



Original Article

# Opposing effects of group size on reproduction and survival in African wild dogs

Scott Creel and Nancy Marusha Creel

Department of Ecology, Montana State University, 302A Lewis Hall, Bozeman, MT 59717, USA

Received 10 February 2015; revised 18 May 2015; accepted 22 May 2015; Advance Access publication 1 July 2015.

For cooperative breeders, we hypothesize that the effects of group size on reproduction and survival might run in opposition if the benefits of grouping cannot be shared without cost. We tested this hypothesis by examining relationships between group size, survival, and reproduction in African wild dogs (*Lycaon pictus*), cooperative hunters with highly cohesive packs within which reproduction is monopolized by the dominant male and female. The production and survival of pups are known to increase with increasing pack size, but the effect of pack size on adult survival has not been examined previously. Data from 366 individuals over a period of 6 years showed that the survival of adults decreased with increasing pack size, with a 25% difference between the largest and smallest packs after controlling for the effects of age, sex, social status, year of study, and pack identity. Several tests confirmed that undetected dispersal is unlikely to have produced this pattern. These results suggest that cooperative breeding in wild dogs cannot be fully explained by mutual direct benefit, thus reinforcing the prior inference that kin selection plays an important role in the evolution of their cooperation. The results also weaken support for the hypothesis that wild dogs are extinction prone due to group-level Allee effects. More broadly, the relationship of effects of group size on survival and reproduction might be predicted by considering whether cooperation yields benefits that accrue to all group members (e.g., through cooperative vigilance) or benefits that must be apportioned to individuals (e.g., through cooperative hunting).

**Key words:** cooperative breeding, group size, survival.

## INTRODUCTION

### Cooperative breeding, cooperative hunting, and the effects of group size on fitness components

In cooperatively breeding species, adults provide care for the offspring of others by guarding them from predation, grooming them, feeding them, and even nursing them (Brown 1987; Koenig and Stacey 1990; Creel et al. 1991; Solomon and French 1997). Following Darwin's (1859) recognition that self-sacrificial behavior presents “a special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory” of evolution by natural selection, decades of research have considered the manner in which cooperative breeding can evolve through a combination of direct fitness benefits and kin selection (Hamilton 1963; Wilson 1975). Emlen (1997) summarized changes in the focus of this research, first from testing whether nonbreeding helpers truly contribute to the successful reproduction of others, thus creating a

positive correlation between group size and the reproductive success of breeders (Skutch 1935; Rowley 1957), to identifying the ecological and demographic conditions that promote nondispersal and helping behavior (Emlen 1982), to using reproductive skew models to test predictions from inclusive fitness theory about the allocation of reproduction among group members (Vehrencamp 1980, 1983; Keller and Reeve 1994; Magrath et al. 2004).

In studies of cooperative breeders, the effects of group size on survival have received considerably less attention than effects on reproduction, and many empirical studies (including our own: Creel et al. 2004) have examined the effects of group size on reproduction but not survival. For example, Solomon and French's (1997) *Cooperative Breeding in Mammals* has 47 index entries for reproduction and reproductive suppression, but none for survival or mortality. Kingma et al. (2014) recently noted that empirical tests of the effect of group size on survival remain relatively rare, and heuristic models of reproductive skew have made widely divergent assumptions about the ways that survival is affected by grouping and helping effort (Hårdling et al. 2003; Cant and Field 2005).

These issues are largely due to the difficulty in collecting adequate data on survival; it is well recognized that such data are

Address correspondence to S. Creel. E-mail: [screel@montana.edu](mailto:screel@montana.edu).

necessary to resolve the relative importance of direct selection and kin selection in the evolution of cooperative breeding. Where adult survival increases with increasing group size (e.g., splendid fairy wrens: Rowley and Russell 1990 and dwarf mongooses: Rood 1990), cooperative breeding might be favored through a combination of kin selection or by-product mutualism. This point was emphasized by Clutton-Brock (2002), who concluded that direct fitness benefits of group augmentation (e.g., improved survival) are common, so that “the direct benefits of helping to the helper’s own fitness have probably been underestimated” and “may be sufficient to maintain cooperative societies.” In contrast to cases in which group augmentation provides direct benefits to helpers, survival might also decrease with increasing group size. In this case, survival costs must be offset by other mechanisms, such as kin-selected benefits of alloparental care, delayed direct benefits through territorial inheritance, or avoiding the costs of dispersal (Emlen 1982; Waser and Jones 1983; Brown 1987). The possibility that grouping might carry survival costs has received relatively little attention, and empirical studies of the effects of group size on both survival and reproduction remain important to resolve the roles of kin selection and direct selection in the evolution of cooperative breeding (Abbot et al. 2011; Kingma et al. 2014).

Here, we test the effect of group size on the survival of African wild dogs for the first time and use the results to re-examine prior inferences about the selection pressures that have shaped cooperative breeding in wild dogs. In general, we hypothesize that:

- 1) The effects of group size on reproduction and adult survival are likely to both be positive (so that group augmentation plays an important role in the evolution of cooperative groups) when the primary fitness benefits of grouping can be shared without cost. For example, the evolution of cooperation is strongly tied to the benefits of cooperative vigilance in the social mongooses (dwarf mongooses: Rood 1978, 1986, 1990, meerkats: Clutton-Brock et al. 1999); all group members can respond to the warnings of a sentinel without constraining the responses of others (Rasa 1986; Koenig and Stacey 1990), so this benefit can be shared without cost.
- 2) The effects of group size on reproduction and survival are more likely to run in opposition (so that group augmentation is less likely to drive evolution of cooperation) when a fitness benefit is directed to or consumed by a single individual and consequently cannot be shared without cost. For example, cooperative hunting allows African wild dogs to hunt more effectively in larger groups (Creel S and Creel NM 1995, 2002), but even when an increase in group size improves foraging success (Creel S and Creel NM 1995, 2002), each kilogram of food can be consumed by only 1 individual, and the direct benefits of cooperative hunting must be apportioned to individuals. In this context, selection is likely to favor individuals who succeeded in obtaining unequally large share for themselves or their own offspring, potentially decoupling the effects of group size on reproduction and adult survival.

