhanced predator defence, improved foraging efficiency, richer learning environment for offspring, and greater vulnerability to parasites and pathogens (Drickamer *et al*., 1996). Reproduction of group-living species may be affected by reproductive suppression by dominant individuals, infanticide, subordinate nonbreeding helpers, and Allee effects. Knowledge of the population dynamics of a species is essential for successful conservation and management and the inclusion of behavioural studies in conservation biology is crucial, especially for species which exhibit complex social organisation, such as the wild dog.

The African wild dog (*Lycoan pictus*) will illustrate the need for the inclusion of behavioural studies in conservation biology and more specifically show the importance of sociality and its effects upon conservation and extinction risk. Wild dogs were chosen due to their very high risk of extinction (IUCN, 2003), complex social organisation and unique *Lycoan* lineage. Once distributed through much of sub-Saharan African, the estimated 2500 or less wild dogs remaining now exist in habitat patches in Southern and Eastern Africa. Very low population densities, approximately 1 adult per 60-100 km^2 and inevitably large dispersal distances, an average of 29.6 km (Creel and Creel, 2002) are a consequence of their huge home ranges, over 1000 km^2, among the largest recorded for carnivores. Average pack size is 10 adults and is composed of a group of related females and a group of related males, with the males and females being unrelated. Only the alpha female, the oldest female, and alpha and beta males, the fittest males, reproduce but litters of 10-11 pups on average are produced (Woodroffe *et al.*, 1997). The breeding female is dependent on cooperative assistance of the other members of the pack to raise pups successfully, by guarding, defence and regurgitating meat. No pair of dogs have ever been observed to successfully rear pups; in Selous a minimum of 5 adults were observed to be required to raise pups successfully (Creel and Creel, 2002). Pack survival is also dependent on subordinate helpers which enhance the defensive ability of the pack by increasing the number of individuals, and the foraging efficiency via cooperative hunting in which the capture prey much larger than themselves (Creel and Creel, 2002; Woodroffe *et al.*, 1997).

The importance of social behaviour in the conservation of the African wild dog will be shown. Current conservation issues, human impact, disease, and interspecific competition, and their consequences on wild dog populations will be reviewed, with reference to the effects of social behaviour. To illustrate how social behaviour affects wild dog population dynamics, the effects on their reproduction and survival will be examined. Predictions made by population viability analyses (PVAs) to quantitative assess of the effects of sociality on population persistence will be used to achieve the goal of identifying the importance of social behaviour.

Conservation Issues

Three main conservation issues which have a negative effect upon wild dog extinction risk have been identified: interspecific competition, human impact, and disease.

Interspecific Competition

Competition between wild dogs and both lions and hyenas falls into three categories, monopolising high prey density areas, direct predation and kleptoparasitism (Gorman *et al.*, 1998; Creel, 2001). Strong negative correlations have been found between wild dog density and both lion and hyena densities (Creel and Creel, 1996). In areas of high prey densities lions and hyenas are abundant, which due to low foraging efficiency and high predation of wild dogs leads to lion and hyena monopolisation (Creel, 2001). Lion predation is a major cause of wild dog mortality (Creel and Creel, 1996). In Kruger National Park 43% of natural adult mortality was a result of lion predation (Mills and Gorman, 1997). Hyenas mostly Compete at kills, by attempting to steal carcasses from wild dogs (Gorman *et al.*, 1998). High kleptoparasitism by hyenas and lions can result in a large reduction of food intake for wild dogs, which results in a larger time hunting to achieve an energy balance as hunting is energetically costly (Woodroffe and Ginsberg 1997; Gorman *et al.*, 1998).

