

Original Article

Direct fitness benefits of delayed dispersal in the cooperatively breeding red wolf (*Canis rufus*)

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The existence of cooperative breeding in diverse animal taxa has inspired much interest in what nonbreeding helpers gain from participation in rearing nondescendent young. A major theoretical explanation for this phenomenon has revolved around the notion of inclusive fitness, where delayed dispersers in a family-based group gain indirect fitness benefits by fostering the viability of close relatives. There is potential, however, for direct fitness benefits in delayed dispersal itself. We explored the relationship between delayed dispersal and lifetime fitness in a reintroduced population of the cooperatively breeding red wolf, *Canis rufus*, which exhibits delayed dispersal but few opportunities to breed in the natal pack. We present evidence that male wolves that delayed dispersal to later ages had lower mortality risk from natural and anthropogenic sources combined and increased probability of becoming reproductive in their lifetimes. Furthermore, delayed dispersal did not result in delayed age at first reproduction. For females, however, the relative costs and benefits of delaying dispersal to later ages were more complex. In general, we provide evidence that there are direct fitness benefits to delaying dispersal in red wolves even in the absence of reproductive opportunities in the natal pack. Thus, we lend support to the hypothesis that direct fitness benefits may in themselves be sufficient to facilitate the evolution of delayed dispersal requisite to cooperatively breeding social systems. *Key words:* age at first dispersal, age at first reproduction, canids, cooperative breeding, lifetime reproductive probability, lifetime reproductive success, survival. [*Behav Ecol* 22:199–205 (2011)]

The evolution of cooperative breeding within family groups has often been described as a consequence of kin selection, where any direct fitness cost of helping behavior by non-breeders is compensated for by gains in indirect fitness, leading to a net increase in inclusive fitness (Hamilton 1963, 1964; Stacey and Koenig 1990). However, although indirect fitness benefits may be influential in some systems, their importance relative to the direct fitness benefits of helping may have been overestimated (Cockburn 1998; Clutton-Brock 2002). In some cases, helping behavior may be costly in terms of energy expenditure and/or delayed reproduction due to delayed dispersal (Heinsohn and Legge 1999). Nevertheless, helping behavior, and the strategy of delayed dispersal that it entails, may also be associated with direct fitness benefits such as reproductive opportunities in the natal territory, group foraging efficiency and/or defense, and reduced dispersal-related mortality risk (Koenig et al. 1992; Cockburn 1998; Ekman et al. 2004).

The presence of delayed dispersal in noncooperatively breeding groups supports the notion that such behavior may confer substantial benefits over and above those associated with indirect fitness, leading to the hypothesis that helping behavior itself may evolve only secondarily to delayed dispersal (Brown 1987; Ligon and Stacey 1991). According to this scenario, selection for delayed dispersal as a stepping-stone to a cooperative breeding strategy will be at least partially related to direct ef-

fects on lifetime fitness. Studies focusing on early-life costs versus benefits of dispersal have shown that optimal dispersal strategy can vary widely across species, social and mating systems, and ecological contexts (reviewed in Solomon and French 1997; Clobert et al. 2001; Koenig and Dickinson 2004). In light of the diversity in potential early-life effects of dispersal, detailed assessment of its effects in relation to fitness-related traits spanning entire life spans are needed across a range of organisms with varying life-history characteristics.

Pioneering studies in group-living birds have shown direct lifetime fitness benefits of both delayed dispersal (Ekman et al. 1999) and delayed breeding (Hawn et al. 2007). Other studies in diverse avian species have demonstrated survival and reproductive benefits of remaining within the natal group (Stacey and Koenig 1990; Koenig and Dickinson 2004). Among mammals, cooperative breeding has been reported primarily within mongoose, rodent, primate, and canid species (Solomon and French 1997), and detailed long-term studies in meerkats (*Suricata suricatta*) and dwarf mongoose (*Helogale parvula*) have demonstrated both survival and intra- and extragroup reproductive benefits of delaying dispersal for subordinates (e.g., Creel and Waser 1994; Waser et al. 1994; Clutton-Brock et al. 2001; Griffin et al. 2003). Nevertheless, little is yet known regarding the direct lifetime fitness implications of delayed dispersal in other cooperatively breeding mammals, particularly among species where breeding opportunities in or around the natal home range are rare, making the benefits of delay less clear.

We tested for direct costs and benefits of delayed dispersal in a population of the red wolf, *Canis rufus* that was derived from a captive breeding program and reintroduced into the Alligator River National Wildlife Refuge in North Carolina

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(McCarley and Carley 1979; USFWS 1984). In this population, red wolves generally live in family groups composed of a socially and genetically monogamous breeding pair, nonbreeding offspring with delayed dispersal, and pups (Sparkman A, unpublished data). Most pups disperse from their natal pack to breed, making age at first dispersal (AFD) the major decision, rather than dispersal versus philopatry per se. Delayed dispersal, therefore, is more likely a function of the benefits of extended tenure on the natal territory, group living, and/or dispersal risk rather than breeding opportunities in the natal group.

