Pup provisioning in the cooperatively breeding African wild dog, *Lycaon pictus*, is driven by pack size, social status and age

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Division of labour, in terms of providing for offspring, in obligate cooperatively breeding mammalian species is poorly understood. To understand offspring provisioning in a cooperatively breeding canid, we analysed a long-term dataset comprising 22 African wild dog, *Lycaon pictus*, denning events (nine packs over nine consecutive years). We investigated the effects of sex, age class, social status, and pack size on the likelihood and frequency of regurgitating food to pups at the den. We found that the interaction of social status and pack size affected the likelihood of regurgitation. Specifically, when in a large (>15) pack, dominant individuals were less likely to regurgitate than subordinate individuals. However, in smaller (≤15) packs, dominant individuals were more likely to regurgitate than subordinate individuals. We also found that the interaction of age and pack size affected the frequency of regurgitation. Specifically, in large packs, yearlings regurgitated more frequently per observation period than adults. Contrastingly, in smaller packs, adults regurgitated more frequently. Sex did not affect pup provisioning. We suggest that these contrasting patterns of helping are best explained by a strong selection pressure for individual behaviour that results in larger pack sizes in this species. When in larger packs, costs are shared as the division of labour spreads amongst individuals. In smaller packs, a division of labour requires individuals that already experience costs (such as reproduction) to be further burdened by provisioning. Overall, our results support that the need for more helpers to care for offspring contributes to the evolutionary consequence of an inverse density dependence.

Keywords: division of labour, helping behaviour, kin selection, pack size, regurgitation.

INTRODUCTION

Care of offspring is shared amongst group members within cooperative breeding social systems (Solomon & French, 1997). Helpers at a nest or den have been documented across diverse taxonomic groups including insects (Wilson, 1971; Shellman-Reeve, 1997), birds (Arnold & Owens, 1999), and mammals (Solomon & French, 1997; Clutton-Brock *et al.*, 2001; Bergmüller, Johnstone, Russell & Bshary, 2007). Non-breeding helpers are typically nulliparous members of a social group (Solomon & French, 1997), related to the breeding pair (Lukas & Clutton-Brock, 2012), that expend time and energy helping to raise offspring born within the group (Harrington & Mech, 1982; Malcolm & Marten, 1982). Helping behaviour is typically interpreted within the theoretical framework of kin selection and inclusive fitness (Hamilton, 1964) which, despite some recent criticism (*e.g.* Nowak, Tarnita & Wilson, 2010), has

received strong support from both theoretical and empirical work across diverse animal systems (Emlen & Wrege, 1991; Hatchwell Gullett & Adams , 2014).

Offspring provisioning has the obvious benefit to offspring of increasing their survival and group-level fitness. With regard to helpers, there are benefits of caring for non-offspring. For example, as African wild dog *Lycaon pictus* pack members are related (Frame, Malcolm, Frame & Lawick, 1979), helpers benefit from the success of non-descendant kin (König, 1997; Griffin & West, 2003). Additionally, gaining experience in the care of offspring (Hrdy, 1976), an enhancement of status (Nicolson, 1987), and an increase in group size fitness *via* offspring survival (Moehlman, 1979; Gilchrist, 2004; Hodge, 2005) are additional benefits to caring for non-offspring. These benefits may also explain the occurrence of unrelated individuals helping to rear offspring despite the likely energetic cost.

Despite a lack of physical specialisation in most mammalian cooperative breeders, the contributions made by individual group members, in terms of offspring provisioning, may vary considerably based on other attributes such as group size, age, sex, and dominance. For example, meerkat, *Suricata suricatta*, helpers in larger groups give fewer food items to pups (Clutton-Brock *et al.*, 2001), adults give more than younger helpers (Clutton-Brock *et al.*, 2001), and dominant meerkats contribute less to pup feeding (Clutton-Brock, Russell & Sharpe, 2004). Further, female meerkats give more food to pups than do males (Clutton-Brock *et al.*, 2001). With regard to canids, the sex of helpers varies with body mass. Smaller canids tend to have female only helpers, compared to larger canids with both male and female helpers (Moehlman & Hofer, 1997).

African wild dogs, considered a large canid (Moehlman & Hofer, 1997), are pack-living carnivores with a complex social structure (Woodroffe, McNutt & Mills, 2004). As obligate cooperative breeders, packs consist of a dominant, breeding pair, and their subordinate helpers (Frame *et al.*, 1979). As breeding is monopolised by a dominant pair, these individuals carry the cost of increased stress (Creel, Creel, Mills & Monfort, 1997). However, reproductive promiscuity in wild dogs has been recorded (Spiering, Somers, Maldonado, Wildt & Gunther, 2009). Additionally, communal nursing has been observed in female wild dogs (Moehlman & Hofer, 1997). Subordinate pack

members (*i.e.* helpers) are usually closely related to the breeding pair in the form of siblings (of one of the dominant pair) or offspring (of both of the dominant pair). Packs consist of 2–50 individuals (Frame *et al.*, 1979), where the costs for small packs are high in terms of hunting success and subsequent energy intake (Creel & Creel, 2002; Rasmussen, Gusset, Courchamp & Macdonald, 2008). Further, at kills, hierarchies exist where younger individuals have priority access (Reich, 1981; Malcolm & Marten, 1982; Creel *et al.*, 1995). In addition to hunting success, wild dog pack size plays a strong role in juvenile survival (Buettner *et al.*, 2007), den site selection and the number of pups raised (Davies, Marneweck, Druce & Asner, 2016), and avoidance of threats (Courchamp & Macdonald, 2001). Breeding occurs annually and, although they are weaned within 3 months, pups are dependent on older pack members to provide them with regurgitated meat from kills and lead them to fresh kills until they are approximately 12 months old (Frame *et al.*, 1979; Malcolm & Marten, 1982). As such, pup provisioning can be costly (Somers, Graf, Szykman, Slotow & Gusset, 2008). Canids are the only mammalian family to provision offspring *via* regurgitations (Moehlman & Hofer, 1997). Despite this complex social structure and behaviour, factors driving the level of contribution by helpers (in terms of pup provisioning) in the endangered, cooperatively breeding wild dog are poorly understood.