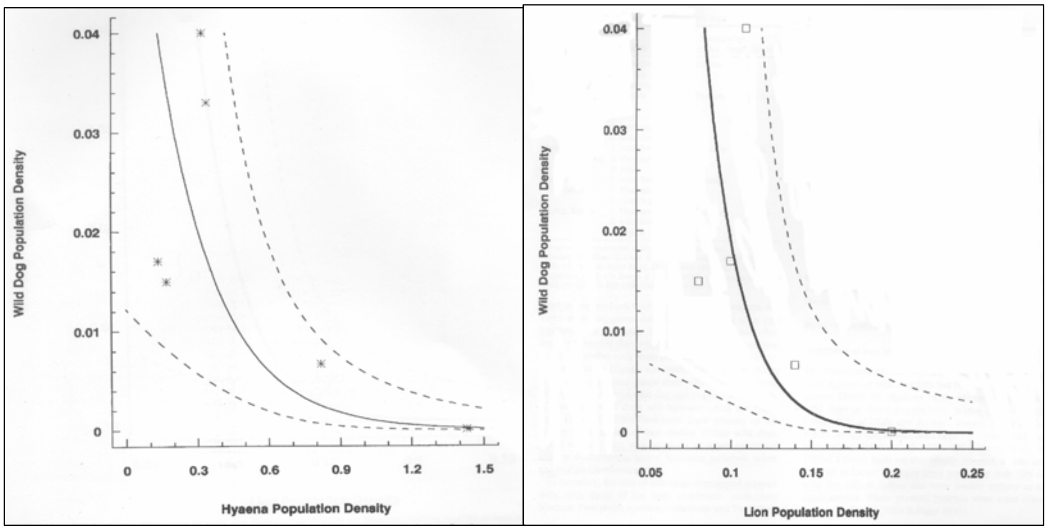

Figure 3. Shows the strong negative correlations found between wild dog density and both lion and hyena density (taken from Creel and Creel, 1996).

Interspecific competition is a result of the dietary overlap of the three species. Even though wild dogs are much smaller than hyenas and wild dogs they have the ability to capture much larger prey through cooperative hunting. This social behaviour and has therefore lead to one of the major causes of wild dog mortality.

Human Impact

Habitat fragmentation has resulted in wild dog's home ranges extend beyond reserve borders, leading to increased mortality risk due to edge effects, persecution by humans, and poaching activity, such as snares which can cause considerable death (Woodroffe and Ginsberg, 1997, 1998; Creel and Creel, 2002). Due to sociality and the effects of interspecific competition wild dogs have large home ranges which and to sustain a demographically effective population size of 500 individuals, an estimated area of 30,380 km^2 is required (Creel and Creel, 2002). The largest nature reserve containing wild dogs, Selous, has an area of 43,600 km^2 and an estimated 880 adult wild dogs (Creel and Creel, 2002).

In the mid 1980's wild dogs became protected (Creel and Creel, 2002), before then they were persecuted within an outside protected areas. Direct persecution of wild dogs within national parks increased during the 20th century as they were considered as vermin. Between 1956 and 1975 in Zimbabwe alone 3404 wild dogs were shot (Childes, 1988). Due to the view of wild dogs being competitors in hunting areas and a threat to livestock, persecution both within and outside protected areas still occurs (Woodroffe and Ginsberg, 1997). Livestock loss to wild dogs is low overall (Rasmussen, 1999; Fuller & Kat, 1990) but it can be high locally (Woodroffe and Ginsberg, 1997).

Over half of adult wild dog mortalities in Hwange National Park, Zimbabwe were found to be due to road deaths caused by a high-speed road (Ginsberg *et al*., 1995; Woodroffe and Ginsberg, 1997; Creel and Creel 2002). In comparison, only one of 23 wild dogs found dead in Selous and Kruger was due a road accident, a result of the lack of substantial roads and application of low speed limits (Ginsberg *et al*., 1995; Woodroffe and Ginsberg, 1997; Creel and Creel 2002).

Disease

Many endangered animals are only present in small, declining populations, which are particularly vulnerable to disease (e.g. the black-footed ferret; Williams *et al*., 1988). Canine distemper virus (CDV), rabies, canine parvovirus (CPV), anthrax (*Bacillus anthracis*) (Creel *et al*., 1995) and other pathogens effect wild dogs (Kat *et al*., 1995; Woodroffe and Ginsberg, 1997; Creel and Creel, 2002). Although the social behaviour of wild dogs increases the transmission rate between individuals within packs it is only usually fatal for when combined with other conservation issues (Fanshawe *et al.*, 1991; Ginsberg *et al*., 1995; Dye, 1996; Creel and Creel, 2002). Interspecific competition and low numbers combined with disease are believed to be responsible the Serengeti wild dog extinctions (Creel, 1992; Burrows *et al.*, 1994; Ginsberg *et al.*, 1995; Morell, 1995; Dye, 1996; East and Hofer, 1996; Creel and Creel, 2002). The main concern over disease in wild dogs is the transmission from other species, particularly domestic dogs (Grenfell and Dobson, 1995; Kat *et al.*, 1995). The threat of disease is likely to be amplified by increased contact between wild dogs and domestic dogs.

