# Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*

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The painted hunting dog or African wild dog, *Lycaon pictus,* is one of the most endangered large carnivores in Africa, with extinction predicted within a few decades if their dramatic decline is not stopped. It has recently been hypothesized that because of their constraining need for helpers, group size was of major importance in obligate cooperative breeding species, and that the resulting likely existence of a threshold number of adults could create an Allee effect, increasing the group extinction risk. One example where the importance for a critical number of adults may have major repercussions for painted hunting dogs concerns baby-sitting, or pup-guarding, a behavior typical of obligate cooperative breeders. We propose that, as forgoing this behavior is costly because pup guards have the potential to decrease pup mortality, its use is costly too, especially in small packs, because helpers are strongly needed for their cooperative foraging (hunting, protecting the kill and bringing back food to the pups). We present a simple model showing how pup-guarding imposes a cost because it implies that less food per hunt is brought back to more individuals at the den. We complete these analyses with empirical tests of the effect of pack size on the probability of pup-guarding, from field data from the Hwange population in Zimbabwe. Our model, as well as our 5 years of empirical data, both suggest a critical threshold at a size of about five individuals. *Key words:* African wild dog conservation, Allee effect, cooperative hunting, inverse density dependence, *Lycaon pictus,* painted hunting dog, pup-guarding. *[Behav Ecol 13:20–27 (2002)]*

T he painted hunting dog, *Lycaon pictus,* often called the African wild dog (but see Rasmussen, 1999) is among the most endangered large carnivores in Africa, and most of the 600–1000 remaining packs are known to be in populations too small to be viable (Woodroffe and Ginsberg, 1997). As a result, complete extinction of the species is predicted imminently unless the precise causes for its decline are rapidly understood and action taken to alleviate them (Fanshawe et al., 1991; Ginsberg and Macdonald, 1990). Even though several causes of mortality in *Lycaon* are well documented (see Creel and Creel, 1998; Woodroffe and Ginsberg, 1999 for reviews), the precise mechanisms endangering this species in particular have not yet been entirely elucidated. In particular, it might be wondered whether natural processes alone (such as competition and predation) can really explain why populations of *Lycaon* are declining more rapidly than those of sympatric carnivores, which also suffered from persecution and habitat fragmentation (Creel and Creel, 1998). *Lycaon* is an obligate cooperative breeder living in packs of up to 20 adults, in which most of the time only the alpha pair breeds; the remaining adults are reproductively suppressed and help to raise the pups (Childes, 1988; Creel and Creel, 1995; Fuller et al., 1992; Maddock and Mills, 1994). Obligate cooperative breeders, such as *Lycaon,* have evolved to such a point that their need for helpers may become a constraint (Clutton-Brock et al., 1999; Jennions and Macdonald, 1994). For ex-

ample, the need for a certain number of helpers to carry out several behaviors essential to the group (including foraging, breeding and survival) may result in a minimum group size, hence an Allee effect (Courchamp et al., 1999; Stephens and Sutherland, 1999). In other words, smaller groups would have increasing difficulties to maintain themselves, to such a point that most packs under a critical number of adults could often be led to extinction.

One advantage of cooperative breeding in *Lycaon* is that a pack member can protect the pups during the months where they cannot follow the hunting party, and it is on this particular aspect of breeding that this work is focused. The common advantages of this behavior in *Lycaon* include: watching pups to prevent loss, alerting them to danger (lions, *Panthera leo,* or spotted hyaenas, *Crocuta crocuta*) thus ensuring they go to the safety of the den, protecting them from smaller predators or conspecifics, and moving them when heavy rain may cause floods at the den (Malcolm and Marten, 1982). Baby-sitting occurs both during the denning and pup caching periods, and both periods are covered by our present data (see below). Evidence that the presence of an adult at the den is beneficial for the pups in terms of survival includes the study by Malcolm and Marten (1982), which provided typical examples of the protection against predators provided by the baby-sitter to the pups. On several occasions, the baby-sitter either ran back to the natal den or went back underground with the pups, or chased away predators close to the den. That study also recorded nine cases where a dog returned to the den to baby-sit after encountering a predator close by. In a similar vein, on one occasion in this study, the presence of at least one lion caused a yearling male baby-sitting 12 week old pups to move them a distance of 1.8 km away from the danger. Other potential advantages of baby-sitting are that first the mother, often an experienced hunter, may be allowed to go back sooner to hunt if a subordinate dog guards the litter and second she

is enabled to get back into vital body condition post whelping so essential to the peripatetic life style of this hypercursorial canid.