Helping behavior is found throughout the *Canis* genus (Moehlman 1986; Mech et al. 1999; Packard 2003) and is widespread among other canids, such as the African wild dog (*Lycaon pictus*) and dhole (*Cuon alpinus*) (reviewed in Moehlman and Hofer 1997). Although behavioral studies have yet to document actual helping behavior other than den attendance in red wolves (Phillips et al. 2003), there is evidence of such behavior in that pups with helpers show increased body size and higher early-life survival at low population density (Sparkman et al. 2010). However, at high population density, pups with helpers show reduced body size and no difference in survival, indicating that in some circumstances, helpers may prioritize their own energetic needs. Thus, as in other cooperatively breeding species (e.g., Malcolm and Marten 1982; Harrington et al. 1983; Clutton-Brock et al. 2000; Gusset and MacDonald 2009), helping behavior in red wolves appears to be facultative. Furthermore, whereas the presence of helpers is positively correlated to lifetime reproductive success (LRS) of female pups, it is negatively correlated to LRS of male pups (Sparkman et al. 2010). Combined, these ambiguous effects of helpers suggest that the evolution of delayed dispersal in wolves may be largely driven by direct rather than indirect fitness benefits.

For our population of red wolves, we predicted a net positive effect of delayed dispersal on direct fitness in spite of limited reproductive opportunities in the natal group, thereby partially accounting for the evolutionary stability of a facultative cooperative breeding system. To test this prediction, we used 16 years of data on radio-collared wolves to ask whether delayed dispersal is associated with 1) decreased early-life mortality risk from natural and anthropogenic sources, 2) increased lifetime probability of reproduction, and/or 3) delayed age at first reproduction. We also assess 4) whether there appears to be a cost to LRS of delaying dispersal for those who become reproductive. Moreover, as sex differences in the ramifications of dispersal strategy are present in some species (e.g., Waser et al. 1994; Ekman et al. 1999; Griffin et al. 2003), we give particular attention to similarities and differences between the sexes in our study system.

MATERIALS AND METHODS

Study system

We studied a population of red wolves successfully reintroduced into the Alligator River National Wildlife Refuge in North Carolina in 1987 after their extinction from their native distribution throughout the southeastern United States (McCarley and Carley 1979; USFWS 1984). Between 1987 and 2007, free-ranging wolves were captured primarily via foothold traps, equipped with very high frequency radio-collars and subsequently monitored intensively to gather detailed information on mortality, dispersal, and reproduction (Phillips et al. 2003). Our analyses focus on wild-born individuals born between 1990 and 2006, which follows the period of initial establishment of the population. This analysis is restricted to animals deemed to be 100% red wolves (see Adams et al. 2007) as dispersal and reproductive behavior of

wolf-coyote hybrids can be confounded by genetic status (Sparkman AM, Adams J, Steury TD, Waits L, Murray DL, manuscript in preparation).

Statistical analyses

AFD was defined as the age at which an individual permanently left his or her natal pack and either joined another pack or became a “floater” outside any established home range. Because animals were monitored for survival and movements twice weekly, dispersal age and timing was known with notable precision (± 14 days). We treated dispersal events as a categorical variable with 3 levels: 0 (6–12 months), 1 (13–24 months), and 2⁺ (25⁺ months). This classification scheme was chosen to reveal costs versus benefits of dispersal on a yearly basis, which is an appropriate unit given that both males and females are annual breeders potentially capable of becoming sexually mature within their first year (Rabon 2009).

Dispersal status was known for 126 individuals, of which 80 dispersed prior to reproduction. The remainder either did not disperse or become reproductive during their lifetimes ($n = 39$) or became reproductive in their natal pack ($n = 7$). Of those that dispersed, 35% dispersed at 0 years, 45% at 1 year, and 20% at 2⁺ years, and 41% became reproductive. A logistic analysis with AFD as the response variable and sex as the dependent variable showed no difference in AFD between sexes ($n = 80$, $\chi^2 = 1.38$, $P = 0.501$).

Because the reintroduced population showed marked growth during the study period and individuals faced potential density-dependent effects, we included natal (year of birth) population density as a covariate in all analyses. Analyses were conducted using SAS 9.2 (SAS Institute, Cary, NC).

Survival

To test for a role of AFD on early-life survival, we constructed logistic mixed models using Proc Glimmix with survival to age 2 (yes or no) as the response variable, AFD and sex as main effects, natal population density as a covariate, all 2-way interactions, and litter as a random effect. We compared the probability of survival from 1 to 2 years of age between 2 major groups: 1) those that dispersed at age 0 and 2) those that remained on the natal territory for age 0—that is, individuals that delayed dispersal to 1 or 2⁺ years of age, died prior to dispersal, or became reproductive on the natal territory. The presence of older siblings that have delayed dispersal (i.e., helpers) has also been shown to affect pup survival to age 2 (Sparkman et al. 2010). As the majority of pups in our sample had helpers present in their natal pack (90/104), we were unable to formally test for an effect of helper presence/absence. However, as those without helpers showed trends in the same direction as those with helpers, and results from analyses conducted both with and without pups that did not have helpers had a similar outcome, we present results from the combined analysis here.