The effects of these conservation issues pose a greater threat to social species as a result of 'inverse density dependence'. Reproductive success and survival rate are pack size dependent,

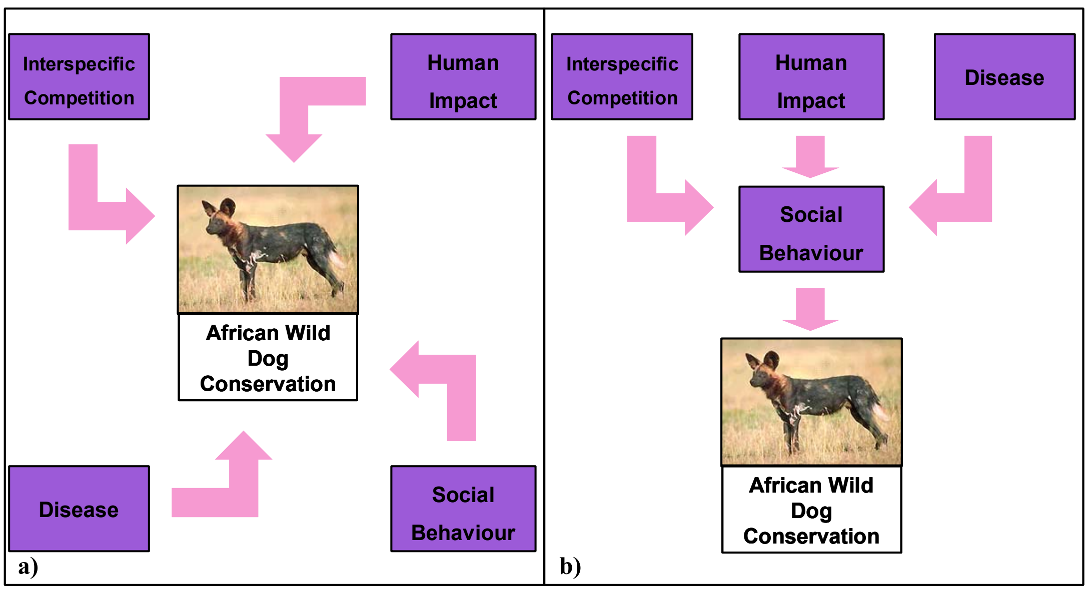

Figure 1. A summary of the threats to African wild dog conservation, a) all acting individually or b) the effects of the conservation issues influenced by social behaviour.

with a larger pack having a smaller extinction risk. Below a critical pack size the extinction risk is increased as reproduction and survival are greatly reduced, thus 'inverse density dependence' occurs. As the conservation issues decrease survival and reproduction they enhance the effects of 'inverse density dependence'. Therefore do the effects of the conservation issues or their effects combined with social behaviour pose the threat to wild dogs (Fig. 1)?

The Role of Social behaviour

The effects of sociality on the extinction risk and conservation of wild dogs will be examined through its effects on the demography of populations, survival and reproduction.

Survival

The survival rate of both wild dog populations and individuals will inevitably have a big impact on extinction risk. Social behaviour within wild dog packs may enhance the threat of disease by increasing the transmission rate between pack members. Like many social species, wild dogs engage in a greeting ceremony involving physical contact, playing and general excitement which may help to cement hierarchy status and social bonds. Licking of mouths often involved in greeting ceremonies, and to stimulate meat regurgitatation, may increase the transmission of rabies and canine distemper between pack members. Disease transmission between packs is limited due to spillover disease transmission from other species and wild dog's large home ranges resulting in low encounter rates (Kat *et al*., 1995; Creel & Creel, 2002).

Dispersal has a high mortality risk for wild dogs but this cost may be reduced by group dispersal. Although dispersal is advantageous in terms of avoiding inbreeding and mate competition, dispersing individuals suffer a higher mortality risk than non-dispersers (Waser, 1996; Creel & Creel, 2002). In wild dogs both sexes disperse equally, usually in groups of same sexed individuals aged 1-2 (McNutt, 1996; Girman *et al*., 1997). The causes of mortality associated with dispersal are unfamiliarity of the habitat and small group size resulting in lower foraging success and weaken defence. Although dispersing groups of wild dogs are much smaller than packs (Creel and Creel, 2002) it could be predicted that dispersing in groups reduces mortality risk. Larger dispersal group would be expected to have greater defence and foraging efficiency and therefore have a reduced dispersal mortality.

Group-living results in a lower risk of mortality for many social species (Drickamer *et al*., 1996) with larger packs having a greater survival rate (Creel and Creel, 1995; Courchamp and Macdonald, 2001). Larger packs have a higher hunting success (greater mass of prey killed and smaller chasing distances) and greater defence of a kill and pups from competitors (Creel and Creel, 1995; Clutton-Brock *et al*., 1999; Courchamp and Macdonald, 2001). Thus, sociality in relation to pack formation, leads to a lower mortality and extinction risk. Larger packs also have a greater reproductive success than smaller packs, due increased litter size and pup survival (Creel and Creel, 1995; Courchamp and Macdonald, 2001; Creel and Creel, 2002).