### Social organization in African wild dogs

Wild dogs (*Lycaon pictus*) are among Africa’s most highly endangered species. The only extant member of their genus, wild dogs diverged from the rest of the wolf-like canids 2–3 million years ago, prior to the radiation of wolves and jackals (*Canis* spp.) (Savage and Russell 1983; Girman et al. 1993). Wild dogs can subsist on a wide range of medium-sized ungulate prey (Creel S and Creel

NM 2002; Hayward and Kerley 2008) and were historically distributed across most of sub-Saharan Africa other than rainforest and desert, though apparently never at high densities (Smithers 1983; Fanshawe et al. 1991; Creel S and Creel NM 2002). Like most other large carnivores, wild dogs have been greatly reduced in number and distribution by human population expansion, habitat degradation and fragmentation, prey depletion, and direct persecution. In addition to these processes, which affect all of Africa’s large carnivores (e.g., Riggio et al. 2013), wild dogs are strongly limited by interspecific competition with lions (primarily via direct killing) and spotted hyenas (primarily via food loss) (Estes and Goddard 1967; Frame GW and Frame LH 1981; Fanshawe and Fitzgibbon 1993; Creel S and Creel NM 1996; Mills and Gorman 1997; Swanson et al. 2014). Even under the best of conditions, wild dogs rarely attain population densities above 17–20 adults/1000 km<sup>2</sup>, though densities as high as 40 adults/1000 km<sup>2</sup> have been observed (McNutt 1996; Creel S and Creel NM 1996, 2002). As a consequence, wild dog populations are small in all but the largest of protected areas. Though population estimates are of varying age and precision, it is thought that perhaps 6000–7000 wild dogs persist across the continent (Fanshawe et al. 1991; Creel S and Creel NM 2002; Woodroffe and Sillero Zubiri 2012). Most populations hold fewer than 100 adults, and genetic data suggest that most populations have an effective size smaller than 30 (Marsden et al. 2012). A few stronghold populations persist, particularly in the Selous and Ruaha–Rungwa–Kisigo ecosystems (Tanzania) and the Kavango–Zambezi Transfrontier Conservation Area (Zambia, Zimbabwe, Botswana, Angola, and Namibia’s Caprivi Strip).

Wild dogs live in highly cohesive packs that range from 2 to 27 adults and yearlings, though packs of 5–15 are most common (Creel S and Creel NM 2002). In the Selous Game Reserve of Tanzania (the site of this study), pack size averaged 8.9 adults (range 2–24 adults) (Creel S and Creel NM 2002). Wild dogs are highly cooperative hunters, and pack size is positively associated with mean prey mass, hunting success (kills per hunt), and the likelihood of making multiple kills, and negatively associated with chase distance (Creel S and Creel NM 1995, 2002). These effects combine to yield a positive relationship between pack size and per capita food intake per kilometer of hunting effort (Creel S and Creel NM 1995, 2002). Larger packs are also more successful at defending their kills from spotted hyenas (Fanshawe and Fitzgibbon 1993; Creel S and Creel NM 1996), and larger packs displace smaller packs in aggressive (sometimes fatal) encounters at the boundaries of adjacent territories (Creel S and Creel NM 2002).

There is an aggressively reinforced dominance hierarchy within each sex, and reproduction is largely monopolized by the dominant individual of each sex through a combination of the behavioral and endocrine consequences of subordination (Frame et al. 1979; Reich 1981; Malcolm and Marten 1982; Creel et al. 1997; Girman et al. 1997). Nonbreeding adult wild dogs routinely cooperate in feeding and guarding pups (Malcolm and Marten 1982), and prior research has shown that litter size increases with pack size in many populations, including Serengeti National Park, Moremi Game Reserve, Kruger National Park, Hwange National Park, and Selous Game Reserve (Reich 1981; Malcolm and Marten 1982; Courchamp et al. 2002; Creel S and Creel NM 2002; Creel et al. 2004). Pup survival also increases as pack size increases, largely because foraging success increases with pack size and pups are usually given first access to carcasses (Malcolm and Marten 1982). Together, these mechanisms allow large packs to raise substantially more offspring than small packs, as shown by extensive data from several populations

(Figure 1) (Creel et al. 2004). Reproductive success is very low in packs with fewer than 5 adults, and the energetic costs of reproduction are so high that unaided pairs very rarely raise offspring; cooperative breeding is almost completely obligate for wild dogs (Creel SR and Creel NM 1991).

Most nonbreeding subordinates of both sexes are related to at least one of the breeders in their pack (Girman et al. 1997). In the Selous population studied here (Creel S and Creel NM 2002), the probability that an individual's parent was still alive remained above 0.5 until age 3, and when a parent died, the probability that the replacement breeder came from within the pack was 0.43 for males and 0.27 for females. Even in cases with an immigrant replacement breeder, it was common for a set of relatives of the same sex to immigrate as a group, or for immigrants to join relatives from prior dispersal events, and microsatellite data showed that relatedness to same-sexed individuals was not detectably lower among individuals who had dispersed than among individuals who had not. As a result of these patterns, the coefficient of relatedness between subordinates and dominant breeders was high for young subordinates (0.34 for yearlings) and declined with age until dropping below 0.10 at age 6, a span of ages that comprises 87% of the population (Creel S and Creel NM 2002). With a strong effect of group size on reproductive success and appreciable relatedness between most helpers and breeders, subordinate wild dogs (particularly young subordinates) gain indirect fitness benefits by helping to raise collateral kin (Creel S and Creel NM 2002).

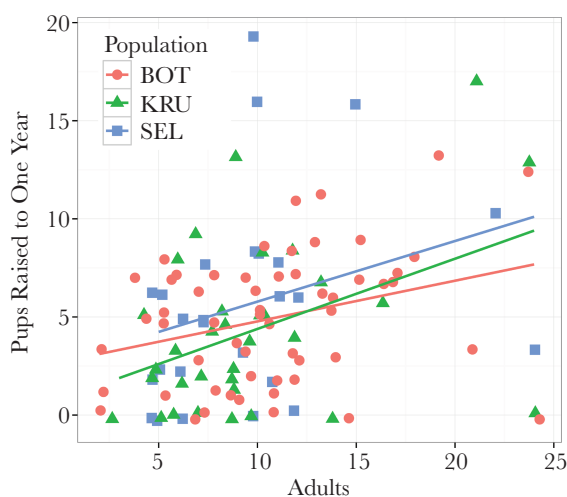
Nonetheless, all of the patterns described above might also be explained without kin selection because the risk of death during the process of dispersal is high for wild dogs. Mortality between emigration from one pack and immigration into another is 20% among males (95% confidence interval [CI]: 0.12–0.28), and 29% among females (95% CI: 0.19–0.37), and nondispersal allows subordinates to avoid this direct fitness cost (Creel S and Creel NM 2002). Nonbreeding adults might also gain direct fitness if their survival is better in larger packs, but surprisingly, no analysis to date has examined this possibility for any wild dog population. Because wild dogs have evolved one of the most cooperative societies described

among vertebrates, filling this information gap has the potential to improve our understanding of the relative strength of direct and indirect selection in social evolution (Darwin 1859; Hamilton 1963, 1964a, 1964b; Dawkins 1979; Abbot et al. 2011). Here, we use a long-term data set from close monitoring of wild dogs in the Selous Game Reserve to test the relationship between pack size and survival for adults (and other age classes), controlling for the effects of age, sex, and social status.