To explore factors affecting whether an individual provisioned pups (in terms of regurgitation, and the frequency of regurgitation), we analysed data collected through direct observations of 22 wild dog denning events in the Kruger National Park (KNP), South Africa, from 1991 to 2000. No sex bias was observed in the population during this time (Maddock & Mills, 1994; Marnewick *et al.*, 2014). Based on current knowledge of wild dog behaviour and social structure, we predicted that: 1) all individuals from smaller packs would be more likely to provision compared to those from larger packs (where packs are considered small when there are 15 or fewer members and large if there are more than 15 members); 2) subordinate individuals would be more likely to provision than dominant individuals; 3) males and females would provision equally, and 4) yearlings would be more likely to provision than older individuals. Further, we expected that when provisioning, 5) all individuals from smaller packs would regurgitate more frequently than those from larger packs; 6) subor-

dinate individuals would regurgitate more frequently than dominant individuals; 7) males and females would regurgitate with equal frequency, and 8) yearlings would regurgitate more frequently than older individuals. Finally, as pack size is an important factor for wild dog success, we expected that 9) there would be an interaction of the above factors with pack size, as larger groups would indicate a higher division of labour.

METHODS

Study area and population

The KNP, encompassing an area of 19 633 km² between 22°25′ and 25°32′ south and 30°50′ and 32°02′ east, supports the only remaining viable, naturally occurring wild dog population in South Africa (Davies-Mostert, Mills & Macdonald, 2015). The area experiences summer rainfall ranging north to south approximately 400 mm to 700 mm per year. Our study was restricted to the southern section of the park (south of the Sabie River) within an area of approximately 4280 km². This area is characterised by knobthorn – marula (*Acacia nigrescens – Sclerocarya birrea)* savanna vegetation. Wild dog numbers ranged from 77 to 157 individuals in our study area over the duration of our study, comprising approximately 36% to 43% of the entire KNP wild dog population, respectively. Besides potential dispersing individuals, the packs included in our study did not consistently range north of the Sabie River (Mills & Gorman, 1997).

Den observations

M.G.L.M. located breeding dens by radio tracking collared pack members from either the air or ground. We then made observations from a stationary vehicle at dens, where packs usually remain for the first 3 months following the birth of a new litter (Malcolm & Marten, 1982). Observation periods coincided with the wild dogs' crepuscular peaks in activity, and ended when no additional activity was observed for at least 30 min ($n = 247$, mean ± S.E. duration of observation period 191 ± 9 min). We sexed individuals based on external genitalia and used pelage patterns to assign individual identities. We classified individuals as pups (0–12 months), yearlings (13–24 months), or adults (>24 months).

We were not able to determine the relative rank of non-breeders from den observations only, thus individuals were categorised as either dominant (*i.e.* the male and female in each pack that

engaged in reproductive and scent marking behaviour) or subordinate (*i.e.* all other group members) (Frame *et al.*, 1979; Maddock & Mills, 1994). In some cases ($n = 2$), a subordinate female also gave birth. Under these circumstances, the litter size for that denning event was the sum of all pups produced by both females that bred. We classified these females as subordinate despite the fact that they bred. All dominant individuals were older than two years (*i.e.* adults).

During each denning event (defined as the total time in a given year that a pack was confined to a den to care for pups), we recorded 1) the total number of adults and yearlings (*i.e.* pack size), 2) the total number of pups (*i.e.* litter size), 3) the total number of regurgitations per individual per observation period, and 4) the individual identity, sex, age class, and social status of the regurgitator.

Ethical note

The wild dogs observed during this study were free-ranging and naturally occurring. All observations at den sites were made passively from vehicles stationed no closer than 25 m from the den. All wild dogs in the KNP are habituated to vehicles due to their continued exposure to people through tourism. At least one individual per pack was fitted with a Very High Frequency radio collar (African Wildlife Tracking cc., Pretoria, South Africa) as part of approved routine of South African National Parks wild dog management in KNP. These collars were fitted when required throughout the study by darting and sedating individuals by qualified veterinarians, and were removed either within the expected 18-month battery life of each device or once the study had concluded. The collars are designed to minimize impact on behaviour while maximizing detectability, as such; the collars weighed no more than 4–5% of the animal's body weight (approximately 450–500 g).

Statistical analyses

To investigate the factors affecting whether or not an individual would regurgitate, we created nine candidate generalized linear mixed effects models with a binomial distribution. We set response to one if an individual regurgitated wihin an observation period and zero if it did not. We then set various combinations of pack size, age, sex, social status, and two-way interactions as fixed effects predictors. We controlled for individual identity as a random factor in all candidate models.