The reintroduced red wolf population has experienced high levels of anthropogenic mortality due to proximity to regions of human activity, such as roads, agricultural fields, and hunting areas. Because our final sample size for survival was too small to distinguish between natural, anthropogenic, and unknown causes of death (36 deaths, 68 survivors), we present results for animals dying of all fates combined. Thus, we assume that factors that make individuals more vulnerable to natural death similarly increase risk from anthropogenic factors. For censored individuals (lost due to radio-collar failure), we assume that death occurred at or around the time of censoring, as results with and without censored individuals were qualitatively similar. This assumption is further justified

by the intensive monitoring of the recovering population, which ascertained that the vast majority of living wolves were located, and reproductive events recorded.

Lifetime probability of reproduction

Tissue samples were collected from each animal at time of capture and used to establish individual identity and parentage from 18 microsatellite loci via genetic exclusion and the program CERVUS 2.0 (Marshall et al. 1998; for detailed genetic methods, see Adams 2006). This information was used to determine whether individuals reproduced successfully in their lifetimes, that is, whether they could be identified as parents for one or more litters. To test for a role of AFD on lifetime probability of reproduction, we constructed logistic mixed models using Proc Glimmix with lifetime reproductive status (yes or no) as the response variable, AFD and sex as main effects, natal population density as a covariate, all 2-way interactions, and litter as a random effect. We compared the lifetime probability of becoming reproductive between the same 2 groups mentioned above: those that dispersed at age 0 and those remained in their natal packs during this time.

Age at first reproduction

Potential costs of dispersal at older ages on age at first reproduction of dispersers were assessed using analysis of covariance (ANCOVA) with age at first reproduction as the dependent variable, AFD (0, 1, or 2⁺) and sex as main effects, and population density as a covariate, and all 2-way interactions. Age at first reproduction in years was treated as a continuous variable and ranged from 1 to 7 years for those for whom dispersal status was known. Because our sample was derived from 34 individuals from 24 litters, we could not introduce litter as a random effect into our model. However, our findings remained consistent even when considering only litters with a single individual represented, demonstrating that any lack of independence among litter mates does not substantially bias our results.

Lifetime reproductive success

We had a small sample of individuals for whom LRS was known ($n = 12$ males, 10 females). LRS was defined as the total number of pups produced in an individual's lifetime (up to 13 years of age, with a mean life span of 3.33 ± 2.66 years) that survived from birth in the spring until the following fall and was estimated as the sum of yearly counts of pups captured in the den and/or observed in a pack during the following months. Only individuals that had helpers present in their natal pack were included in the analysis as the presence of helpers has been shown to influence LRS in red wolves (Sparkman et al. 2010), and our sample for packs without helpers was negligible. We constructed ANCOVA models with AFD (0, 1, or 2⁺) as a main effect and natal population density as a covariate. We conducted these analyses by sex because we had information on LRS for only a single male dispersing at age 0. At least 3 individuals were available for each dispersal age in our sample of females. Litter was not included as a random effect as only 4/18 litters in our sample contained more than 1 individual, and stepwise exclusion of these litters did not alter our findings.

RESULTS

Survival

The final model for early-life survival contained AFD, population density, and litter as a random effect (Table 1). There was a significant effect of AFD on survival to age 2, with wolves dispersing at age 0 having a lower probability of survival (Figure 1A). Though there was no significant interaction be-

Table 1

Mixed model analysis of survival to age 2 and lifetime probability of reproduction in red wolves with litter included as a random effect ($n = 104$, 34 litters)

		df	χ^2	<i>P</i>
Survival to age 2	AFD	1,69	7.08	0.010
	Population density	1,69	5.63	0.020
Lifetime probability of reproduction	AFD	1,67	1.20	0.277
	Sex	1,67	1.52	0.223
	AFD \times sex	1,67	3.93	0.052
	Population density	1,67	8.71	0.004

df, degrees of freedom.

tween AFD and sex, this relationship appeared to be primarily driven by males as analyses conducted by sex show a significant difference between males ($P = 0.0108$) but not females ($P = 0.624$) that dispersed at age 0 versus those that delayed dispersal. There was also a significant effect of natal population density, with both sexes being less likely to survive to age 2 at higher density.

