



## Evidence for a genetic basis for delayed dispersal in a cooperatively breeding canid

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Among cooperatively breeding species, delayed dispersal provides an opportunity for older siblings to help rear young. There is considerable variation in the extent to which cooperative breeders delay dispersal, however, and while delayed dispersal may be a consequence of adaptive evolution favouring family living, evidence for a genetic basis is lacking. Furthermore, the extent to which dispersal behaviour itself is under direct selection, or evolves indirectly in response to selection on correlated life-history traits, remains unclear. We tested for evidence of inter- and intraspecific quantitative genetic variation in age at first dispersal in a reintroduced population of the red wolf, *Canis rufus*, that naturally hybridizes with the coyote, *Canis latrans*, which delays dispersal to a lesser extent than the red wolf. Using analyses based on individual relationships to population founders and sire–offspring regressions, we found evidence for intraspecific genetic variation in dispersal age in male, but not female, red wolves. We also found evidence for interspecific genetic variation, in that red wolves had later dispersal age than coyote–red wolf hybrids. Intraspecific variation in dispersal age was not explained by variation in social and environmental factors nor alternative targets of selection such as body mass or age at first reproduction. Thus, selection may act directly on dispersal-related behaviours. However, life-history traits may continue to be influential in creating interspecific differences in dispersal age, as hybrids also showed earlier reproduction. Our findings suggest that evolution of delayed dispersal may be due to both direct and indirect selection on existing quantitative genetic variation, and that genetic and environmental mechanisms underlying dispersal may differ between the sexes.

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The phenomenon of cooperative breeding, where one or more nonbreeding helpers assist in the rearing of young, has evolved multiple times in the vertebrate phylogeny, and appears in a variety of mammals, birds and fish (Solomon & French 1997; Koenig & Dickinson 2004). However, there is considerable variability in the degree to which a cooperative breeding strategy is employed. In fact, few species are obligate cooperative breeders (Ligon & Burt 2004). Instead, cooperative breeding is largely facultative, with many breeders successfully rearing young without helpers. Whether or not helping behaviour occurs is contingent on a variety of factors, such as condition of potential helpers, population density and/or food availability (e.g. Malcolm & Marten 1982; Harrington et al. 1983; Clutton-Brock et al. 2000; Gusset & Macdonald 2009). At the most basic level, however, helping behaviour in many kin-based cooperative breeding systems is ultimately contingent on

dispersal decisions that will determine whether or not there is temporal overlap between consecutive broods at the natal site. Thus, the evolution of dispersal behaviour, which involves decisions regarding whether and/or when to disperse from the natal site, is central to the evolution of cooperative breeding. However, little is known regarding how dispersal decisions evolve, as the major genetic and environmental mechanisms that shape dispersal can be difficult to pin down (Bekoff 1977; Clobert et al. 2001).

The gradual evolution of delayed dispersal and cooperative breeding from an occasional to a widespread occurrence is particularly evident in the Canidae. Among canids, the ability of a family group to exhibit cooperative breeding is directly linked to tenure of individuals in their natal pack, as most canids are annual breeders and older siblings must delay or forgo dispersal to overlap with a new litter of pups. Extant canids fall into two main lineages, the fox and fox-like canids, which contain the bat-eared fox, *Otocyon megalotis*, raccoon dogs, *Nyctereutes procyonoides*, and ‘true’ foxes (*Vulpes* spp.), and the wolf-like canids, containing jackals, wolves and wild dogs (Agnarsson et al. 2010). Fox and fox-like species have

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been reported as delaying or forgoing dispersal, with helping behaviour observed in some species (Macdonald 1979; Hersteinsson & Macdonald 1982; Malcolm 1986). However, early dispersal is widespread in this group, often precluding the expression of helping behaviour (reviewed in Waser 1996). In contrast, a number of the larger wolf and wolf-like canids may delay dispersal for one or more years, and in many of these species helping behaviour appears to be the norm (reviewed in Moehlman 1997). Furthermore, considerable variation in the duration of family bonds exists even within this lineage. For instance, in the coyote, *Canis latrans*, many individuals disperse within their first year, but delayed dispersal and helping behaviour, up to but seldom exceeding the second year, can also occur (Harrison 1992; Hatier 1995). In contrast, in the grey wolf, *Canis lupus*, some individuals may delay dispersal from 2 to 5 years, and show overlap among multiple generations of offspring (Mech & Boitani 2003). Canids are also notable in that, while there can be a great deal of intraspecific plasticity (e.g. Roemer et al. 2001; Iossa et al. 2009), the fox lineage frequently shows sex-biased dispersal, with female-biased philopatry, whereas the wolf lineage often shows similar dispersal patterns in both sexes, or in some cases male-biased philopatry (reviewed in Mech & Boitani 2003; Macdonald & Sillero-Zubiri 2004). Given this diversity among evolutionary lineages, among closely related species within lineages and between the two sexes, the canids represent an ideal model system in which to examine the evolution of delayed dispersal in the context of cooperative breeding.