To investigate how frequently an individual

regurgitated during each observation period, we created a further nine candidate generalized linear mixed effects models with a Poisson distribution. We set the number of regurgitations as the response, and various combinations of pack size, age, sex, social status, and two-way interactions as fixed effects predictors. We set individual identity as a random factor, and length of observation period as an offset factor in all candidate models.

We assessed collinearity between independent explanatory variables prior to analysis using variance inflation factors (VIF) and Spearman rank correlation tests. Where high levels of correlation (Spearman's rho > 0.5) were found between variables, one was discarded from the analysis, ensuring that all variables had VIF values below 2 in the final statistical models. Litter size was correlated with pack size and, as pack size has such an important effect on wild dog success (Buettner *et al.*, 2007; Davies *et al.*, 2016), litter size was discarded from both analyses. To identify the best model(s), we used model selection based on Akaike Information Criterion (AIC*c*). We performed all statistical analyses and created all figures in RStudio v 1.0.136 (Core Team, 2008) for Windows, using functions in the packages lme4 (Bates *et al.*, 2014) and MuMIn (Bartoň, 2013).

RESULTS

We recorded 2199 regurgitations throughout the study, and 79% of all individuals in the study were recorded regurgitating at least once (Table 1).

Pack size, status, and an interaction between pack size and status were the most important predictors of whether a wild dog would regurgitate, where the top model explained 100% of the variation (Figure 1; Table 2). When in a small pack, dominant individuals are more likely to regurgitate than subordinate individuals. In contrast, when in a large pack, subordinate individuals are more likely to regurgitate than dominant individuals.

Pack size, age, and an interaction between pack size and age were the most important predictors of frequency of regurgitation, where the top model explained 70% of the variation (Figure 2; Table 3). Adults regurgitated more frequently in smaller packs, whereas yearlings regurgitated more frequently in larger packs.

DISCUSSION

Understanding the factors driving the evolution of helping behaviour, and provisioning of young in particular, is a challenge. Our analyses of individual factors influencing whether, and how often, wild dogs provisioned for pups provide valuable

Table 1. Summary of pack structure for all packs included in the study.

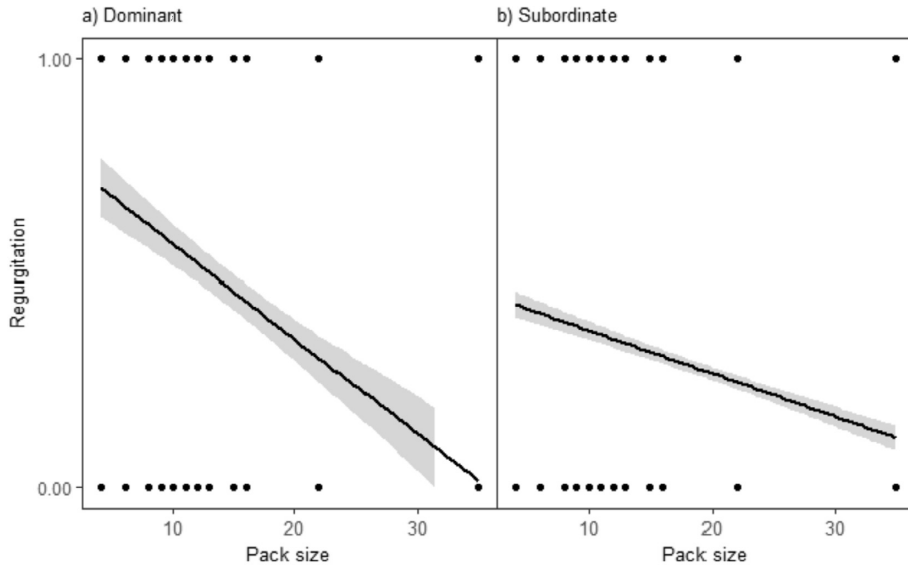| Pack ID /year	Pack size (adults & yearlings)	Number of males (adults & yearlings)	Number of females (adults & yearlings)	Litter size	Pack regurgitation rate (regurgitations per hour)
DP 94	35	15	20	28	4.12
DP 93	22	11	11	17	2.21
MB 99	16	8	8	18	0.50
PK 92	16	7	9	13	1.66
MB 98	15	10	5	17	3.93
DP 92	12	6	6	19	1.22
TK 98	12	6	6	13	3.72
DP 96	11	4	7	13	3.02
GD 91	11	8	3	11	1.95
GD 94	11	6	5	11	1.57
DP 91	10	6	4	16	1.19
MB 97	10	8	2	9	8.19
SK 91	10	5	5	13	1.96
SR 91	10	5	5	12	0.37
SR 92	10	5	5	13	1.30
TK 97	10	8	2	11	8.93
TK 96	9	7	2	13	3.20
BM 98	8	3	5	8	1.32
MB 92	8	4	4	13	2.51
BM 00	6	4	2	17	3.15
MB 91	6	2	4	13	0.71
SH 96	4	2	2	10	1.02

Fig. 1. Regurgitation (1 = yes, 0 = no) by (**a**) dominant and (**b**) subordinate individuals with increasing pack size. Shaded region represents 95% confidence intervals.

insight into these mechanisms. Our results show that for wild dogs, pack size, status, and age influence an individual's contribution to pup rearing. Specifically, in larger packs, subordinate individuals were more likely to regurgitate for pups compared to smaller packs where dominant individuals were more likely to regurgitate. With regard to frequency of regurgitation, in larger packs, yearlings regurgitated more frequently, compared to smaller packs where adults regurgitated more frequently.