The main apparent disadvantage of baby-sitting is that the individual assuming this task cannot participate in the hunts. Because *Lycaon* hunt cooperatively, and its hunting success is related to the hunting party size (Creel, 1997; Creel and Creel, 1995), small packs will tend to have a lower hunting efficiency than larger packs. Though a single dog has been recorded to kill an adult kudu, *Tragelaphus strepsiceros,* cow (this study), they will generally also be less likely than larger packs to tackle large prey. Moreover, larger hunting parties are less likely to lose kills to kleptoparasites because they reduce carcass access time and the presence of a single individual may make a difference (Carbone et al., 1997; Creel and Creel, 1996; Fanshawe and Fitzgibbon, 1993; Gorman et al., 1998). Finally, and most importantly here, adults regurgitate food back at the den for the pups once they are able to eat solid food at the age of 2 to 3 weeks and during the ensuing 2 to 3 months (Estes and Goddard, 1967; Malcolm and Marten, 1982; McNutt, 1996). Pups are dependent on regurgitation until they can follow the hunting party and feed directly at the kill (Malcolm and Marten, 1982; Rasmussen, 1997). Leaving a guard with the pups during hunts is thus energetically detrimental for three reasons. First, the total amount of food regurgitated by the hunters will be lower if one adult did not participate in hunts (and this may be exacerbated by the lower hunting efficiency of smaller hunting parties). Second, the individual guarding the pups, especially if it is the lactating mother, will consume part of the meat regurgitated by the hunters (Kühme, 1965; Malcolm and Marten, 1982), a part which will thus not be available to the pups. This energetic disadvantage can be increased if more than one adult baby-sits, as has sometimes been observed (Malcolm and Marten, 1982). Third, reduced intakes will lead to supplementary hunts which expose the pack to additional risks associated with hunting and high energy expenditure (Gorman et al., 1998).

This behavior is generally called baby-sitting when the pack member is a nonbreeding helper, but in our study we must consider all instances where a pack member was left with the pups (either the mother or a helper). In addition, when a pack member is left at the den, it is most often the alpha female (89.7% of the pup-guarding occurrence in our data set). For these reasons, we will from now on refer to ''pup-guarding'' rather than ''baby-sitting.''

Nonbreeders guard the young at the den in a variety of cooperative carnivores (Solomon and French, 1996) and virtually all studies of vertebrates with such guarding behavior show that removal of guards leads to a substantial reduction of offspring (Clutton-Brock, 1991). As it is for the benefits, the presence of pup-guarding cost seems widespread, although it may differ among species. For example in suricates, *Suricata suricatta,* individuals forego foraging for the duration of pup-guarding, which is very costly (Clutton-Brock et al., 1998; Doolan and Macdonald, 1999). Although in suricates the cost seems to be borne by the pup guard only, this cost has been shown to increase as group size decreases. Because the probability of leaving a pup guard does not increase with group size in suricates, each individual will perform this costly task more often in small groups (Clutton-Brock et al., 1998).

For all the above reasons, it appears sensible to predict that in *Lycaon* the cost of leaving a pup guard will be higher for small packs, and that the smallest packs may not be able to afford such cost. As a consequence, smaller packs may be confronted with a trade-off of allocation: either leave a pup guard and suffer reduced provisioning efficiency, or do not and suffer increased pup mortality through predation, loss or drown-ing. Alternatively, adults might compensate for the lesser amount of food obtained from a hunt by increasing the number of daily hunts, but this then increases costs and risks associated with the hunt. The aim of this article is to explore this trade-off. It may be worth emphasizing at this point that we entirely agree that small packs may sometimes do fine, especially when they involve experienced individuals. There are some good anecdotes of small packs breeding and even pairs or single dogs surviving for some time. Our point is a different one—namely that statistically the break point between success and failure hovers around a pack size threshold, in this case around five adults: the breeders and around three helpers.

Because pup-guarding is well suited to illustrate the probable Allee effect in *Lycaon,* it provides an interesting example of the importance of pack size for the survival of this species. In a previous work, we provided evidence from the literature of the likelihood of a minimum pack size in *Lycaon* (Courchamp and Macdonald, 2001). In addition, we provided a mathematical model of the dynamical consequences such an effect would have, and showed that the existence of this threshold increased the probability of extinction at both the pack and population levels (Courchamp et al., 2001). These two previous papers highlighted the importance of this threshold for the conservation of this species, but the illustration of the mechanism through which the behavior could act on population dynamics remained to be presented. Here, we do so by presenting a simple model that describes how the presence of a pup guard imposes an energetic constraint at pack level and how this cost is related to pack size. We first test the results of this model by analyzing published data on pup-guarding. Finally, we present new empirical data from the Hwange population of *Lycaon* in Zimbabwe, which confirm the importance of pack size for pup-guarding, and which support the proposition that there is a threshold pack size beneath which pup-guarding may become unsustainable.

## MATERIAL AND METHODS

### Model

We construct a simplistic model, which features the main processes contributing to the energetic costs to *Lycaon* of pup feeding: amount of food needed for each individuals and amount of food obtained from a hunt by each hunter. For the sake of simplicity, we will assume that yearlings are equivalent to adults in the model. We will therefore only distinguish between adults and pups. That yearlings are less efficient at hunting and maybe less generous in terms of regurgitation will only underestimate the importance of pack size in our model, thereby strengthening our conclusions (but see discussion). For the model, as well as the empirical data below, we define a hunt as the period during which the dogs are away from the den and involved in any phase of hunting activity. A hunt can thus include multiple kills (two hunts are counted if the hunters come back to the den in between); it corresponds to a foraging period of about 3.5 h (sensu Gorman et al., 1998). Calling r the gut content of each adult, we consider that a pack of A adults will provide regurgitated food from a hunt in sufficient amount for P pups and themselves if and only if $rA \geq Pe_p + Ae_a$ where $e_p$ and $e_a$ are the food requirements of pups and adults, respectively. Then, if one of the adults acts as a pup guard, A-1 adults bring back food to the den, and they have to share r(A-1) between the same number of individuals. We also assume that an adult which guards the pups has a lower energy requirement than the hunting adults. If we call $e_g$ the food requirement of the pup guard, leaving a pup guard at the den while hunting is energetically