Reproduction

A low reproductive success will increase the vulnerable of a species to extinction. Factors affecting reproductive success in wild dogs are pack size and reproductive suppression. Larger packs have a greater reproductive success due to increased foraging efficiency, greater defensive ability and more helpers to raise enormous litters successfully. Reproductive success can be directly affected by pup predation, by hyenas and lions (Creel and Creel, 2002). Predation is reduced in larger packs by more members resulting in better defence of pups and adults. Subordinates help in raising young by pup-guarding and regurgitating meat for the pups and the mother. The number of hunters increases foraging efficiency, thus pups and adults in larger packs have an increased energy intake. Nonbreeders are essential for reproductive success; no observations have been made of a pair of wild dogs successfully raising pups and in Selous a minimum of 5 adults were observed to be required to successfully raise pups to independence (Creel and Creel, 2002). Packs of 10 adults have twice as many pups in litters and raise three times as many pups to yearlings than pack of 9 adults or less (Creel and Creel, 2002).

The relationship between pack size and both reproductive success and survival may lead to a decrease in wild dog population persistence due to 'inverse density dependence'. As a result of there need for helpers, it has been hypothesised that cooperative breeders have a critical pack size (Courchamp *et al*., 1999, 2000; Courchamp and Macdonald, 2001). Below the critical pack size 'inverse density dependence will occur', which leads to low survival and reproductive rates due to the low number of helpers and inevitably results in further decline of numbers. This can create an Allee effect which will result in an increased extinction risk (Courchamp *et al*., 1999; Stephens and Sutherland, 1999; Courchamp *et al*., 2000; Courchamp and Macdonald, 2001). Courchamp *et al*. (2000) also suggest that an Allee effect at the pack level could generate an Allee effect at the population level as a critical number of packs may exist. This could result in conservation issues, such as fragmentation and human impact, amplifying the effects of inverse density dependence and thus having an enhanced effect upon cooperative breeding species (Courchamp *et al*., 2000).

The presence of reproductively suppressed helpers has the benefit of increasing the reproductive success and survival of the pack but reproductive suppression could also threaten wild dog persistence. Due to such stringent breeding requirements wild dogs are not adapted to respond to breeding opportunities or recover from stochastic events which may increase their extinction risk (Frank and Woodroffe, 2001). The effects of demographic stochasticity, in terms of fecundity variability, is amplified in species which exhibit reproductive suppression as the number of breeding units is the pack rather than the individual (Vucetich *et* *al*., 1997). Thus, to reduce the effects of demographic stochasticity the number of packs has to increase not the number of individuals (Vucetich *et al*., 1997).

Reproductive suppression can affect genetic variability by greatly reducing the gene pool. The skewed reproductive success caused by reproductive suppression leads to a large reduction in genetic effective population size (N_e) (Lande and Barrowclough, 1987) as this only counts reproducing individuals, inevitably this will result in the loss of genetic variability through genetic drift and increased risk of extinction (Creel, 1998; Creel and Creel, 2002). Creel and Creel (2002) estimate that a reserve area of 77,420 km^2 is required to maintain a wild dog population with $N_e = 500$, which is a value that has been suggested to maintain a population's genetic diversity (Franklin, 1980, cited in Creel and Creel, 2002).

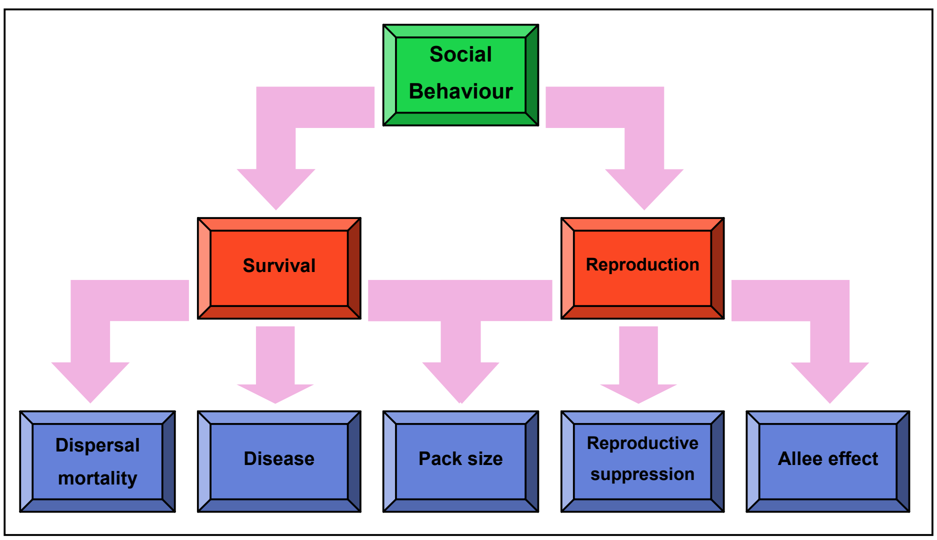

Figure 2. The possible ways in which social behaviour can affect the population dynamics of the African wild dog.