The social niche specialisation hypothesis (Bergmüller & Taborsky, 2007; Bergmüller, Schürch & Hamilton, 2010) suggests that consistent individual differences in behaviour will be favoured where there is within-group conflict over limited resources, such as food or breeding opportunities, and there are fitness benefits to niche specialisation as it reduces this conflict. Within cooperatively breeding species, such as the wild dog, there is potential for within-group conflict over breeding opportunities, and social niches (*i.e.* breeder, non-breeder status) alleviate such conflict. Breeding individuals will incur greater costs when also contributing to pup provisioning, as they also carry the cost of dominance and reproduction (Creel *et al.*, 1997; Creel, Creel & Monfort, 1998; Young, 2005; Hodge, 2007). However, in larger wild dog packs, a higher degree of labour division means that pup provisioning can be shared amongst many group members, alleviating breeders of the burden. Larger packs are also able

Table 2. The nine candidate models used to investigate factors affecting whether an individual regurgitated. Top model indicated in bold where ΔAICc ≤ 2 following (Burnham & Anderson, 1998). Status:Age was not included as no yearlings were dominant.

| Rank	Form of regression	d.f.	loglikelihood	AICc	ΔACc	w_i
1	**Status + Pack size + Status:Pack size**	**5**	**−1797.06**	**3604.14**	**0.00**	**1.00**
2	Sex + Pack size + Sex:Pack size	5	−1805.47	3620.96	16.82	0.00
3	Age + Pack size + Age:Pack size	5	−1807.39	3624.80	20.66	0.00
4	Pack size	3	−1811.17	3628.35	24.20	0.00
5	Status + Sex + Status:Sex	5	−1829.19	3668.39	64.25	0.00
6	Status	3	−1837.98	3681.98	77.83	0.00
7	Sex + Age + Sex:Age	5	−1841.57	3693.15	89.01	0.00
8	Sex	3	−1857.28	3720.57	116.42	0.00
9	Age	3	−1863.72	3733.44	129.30	0.00
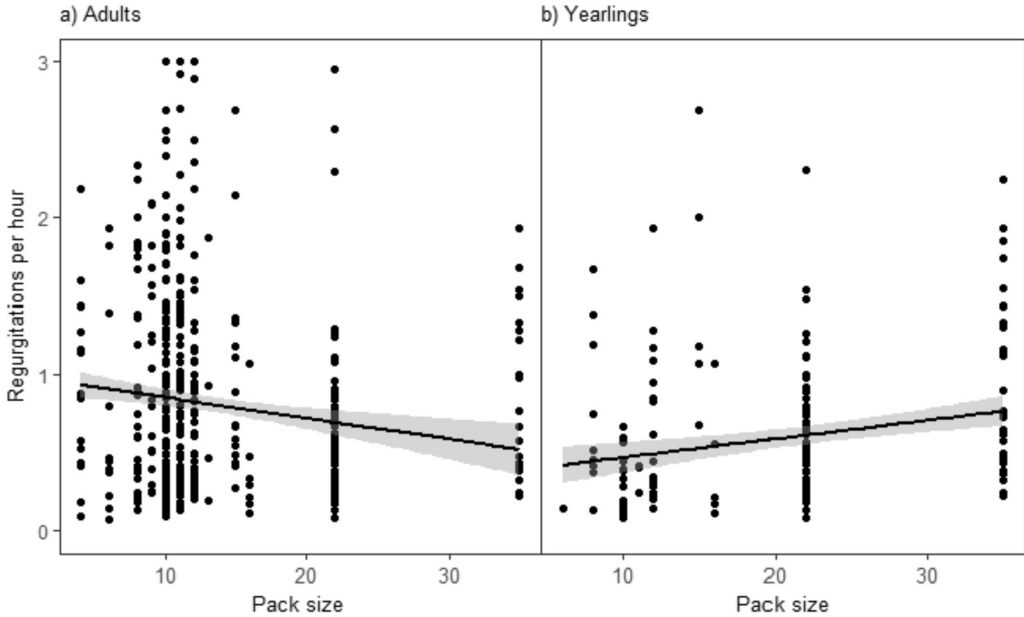
Fig. 2. The number of regurgitations per hour by (**a**) adults and (**b**) yearlings with increasing pack size. Shaded region represents 95% confidence intervals.

to hunt larger prey (Pole, Gordon, Gorman & MacAskill, 2004), have greater hunting success (Creel & Creel, 2002), choose optimal den sites (Davies *et al.*, 2016), and have greater breeding success both in terms of number of pups emerging from the den at three weeks of age as well as number of pups successfully reared to independence (Creel *et al.*, 1998; Buettner, Davies-Mostert, du Toit & Mills, 2007). Reduced costs of provisioning in larger packs may enable pack members to devote more energy to other essential aspects of pack survival, such as pup guarding and territory defence. This further emphasizes the importance of group size for cooperatively breeding species.

The need for a minimum number of helpers to provide for young creates an inverse density dependence that predisposes small wild dog packs to extinction (Courchamp, Rasmussen & Macdonald, 2002). Similar arguments have been evoked to explain the increased survival of young with increasing group size in other cooperatively breeding mammals, such as Ethiopian wolves, *Canis simensis* (Sillero-Zubiri, 1994).