## METHODS

Demographic data come from 1068 annual records for 366 individually recognized wild dogs living in 11 packs on a 2600 km<sup>2</sup> site in Tanzania's Selous Game Reserve, from 1991 to 1996. Detailed methods have been described previously (Creel S and Creel NM 2002). Briefly, we radio-collared 2 adults in each pack using Telonics MOD-400 VHF radio collars, with permission from the Tanzania Commission on Science and Technology, the Tanzania Department of Wildlife, and the Project Manager of Selous Game Reserve, using a protocol approved by Purdue University's IACUC. These radio collars weighed less than 2% of body mass and did not detectably affect behavior, survival, or glucocorticoid levels (Creel S and Creel NM 2002). Using frequent observations ( $\bar{X}$  = 140 observation days/year), we recorded whether each individual was alive in each of the 6 years of study, by recording all daily observations of each individual and collapsing these sightings into 366 individual records of annual detection/nondetection. Study years began on 15 June to align with the onset of the annual denning period. To relate survival to pack size, it is necessary to standardize the manner in which pack size is measured: we recorded the size of each pack during a window centered on 15 June, including all individuals that we observed with each pack within several weeks of that date, provided that they had no known period of absence from the pack. The period over which pups must be fed and protected is the most energetically demanding portion of the year for wild dogs, so we reasoned that measuring pack size at the onset of pup rearing would provide the most power to detect relationships with survival.

Wild dogs have unusually distinct markings that allow reliable individual recognition, so that misidentification or the loss of marks does not complicate the estimation of survival rates. Radio-collared individuals were known to be alive on-site or had died on-site in 87 of 88 cases monitored for a full year, and only 21 (2%) of 1068 annual records were adults of unknown origin. Both of these results indicate that only 1–2% of individuals entered or exited the study population annually (Creel S and Creel NM 2002), confirming that such movements were too infrequent to have an appreciable effect on inferences about the factors affecting annual survival within the study population (also see Results for further tests of this assumption). With no loss of marks and near-complete geographic closure, generalized linear models with a binomial distribution and a logit link are suitable to test the association between survival and pack size. We first tested the suitability of this known-fate modeling approach by estimating annual detection probability ( $\hat{p}$ ) using the Cormack–Jolly–Seber (CJS) model, fit with the *RMark* 2.1.8 package (Laake 2014) in R (R Core Development Team 2008). This preliminary analysis confirmed that estimated annual detection ( $\hat{p}$ ) was close to 1, was estimated precisely (mean = 0.984, Agresti–Coull 95% binomial CI: 0.974–0.990), and was not detectably affected by age class, sex, social status, pack size, pack identity, or year. For wild dogs, it is logically expected that individual attributes should have little effect on  $\hat{p}$  because individuals of all ages, sexes,



**Figure 1**

Prior studies of wild dogs in several ecosystems, including the Selous GR (SEL) population studied here and well-studied populations in Moremi GR (BOT) and Kruger NP (KRU) have shown that the number of pups born and the number of pups raised to 1 year of age increase with pack size. From data reported in Creel et al. (2004).

and ranks were normally observed each time their pack was located (and typically followed for several days). Using *RMark*, Change in Akaike's Information Criterion ( $\Delta\text{AIC}$ ) values showed that a CJS model with a single mean probability of detection  $\hat{p}(\cdot)$  outperformed models in which  $\hat{p}$  was estimated as a function of age class, sex, social status, pack size, pack identity, or year. When AIC scores select the  $\hat{p}(\cdot)$  model for detection, known-fate approaches yield inferences about effects on survival that are identical to inferences from estimates of apparent survival ( $\phi$ ) from the CJS model.

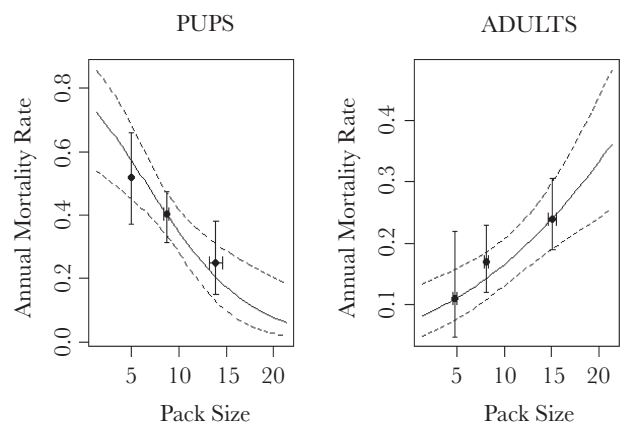
On the basis of these preliminary results, we report results from generalized linear mixed models, which allowed us to include random effects of individual identity and pack identity in a well-understood manner. Each individual contributed an average of 2.9 annual records to the data set and 10 of the 11 packs were observed in more than 1 year, so we included random effects on the intercept for pack identity, individual identity, and year. We examined effects on survival using mixed logistic regression models fit by maximum likelihood using the Laplace method, implemented with the *glmer()* function of the *lme4* package in R. To fit models with a nesting structure appropriate for the data, we tested whether the inclusion of random effects for individual identity or pack identity (or both) affected inferences, for the entire data set and for each subset of the data discussed below (subsets were examined to assess geographic population closure). From the perspective of model selection, models with a random effect of individual identity had Change in Akaike's Information Criterion, corrected for sample size ( $\Delta\text{AICc}$ ) scores at least 8.0 units worse than otherwise identical models that excluded the random effect, and models with a random effect of pack identity had  $\Delta\text{AICc}$  scores between 3.6 and 8.0 units worse than otherwise identical models that excluded random effects. For the question of focal interest, the exclusion or inclusion of these random effects had only minor effects on the estimated effect of pack size on survival and did not alter inferences. However, to be conservative in our inferences about effects of pack size, we report results from a generalized linear mixed model of survival (binomial distribution, logit link) that included random effects of pack identity and year, together with fixed effects of pack size, sex, age and social status (alpha/subordinate). Because the question of primary interest was to test the effect of group size on survival, we included covariates whose omission might bias the estimated effect of group size, rather than employing a model selection approach based on parsimony. Finally, because prior results for wild dogs show that age-related variation in survival is mainly due to differences between pups, yearling, and adults, with little variation among adult age classes (Creel S and Creel NM 2002; Creel et al. 2004), we included a quadratic effect of age.

Neither CJS nor known-fate models distinguish between death and permanent disappearance, so we used several strategies (in addition to confirming low rates of emigration by radio-collared animals and immigration by unknown adults, described above) to test whether undetected emigration was likely to affect the patterns we observed. First, we tested whether the effect of pack size on survival differed for subordinates and dominants, because dominant wild dogs rarely if ever disperse (Creel S and Creel NM 2002). Thus, a lack of interaction between alpha status and the effect of pack size on survival would suggest that undetected dispersal does not drive the observed effect. Second, we tested whether the effect of pack size on survival differed for animals in young age classes (1 and 2) that were most likely to disperse and older age classes that were less likely to disperse (Creel S and Creel NM 2002). If effects of group size on survival were equally strong (or stronger: see Results)

in the age classes with low rates of dispersal, this would again suggest that undetected dispersal does not underlie the observed effect. Finally, we tested for an interaction between the effect of pack size on survival and the year of study. If undetected dispersal was important, it should have been more common at the beginning of the study, so constant (or decreasing: see Results) mean survival through time would again suggest that undetected dispersal did not drive observed relationships between pack size and survival.