Lifetime probability of reproduction

The final model for lifetime probability of reproduction contained AFD, sex, sex \times AFD, population density, and litter as a random effect (Table 1). There was a borderline significant interaction between AFD and sex, and comparison of least square means reveals that males dispersing at age 0 were less likely to become reproductive than those that were delayed ($P = 0.0416$) (Figure 1B). No difference was evident between

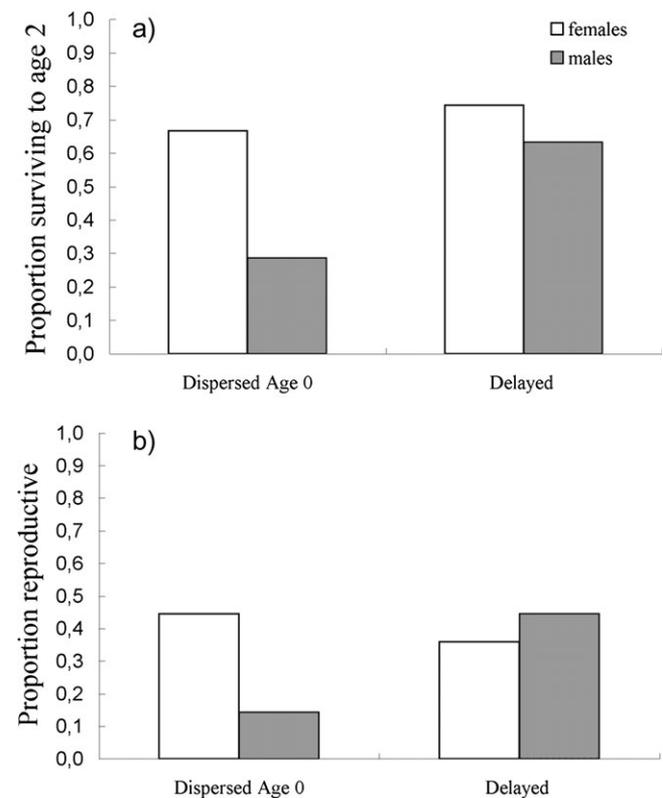


Figure 1

Proportion of wolves surviving to age 2 (A) and proportion attaining reproduction in their lifetimes (B) in relation to dispersal age for red wolves ($n = 104$).

dispersal groups for females. There was also a significant effect of natal population density, with both sexes being less likely to become reproductive at higher density.

Age at first reproduction

The final model for age at first reproduction contained AFD and sex, and sex \times AFD as main effects (Table 2). Population density and its interaction with sex were nonsignificant ($P > 0.1$) and were therefore dropped from the model. There was a significant relationship between AFD and age at first reproduction, however, a marginally significant interaction between sex and AFD suggests that this relationship is driven predominantly by females (Figure 2). Comparisons of least square means revealed that females delaying dispersal to 2⁺ years had later ages at first reproduction (0 vs. 2⁺: $P = 0.0843$; 1 vs. 2⁺: $P = 0.0006$). However, there was no significant difference in age at first reproduction between individuals dispersing at age 0 or 1 ($P = 0.417$). Finally, females had marginally significantly later age at first reproduction than males, as previously reported in a larger sample (Sparkman et al. 2010).

Lifetime reproductive success

Females dispersing at age 1 had marginally significantly greater LRS than females dispersing at either age 0 or 2⁺ (Table 2; Figure 3). As previously reported, there was a significant decrease in LRS with increasing population density (Sparkman et al. 2010). Male LRS did not differ with AFD or density, though our analysis for this sex is limited to showing a lack of difference between dispersers at 1 and 2⁺ years.

DISCUSSION

Direct fitness benefits of delaying dispersal in group-living species are a function of both survival and reproductive costs and benefits. Survival to reproductive age is a critical component of lifetime fitness, and dispersal has been shown to be a high risk endeavor in diverse taxa, perhaps due to dangers associated with independently traveling long distances in unfamiliar territory (e.g., Peterson et al. 1984; Fuller 1989; Harrison 1992; Ridley et al. 2008; Devillard and Bray 2009). In species that show little or no natal philopatry, however, such risks are unavoidable. In this case, the question becomes whether adjusting AFD can influence the relative risk of dispersal; indeed, there is already some evidence to suggest this is the case (e.g., Harrison 1992; Waser et al. 1994). However, the ramifications of age at dispersal for lifetime fitness do not necessarily end there as an individual's lifetime probability of reproduction, age at first reproduction, and ultimately,

Table 2
ANCOVA of age at first ($n = 34$) and LRS in red wolves ($n = 12$ males, $n = 10$ females)

	Effect	df	F	P	
Age at first reproduction	AFD	1,28	5.574	0.009	
	Sex	1,28	3.907	0.058	
	AFD \times sex	2,28	3.002	0.066	
LRS	Males	AFD	1,9	0.464	0.513
		Population density	1,9	2.077	0.183
	Females	AFD	1,6	4.880	0.069
		Population density	1,6	4.511	0.064

df, degrees of freedom.