Our results also show that, in larger packs, subordinate individuals are more likely to regurgitate to pups than dominant individuals. Breeding individuals (*i.e.* dominant) experience greater costs by provisioning than non-breeders, as they

Table 3. The nine candidate models used to investigate factors affecting the rate of regurgitation. Top model indicated in bold where ∆AIC*c* ≤ 2 following (Burnham & Anderson, 1998). Status:Age was not included as no yearlings were dominant.

Rank	Form of regression	d.f.	loglikelihood	AICc	∆AICc	w_i
1	**Age + Pack size + Age:Pack size**	**5**	**−2257.43**	**4524.92**	**0.00**	**0.70**
2	Sex + Age + Sex:Age	5	−2258.70	4527.46	2.55	0.20
3	Status + Sex + Status:Sex	5	−2259.57	4529.20	4.29	0.08
4	Age	3	−2263.03	4532.09	7.17	0.02
5	Sex	3	−2266.78	4539.58	14.67	0.00
6	Status	3	−2267.94	4541.91	16.99	0.00
7	Sex + Pack size + Sex:Pack size	5	−2266.17	4542.40	17.49	0.00
8	Status + Pack size + Status:Pack size	5	−2266.32	4542.70	17.78	0.00
9	Pack size	3	−2270.87	4547.76	22.85	0.00

would need to divert resources away from reproduction (Clutton-Brock *et al.*, 2002). This is particularly relevant for females, who carry costs of gestation and lactation (Clutton-Brock, Albon & Guinness, 1989). Moreover, dominant wild dogs chase other predators and protect the den more often than subordinate individuals (Malcolm & Marten, 1982). As dominant wild dogs carry costs of status and reproduction (Malcolm & Marten, 1982; Clutton-Brock *et al.*, 1989; Creel *et al.*, 1997), this helping behaviour from subordinate individuals in large packs alleviates the additional cost of provisioning from dominant individuals. Dominant meerkats also contribute to pup provisioning less than other adults (subordinate individuals) (Clutton-Brock *et al.*, 2004), and our results support previous findings of increased pup survival in larger wild dog packs (McNutt & Silk, 2008; Creel & Creel, 2015).

Within subordinate wild dogs, yearlings regurgitated more frequently per period than adults in large packs. In species where foraging success increases with age, individual contributions to rearing young increases accordingly (Brotherton *et al.*, 2001; Koenig & Walters, 2011). In wild dogs, however, pack members contribute equally to hunting from the time they are 12 months old (*i.e.* from the time they become yearlings). Thus, all yearlings and adults have the potential to achieve equal foraging success (McNutt, 1996). Further, yearlings have priority access to food at kills (Reich, 1981; Malcolm & Marten, 1982; Creel *et al.*, 1995). As older individuals carry the cost of lower feeding rank, the helping behaviour from yearlings in large packs alleviates the additional cost of provisioning from adults.

Contrastingly, in smaller packs, dominant individuals are more likely to regurgitate. A similar pattern is observed in meerkats where, although dominant meerkats contribute less than subordinate individuals, their provisioning increases when group size decreases (Clutton-Brock *et al.*, 2004). Smaller wild dog packs have lower hunting success (Creel & Creel, 2002) meaning lower food availability in comparison to larger packs. This can lead to a 'poverty trap' as described by Rasmussen *et al.* (2008), where smaller packs are less successful hunters, produce smaller litters, and are subsequently more vulnerable to extinction. When food availability is low, individuals with the highest investment, *i.e.* the parents of the offspring, are not likely to alter their provisioning as non-parents may. This has been shown in banded

mongooses, *Mungos mungos*, where breeding females and adult males maintained their pup provisioning as food supply decreased, in comparison to non-breeding females and juvenile males who helped less when food was scarce (Nichols *et al.*, 2012). Graf *et al.* (2006) also highlight the importance of group size in wild dogs, where a small pack of wild dogs accepted and integrated an unrelated female and her pups. This shows that, although immigration is rare (Frame *et al.*, 1979; McNutt, 1996), group augmentation is acceptable when the number of group members is low, and the pack could benefit from more helpers. Additionally, we found that adult wild dogs regurgitated more frequently per period than yearlings. When food availability is low, adult wild dogs continue to regurgitate for pups, whereas yearlings do not (Malcolm & Marten, 1982). Malcolm and Marten (1982) further note that adult helpers appear to make substantial contributions to pup survival, whereas the effect of yearlings on pup survival depends on food availability. This is likely due to the growth still occurring for yearling wild dogs, who require food to develop body size and are thus less likely to give up scarce resources than adults.

We found that sex did not affect whether an individual would regurgitate to pups or the frequency of regurgitations. Sex differences in helping behaviour are a result of sex differences in philopatry (Clutton-Brock *et al.*, 2002). No sex bias was observed in the KNP wild dog population (Maddock & Mills, 1994; Marnewick *et al.*, 2014), with both sexes contributing to hunting and pup guarding (Malcolm & Marten, 1982). Although male wild dogs have been described previously as being more philopatric in a male biased population (McNutt, 1996), we suggest that this is not a factor for wild dogs in a population with no sex bias.

Differing ecological conditions can cause variation in the degree of helping behaviour from individuals (Macdonald, 1983; Gusset & Macdonald, 2010). The reliance on helpers can be less pronounced when inter-specific competition is low (*e.g.* Somers *et al.*, 2008). As such, our results may be specific to the KNP. However, as we utilised data spanning 9 years and thus some fluctuating ecological conditions, we are confident that our results provide insight into pup provisioning by wild dogs.