Predicting Population Persistence

To quantitatively assess the effects of sociality on extinction risk and predict future population persistence, population viability analysis (PVA's) can be used. PVA's are models which predict the size and risk of extinction for a population in the future (Boyce, 1992; Coulson *et al*., 2001; Beissinger and McCullough, 2002; Morris and Doak, 2002).

VORTEX Population Models

Ginsberg and Woodroffe (1997) conducted a PVA using VORTEX computer package (Lacy *et al*., 1995, cited in Woodroffe *et al*., 1997) to simulate wild dog populations. The issues addressed include inbreeding, population size, age-dependent mortality, and catastrophes such as drought, flooding, disease, and persecution. The model predicted that inbreeding has little effect on population persistence and if not linked to other populations, fragmentation will only affect populations under 50 adults. Catastrophes only had an affect on the probability of extinction in populations of 20 dogs or less. Adult and yearling mortality has more of an affect on persistence than juvenile mortality, but population size (20, 50 or 100 adults) will affect population persistence the most (Ginsberg and Woodroffe, 1997).

The reliability of simple models, such as that used by Ginsberg and Woodroffe (1997), to predict population persistence have been questioned, especially when used for species which exhibit social structure or complex ecological interactions (Boyce, 1992; Caughley, 1994; Vucetich *et al*., 1997; Coulson *et al*., 2001; Creel and Creel, 2002; Ellner *et al*., 2002; Reed *et al*., 2002; McCarthy *et al*., 2003). PVA's are models, therefore its validity depends on the data and model structure used (Creel and Creel, 2002; Reed *et al*., 2002). The ease of use make PVA models a valuable tool in conservation biology but simplicity results in assumptions being made about demography, social structure and ecological interactions (Durant, 2000; Creel and Creel, 2002; Grim *et al*., 2003). If the assumptions of the model do not represent the population biology of the species being used the viability of the results is inevitably reduced. Vucetich and Creel (1999) state that "Using a generalised PVA model to predict viability when the population's biology does not fit the PVA model assumptions is analogous to drawing inferences from a statistical test for data that do not meet its assumptions".

Ginsberg and Woodroffe (1997) attempted to incorporate aspects of wild dog social organisation into the simple VORTEX model by including only 58% of females, an approximation of the number of breeding females in real populations, and assuming mating was monogamous. VORTEX is not designed to include social structure within the model so the results should be questioned and a model which incorporates social structure should be used instead (Heinsohn, 1992; Ginsberg and Woodroffe, 1997).

Individual Based Models

Aspects of social behaviour and ecological interactions which affect population dynamics can be included in individual based models by the use characteristics of individuals (DeAngelis and Gross, 1992; Vucetich *et al*., 1997; Vucetich and Creel, 1999; Creel and Creel, 2002; Grimm *et al*., 2003). Demographic and ecological data from a 6 year study of wild dogs in Selous Game Reserve, Tanzania, were used to conduct a PVA using an individual based model (Vucetich and Creel, 1999; Creel and Creel, 2002). The effects of lion density on wild dog population persistence were the main focus of the model. The sensitivity of the population's extinction risk, under high (131 lions/1000 km^2) or moderate (100 lions/100 km^2) lion density, to disease (rabies, CDV, CPV), immigration (0-1 immigrant groups per year), litter size (5-12 pups) and pack size (2-20 dogs per pack) were predicted. High lion density, disease and lion density acting additively, reducing immigration under high lion density, decreasing litter size to less than 6 pups per litter under both lion densities and lower pack sizes under both lion densities were all predicted to lower probabilities of population persistence. Additionally, immigration did not affect the predicted population persistence under moderate lion density and reducing pack size under high lion density increases the predicted extinction risk of wild dogs more rapidly than under moderate lion density.