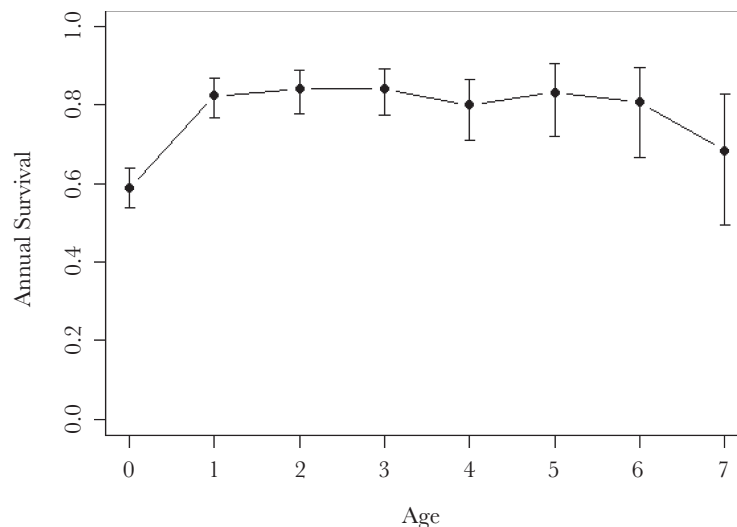
## RESULTS

The full generalized linear model of annual survival provided a substantially better fit to the data than a null model that included only random effects on the intercept of pack identity and year (deviance of full model = 646.4, deviance of null model = 992.9,  $\chi^2 = 346.5$ ,  $P \ll 0.001$ ). With regard to the effect of primary interest, the annual survival of adults (excluding pups and yearlings) declined significantly as pack size increased (Figure 2:  $b = -0.092 \pm 0.027$ ,  $P \ll 0.001$ ;  $b \pm$  standard error<sub>*b*</sub> with  $P$  value for  $z$  test of overlap of effect's 95% CI with 0, here and subsequently). This slope represents a 1.4% decline in annual survival per additional group member or a 25% difference in annual survival between the largest and smallest pack sizes observed in this study (Figure 2). Controlling for social status, sex, and age (and including random effects of year, individual identity, and pack identity) the decrease in adult survival with increasing pack size remained highly significant ( $b = -0.025 \pm 0.008$ ,  $P = 0.004$ ). Although dominant adults tended to survive better than subordinates, this effect was highly variable ( $b = 0.36 \pm 0.37$ ,  $P = 0.33$ ), and the effect of pack size on survival was similar for dominant and subordinate adults (interaction of pack size  $\times$  rank:  $b = 0.0073 \pm 0.032$ ,  $P = 0.82$ ). Pup survival was lower than that of adults (Figure 3), but subsequent survival was virtually constant among the adult age classes up to 8 years of age (Figure 3), which comprised more than 95% of the adult population (Creel S and Creel NM 2002; Creel et al. 2004). Consistent with these patterns, both the linear ( $b = 0.57 \pm 0.14$ ,  $P < 0.001$ ) and quadratic ( $b = 0.036 \pm 0.015$ ,  $P = 0.015$ ) effects of age on survival



**Figure 2**

Relationships between annual mortality rates and pack size in African wild dogs: pups (left) and adults (right). For each panel, the back-transformed generalized linear model and its 95% confidence limits are shown, together with the raw data shown as means ( $\pm 95$  confidence limits on both axes) for small ( $\leq 5$  adults), medium sized (6–10 adults), and large packs ( $> 10$  adults). Pack size was measured as the number of adults ( $\geq 2$  years old) present at the onset of the pup-rearing period. Yearlings were not included in the analysis of adult survival (see text for details).



**Figure 3**

The survival of pups was substantially lower than that of adults, whereas survival was relatively constant across older age classes.

were strong for the data set as a whole (including pups and yearlings), but there was no detectable relationship between survival and age for adults. Males tended to survive better than females, but the effect was highly variable with a CI that heavily overlapped 0 ( $b = 0.14 \pm 0.19$ ,  $P = 0.45$ ).

As has been reported previously for wild dogs in Selous and elsewhere (Creel et al. 2004), the survival of pups increased substantially with increasing pack size (Figure 2). The effect of pack size on the survival of yearlings was intermediate between the patterns observed for pups and adults, so that yearling survival showed no tendency to vary with pack size ( $b = 0.002 \pm 0.025$ ,  $P = 0.96$ ).

Several results suggest that undetected dispersal is not a likely explanation for the observed relationships between pack size and survival. First, the mean annual rate of detected dispersal was 21% (95% CI: 0.18–0.27) for males and 33% (95% CI: 0.28–0.41) for females (Creel S and Creel NM 2002, chapter 8). By itself, the high frequency of observed dispersal suggests that undetected dispersal was not common, because dispersal rates would have had to have been exceptionally high for much additional dispersal to have gone undetected. Second, although we directly observed 296 individuals during the process of dispersal (in 58 dispersing units), no dominant breeder was ever observed to disperse (Creel S and Creel NM 2002). Despite this clear difference in dispersal tendency, the effect of pack size on adult survival did not detectably differ for subordinates and dominants. In fact, the negative effect of pack size on adult survival tended to be stronger among dominants (2-way interaction:  $b = -0.53 \pm 0.42$ ,  $P = 0.70$ ). Third, prior analysis has shown that yearlings and 2 year olds disperse more frequently than older age classes (Creel S and Creel NM 2002). Thus, if undetected dispersal created a spurious relationship between pack size and survival, one would expect a stronger negative relationship (i.e., larger effect size) among the younger age classes, but when the data are restricted to 1 and 2 year olds, the observed relationship is weaker and tends to be positive ( $b = 0.026 \pm 0.020$ ,  $P = 0.208$ ). Finally, undetected dispersal should have been most common early in the study when fewer individuals were radio collared, so that an increase in estimated survival through time would support the hypothesis that undetected dispersal affected estimates of survival. Contrary to this hypothesis, estimated survival rates

decreased through time ( $b = -0.29 \pm 0.09$ ,  $P = 0.0015$ , treating year as an ordered fixed effect).