Helping behaviour in a number of group-living species can be explained by high levels of intra-group relatedness (Clutton-Brock, 2002;

Arnold & Owens, 2005). Relatedness in wild dog packs is high (Girman, Mills, Geffen & Wayne, 1997), and anecdotal evidence that unrelated individuals are less likely to provision pups does exist (Potgieter, O'Riain & Davies-Mostert, 2015). Unfortunately, we were unable to record relatedness between individuals in our study and, therefore, could not assess its influence on provisioning. Future studies should further investigate the role that relatedness plays in the provisioning of pups in wild dogs. Interestingly, behavioural type (or personality) explained the variation in helping behaviour of the cooperatively breeding cichlid, *Neolamprologus pulcher*, rather than relatedness (Le Vin, Mablea, Taborsky, Heg & Arnold, 2011). Kinship did not affect the frequency of provisioning by meerkat helpers (Clutton-Brock *et al.*, 2001), and no relationship between relatedness and provisioning was observed in a Serengeti population of wild dogs (Malcolm & Marten, 1982). Further, pack augmentation with unrelated individuals has been recorded (Graf *et al.*, 2006). Thus, perhaps the level of relatedness is not such a heavily influencing factor but, again, this requires further study in wild dogs.

In conclusion, our results provide key insight into the factors driving pup provisioning in wild dogs. By fully understanding the social structure leading to pup provisioning, we can further understand population dynamics of wild dogs as a whole. For example, our results show that pack size has a significant effect on pup provisioning, where smaller packs require help from individuals carrying other costs (*i.e.* dominant individuals and adults) in comparison to larger packs where these individuals are not required to provision due to a division of labour. This gives us key insight into how large packs outcompete smaller packs in multiple aspects of wild dog ecology. Moreover, with increasing pack size being a fundamental factor that positively influences hunting success (Creel & Creel, 2002), optimal den site selection (Davies *et al.*, 2016), breeding success (Creel & Creel, 2002), juvenile survival (Buettner *et al.*, 2007) and avoidance of threats (Courchamp & Macdonald, 2001), we suggest that this is a key driver in wild dog population ecology. With the endangered status of wild dogs, understanding factors that limit and promote the population is of key importance to researchers and managers alike. Our results support the notion that needing more helpers to provide for more offspring may have contributed to the evolutionary consequence of an inverse density dependence that has been reported in other cooperatively breeding carnivores, such as dwarf mongooses, *Helogale parvula* (Creel & Creel, 1991) and meerkats (Clutton-Brock *et al.*, 1999).

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REFERENCES

Arnold, K.E. & Owens, I.P.F. (1999). Cooperative breeding in birds: the role of ecology. *Behavioral Ecology*, 10, 465–471.

Arnold, K.E., Owens, I.P.F. & Goldizen, A.W. (2005). Division of labour within cooperatively breeding groups. *Behaviour*, 142, 1577–1590.

Bartoñ, K. (2013). MuMIn: Multi-model inference. R package version 1.9. 13. *The Comprehensive R Archive Network (CRAN)*, *Vienna, Austria*.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G. & Green, P. (2014). Package 'lme4'. *R Foundation for Statistical Computing*, *Vienna*, *12*.

Bergmüller, R., Johnstone, R.A., Russell, A.F. & Bshary, R. (2007). Integrating cooperative breeding into theoretical concepts of cooperation. *Behavioural Processes*, 76, 61–72.

Bergmüller, R., Schürch, R. & Hamilton, I.M. (2010). Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. *Philosophical Transactions of the Royal Society B*, 365, 2751–2764.
DOI: 10.1098/rstb.2010.0124

Bergmüller, R. & Taborsky, M. (2007). Adaptive behavioural syndromes due to strategic niche specialization. *BMC Ecology*, 7, 7–12.

Brotherton, P.N.M., Clutton-Brock, T.H., O'riain, M.J., Gaynor, D., Sharpe, L., Kansky, R. & McIlrath, G.M. (2001). Offspring food allocation by parents and helpers in a cooperative mammal. *Behavioral Ecology*, 12, 590–599.

Buettner, U.K., Davies-Mostert, H.T., du Toit, J.T. & Mills, M.G.L. (2007). Factors affecting juvenile survival in African wild dogs (*Lycaon pictus*) in Kruger National Park, South Africa. *Journal of Zoology*, 272, 10–19.
DOI: 10.1111/j.1469-7998.2006.00240.x

Clutton-Brock, T.H. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, 296, 69–72.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature*, 337, 260–262.

Clutton-Brock, T.H., Brotherton, P.N.M., O'riain, M.J., Griffin, A.S., Gaynor, D., Kansky, R., Sharpe, L. & McIlrath, G.M. (2001). Contributions to cooperative rearing in meerkats. *Animal Behaviour*, 61, 705–710.

Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D. & Brotherton, P.N.M. (1999). Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology,* 68, 672–683.
DOI: 10.1046/j.1365-2656.1999.00317.x

Clutton-Brock, T.H., Russell, A.F. & Sharpe, L.L. (2004). Behavioural tactics of breeders in cooperative meerkats. *Animal Behaviour*, 68, 1029–1040.