The main aspect of sociality that was included in the individual based model was the dependence of reproductive success on pack size and the rules for dispersal (Creel and Creel, 2002). The relationship between pack size and reproductive success was included by litter size being determined by pack size and only one litter added annually to a pack that contained at least one male and one female. Dispersal was modelled so that it was similar to that observed in the Selous population, by all the yearling of one sex from a pack that exceeded 12 dogs dispersing to the smallest pack, if the predicted number of packs was less than the actual number the members of the smallest pack dispersed into randomly selected packs, and with a 0.5 chance of dispersal mortality. Therefore pack size was affected by mortality and fecundity and the number of packs affected by ecological factors (Vucetich and Creel, 1999; Creel and Creel, 2002).

This individual based model includes important factors of wild dog social behaviour which affect population dynamics, but some factors have not been incorporated or underestimated. The effects of reproductive suppression were underestimated, as one litter was added to a pack which contained one male and one female, yet in Selous no pack under 5 dogs where found to raise pups successfully (Creel and Creel, 2002). I suggest that incorporating the dependency of survival on pack size as well as the dependency of reproductive success on pack size will incorporate the effects of reproductive suppression more thoroughly. Small packs would then suffer from small litters and decreased pup and adult survival. Survival was incorporated into the model by age-specific mortality and dispersal mortality only. Small packs have a lower survival rate than larger packs as a consequence decreased foraging efficiency and defensive ability, and lower reproductive success (Clutton-Brock *et al*., 1999; Courchamp *et al*., 2000; Courchamp and Macdonald, 2001; Courchamp *et al*., 2002). Further declines in size of small packs occur due to decreased survival and reproductive success, thus small packs suffer from ‘inverse density dependence’ and an Allee effect may occur, which are likely to have implications on wild dog population persistence. Pack size dependent mortality is an important factor and should be incorporated in to the PVA models. I hypothesise that the integration of pack size dependent mortality, which includes ‘inverse density dependence’ and an Allee effect, into this individual based model will affect the extinction risk of the population.

The social behaviour of wild dogs may result in a greater rate of disease transmission between pack members, which will increase the threat of disease. Smith and Wilkinson (2002) found that increased probability of contact between individual badgers lead to a greater spread of rabies. Disease transmission rate was not included in the individual based model, so the effects of disease on population persistence may be underestimated. I hypothesise that the inclusion of disease transmission rate will affect the population persistence of wild dogs.

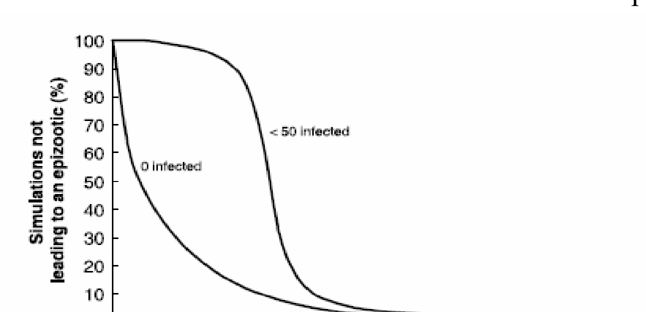

Fig. 4. The effect of increasing contact probability on the spread of rabies. Density-independent (DI) contact probabilities were used, with an overall main sett density of 0·2, a carrying capacity of one, and mortality rates multiplied by 1·2. The line labelled ‘0 infected’ represents the percentage of simulations where rabies failed to spread at all. The line labelled ‘< 50 infected’ represents the percentage of simulations where rabies spread to less than 50 animals.

Although both the VORTEX and the individual based model show important factors of wild dog conservation their predictions can not be compared to show the importance of sociality. A comparison can be made between the predictions of a model with and another without social behaviour incorporated to discover the importance of social behaviour. Disease is the only conservation issue which the VORTEX and individual based model both address, but not at the same probability of occurrence, thus a comparison can not be made.

Other Species

The effects of social behaviour on population extinction risk have been addressed by two studies, one for the gray wolf, *Canis lupus*, (Vucetich *et al*., 1997) and for the alpine Marmot, *Marmota marmota* (Grimm *et al*., 2003). Vucetich *et al*. (1997) used empirical data on a gray wolf population in Michigan, collected between 1959 and 1995, to compare the predictions of an individual based model with the predictions of a diffusion model, which does not incorporate social behaviour. Similar to Creel and Creel (2002), the effects of reproductive suppression were incorporated into the model by one litter of pups being added annually to a pack that contained one male and one female.

The comparison between this model's predictions and the diffusion model predictions shows the effects of reproductive suppression on extinction risk, but it must be noted that the individual based model does not incorporate important factors, such as the relationship between pack size and both reproductive success and survival rate. As a consequence of the inclusion of reproductive suppression, the individual based model predicts that demographic stochasticity decreases with a larger number of social groups rather than number of individuals as found with the diffusion model. Thus, sociality amplifies the effects of demographic stochasticity and increases extinction risk by restricting the number of breeding units to the number of social groups (Vucetich *et al*., 1997).