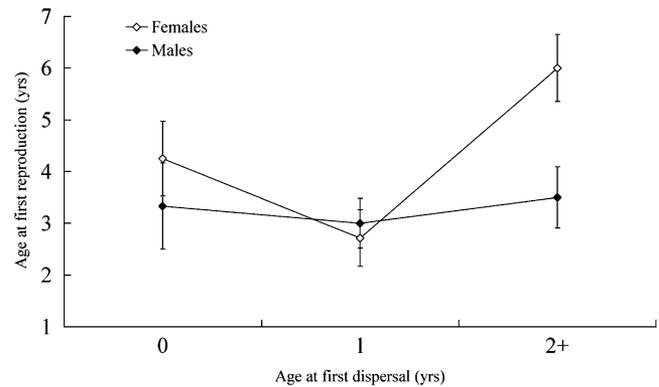


Figure 2
Relationship between age at first reproduction and AFD in red wolves ($n = 34$). Least square means and standard errors of the means are shown.

LRS are determined not only by survival to reproductive age but also by other critical factors—such as body condition, ability to acquire a mate, and parenting skills—that may be influenced by the amount of time spent on the natal territory (Solomon and French 1997; Cockburn 1998). In this study, we present evidence that delaying dispersal can confer both direct survival and reproductive fitness benefits in a large cooperatively breeding carnivore but that these benefits may differ between the sexes.

For male red wolves, the ramifications of delayed dispersal were straightforward: delaying dispersal had a strong positive relationship to direct fitness. Wolves dispersing at age 0 had lower survivorship to age 2 than those that remained in their natal pack during this time (Figure 1A). Given that less than 5% of wolves reproduce prior to age 2, it is not surprising, therefore, that early dispersers also showed decreased lifetime probability of reproduction (Figure 1B). Approximately half of wolves surviving to age 2 become reproductive, but this percentage was consistent for both early and late dispersers (see Figure 1). The relationship between lifetime probability of reproduction and AFD, therefore, appears to be primarily driven by survival to reproductive age. This evidence for a survival cost to early dispersal in male red wolves is consistent with studies in coyotes (*C. latrans*) and dwarf mongoose (*H. parvula*) where early dispersers had lower survivorship (Harrison 1992; Waser et al. 1994).

Although increased mortality and decreased probability of reproduction in early dispersers represents a clear fitness cost,

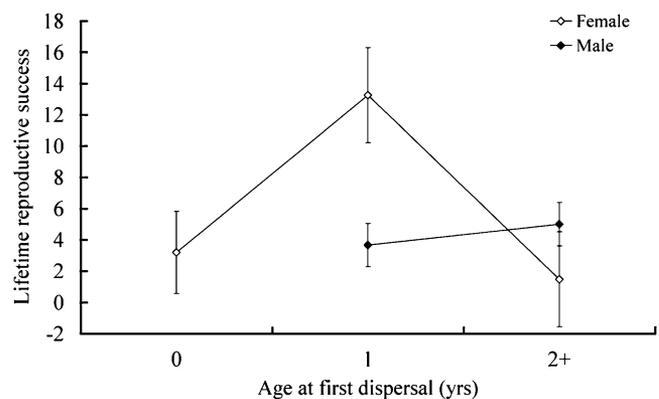


Figure 3
Relationship between LRS and AFD for red wolves (10 females, 12 males). Least square means and standard errors of the means are shown.

there is also a possibility that this cost could trade off with a fitness benefit, such as earlier age at first reproduction. However, the marginally significant sex \times AFD interaction indicates that delaying AFD did not result in delayed reproduction in males as it did in females (Figure 2), suggesting that the major decision for males may be whether to “float” or remain in the natal pack prior to reproduction rather than to negotiate a trade-off between survival and timing of reproduction per se. This is consistent with findings in gray wolves (*C. lupus*), where individuals dispersing at older ages were more successful in pairing and denning subsequent to dispersal than those dispersing as pups (Gese and Mech 1991). We were unable to assess LRS for age 0 dispersers, but we do provide evidence that LRS does not differ between for 1 and 2⁺ dispersers (Figure 3). Combined, these data on survival and reproduction suggest that for males, there are substantial benefits to delaying dispersal to at least 1 year of age and that delaying to 2⁺ does not carry long-term costs for reproductive success relative to dispersing at age 1. Thus, there appear to be direct fitness benefits to delaying dispersal for males, over and above any indirect fitness benefits of helping rear younger siblings while remaining in the natal pack.

Evidence for a strong mortality cost for dispersal at age 0 in females was weak—though there was no significant interaction between sex and AFD, analyses conducted by sex suggest that the significant effect of AFD in the combined analysis was driven largely by males (Figure 1A). Thus, the lack of a significant 2-way interaction between sex and AFD may be a result of low power. Whether or not females dispersing at this age do experience a slight increase in mortality risk is a moot point from a fitness perspective, however, given that there was no difference in lifetime probability of reproduction for early versus late dispersing females (Figure 1B). The only sign of a cost to delayed dispersal was found in a delay in age at first reproduction for females delaying to 2⁺ years of age (Figure 2). This delay could potentially result in a cost to LRS as individuals with earlier ages at first reproduction tend to have longer reproductive life spans and consequently higher LRS (Sparkman AM, Adams J, Steury TD, Waits L, Murray DL, manuscript in preparation). Interestingly, we found that LRS was highest for individuals dispersing at 1 year relative to those dispersing at 0 or 2⁺ years (Figure 3). Although the small sample size requires that any conclusions from these findings must be made cautiously, it appears that at the very least there is no tangible cost to delaying dispersal to 1 year (and that there may be a benefit), but delaying longer than this may carry a cost via reduced reproductive life span due to delayed reproduction.