Clutton-Brock, T.H., Russell, A.F., Sharpe, L.L., Young, A.J., Balmforth, Z. & McIlrath, G.M. (2002). Evolution and development of sex differences in cooperative behavior in meerkats. *Science*, 297, 253–256.

Core Team, R. (2008). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Courchamp, F. & Macdonald, D.W. (2001). Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Animal Conservation*, 4, 169–174.

Courchamp, F., Rasmussen, G.S.A. & Macdonald, D.W. (2002). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology*, 13, 20–27.

Creel, S. & Creel, N.M. (2002). *The African wild dog: behavior, ecology, and conservation*. Princeton, U.S.A.: Princeton University Press.

Creel, S. & Creel, N.M. (2015). Opposing effects of group size on reproduction and survival in African wild dogs. *Behavioral Ecology*, 26(5), 1414–1422.
DOI: 10.1093/beheco/arv100

Creel, S., Creel, N.M., Matovelo, J.A., Mtambo, M.M.A., Batamuzi, E.K. & Cooper, J.E. (1995). The effects of anthrax on endangered African wild dogs (*Lycaon pictus*). *Journal of Zoology* 236, 199–209.

Creel, S., Creel, N.M., Mills, M.G.L. & Monfort, S.L. (1997). Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. *Behavioural Ecology*, 8, 298–306.

Creel, S., Creel, N.M. & Monfort, S.L. (1998). Birth order, estrogens and sex-ratio adaptation in African wild dogs (*Lycaon pictus*). *Animal Reproduction Science*, 53, 315–320.

Creel, S.R. & Creel, N.M. (1991). Energetics, reproductive suppression and obligate communal breeding strategies in carnivores. *Behavioral Ecology and Sociobiology*, 28, 263–270.

Davies-Mostert, H.T., Mills, M.G.L. & Macdonald, D.W. (2015). The demography and dynamics of an expanding, managed African wild dog metapopulation. *African Journal of Wildlife Research*, 45, 258–273.

Davies, A.B., Marneweck, D.G., Druce, D.J. & Asner, G.P. (2016). Den site selection, pack composition, and reproductive success in endangered African wild dogs. *Behavioral Ecology*, 27, 1869–1879.
DOI: 10.1093/beheco/arw124

Emlen, S.T. & Wrege, P.H. (1991). Breeding biology of white-fronted bee-eaters at Nakuru: the influence of helpers on breeder fitness. *The Journal of Animal Ecology*, 60, 309–326.

Frame, L.H., Malcolm, J.R., Frame, G.W. & Lawick, H. (1979). Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania 1967–1978. *Ethology*, 50, 225–249.

Gilchrist, J.S. (2004). Pup escorting in the communal breeding banded mongoose: behavior, benefits, and maintenance. *Behavioral Ecology*, 15, 952–960.
DOI: 10.1093/beheco/arh071

Girman, D.J., Mills, M.G.L., Geffen, E. & Wayne, R.K. (1997). A molecular genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycaon pictus*). *Behavioural Ecology and Sociobiology*, 40, 187–198.

Graf, J.A., Gusset, M., Reid, C., van Rensburg, S.J., Slotow, R. & Somers, M.J. (2006). Evolutionary ecology meets wildlife management: artificial group augmentation in the re-introduction of endangered African wild dogs (*Lycaon pictus*). *Animal Conservation*, 9(4), 398–403.
DOI: 10.1111/j.1469-1795.2006.00048.x

Griffin, A.S. & West, S.A. (2003). Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science*, 302, 634–636.

Gusset, M. & Macdonald, D.W. (2010). Group size effects in cooperatively breeding African wild dogs. *Animal Behaviour*, 79, 425–428.
DOI: 10.1016/j.anbehav.2009.11.021

Hamilton, W.D. (1964). The genetical evolution of social behaviour. II. *Journal of theoretical biology*, 7, 17–52.

Harrington, F.H. & Mech, L.D. (1982). Patterns of homesite attendance in two Minnesota wolf packs. In F.H. Harrington & P.C. Paupet (Eds), *Wolves: behaviour, ecology conservation*. Park Ridge, NJ: Noyes Publications.

Hatchwell, B.J., Gullett, P.R. & Adams, M.J. (2014). Helping in cooperatively breeding long-tailed tits: a test of Hamilton's rule. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 369, 20130565.

Hodge, S.J. (2005). Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. *Proceedings of the Royal Society of London B: Biological Sciences*, 272, 2479–2484.
DOI: 10.1098/rspb.2005.3255

Hodge, S.J. (2007). Counting the costs: the evolution of male-biased care in the cooperatively breeding banded mongoose. *Animal Behaviour*, 74, 911–919.

Hrdy, S.B. (1976). The care and exploitation of nonhuman primate infants by conspecifics other than the mother. In J.S. Rosenblatt, R.A. Hinde, E. Shaw & C. Beer (Eds), *Advances in the study of behavior* (Vol. 6) (pp. 251–383). New York, U.S.A.: Academic Press.

Koenig, W.D. & Walters, E.L. (2011). Age-related provisioning behaviour in the cooperatively breeding acorn woodpecker: testing the skills and the pay-to-stay hypotheses. *Animal Behaviour*, 82, 437–444.

König, B. (1997). Cooperative care of young in mammals. *Naturwissenschaften*, 84, 95–104.

Le Vin, A. L., Mablea, B.K., Taborsky, M., Heg, D. &

African Journal of Wildlife Research Vol. 48, No. 1, 2018

Arnold, K.E. (2011). Individual variation in helping in a cooperative breeder: relatedness versus behavioural type. *Animal Behaviour*, 82, 467–477.