profitable only if the amount brought back by A-1 hunters [thus $r(A-1)$] is at least equal to the needs of P pups (thus $Pe_p$), plus the needs of these A-1 hunters [thus $(A-1)e_a$] and those of the pup guard ($e_g$). We can deduce the number of adults A needed for the energetic balance to be positive:

$$r(A-1) \geq Pe_p + (A-1)e_a + e_g \Leftrightarrow A \geq \frac{Pe_p + e_g}{r - e_a} + 1. \quad (1)$$

The value of the gut contents of an adult *Lycaon,* r, is taken from Reich's work: 4.4 kg (in McNutt, 1996; also used in Carbone et al., 1997). The amount needed for an adult is considered to be between 2.5 and 3.5 kg (Gorman et al., 1998) or between 2 and 2.5 kg (Creel and Creel, 1995). We consider in our numerical illustration of Equation 1 that for each of these two ranges, the lower value corresponds to the metabolic need of a dog with low energy requirement (pup guard, if it is not at the same time suckling the pups), while the upper value is needed to achieve energy balance for the individuals participating in hunts, which involves a higher daily energy expenditure. One can alternatively consider that this lower value corresponds to the lesser amount of food provided by regurgitation to the pup guard, regardless of its energy requirement (Malcolm and Marten, 1982 showed that pup guards often get a lesser amount of regurgitate). It has been estimated that, on average, each adult regurgitates about 1 kg of meat after a full meal (Malcolm, 1979, in Fuller and Kat, 1990). This coincides with the values of 4.4 kg for gut content and 3.5 kg eaten per adult per day. Since it is not specified whether the 1 kg of meat regurgitated is for one or several pups, we will assume here that it is for one pup only (taking half this value provides essentially the same results). As a first step, we consider that dogs always obtain the maximum amount of meat from the hunt (in terms of prey availability and hunting success), since they are considered excellent hunters (Creel and Creel, 1998; Fanshawe and Fitzgibbon, 1993; Fuller and Kat, 1993). We use the conversion factor of 6862 kJ/kg of meat obtained by Creel (1997) to express our results in energy units.

The previous relationship (Equation 1) provides the minimum number of adults necessary in a pack for the use of a guard during a hunt not to be energetically detrimental. However, smaller packs might compensate for this disadvantage in numbers by hunting more often. We thus modify Equation 1 in order to account for the potential to increase the amount of food brought to the den by hunting several times a day: H is the number of hunts performed by a pack per day. By one hunt we actually mean here one foraging period: one hunt can involve multiple kills, as is often observed for large packs (Creel and Creel, 1995). In addition, the amount of food obtained by each dog should be modified to account for the differential foraging success (including efficiency of capture, kill and evisceration of prey and defense of carcass) of *Lycaon* in small and in large packs (Creel and Creel, 1995, 1996). For this, we consider that this amount is a function of the number of adults A and we use the data of Creel (1997) linking foraging success (in kJ/dog/day) to the number of adults in the pack. Equation 1 becomes:

$$H f_{A-1}(A-1) \geq Pe_p + (A-1)e_a + e_g \quad (2)$$

which yields:

$$H \geq \frac{Pe_p + (A-1)e_a + e_g}{(A-1)f_{A-1}}$$

where $f_{A-1}$ is the foraging success of A-1 hunters (in kJ/dog/day), and takes into account differences due to the size of the hunting party. Following the same reasoning, the number of
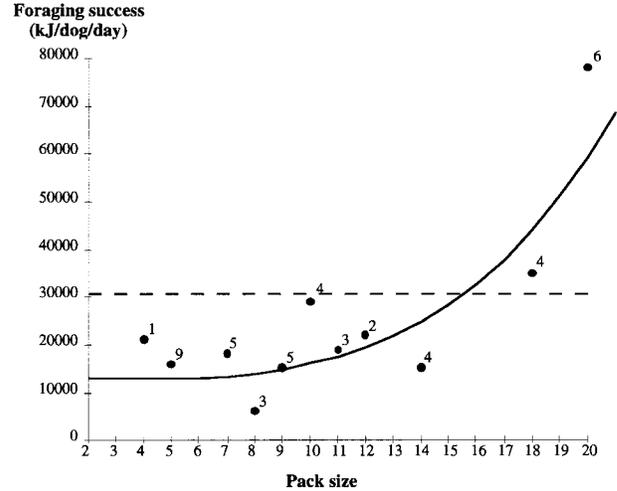