## DISCUSSION

For wild dogs in the Selous population, the production and survival of pups increase substantially in larger packs (this study, Creel S and Creel NM 2002; Creel et al. 2004), whereas the survival of adults decreases comparably. Large packs are more efficient and effective hunters (Creel S and Creel NM 1995), but the benefits of cooperation are not allocated evenly among individuals. Consequently, the grouping decisions of nonbreeding subordinates (which comprise 78% of the adult population) yield indirect fitness benefits (Malcolm and Marten 1982; Creel S and Creel NM 2002), but they also carry direct fitness costs in the form of lower annual survival. Although the mechanistic cause of this mortality is not well understood (because most deaths are not directly observed), we suggest that the process is ultimately driven by the risks and energetic demands of hunting to provide for a larger number of dependents (Creel S and Creel NM 2002). Alternatively, it is possible that social conflict is greater in larger groups, with consequences for adult survival.

Previous inclusive fitness calculations for wild dogs did not account for this direct survival cost, but nonetheless showed the indirect fitness benefits of nondispersal exceeded the direct benefits for subordinates younger than 5 years of age (Creel S and Creel NM 2002). By reducing net direct benefits, the direct costs detected here strengthen prior inferences about the relative importance of indirect fitness in shaping the grouping decisions of subordinate wild dogs. In cases where survival decreases as pack size increases, the immediate effect of “group augmentation” is to decrease the direct fitness of nonbreeders, though offsetting delayed direct benefits remain a possibility (Brown 1987; Creel 1990; Kingma et al. 2014). The role of kin selection does not emerge as clearly when the survival of nonbreeding adults increases with pack size, as has been found for dwarf mongooses, *Helogale parvula* (Rood 1990), meerkats, *Suricata suricatta* (Clutton-Brock 2002), bicolor wrens (*Campylorhynchus griseus*) (Rabenold 1990), Florida scrub jays (*Aphelocoma coerulescens*) (Woolfenden and Fitzpatrick 1990), acorn woodpeckers (*Melanerpes formicivorus*) (Koenig and Stacey 1990), and

Lake Tanganyika cichlids (*Neolamprologus pulcher*) (Heg et al. 2005). For species such as these, living in large groups provides direct fitness benefits to both breeders and helpers and may provide both direct and indirect benefits to helpers—though neither of these patterns constitutes a logical argument against inclusive fitness theory or the evolutionary role of indirect selection (Dawkins 1979; Reeve and Keller 2001).

Data from Selous also suggest that subordinate wild dogs tolerate nonbreeding status and direct survival costs to avoid the increased risk of death that accompanies dispersal (Emlen 1982; Kokko and Ekman 2002). All portions of the study site with suitable habitat and prey were occupied by resident packs, and many areas were overlapped by the ranges of more than 1 pack, with as many as 6 packs simultaneously ranging in some areas (Creel S and Creel NM 2002). With such habitat saturation, options for dispersing individuals are constrained, which promotes nondispersal, particularly in species for which dispersal carries a high risk of death. For Selous wild dogs, comparison of the sizes of immigrating and emigrating groups (Creel S and Creel NM 2002) suggest that mortality during the process of dispersal was 20% for males (95% CI: 0.12–0.28) and 29% for females (95% CI: 0.19–0.37). Nondispersal allows subordinates to avoid this fitness cost, which is closely comparable with the difference in adult survival rates for the smallest and largest packs. It is noteworthy that the mortality risk of dispersal is probably not an effect of the small size of dispersing groups, given the results presented here. Instead, factors such as aggression during attempts to immigrate or increased use of areas that are little used by resident packs, and thus increased exposure to predation by lions (Creel S and Creel NM 1996; Mills and Gorman 1997; Swanson et al. 2014) might underlie the costs of dispersal, as has been shown experimentally for other species (Heg et al. 2004).

Because pups do not hunt effectively and are given first access to carcasses (Malcolm and Marten 1982), it is perhaps not surprising that adult survival is compromised by heavy energetic investment in raising the large number of pups typical of large packs. It is interesting to note that yearlings are behaviorally intermediate between pups and adults in many ways. For example, yearlings sometimes hunt but sometimes trail behind the hunting pack. For this reason, prior analysis has excluded yearlings from consideration as part of a pack's effective size for hunting (Creel S and Creel NM 1995). Like pups, yearlings are sometimes given priority of access to carcasses, but sometimes they are not, particularly when the adults are not well fed. The lack of a detectable effect of pack size on the survival of yearlings (intermediate between the positive effect on pups and the negative effect on adults) is congruent with these intermediate patterns of behavior. All of these patterns are congruent with the broader hypothesis that the effects of group size on reproduction and survival are more likely to be uncorrelated or of opposite sign in cases where the benefits of grouping cannot be shared without cost.

CJS and known-fate models do not distinguish between undetected dispersal and death, and there is no complete solution to this problem, but several tests suggest that undetected permanent emigration was too rare to produce the observed effect of group size on survival. The estimated probability of annual detection was high ( $\bar{X}$  = 0.984, Agresti–Coull 95% CI: 0.974–0.990) for all classes of individuals in all packs and all years, and 98.9% of radio-collared individuals remained on the study site each year. In addition, patterns that would be expected if undetected dispersal was common were not seen in comparisons of breeders versus subordinates, young versus old adults, and early versus late years of

study. We suggest that undetected dispersal was uncommon simply because we directly observed a large proportion of dispersers during the process of dispersal (296 observations in 1068 individual-years). This high frequency of detected dispersal may have been due to the long duration of “floating” between packs, which was  $145 \pm 18$  days in this population (Creel S and Creel NM 2002). In addition, the study area was bounded to the south by the Rufiji River, which was a substantial barrier to wild dog movements. Although wild dogs are quite capable of crossing large rivers, they were rarely detected to do so on this site (only 2 such movements were detected in 6 years). The areas to the east and north of the study site were occupied by people engaged in rice farming, small-scale charcoal production, pit sawing, and the legal and illegal harvest of wildlife. Wild dogs are capable of movement through such landscapes, but were rarely observed to do so on this site (e.g., the home range boundaries of several packs were highly congruent with the boundary of the game reserve: see chapter 3 of Creel S and Creel NM 2002). Collectively, a broad range of tests and observations consistently suggest undetected dispersal had relatively little effect on the patterns of survival that we observed.