Lukas, D. & Clutton-Brock, T.H. (2012). Cooperative breeding and monogamy in mammalian societies. *Proceedings of the Royal Society of London B: Biological Sciences*, 279, 2151–2156.

Macdonald, D.W. (1983). The ecology of carnivore social behaviour. *Nature*, 301, 379–384.

Maddock, A.H. & Mills, M.G.L. (1994). Population characteristics of African wild dogs *Lycaon pictus* in the eastern Transvaal lowveld, South Africa, as revealed through photographic records. *Biological Conservation*, 67, 57–62.

Malcolm, J.R. & Marten, K. (1982). Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behavioral Ecology and Sociobiology*, 10, 1–13.

Marnewick, K., Ferreira, S.M., Grange, S., Watermeyer, J., Maputla, N. & Davies-Mostert, H.T. (2014). Evaluating the status of and African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* through tourist-based photographic surveys in the Kruger National Park. *PLOS ONE*, 9, e86265. DOI: 10.1371/journal.pone.0086265

McNutt, J.W. (1996). Sex-biased dispersal in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, 52, 1067–1077.

McNutt, J.W. & Silk, J.B. (2008). Pup production, sex ratios, and survivorship in African wild dogs, *Lycaon pictus*. *Behavioral Ecology and Sociobiology*, 62, 1061–1067. DOI: 10.1007/s00265-007-0533-9

Mills, M.G.L. & Gorman, M.L. (1997). Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology*, 11, 1397–1406.

Moehlman, P.D. (1979). Jackal helpers and pup survival. *Nature*, 277, 382–383.

Moehlman, P.D. & Hofer, H. (1997). Cooperative breeding, reproductive suppression, and body mass in canids. In N.G. Solomon & J.A. French (Eds), *Cooperative breeding in mammals* (pp. 76–128). Cambridge, U.K.: Cambridge University Press.

Nichols, H.J., Amos, W., Bell, M.B.V., Mwanguhya, F., Kyabulima, S. & Cant, M.A. (2012). Food availability shapes patterns of helping effort in a cooperative mongoose. *Animal Behaviour*, 83 1377–1385.

Nicolson, N.A. (1987). Infants, mothers, and other females. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker (Eds), *Primate societies* (pp. 330–342). Chicago, U.S.A.: University of Chicago Press.

Nowak, M.A., Tarnita, C.E. & Wilson, E.O. (2010). The evolution of eusociality. *Nature*, 466, 1057–1062.

Pole, A., Gordon, I.J., Gorman, M.L. & MacAskill, M. (2004). Prey selection by African wild dogs (*Lycaon pictus*) in southern Zimbabwe. *Journal of Zoology*, 262, 207–215. DOI: 10.1017/s0952836903004576

Potgieter, K.R., O'Riain, MJ. & Davies-Mostert, H.T. (2015). Behavioural cues can be used to predict the outcome of artificial pack formation in African wild dogs (*Lycaon pictus*). *African Journal of Wildlife Research*, 45, 215–222. DOI: 10.3957/056.045.0215

Rasmussen, G.S., Gusset, M., Courchamp, F. & Macdonald, D.W. (2008). Achilles' heel of sociality revealed by energetic poverty trap in cursorial hunters. *The American Naturalist*, 172(4), 508–518. DOI: 10.1086/590965

Reich, A. (1981). *The behaviour and ecology of the African wild dog (Lycaon pictus) in the Kruger National Park.* (Ph.D. thesis). New Haven, U.S.A.: Yale University.

Shellman-Reeve, J.S. (1997). The evolution of social behaviour. In J.C. Choe & B.J. Crepsi (Eds), *The evolution of social behaviour in Insects and Arachnids.* (pp. 52–93). Cambridge, U.K.: Cambridge University Press.

Sillero-Zubiri, C. (1994). *Behavioural ecology of the Ethiopian wolf, Canis simensis.* (Ph.D. thesis). Oxford, U.K.: University of Oxford,

Solomon, N.G. & French, J.A. (1997). *Cooperative breeding in mammals*. Cambridge, U.K.: Cambridge University Press.

Somers, M J., Graf, J.A., Szykman, M., Slotow, R. & Gusset, M. (2008). Dynamics of a small re-introduced population of wild dogs over 25 years: allee effects and the implications of sociality for endangered species' recovery. *Oecologia*, 158, 239–247.

Spiering, P.A., Somers, M.J., Maldonado, J.E., Wildt, D.E. & Gunther, M.S. (2009). Reproductive sharing and proximate factors mediating cooperative breeding in the African wild dog (*Lycaon pictus*). *Behavioral Ecology and Sociobiology*, 64, 583–592. DOI: 10.1007/s00265-009-0875-6

Wilson, E.O. (1971). *The insect societies*. Cambridge, U.K.: Belknap Press.

Woodroffe, R., McNutt, J.W. & Mills, M.G.L. (2004). African wild dog (*Lycaon pictus*) In C. Sillero-Zubiri, M. Hoffmann & D.W. Macdonald (Eds), *Canids: foxes, wolves, jackals, and dogs: status survey and conservation action plan* (pp. 174–182). Gland, Switzerland: IUCN

Young, A.J., Carlson, A.A. & Clutton-Brock, T. (2005). Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Animal Behaviour*, 70, 829–837.

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