**Figure 1**
Foraging efficiency as a function of pack size (adults + yearlings). There is a significant, nonlinear relationship between the number of hunters and the daily energy gained by hunter per day. This is because larger groups are more efficient at killing, have access to larger prey, clean up a carcass faster and can defend it longer against kleptoparasites. The constant value of 4.4 kg used in the first model (r in Equation 1) is indicated by a dashed line. It shows that the use of a constant value for foraging efficiency overestimates the amount brought back to the den: the model using the nonlinear relationship more precisely matches biological reality. Numbers beside the points represent the number of observations for each pack size. Modified from Creel (1997).

hunts needed to feed P pups when all A adults participate in the hunts (no pup-guarding) is

$$\frac{Pe_p + Ae_a}{A f_A}.$$

The expression of $f_A$ (i.e., foraging success of A hunters) is obtained by fitting the data of Creel (1997) to a model of the form:

$$f_A = (\lambda + \beta A^\mu). \quad (3)$$

We fitted the regression to these data, and obtained a fit at the $\alpha$ level of 0.001 for $\lambda = 12826$; $\beta = 1.24$ and $\mu = 3.58$ (Figure 1).

## Field data

The empirical study was conducted by one of us (GR) between April 1994 and October 1999 in Hwange and adjacent areas totaling 5500 km². Focal packs were those that either resided entirely in areas contiguous with the park or had their home range within a 60 km zone on the park border. Lions and hyaenas were present throughout the study area. Data came from 13 denning period events from eight packs, a pack being defined as a potential breeding unit containing at least one adult of each sex (Malcolm, 1979; Reich, 1981). We avoided pseudoreplication by comparing results among packs (observations averaged within packs). Denning period is when the pups are too young to follow the adults during long trips, and the pack exhibits refuging rather than nomadic behavior. This period is of about 12 weeks. Pup caching occurs when pups are 12 weeks old at least and the pack is mobile. Since the pups are too young to follow the pack all day long, they are hidden during some foraging periods. Our data set includes this event as pup-guarding occurs when pups are

cached as well. In all instances of pup caching the data were obtained by remaining with the pups.

Dogs were categorized into age classes as follows: pups (<1 year old), yearlings (≥1–<2 y.o.) and adults (≥2 y.o.). Pups were identified at emergence providing a record of the number of dogs in each class category at all times. In six packs, data were obtained through radio-collared individuals, either by following packs on hunts to see which individuals were hunting, or by den watching. The latter was used only on packs that had been followed for more than 9 months and were deemed habituated to observer presence at this critical time. Individuals were radio-collared when conditions were favorable in terms of habitat density and time of day. In thicker bush the anaesthetic doses were kept at the higher end of the range specified to reduce knockdown time and thus the likelihood of an individual being darted and subsequently lost. Capture was not undertaken if the risk of the animal being lost was too important (thick bush). Immobilization was only undertaken in the mornings in order to reduce predation risk (dogs are more vulnerable at night, and by that time they should have completely recovered from anesthesia). Only adults over the age of 14 months were collared, with the first individual to be collared being selected at random. When a second radio collar was put on a pack, an adult of the opposite sex was usually selected. Retroreflective protective collars, which often had no radio unit were fitted to any individual that could be immobilized providing they were old enough. These collars, though fitted in an attempt to reduce road mortality, helped to reveal which individuals were hunting/pup-guarding at night. Proven breeding alpha females were never collared because Ketamine is known to cross the placental barrier, though one female subordinate at the time of collaring, subsequently acquired alpha status. No pup-guarding data are presented within 5 days after collaring.

All dogs were chemically immobilized using a 5.5:1 Ketamine HCl (Fort Dodge): Xylazine (Bayer). Administration of the drug was intramuscular in the rear quarter by dart ($n =$ 9). Darting was achieved using 1.8 mm Daninject darts and a 1M rifle with doses ranging from 180 mg:33 mg to 220 mg:40 mg depending on age, condition, and size. All procedures on anaesthetized animals were carried out in situ with the dogs being laid onto a canvas reserved solely for this purpose. As the depth of anesthesia could not be measured, precautions were taken to reduce possible stress from awareness of close proximity with humans. These measures involved the dogs being blindfolded and fitted with earmuffs specially designed to allow easy removal by the study animal in case of a bolt recovery. Also communications were kept silent and carried out by predetermined hand signals. As frequently other members of the pack were waiting close by, personnel assisting adopted no erect postures. When vital reflex signs indicated that the Ketamine (the half-life of which is considerably shorter than Xylazine) was nearly metabolized, immobilization was reversed, using 4–6 mg of Antipamezole (Pfizer) administered intramuscularly.