Grimm *et al.* (2003) used individual based models to compare social and non-social predictions, thus improving upon the model by Vucetich *et al*., (1997) by controlling the model type. A conservative approximation to the truly non-social version was used as it is not possible to create an imaginary non-social marmot (Grimm *et al*., 2003). The social aspects incorporated are reproductive suppression (reproduction only occurs in the presence of a territorial male and female), the relationship between group size and both survival (winter mortality) and reproductive success (litter size and weaning weight), and dispersal rules (floaters, recolonisation and dispersal mortality).

The models show that sociality has a positive effect on the persistence of marmot populations by decreasing the winter mortality of the territorial couple which is analogous to making the environment more favourable (Grimm *et al*., 2003). One or two subordinates present increases the winter survival of a territorial marmot by more than 30% and 50% respectively (Grimm *et al*., 2003). Consequently, sociality increases the population growth rate of marmots.

Wild dogs are more likely to suffer from the inflated demographic stochasticity as a result of a decreased number of reproductive units found by Vucetich *et al*. (1997) than increased population growth due to the presence of helpers found by Grimm *et al*. (2003). Inflated demographic stochasticity due to reproductive suppression will have more of an effect on wolves and wild dogs, which have larger pack sizes, than on marmots. Grimm *et al*. (2003) found that marmot populations can easily recover from small sizes due to presence of subordinate helpers. It is known that wild dogs do not easily recover from small sizes due to 'inverse density dependence' which results in small pack sizes having reduced survival and reproductive success which further decreases numbers (Courchamp *et al*., 2000; Courchamp and Macdonald, 2001). Grimm *et al*. (2003) suggests that sociality introduces reliability at the level of reproductive unit because reproductive failure is prevented. This applies to wild dog packs which are above a critical size as the presence of helpers prevents the failure of the pack as a reproductive unit. Below a critical size the presence of helpers does not ensure reproductive success of the pack due to 'inverse density dependence'.

The work of Grimm *et al*. (2003) and Vucetich *et al*. (1997) show that sociality is an important aspect of the extinction risk and conservation of obligate cooperative breeders and should be included in conservation biology and PVAs. Grimm *et al*. (2003) and Vucetich *et al*. (1997) conclude that PVA's which do not incorporate complex social behaviour should not be relied upon to predict population persistence and species-specific models should be used when appropriate. They also suggest that the pack should be the unit at which management is aimed at and detrimental effects on social behaviour caused by management should be prevented.

To discover the importance of social behaviour for wild dogs further work is required. A similar approach to that of Grimm *et al*. (2003) should be taken, using two individual based models, one including sociality and the other using a conservative approximation to the truly non-social version and then comparing the predictions. Important aspects of social behaviour which should be included in the structure of the model include pack size dependent reproductive success and survival rate, reproductive suppression, disease transmission rate, 'inverse density dependence' resulting in an Allee effect and rules for dispersal (Table 2). It can be hypothesised that all these factors will have an effect upon the sensitivity of wild dog population persistence to conservation issues such as interspecific competition, disease and human impact (Figure 1b). Thus, the inclusion of social behaviour in the conservation of

African wild dogs is very important as it may explain wild dog's sensitivity to conservation issues and their continuing decline in number when other conspecifics have stopped.

Conclusion

It has been shown that complex social behaviour has a large influence on the population dynamics of a species. The relationship between pack size and both reproductive success and survival results in larger packs having a lower extinction risk due to increased defence, foraging efficiency and help in raising pups (Clutton-Brock *et al*., 1999; Courchamp and Macdonald, 2001; Creel and Creel, 2002). Yet it has been hypothesised that this relationship could also lead to an increased extinction risk as a critical pack may exist, under which 'inverse density dependence' occurs. Thus, when pack size is below a critical size it has a low probability of persistence due to low survival and reproductive success leading to further decline in numbers, thus an Allee effect may exist (Courchamp *et al*., 2000). Reproductive suppression can increase extinction risk through amplifying the effects of demographic stochasticity. To decrease the effects of demographic stochasticity in a species which exhibits reproductive suppression, the number of packs/groups must be increased not the number of individuals as in non-reproductively suppressed species (Vucetich *et al*., 1997). Reproductive suppression can also lead to a larger loss of genetic variation through a decreased gene pool as the genetic effective population size (N_e) is reduced. These influences of social behaviour upon population dynamics can greatly amplify the effects of threats such as fragmentation and persecution (Courchamp *et al*., 2000). Therefore, sociality has clear implications on the population dynamics of the species, and social species may be at a greater risk of extinction than non-social (Table 1b).