In light of these findings, it appears that the direct fitness costs and benefits of delaying dispersal are not as easily resolved for female red wolves as for males. Other work suggests that females, which are smaller in general, may suffer reductions in body mass to a greater extent than males when faced with competition for resources (Sparkman et al. 2010). Thus, it is possible that females are more plastic with regard to both dispersal age and reproductive success, making a consistent strategy more difficult to discern. Nevertheless, females can and do delay dispersal to later ages in equal proportion to males, suggesting that if direct benefits do not in fact suffice, indirect fitness benefits associated with cooperative breeding (if they exist) could play a more critical role for females than for males in the evolutionary maintenance of a delayed dispersal strategy.

One difficulty with observational studies of this kind is their limited ability to establish actual targets of selection from other correlated traits (Lande and Arnold 1983). Is it in fact dispersal strategy that results in the specific costs and benefits discussed here or is dispersal age merely incidental to other

pivotal traits, such as body size, that may more directly affect survivorship and reproductive potential? The mechanisms underlying dispersal decisions are notoriously difficult to discern, even within a single species, though body size and/or social dominance have been implicated in some studies (e.g., Gese et al. 1996; Koopman et al. 2000; Ekman et al. 2002; Zedrosser et al. 2007). Some studies in canids have suggested that there is no clear association between pup body size and dispersal age (e.g., Gese and Mech 1991; Soulsbury et al. 2008). However, in red wolves, it appears that male pups that either disperse at age 0 or delay to 2+ years are larger than those dispersing at age 1 (Sparkman A, unpublished data). Thus, if larger body size is any indication, individuals dispersing at age 0 do not appear to be in poorer condition than those remaining in their natal pack. This suggests that it may indeed be age-specific vulnerability to dispersal risks (due to lack of experience, e.g., in skills such as foraging and self defense), rather than increased vulnerability of dispersers in poor condition, that results in reduced survivorship for males dispersing at age 0. However, it is not yet clear whether potential targets of selection involve developmental or behavioral mechanisms rather than body size per se (reviewed in Bekoff 1977; Clobert et al. 2001). Whatever the case, there is some evidence that AFD is a heritable trait in red wolves (Sparkman AM, Adams J, Steury TD, Waits L, Murray DL, manuscript in preparation), and the positive association we report between delayed dispersal and fitness-related traits suggests that it may be under either direct or indirect selection.

In addition to evidence for an effect of AFD on survival and probability of reproduction, we also found evidence for an effect of population density. Both survival and lifetime probability of reproduction decreased with increasing density in both sexes (Table 1). In other studies on this population, we report negative effects of density on reproductive life span, lifetime number of reproductive events, and overall LRS (Sparkman et al. 2010), as well as a negative relationship between density and body mass (Sparkman AM, Adams J, Steury TD, Waits L, Murray DL, manuscript in preparation). However, we have found no effect of density on either age at first reproduction (Sparkman et al. 2010) or AFD (Sparkman AM, Adams J, Steury TD, Waits L, Murray DL, manuscript in preparation). Thus, it would appear that though the high population density which the reintroduced red wolf population has currently reached can negatively impact survival, it does not have a strong effect on dispersal timing. This is interesting, given that in some species, propensity to stay or leave the natal group is strongly affected by population density, which can have important ramifications for resource and/or home range availability (reviewed in Lambin et al. 2001). This is most dramatically demonstrated in the Ethiopian wolf (*C. simensis*), where habitat saturation is thought to lead to lifetime natal philopatry in the majority of males (Sillero-Zubiri et al. 1996). The mechanisms underlying the relationship between density, survival, dispersal, and important ecological factors such as resource availability should be explored in more detail in future studies in the red wolf, to further understand how the effects of density on survival and AFD can be uncoupled.