All immobilized dogs were monitored for 24 h post anesthesia to ensure their safe return and integration into their pack. The knockdown time ranged from 45–95 min (mean 65 min). Recovery was seemingly full by the late afternoon prior to the evening hunt. Response to the collar by the wearer was indifference. Any pups in the pack would show interest in the collar, however this interest would wane to none after 7–10 days. There was no other observable effect of the collars. Protective collars remained on individuals, with MOD 400 collars being replaced with Sirtrack collars where possible. No hair slip was noted with protective collars and minimal slip was noted in MOD 400 collars.
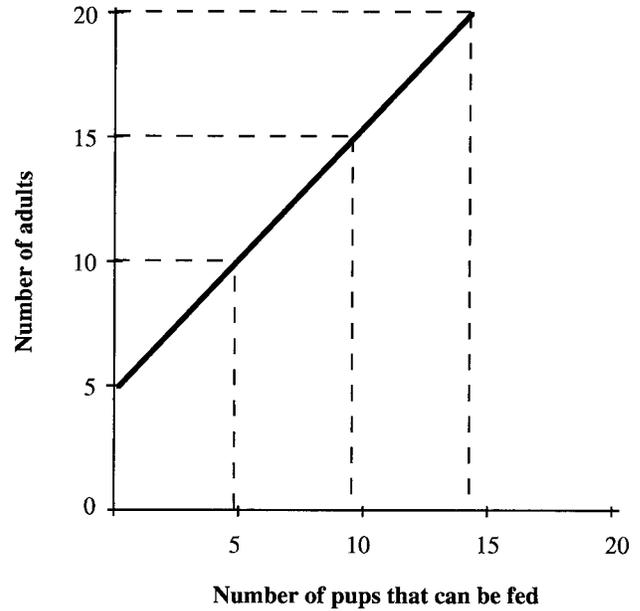


**Figure 2**
Predicted minimum number of adults needed to both feed a given number of pups from the product of one hunt and guard them during this hunt. The threshold, as found by the first model (foraging efficiency is constant), is five adults.

## RESULTS

### Model

Figure 2 shows the predicted minimum number of adults needed to both feed the pups from the product of one hunt and guard them during this hunt. This shows that, in theory, packs of five adults cannot feed pups sufficiently if they are to use one hunter as a pup guard. This however does not account for the higher foraging success of large hunting parties, which could increase the difficulty of leaving a guard in small packs. We take this into account by replacing the constant amount of food obtained for a hunt, by a function of the hunting party size (Equation 3 and Figure 1). We use the model of Equation 3 in Equation 2 to express the number of hunts H that must be completed to feed a pack with P pups, A-1 hunters and one pup guard. We first show the number of hunts that must be achieved in theory for a pack of a given size to be able to feed a litter of a given size (Figure 3a). This figure also shows how, regardless of the use of a pup guard, smaller packs will have to increase the number of hunts (and the associated costs and risks) to raise the same number of pups as do larger packs.

It is then possible to calculate the number of additional hunts that must be performed to compensate for the absence of one hunter which stays to protect the pups at the den:

$$\frac{Pe_p + Ae_a}{Af_A} - \frac{Pe_p + (A\text{-}1)e_a + e_g}{(A\text{-}1)f_{A\text{-}1}}.$$

This is shown in Figure 3b: for packs of more than five adults, and regardless of the number of pups, there is no need to increase the number of daily hunts in order to feed the litter and guard it at the same time. In contrast, packs of five adults and less need to increase their number of hunts per day to achieve the same results. For packs of five and four, adults will need to hunt once more each day if a pup guard is to be used, while packs of three adults will require a second additional daily hunt for large litters. Pairs will have to perform
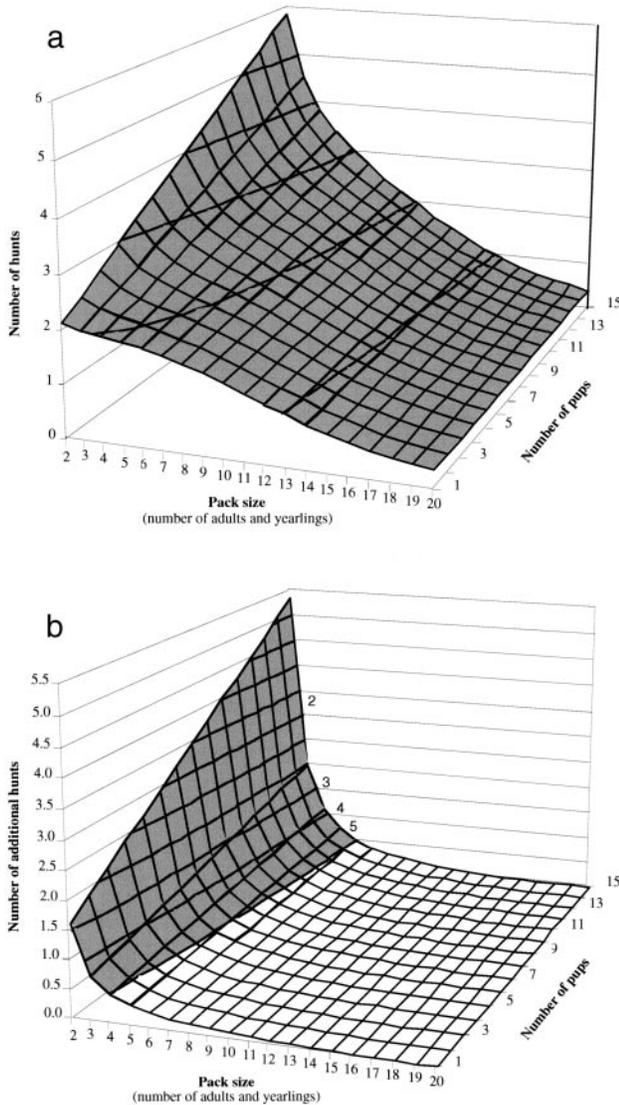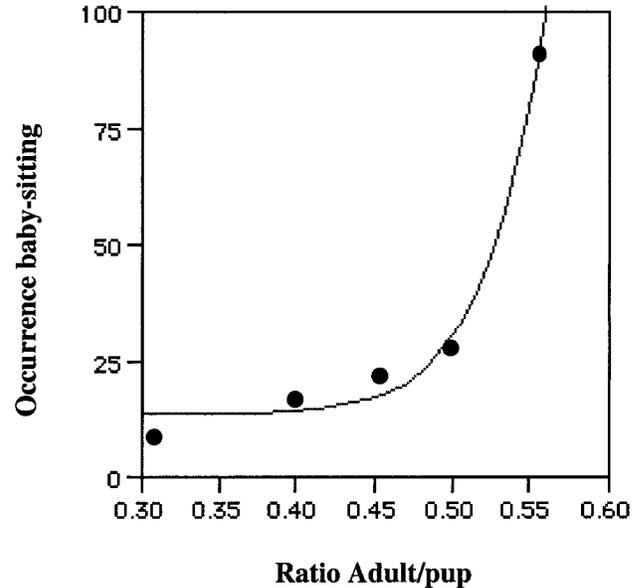
**Figure 3**
(a) Number of hunts that must theoretically be achieved by a pack of a given number of adults and pups if energetic balance is to be attained, when all adults participate in hunts (no pup guard). This graph shows that, regardless of the use of a pup guard, smaller packs will have to increase the number of hunts (and the associated costs and risks) to raise the same number of pups as larger packs. (b) Number of additional hunts needed by packs of a given number of adults and pups to compensate for the use of a pup guard. Regardless of the number of pups, there is no need to increase the number of daily hunts for packs of more than five adults (white area). In contrast, packs of five adults and less need to increase their number of hunts per day to feed their pups, if they are to use a pup guard.