To assess the effects of sociality on the extinction risk of wild dogs, population viability analyses (PVAs) were examined. Two PVAs for wild dog population have been conducted. Ginsberg and Woodroffe (1997) used the VORTEX computer program to predict the persistence of wild dog populations, and found that population size had the greatest effect on population persistence. Larger populations are under less pressure from stochastic events as they are able to recover more easily. By using VORTEX the possible effects of social behaviour were not included and the viability of results of this model must be questioned. The individual based model by Creel and Creel (2002) included aspects of social behaviour, the dependence of reproductive success on pack size and rules for dispersal. The model predicted that competition and predation by lions could have a large impact on population persistence, especially when acting with disease, small litter size and pack size, and low immigration. Although this model is more viable than the VORTEX model, I hypothesise that the inclusion of the dependency of survival on pack size, rather than just age-dependent mortality, and disease transmission rate will affect the predictions of the model. By including pack size dependent reproductive success and survival, inverse density dependency below a critical size can be incorporated, which will result in increased extinction risk to small packs.

To assess the importance of sociality on conservation and extinction risk the predictions of models with and without incorporating social behaviour can to be compared. A comparison of the VORTEX model with the individual based model of wild dogs is not possible as they do not consider the same conservation issues. Two studies, one on gray wolves (Vucetich *et al*., 1997) and one on alpine marmots (Grimm *et al*., 2003), looked at the effects of sociality on extinction risk. Vucetich *et al*. (1997) concluded that reproductive suppression inflates the effects of demographic stochasticity, thus increasing the extinction risk. Model type was controlled for by Grimm *et al*. (2003) and sociality was found to increase population growth of the marmots, leading to decreased extinction risk (Grimm *et al*., 2003). Wild dogs are dependent on greater degree of pack size increase than marmots so the result of Grimm *et al*. (2003) are difficult to infer on to wild dog populations. The predictions made by Vucetich *et al*. (1997) can be inferred on to wild dog populations as these species are similar behaviourally but it must be noted that this model did not include important aspects of sociality. From these models it can be seen that to successfully manage and protect social species the inclusion of sociality in PVAs and conservation biology is essential.

It can be concluded that sociality has an influence on the population dynamics, and therefore the extinction risk and conservation of wild dogs. This influence includes inflating the effects of demographic stochasticity due to reproductive suppression and amplifying the effects of conservation issues as a result of the dependency of reproductive success and survival on pack size (Vucetich *et al*., 1997; Courchamp *et al*., 2000). To fully understand the importance of sociality on the extinction risk and conservation of the wild dogs the comparison of predictions from models of wild dog populations is required. The predictions made by the individual based model by Creel and Creel (2002) with the addition of pack size dependent mortality and disease transmission rate, could be compared with the predictions of an individual based model structured on a conservative approximation to the truly non-social version, as done by Grimm *et al*. (2003) for marmots.

Although PVA models are useful for predicting population persistence and identifying specific factors that can be managed, it must noted that they are models and their validity can not be assumed without thorough tests and evaluations. In terms of applying the predictions of population viability analyses to management strategies, it is essential that it is treated as an experiment. Two similar areas or populations should be used, one as a control, that has nothing altered, and the other as a treatment, where a management strategy is applied. Only by doing this will it be possible to identify whether the management and not other factors are effective at increasing the population persistence, therefore testing the accuracy of PVAs.

PVAs indicate areas in which management can increase wild dog population persistence. Habitat fragmentation is one of their biggest threats due to their need for extensive home ranges, therefore large areas where wild dogs are protected from human persecution need to be maintained (Woodroffe and Ginsberg, 1999). Creel and Creel (2002), found that immigration increased population persistence so the possibility of establishing corridors and translocating dogs should be considered. Interspecific competition is a large threat to wild dog persistence (Creel and Creel, 2002) but the control of lion and hyena numbers is not realistic, especially due to their tourism appeal. Wild dog populations in small areas have a greater extinction risk and specific management strategies should be devised for these populations. These could include minimising persecution through education and livestock husbandry, reducing accidental deaths by enforcing lower speed limits on roads and increasing antipoaching activities, and preventing contact with domestic dogs to minimise the threat of disease (Woodroffe and Ginsberg, 1997, 1999). From this work it is clear that the social behaviour of wild dogs, in terms of their reproductive suppression and dependency on pack size for both reproductive success and survival, have implications for population persistence. The management of large populations and packs to reduce these effects of sociality and the inclusion of social behaviour in extinction risks and conservation should be a necessary aspect of increasing wild dog population persistence.

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