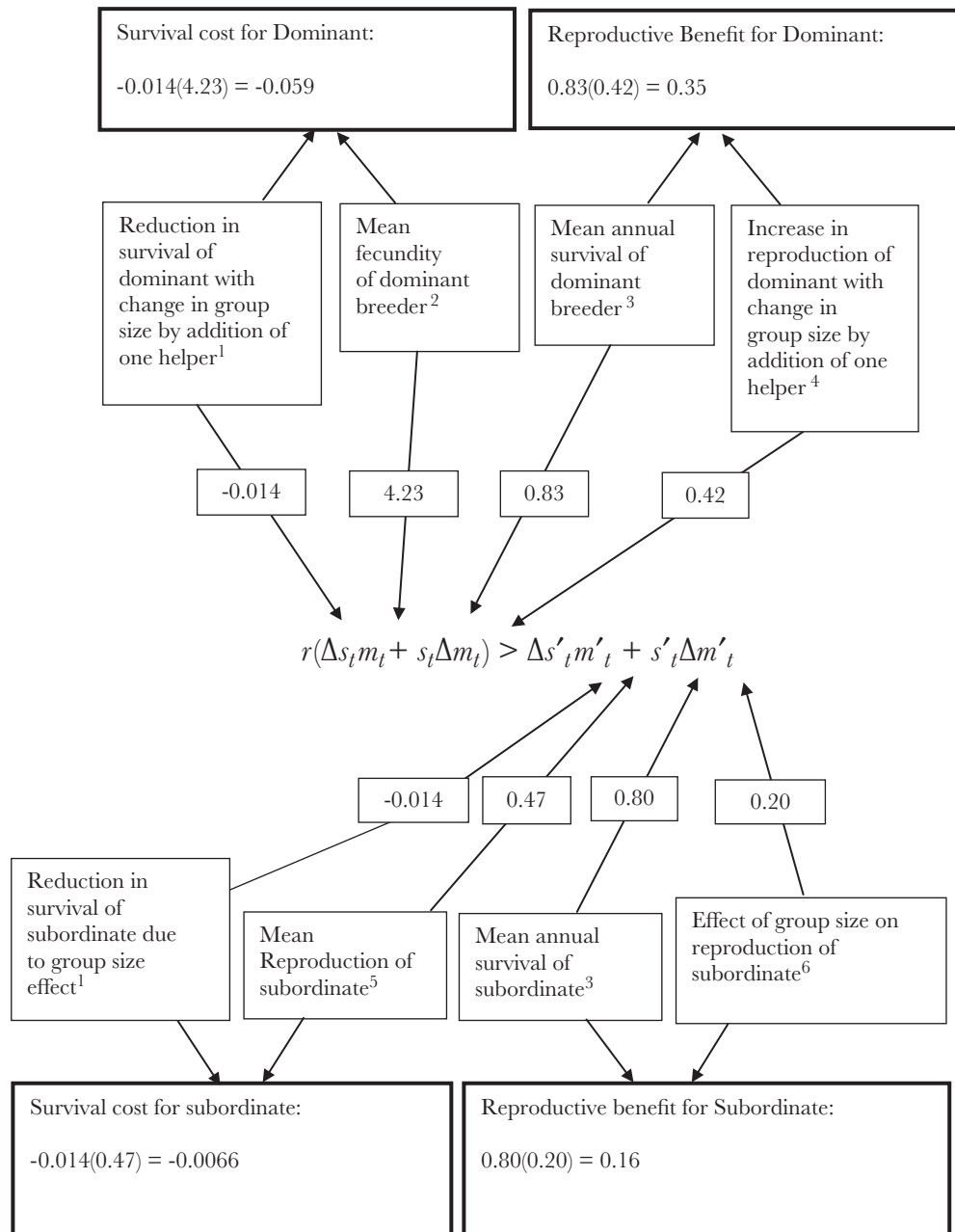
Some individuals were first observed as adults, and thus their age was estimated based on size, tooth wear, and pelage (particularly on the head). However, survival was quite constant within the adult age class (Figure 3) (Creel et al. 2004) so that our primary inference would only be affected by misclassification of juveniles as adults, an error that is not likely for wild dogs.

Given that the effects of group size on adult survival and reproduction run in opposition, it would clearly be of interest to quantify the effect group size on inclusive fitness, but our data are not sufficient for precise estimates of all the required parameters. Even if restricted to immediate effects, a full analysis of the effect of pack size on the inclusive fitness of helpers would require application of Equation 1 across a range of group sizes, with data partitioned by sex and age (and any other variables that affect demography or within-group relatedness).

$$r(\Delta s_t m_t + s_t \Delta m_t) > \Delta s'_t m'_t + s'_t \Delta m'_t \quad (1)$$

This equation is an extension of Hamilton's rule,  $rb > c$ , specifying the conditions under which natural selection favors interactions with a fitness cost  $c$  for the donor and fitness benefit  $b$  for the recipient, between a pair of individuals with relatedness  $r$ . In Equation 1, we have expressed  $b$  and  $c$  as effects on the survival ( $s_t$ ) and reproduction ( $m_t$ ) of the dominant breeder (recipient) and subordinate nonbreeder (donor). Parameters with a prime denote the subordinate whose decision to remain in the group is being evaluated. Values without a prime denote the group's dominant breeders.  $\Delta$  indicates the change in  $s_t$  or  $m_t$  when pack size changes by 1 adult. Subscript  $t$  denotes the current year (a generalization of this equation to consider subsequent years would require a structure parallel to the equation for reproductive value). Figure 4 illustrates a highly simplified numerical application of this equation, but the effects of changes in group size on inclusive fitness are not fully resolved for African wild dogs, as is true for most cooperative breeders.

Finally, reduced adult survival in larger packs is pertinent to the conservation of wild dogs. It has quite reasonably been suggested that “a pack in which membership drops below a critical size may be caught in a positive feedback loop: poor reproduction and low survival further reduce pack size, culminating in failure of the whole pack ... [creating] an Allee effect with consequences for the conservation of this species, and of other obligate cooperators” (Courchamp and Macdonald 2001). However, our results show that



**Figure 4**

A simplified application of Equation 1 to illustrate calculation of inclusive fitness effects of a change in group size that alters both survival and reproduction. This calculation identifies the coefficient of relatedness necessary for the net inclusive fitness effect of nondispersal to be positive ( $rb > c$ ) for a typical subordinate wild dog with all parameters/effects at their means. A more detailed application might compare net inclusive fitness effects for 2 alternative strategies ( $r_1 b_1 - c_1$  vs.  $r_2 b_2 - c_2$ ) and would ideally consider the functional form of relationships between group size, survival, and reproduction, with data partitioned among age–sex classes with differences in demographic rates and relatedness to group mates. <sup>1</sup>From generalized linear mixed model of Figure 2, mean slope of the regression of adult survival on group size, back-transformed to linear scale. <sup>2</sup>Mean fecundity = 4.7 offspring raised to independence, of which ~90% are produced by alphas (Creel S and Creel NM 2002). <sup>3</sup>Mean from generalized linear mixed model of Figure 2 with all other effects at their means. <sup>4</sup>From regression of pups raised to 1 year of age on pack size (Figure 1). In this illustration, we assume that reproduction in future years is not affected. <sup>5</sup>Mean fecundity = 4.7 offspring raised to independence, of which ~10% are produced by subordinates.  $4.7(0.1) = 0.47$ . For this illustration, we assume that future reproduction of subordinate is not affected by changes in current group size and that the individual whose decision is being examined will remain a subordinate (see Creel 1990 and Kingma et al. 2014 for more complex possibilities). <sup>6</sup>Assuming that the effect of group size on reproduction is the same for subordinates as for alphas (see note 4), which need not be true,  $0.47(0.42) = 0.20$ .