up to five more hunts if they need to split to guard and hunt (and this assumes that the hunter is experienced enough to kill prey alone).

Although we do not aim to provide an accurate estimate of the number of hunts needed to compensate for pup-guarding, it would be interesting at this point to estimate how many times a day a *Lycaon* is able to hunt. In a previous study, the maximum number of hunts per day was eight (Creel and Creel, 1995). Although this may only reflect the number of hunts that dogs need to satisfy their requirements, eight hunts per day might be close to a maximum a dog can sustain. This
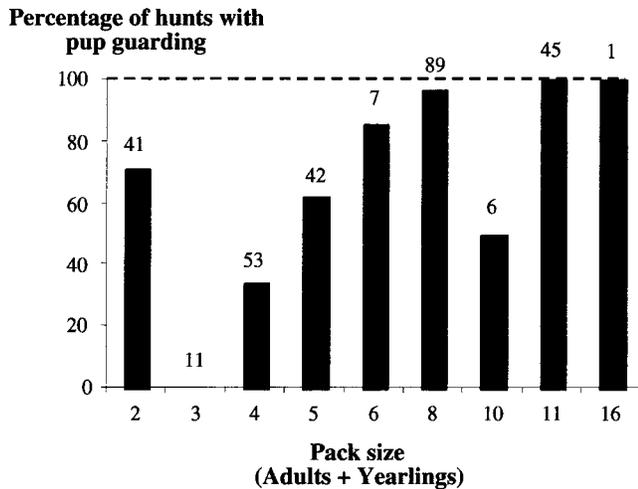


**Figure 4**
Relationship between ratio of adults to pups in a pack and number of times this pack was observed using a pup guard (each dot represents one pack; data from Malcolm and Marten, 1982). The significant, nonlinear relationship highlights that there might be a threshold of around two pups per adult, below which the probability of using a pup guard drops dramatically. Since the average litter size is around 10 pups, this threshold should be around five adults.

number is however less than our prediction of the number required by the smallest packs to compensate for the use of a pup guard (Figure 3). A recent analysis of the energetic constraints of hunting showed that hunting for an average of 3.5 h daily, *Lycaon* is already close to its physiological limits (Gorman et al., 1998). It may be difficult to equate time spent hunting and number of hunts in those two studies, but, clearly, small groups may be unable to cope with the number of additional hunts required daily to compensate for the loss of a hunter, and may instead forgo pup-guarding.

**Literature data**

We re-analyzed some of the results of a published study of a Tanzanian population of *Lycaon* (Malcolm and Marten, 1982). This study presented the distribution of pup-guarding occurrences for the different members of five studied packs. Since the numbers of adults was similar for each pack (there were no yearlings these years), we plotted the number of pup-guarding occurrences against the ratio of adults over pups (Figure 4). This figure shows a nonlinear relationship, significant at the $\alpha$ level of 0.001, between ratio of adults over pups in the pack and occurrence of pup-guarding. It is interesting in this regard to observe that there seems to be a threshold set slightly under two pups per adult, below which pup-guarding becomes much less likely. If one takes 10.31 as the average litter size (calculated over 165 litters from published data: Burrows et al., 1994; Fuller et al., 1992; Maddock and Mills, 1994), then this threshold is under 5.16 adults. This is suggestive of a cost of pup-guarding when fewer adults are in charge of more pups. This analysis supports the prediction of our model. In a given ecosystem and for the same years, packs where adults had to feed fewer pups more often used a pup guard than did other packs. Note however that few packs were available for this analysis, and all were of a rather small size (four or five adults).