An important caveat to bear in mind when interpreting our results is that, due to small sample sizes, it was necessary to group individuals with all causes of death—natural, anthropogenic, and unknown—for our analyses. As this study concerns a reintroduced population residing in an area with high levels of anthropogenic activity, resulting in deaths due to vehicle collision and illegal hunting, it is possible that the survival advantages of delaying dispersal are accentuated to a greater degree by anthropogenic sources of mortality. Future work should investigate the dynamics of cause-specific mortality in this

population and determine whether anthropogenic risk is additive or compensatory to natural risk (Murray et al., 2010). It is also important to bear in mind that our analysis is based on the single remaining extant population of the red wolf, and we are unable to evaluate the extent to which our findings are generalizable to other populations of the same species in differing ecological contexts. However, we hope that future studies in wild populations of the closely related Eastern wolf (*C. lycaon*) and other large-bodied canids, such as the gray wolf and the coyote, will explore similar questions. An interspecific comparative context will be particularly of interest because red wolves are intermediate in dispersal strategy to the coyote and the gray wolf, with delayed dispersal in 65% of pups. In the coyote (*C. latrans*), many individuals disperse within their first year, though delayed dispersal and helping behavior, up to but seldom exceeding the second year, can also occur (Harrison 1992; Hatier 1995). In contrast, in the gray wolf (*C. lupus*), helping behavior is common, and some individuals may delay dispersal from 2 or 3 to as many as 5 years and exhibit overlap among multiple generations of offspring (Mech and Boitani 2003). Thus, one would predict the fitness benefits of delayed dispersal to be strong in gray wolves, as they appear to be in red wolves, but weaker in coyotes, where family bonds are of shorter duration.

It remains to be determined whether helping behavior itself, above and beyond delayed dispersal, is simply a facultative result of sociality in canids, where cohesive behaviors such as group foraging and defense are naturally extended to younger siblings, or whether it evolves as a result of net benefits to inclusive fitness. Nevertheless, in this reintroduced population of red wolves, we provide evidence for direct fitness benefits of delayed dispersal, especially among males, suggesting that the evolution of delayed dispersal may itself be sufficient cause for the formation of family groups conducive to a cooperative breeding strategy, even in the absence of reproductive opportunities within the natal group.

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REFERENCES

- Adams JR. 2006. A multi-faceted molecular approach to red wolf (*Canis rufus*) conservation and management [PhD thesis]. Moscow (ID): University of Idaho.
- Adams JR, Lucash C, Schutte L, Waits LP. 2007. Locating hybrid individuals in the red wolf (*Canis rufus*) experimental population area using a spatially targeted sampling strategy and faecal DNA genotyping. *Mol Ecol*. 16:1823–1834.
- Bekoff M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *Am Nat*. 111:715–732.
- Brown JL. 1987. Helping and communal breeding in birds. Princeton (NJ): Princeton University Press.
- Clobert J, Danchin E, Dhondt AA, Nichols JD. 2001. Dispersal. Oxford: Oxford University Press.
- Clutton-Brock T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*. 296:69–72.
- Clutton-Brock TH, Brotherton PNM, O'Riain MJ, Griffin AS, Gaynor D, Sharpe L, Kansky R, Manser MB, McIlrath GM. 2000. Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proc Biol Sci*. 267:301–305.
- Clutton-Brock TH, Russell AF, Sharpe LL, Brotherton PNM, McIlrath GM, White S, Cameron EZ. 2001. Effects of helpers on juvenile development and survival in meerkats. *Science*. 293:2446–2449.
- Cockburn A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annu Rev Ecol Syst*. 29:141–177.
- Creel SR, Waser PM. 1994. Inclusive fitness and reproductive strategies in dwarf mongooses. *Behav Ecol*. 5:339–348.
- Devillard S, Bray Y. 2009. Assessing the effect on survival of natal dispersal using multistate capture-recapture models. *Ecology*. 90:2902–2912.
- Ekman J, Bylin A, Tegelstrom H. 1999. Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. *Proc R Soc B Biol Sci*. 266:911–916.
- Ekman J, Eggers S, Griesser M. 2002. Fighting to stay: the role of sibling rivalry for delayed dispersal. *Anim Behav*. 64:453–459.
- Ekman J, Hatchwell BJ, Dickinson JL, Griesser M. 2004. Delayed dispersal. In: Koenig W, Dickinson J, editors. *Ecology and evolution of cooperative breeding birds*. Cambridge (UK): Cambridge University Press.
- Fuller TK. 1989. Population dynamics of wolves in North-Central Minnesota. *Wildl Monogr*. 105:3–41.
- Gese EM, Mech LD. 1991. Dispersal of wolves (*Canis lupus*) in north-eastern Minnesota, 1969–1989. *Can J Zool*. 69:2946–2955.
- Gese EM, Ruff RL, Crabtree RL. 1996. Social and nutritional factors influencing the dispersal of resident coyotes. *Anim Behav*. 52:1025–1043.
- Griffin AS, Pemberton JM, Brotherton PNM, McIlrath G, Gaynor D, Kansky R, O'Riain J, Clutton-Brock TH. 2003. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behav Ecol*. 14:472–480.
- Gusset M, Macdonald DW. 2009. Group size effects in cooperatively breeding African wild dogs. *Anim Behav*. 79:425–428.
- Hamilton WD. 1963. The evolution of altruistic behavior. *Am Nat*. 97:354–356.
- Hamilton WD. 1964. The genetical evolution of social behaviour. II. *J Theor Biol*. 7:17–52.
- Harrington FH, David Mech L, Fritts SH. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. *Behav Ecol Sociobiol*. 13:19–26.
- Harrison DJ. 1992. Dispersal characteristics of juvenile coyotes in Maine. *J Wildl Manage*. 56:128–138.
- Hatier KG. 1995. Effects of helping behaviors on coyote packs in Yellowstone National Park, Wyoming. Bozeman (MO): Montana State University.
- Hawn AT, Radford AN, du Plessis Morné A. 2007. Delayed breeding affects lifetime reproductive success differently in male and female green woodhoopoes. *Curr Biol*. 17:844–849.
- Heinsohn R, Legge S. 1999. The cost of helping. *Trends Ecol Evol*. 14:53–57.
- Koenig W, Dickinson J. 2004. *Ecology and evolution of cooperative breeding birds*. Cambridge (UK): Cambridge University Press.
- Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT. 1992. The evolution of delayed dispersal in cooperative breeders. *Q Rev Biol*. 67:111–150.
- Koopman ME, Cypher BL, Scrivner JH. 2000. Dispersal patterns of San Joaquin kit foxes (*Vulpes macrotis mutica*). *J Mammal*. 81:213–222.
- Lambin X, Aars J, Pieltney SB. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p. 110–122.
- Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution*. 37:1210–1226.
- Ligon JD, Stacey PB. 1991. The origin and maintenance of helping behavior in birds. *Am Nat*. 138:254–258.
- 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.
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol Ecol*. 7:639–655.
- McCarley H, Carley CJ. 1979. Recent changes in distribution and status of wild red wolves (*Canis rufus*). In: *Endangered Species Report 4*. Albuquerque (NM): US Fish Wildlife Service. p. 38.