the effect of pack size on survival run in opposition to the postulated effect, with trade-offs between reproduction and adult survival, and between juvenile survival and adult survival. With such trade-offs, a reduction in pack size has both positive and negative effects on vital

rates for wild dogs: the net effect on population growth is difficult to assess because the costs and benefits of grouping differ for age classes with large differences in reproductive value. This point may be moot, however, because to our knowledge there is no evidence

for a relationship between pack size and population density within or between wild dog populations (Creel S and Creel NM 2002), as would be necessary for reductions in pack size to exacerbate the likelihood of local extinction through Allee effects. Instead, substantial evidence from many populations suggests that wild dogs are primarily vulnerable to extinction due to anthropogenic threats that affect all large African carnivores, including habitat loss, prey depletion, snaring, and poisoning (Woodroffe and Ginsberg 1999; Gusset et al. 2009; Becker et al. 2013), coupled with large area requirements (Woodroffe and Ginsberg 1998; Creel S and Creel NM 2002) and strong limiting effects of competition with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (Estes and Goddard 1967; Kruuk 1972; Fanshawe and Fitzgibbon 1993; Creel S and Creel NM 1996; Mills and Gorman 1997; Creel 2001).

## FUNDING

This work was supported by the Frankfurt Zoological Society (FZS 1112/90) and the National Science Foundation (IBN-9419452 and IBN-9712613).

We thank the Tanzania Wildlife Department, the Tanzania Commission for Science and Technology (COSTECH), and the Tanzania Wildlife Research Institute (TAWIRI) for the permission to work in the Selous Game Reserve. Our thanks to Dr M. Borner and the late Dr R. Faust of the Frankfurt Zoological Society and the staff of the Selous Game Reserve for support of the research in many ways. Special thanks to G. Bigurube, W. Minja, M. Kachui, and R. Nguwasi. Thanks also to 3 anonymous reviewers for their helpful comments on a prior version.

**Handling editor:** Madeleine Beckman

## REFERENCES

- Abbot P, Abe J, Alcock J, Alizon S, Alpedrinha JA, Andersson M, Andre JB, van Baalen M, Balloux F, Balshine S, et al. 2011. Inclusive fitness theory and eusociality. *Nature*. 471:E1–E4.
- Becker M, McRobb R, Watson F, Dröge E, Kanyembo B, Murdoch J, Kakumbi C. 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biol Conserv*. 158:26–36.
- Brown JL. 1987. Helping and communal breeding in birds. Princeton (NJ): Princeton University Press.
- Cant MA, Field J. 2005. Helping effort in a dominance hierarchy. *Behav Ecol*. 16:708–715.
- Clutton-Brock T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*. 296:69–72.
- Clutton-Brock TH, Gaynor D, McIlrath GM, MacColl ADC, Kinsky R, Chadwick P, Brotherton PNM. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J Anim Ecol*. 68:672–683.
- Courchamp F, Macdonald DW. 2001. Crucial importance of pack size in the African wild dog *Lycyaon pictus*. *Anim Conserv*. 4:169–174.
- Courchamp F, Rasmussen GSA, Macdonald DW. 2002. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycyaon pictus*. *Behav Ecol*. 13:20–27.
- Creel S. 1990. The future components of inclusive fitness: accounting for interactions between members of overlapping generations. *Anim Behav*. 40:127–134.
- Creel S. 2001. Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conserv Biol*. 15:271–274.
- Creel SR, Creel NM. 1991. Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behav Ecol Sociobiol*. 28:263–270.
- Creel S, Creel NM. 1995. Communal hunting and pack size in African wild dogs, *Lycyaon pictus*. *Anim Behav*. 50:1325–1339.
- Creel S, Creel NM. 1996. Limitation of African wild dogs by competition with larger carnivores. *Conserv Biol*. 10:526–538.
- Creel S, Creel NM. 2002. The African wild dog: behavior, ecology and conservation. Princeton (NJ): Princeton University Press.
- Creel S, Creel NM, Mills MG, Monfort SL. 1997. Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. *Behav Ecol*. 8:298–306.
- Creel S, Mills MGL, McNutt JW. 2004. Demography and population dynamics of African wild dogs in three critical populations. In: Macdonald DW, Sillero-Zubiri C, editors. *Biology and conservation of wild canids*. Oxford: Oxford University Press. p. 337–350.
- Creel SR, Monfort SL, Wildt DE, Waser PM. 1991. Spontaneous lactation is an adaptive result of pseudopregnancy. *Nature*. 351:660–662.
- Darwin C. 1859. *On the origin of species by means of natural selection*. London: John Murray.
- Dawkins R. 1979. Twelve misunderstandings of kin selection. *Z Tierpsychol*. 51:184–200.
- Emlen ST. 1982. The evolution of helping. I. An ecological constraints model. *Am Nat*. 119:29–39.
- Emlen ST. 1997. Predicting family dynamics in social vertebrates. In: Krebs JR, Davies NB, editors. *Behavioural ecology*. Oxford: Blackwell Scientific. p. 228–253.
- Estes RD, Goddard J. 1967. Prey selection and hunting behavior of the African wild dog. *J Wildl Manage*. 31:52–70.
- Fanshawe JH, Fitzgibbon CD. 1993. Factors influencing the hunting success of an African wild dog pack. *Anim Behav*. 45:479–490.
- Fanshawe JH, Frame LH, Ginsberg JR. 1991. The wild dog—Africa's vanishing carnivore. *Oryx*. 25:137–146.
- Frame GW, Frame LH. 1981. *Swift and enduring: cheetahs and wild dogs of the Serengeti*. New York: E.P. Dutton.
- Frame LH, Malcolm JR, Frame GW, Lawick H. 1979. Social organization of African wild dogs (*Lycyaon pictus*) on the Serengeti plains, Tanzania 1967–1978. *Z Tierpsychol*. 50:225–249.
- Girman DJ, Kat PW, Mills MG, Ginsberg JR, Borner M, Wilson V, Fanshawe JH, Fitzgibbon C, Lau LM, Wayne RK. 1993. Molecular genetic and morphological analyses of the African wild dog (*Lycyaon pictus*). *J Hered*. 84:450–459.
- Girman DJ, Wayne RK, Mills MGL, Geffen E. 1997. A molecular genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycyaon pictus*). *Behav Ecol Sociobiol*. 40:187–198.
- Gusset M, Swarner MJ, Mponwane L, Keletile K, McNutt JW. 2009. Human-wildlife conflict in northern Botswana: livestock predation by endangered African wild dog *Lycyaon pictus* and other carnivores. *Oryx*. 43:67–72.
- Hamilton WD. 1963. The evolution of altruistic behavior. *Am Nat*. 97:354–356.
- Hamilton WD. 1964a. The genetical evolution of social behaviour. I. *J Theor Biol*. 7:1–16.
- Hamilton WD. 1964b. The genetical evolution of social behaviour. II. *J Theor Biol*. 7:17–52.
- Hårdling R, Kokko H, Arnold KE. 2003. Dynamics of the caring family. *Am Nat*. 161:395–412.
- Hayward MW, Kerley GI. 2008. Prey preferences and dietary overlap amongst Africa's large predators. *S Afr J Wildl Res*. 38:93–108.
- Heg D, Bachar Z, Brouwer L, Taborsky M. 2004. Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proc Biol Sci*. 271:2367–2374.
- Heg D, Brouwer L, Bachar Z, Taborsky M. 2005. Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*. 142:1615–1641.
- Keller L, Reeve HK. 1994. Partitioning of reproduction in animal societies. *Trends Ecol Evol*. 9:98–102.
- Kingma SA, Santema P, Taborsky M, Komdeur J. 2014. Group augmentation and the evolution of cooperation. *Trends Ecol Evol*. 29:476–484.
- Koenig WD, Stacey PB. 1990. Acorn woodpeckers: group living and food storage under contrasting ecological conditions. In: Stacey PB, Koenig WD, editors. *Cooperative breeding in birds*. Cambridge: Cambridge University Press. p. 415–453.
- Kokko H, Ekman J. 2002. Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *Am Nat*. 160:468–484.
- Kruuk H. 1972. *The spotted hyena: a study of predation and social behavior*. Chicago: University of Chicago Press.
- Laake J. 2014. RMark: R code for MARK analysis. Vienna (Austria): The Comprehensive R Archive Network. Available from: <http://cran.r-project.org/>.
- Magrath RD, Heinsohn RG, Johnstone RA. 2004. Reproductive skew. In: Koenig W, Dickinson J, editors. *Ecology and evolution of*