**Percentage of hunts with pup guarding**



**Figure 5**
Relationship between pack size (number of adults and yearlings) and the proportion of hunts observed with pup-guarding in the Hwange population. As its size increases, the pack gets more likely to leave a pup guard during the hunt. Packs of more than five adults almost always leave a pup guard. Statistically, the largest difference is between packs of five dogs or less and packs of more than five dogs (see text).

### Field data

For this analysis we used results from a different population, in Zimbabwe. Pack size and pup-guarding status was known for 246 hunts out of a potential of 314 hunts for the 13 denning periods. Of these, 33% were undertaken by the whole pack, the remaining 167 hunts involving one pack member as a pup guard. Hunts that took place during the night (22 hunts), that is when the risk of pup predation is high, invariably involved a guard remaining with the pups, whereas pups were left alone during 39% of diurnal hunts ($\chi_1^2 = 11.709$; $p = .0006$). Furthermore, pup-guarding was significantly more likely in larger packs: the eight packs of less than five individuals left a guard with the pups in $34.7 \pm 0.1\%$ of their hunts, while the five packs of more than five individuals left a guard in $88.5 \pm 0.1\%$ of their hunts (Mann-Whitney $Z = -2.635$; $p = .0084$).

We tested the effect of both time of hunt (day or night) and pack size on the probability of pup-guarding through a logistic regression (binomial error), creating *ad hoc* groups for each size-pack (18 groups). Probability of pup-guarding strongly differed between groups ($\chi_{17}^2 = 17.90$; $p < 10^{-4}$). This difference between packs is explained by their size (size nested within group, $F_{16}^1 = 9.25$; $p = .008$). In addition, probability of pup-guarding differed between hunting periods (a.m., p.m., and night, $\chi_2^2 = 11.67$; $p = .003$). The effect of hunting period on probability of pup-guarding was the same between group (interaction group—hunting period, $\chi_{11}^2 = 17.90$; $p = .08$). The distribution of the pup-guarding occurrences for packs of different sizes is shown in Figure 5. The largest difference in the number of hunts with or without pup-guarding was between packs of five or less and packs of more than five dogs ($\chi_1^2 = 89.345$; $p < 10^{-4}$), suggesting once more a threshold of five individuals for pup-guarding in *Lycaon*. When a distinction was made between yearlings and adults, the significant effect of pack size on the probability of pup-guarding was lost if yearlings were not taken into account, probably because too few packs were available. The presence of yearlings in the pack was however a significant predictor of the probability of pup-guarding (Mann-Whitney $Z = -2.143$;

$p = .0321$). To facilitate comparison between our data and that published by Malcolm and Marten (1982), we explored the effect of the ratio of pack size (adults plus yearlings, when present) to number of pups. We found that there was a highly significant difference between packs with a ratio below 0.5 (29.8% of pup-guarding) and packs with a ratio above 0.5 (75.5% of pup-guarding; $\chi_1^2 = 35.664$; $p < 10^{-4}$). Pup-guarding occurrences were too few for small pack sizes to test whether small packs undertook more daily hunts if they used a pup guard than if they did not use one. Packs of three never left a pup guard, which supports the prediction of our model, although the lack of observation of the pups of one of the packs of three during their first weeks may account in part for this result. Results for packs of four and five were not significant. However, packs of two performed 11 times an additional hunt over the 18 days when they left a pup guard, compared with no additional hunt for the 12 days when they did not leave a guard, which makes a significant difference ($\chi_1^2 = 11.579$; $p = .0007$). This result confirms our prediction of a high cost of pup-guarding for small packs.

### DISCUSSION

Combining theoretical and empirical approaches, we showed that in *Lycaon,* leaving or not leaving a pup guard amounts to choosing between two costs. The absence of a pup guard may risk high pup mortality, whereas presence of a pup guard may lead to higher mortality through lost hunting efficiency. In small packs, employing a pup guard during the hunt may result in crucially diminished amounts of food brought back to the den by the remaining adults. Consequently, adults in small packs may have to complete additional costly and risky hunts each day to compensate for the loss of a hunter to pup-guarding. Yet, dispensing with a pup guard may be hazardous as it is generally agreed that pup guards have the potential to prevent loss of pups and pup predation. High mortality of pups (around 40%) by predation from intraguild competitors has been reported in several studies (van Heerden et al., 1995; Ginsberg et al., 1995; Mills and Gorman, 1997). Although logistically difficult, it would be interesting to collect enough observational data to be able to test the extent to which pup mortality changes with the presence or absence of a guard, controlling for pack size. Here we show that a pup guard was systematically used during hunts at night, when lions and hyaenas are active and a threat to unattended pups. We demonstrate theoretically that using a pup guard is costly in terms of energy for the whole pack, and that only large packs, or packs with few pups, can afford it. We also show that smaller packs need to hunt more often to feed their pups, especially when using a pup guard.