- Mech LD, Boitani L. 2003. Wolf social ecology. In: Mech LD, Boitani L, editors. *Wolves: behavior, ecology and conservation*. Chicago (IL): University of Chicago Press.
- Mech LD, Wolf PC, Packard JM. 1999. Regurgitative food transfer among wild wolves. *Can J Zool*. 77:1192–1195.
- Moehlman PD. 1986. Ecology and cooperation in canids. In: Rubenstein DI, Wrangham RW, editors. *Ecological aspects of social evolution: birds and mammals*. Princeton (NJ): Princeton University Press.
- Moehlman PD, Hofer H. 1997. Cooperative breeding, reproductive suppression and body mass in canids. In: Solomon NG, French JA, editors. *Cooperative breeding in mammals*. Cambridge (UK): Cambridge University Press.
- Murray DL, Smith DW, Bangs EE, Mack C, Oakleaf J, Fontaine J, Boyd D, Jiminez M, Niemeyer C, Meier TJ, et al. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biol Conserv*. 143:2514–2524.
- Packard JM. 2003. Wolf behavior: reproductive, social and intelligent. In: Mech LD, Boitani L, editors. *Wolves: behavior, ecology and conservation*. Chicago (IL): University of Chicago Press.
- Peterson RO, Woolington JD, Bailey TN. 1984. *Wolves of the Kenai Peninsula, Alaska*. Wildl Monogr. 88:3–52.
- Phillips MK, Henry VG, Kelly BT. 2003. Restoration of the red wolf. In: Mech LD, Boitani L, editors. *Wolves: behavior, ecology and conservation*. Chicago (IL): University of Chicago Press.
- Rabon DR. 2009. *Factors affecting reproduction in the red wolf (Canis rufus)*. Raleigh (NC): North Carolina State University.
- Ridley AR, Raihani NJ, Nelson-Flower MJ. 2008. The cost of being alone: the fate of floaters in a population of cooperatively breeding pied babblers *Turdoides bicolor*. *J Avian Biol*. 39:389–392.
- Sillero-Zubiri C, Gottelli D, Macdonald DW. 1996. Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behav Ecol Sociobiol*. 38(5):331–340.
- Solomon NG, French JA. 1997. *Cooperative breeding in mammals*. Cambridge (UK): Cambridge University Press.
- Soulsbury C, Baker P, Iossa G, Harris S. 2008. Fitness costs of dispersal in red foxes (*Vulpes vulpes*). *Behav Ecol Sociobiol*. 62: 1289–1298.
- Sparkman AM, Adams J, Beyer A, Steury TD, Waits L, Murray DL. 2010. Helper effects on pup lifetime fitness in the cooperatively breeding red wolf (*Canis rufus*). *Proc R Soc B Biol Sci*. doi:10.1098/rspb.2010.1921.
- Stacey PB, Koenig WD. 1990. *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge (UK): Cambridge University Press.
- USFWS. 1984. *Red Wolf recovery plan*. Atlanta (GA): US Fish Wildlife Service.
- Waser PM, Creel SR, Lucas JR. 1994. Death and disappearance—Estimating mortality risks associated with philopatry and dispersal. *Behav Ecol*. 5:135–141.
- Zedrosser A, Støen O-G, Sæbø S, Swenson JE. 2007. Should I stay or should I go? Natal dispersal in the brown bear. *Anim Behav*. 74: 369–376.