- cooperative breeding in birds. Cambridge: Cambridge University Press. p. 157–176.
- Malcolm JR, Marten K. 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behav Ecol Sociobiol.* 10:1–13.
- Marsden CD, Woodroffe R, Mills MGL, McNutt JW, Creel S, Groom R, Masenga E, Cleaveland S, Kat P, Rasmussen G, et al. 2012. Spatial and temporal patterns of neutral and adaptive genetic variation in the endangered African wild dog (*Lycaon pictus*). *Mol Ecol.* 21:1379–1393.
- McNutt JW. 1996. Sociality and dispersal in African wild dogs, *Lycaon pictus* [PhD dissertation]. [Davis (CA)]: University of California.
- Mills MGL, Gorman ML. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv Biol.* 11:1397–1406.
- Mills MGL, Martyn LG. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv Biol.* 11:1397–1406.
- Rabenold KN. 1990. *Campylorhynchus* wrens: the ecology of delayed dispersal and cooperation in the Venezuelan savanna. In: Stacey PB, Koenig W, editors. *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge: Cambridge University Press. p. 157–196.
- Rasa OAE. 1986. Coordinated vigilance in dwarf mongoose family groups: the ‘watchman’s song’ hypothesis and the costs of guarding. *Z Tierpsychol.* 71:340–344.
- R Core Development Team. 2008. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Reeve HK, Keller L. 2001. Tests of reproductive-skew models in social insects. *Annu Rev Entomol.* 46:347–385.
- Reich A. 1981. The behavior and ecology of the African wild dog, *Lycaon pictus*, in the Kruger National Park [PhD dissertation]. [New Haven (CT)]: Yale University.
- Riggio J, Jacobson A, Dollar L, Bauer H, Becker M, Dickman A, Funston P, Groom R, Henschel P, de Iongh H, et al. 2013. The size of savannah Africa: a lion’s (*Panthera leo*) view. *Biodivers Conserv.* 22:17–35.
- Rood JP. 1978. Dwarf mongoose helpers at the den. *Z Tierpsychol.* 48:277–287.
- Rood JP. 1986. Ecology and social evolution in the mongooses. In: Rubenstein DI, Wrangham RW, editors. *Ecological aspects of social evolution*. Princeton (NJ): Princeton University Press. p. 131–152.
- Rood JP. 1990. Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Anim Behav.* 39:566–572.
- Rowley I. 1957. Co-operative feeding of young by superb blue wrens. *Emu.* 57:356–357.
- Rowley I, Russell E. 1990. Splendid fairy-wrens: demonstrating the importance of longevity. In Stacey PB, Koenig WD, editors. *Cooperative breeding in birds: long-term studies of ecology and behaviour*. Cambridge (UK): Cambridge University Press, p.3–29.
- Savage DE, Russell DE. 1983. *Mammalian paleofaunas of the world*. Menlo Park (CA): Benjamin/Cummings.
- Skutch AF. 1935. Helpers at the nest. *The Auk.* 52:257–273.
- Smithers RHN. 1983. *The mammals of the southern African subregion*. Pretoria (South Africa): University of Pretoria.
- Solomon NG, French JA. 1997. *Cooperative breeding in mammals*. Cambridge: Cambridge University Press.
- Swanson A, Caro T, Davies-Mostert H, Mills MG, Macdonald DW, Borner M, Masenga E, Packer C. 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions. *J Anim Ecol.* 83:1418–1427.
- Vehrencamp SL. 1983. A model for the evolution of despotic versus egalitarian societies. *Anim Behav.* 31:667–682.
- Vehrencamp S. 1980. To skew or not to skew? *Proceedings of the XVII International Ornithological Society*. Berlin (Germany): Deutsche Ornithologen-Gesellschaft. 869–874 pp.
- Waser PM, Jones WT. 1983. Natal philopatry among solitary mammals. *Q Rev Biol.* 58:355–390.
- Wilson EO. 1975. *Sociobiology: the new synthesis*. Cambridge (MA): Harvard University Press.
- Woodroffe R, Ginsberg JR. 1998. Edge effects and the extinction of populations inside protected areas. *Science.* 280:2126–2128.
- Woodroffe R, Ginsberg JR. 1999. Conserving the African wild dog *Lycaon pictus*. I. Diagnosing and treating causes of decline. *Oryx.* 33:132–142.
- Woodroffe R, Sillero-Zubiri C. 2012. *Lycaon pictus*. The IUCN Red List of Threatened Species. Version 2015.2. Available from: [www.iucnredlist.org](http://www.iucnredlist.org).
- Woollfenden GE, Fitzpatrick JW. 1990. Florida scrub jays: a synopsis after 18 years of study. In: Stacey PB, Koenig WD, editors. *Cooperative breeding in birds: long term studies of ecology and behavior*. Cambridge: Cambridge University Press. p. 24–266.