The simplistic mathematical model we used here indicated a relationship between pack size and energetic cost involved with pup-guarding. Yet, in this model, many points could be improved. For example, we focused on pack size only, but individuals that have different social status will have different individual costs and benefits at guarding the pups of the pack breeders. Similarly, we did not focus on the precise value that should be taken by the amount eaten by the guard. As shown by Malcolm and Martens (1982), the guard often eats less that the other adults, or even not at all in some cases. In that case, the lower value used for the amount eaten by the guard does not reflect its energy requirement (especially if it is the lactating mother). As, in this case, the cost of pup-guarding is also borne by the guard itself, a need for more food that may prevent individuals from pup-guarding as much as they would in absence of this food stress. To be more realistic, our model should have used a larger value for $e_b$. However, doing so would lead to an exacerbation of the effect we predict in this

paper, which only strengthens our point. It also is noteworthy that we hypothesized that only one guard was left at a time, regardless of the number of pups. A more realistic alternative might be to consider that very large litters would require two or more simultaneous guards, and that this could be afforded only when the pack size is sufficiently high. This possibility, which has been observed in the wild (Malcolm and Marten, 1982), would also increase the trade-off between pup-guarding and hunting. Note that if a linear relationship was used instead of the model used in Equation 3 for the foraging success of A hunters, the results would be qualitatively unchanged and would quantitatively more strongly emphasize the importance of pack size.

Re-analysis of published data showed a positive relationship between the occurrence of pup-guarding and the ratio of adults to pups, partially confirming the prediction of our mathematical model. An analysis of new empirical data completes this, by confirming the relationship between pack size and the probability of pup-guarding. These analyses also show that yearlings play an important role in this regard, which supports our pooling of adults and yearlings in the model. It is interesting to note that Burrows (1995) also found an effect of pack size on pup survival, which was significant only if yearlings were taken into account. Although yearlings are not yet experienced hunters, their presence contributes to foraging efficiency. It is generally the alpha male or the alpha female which leads the hunt, but yearlings nonetheless contribute to several aspects of cooperative hunting, including the diminution of kleptoparasitism, by decreasing the carcass access time (increased cleaning efficiency) and increasing the ratio of dogs/hyaenas (see Carbone et al., 1997; Fanshawe and Fitzgibbon, 1993). In addition, by regurgitating meat to the begging pups back at the den, (Estes and Goddard, 1967; Malcolm and Marten, 1982), yearlings' stomachs can act as ''the storage and preparation containers for the pups' food'' (Kühme, 1965). This also allows a rapid ''transport of the hastily dismembered prey into safe cover'' (Kühme, 1965). For these reasons, the pack may chose to use a pup guard when the cost of doing so is offset to the presence of yearlings to increase the hunting party.

Another solution enabling the adults to lower the costs of this trade-off might be to alternate strategies. If pup-guarding is used only occasionally (e.g., only if a predator is around or in case of heavy rains, when the pups risk drowning in the den), this may lower the risk of pup mortality, while avoiding under-nourishment (or hunting injuries). By constantly adjusting their strategy, adults may be able to feed sufficiently all pack members as often as possible, thereby maintaining all dogs in good condition, so that when a pup guard must be used, the associated loss of energy (less food or more hunts) is not too costly. Therefore, we predict that pup guards should be used for only a proportion of the hunts, and this proportion should increase with pack size. Both the published literature and our data suggest that this is indeed the case.

We approached this problem through four independent analyses, and each led to the same estimate of a critical threshold around five adults (see Figures 2, 3b, 4, and 5). Of course, the simplifications involved mean that we do not expect our estimates to be precise values of the number of adults needed for a pup guard to be affordable. Similarly, the number of additional hunts is given as only an indication of a likely process. Individual differences, such as the experience of hunters (the pup guard is often the mother and it is also often one of the most experienced hunters), and the environment (prey availability and characteristics of the habitat) are major factors that will change these values. Our main aim has been to demonstrate that a threshold pack size exists, rather than to be precise about its value. Yet it is striking that, as was the case

with four approaches used independently in this article, other authors have reported that packs of more than four to six *Lycaon* have advantages over smaller packs (Carbone et al., 1997; Creel et al., 1998; Estes and Goddard, 1967; McNutt, 1996).

As *Lycaon* is among the most endangered canid species (Woodroffe and Ginsberg, 1997), our findings have noteworthy implications for their conservation biology. This is particularly pertinent as this species is a victim of negative attitudes (Rasmussen, 1999) and anthropogenic mortality, the impact of which has the capacity to reduce numbers to below a sustainable threshold and where the loss of one or two individuals can impact on pack integrity and ability to survive (Rasmussen, 1996, 1997). The relationship between survival and group size, upon which this work is focused, is not specific to *Lycaon,* nor is pup-guarding the sole aspect to which such a trade off may apply: this concept could also be applied to other cooperative breeders, many of which are also vulnerable to extinction and currently endangered.

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