Considerable theory exists regarding the adaptiveness of delayed dispersal in vertebrates, with regard to group-living benefits, inbreeding avoidance or optimality, mate competition and resource competition (Johnson & Gaines 1990; Koenig et al. 1992). A baseline requirement for the evolution of delayed dispersal, however, is the existence of genetic variation upon which selection can act. Although studies in this area are limited, there is growing evidence for an intraspecific genetic basis for dispersal propensity and dispersal distance in mammals (Myers & Krebs 1971; Krackow 2003; Selonen & Hanski 2010), birds (Hansson et al. 2003; Pasinelli et al. 2004; Doligez et al. 2009) and reptiles (Massot et al. 2003; Sinervo et al. 2006). Nevertheless, only one landmark study in male rhesus macaques, *Macaca mulatta*, has demonstrated a clear genetic basis for age at first dispersal in vertebrates (Trefilov et al. 2000), a trait central to the evolution of family life from relatively short to longer-lasting family bonds.

We tested the hypothesis that taxonomic diversity in dispersal strategy is due, in part, to genetic differences by testing for quantitative genetic variation in dispersal age both within and across two canid species. Our study was conducted on a reintroduced population of the cooperatively breeding red wolf, *Canis rufus*, which has experienced a number of natural hybridization events with the closely related coyote. The red wolf was declared extinct from the wild in 1980, but was recovered beginning in 1987 with the reintroduction of captive-born wolves derived from wild-caught founders in a captive breeding programme (McCarley & Carley 1979; USFWS 1984). Intensive radiocollaring, monitoring and genetic sampling of the recovering population has provided almost complete pedigree information for several hundred red wolves and hybrids, as well as detailed information on life-history traits, including dispersal age. Thus, we were able to test for intraspecific quantitative genetic variation in dispersal age in both male and female red wolves by testing for (1) a founder line effect on dispersal age and (2) heritability of dispersal age via sire–offspring regressions. In addition, we tested for interspecific genetic variation in dispersal age by (3) comparing red wolves and coyote–red wolf hybrids. While many coyote pups disperse during their first year of life (Harrison 1992), 65% of red wolf pups in our

population delayed dispersal to one or more years of age, with no sex bias in dispersal rate (Sparkman et al. 2011b). Thus, we predicted earlier dispersal age in hybrids, indicating an intermediate, or more coyote-like, phenotype.

We have previously reported that delayed dispersal age in red wolves is associated with higher lifetime probability of reproduction in males (Sparkman et al. 2011b). This finding suggests that, given a genetic basis, dispersal age may be under strong selection. However, since dispersal age itself may be influenced by genes affecting body mass and age at first reproduction (reviewed in: Howard 1960; Ims & Hjermann 2001), it may be under indirect rather than direct selection. Thus, we also tested for evidence of founder line and hybridization effects on these additional traits, in an attempt to determine whether there is correlated variation for other potential targets of selection. In addition, we tested for effects of social factors such as litter size and litter sex ratio on dispersal age. Furthermore, as the reintroduced population has experienced a dramatic increase in density over time, which may influence dispersal decisions via resource competition or home range saturation (reviewed in Lambin et al. 2001), we tested for an effect of natal population density on all three life-history traits in question.

## METHODS

### Study System

We studied red wolves reintroduced into the Alligator River National Wildlife Refuge in North Carolina, U.S.A., in 1987, following extinction from their native distribution throughout the southeastern United States (McCarley & Carley 1979; USFWS 1984). Between 1987 and 2007, free-ranging wolves were captured primarily via foothold traps, equipped with very high frequency (VHF) radiocollars and monitored intensively to gather detailed information on life-history traits and home range characteristics (Phillips et al. 2003). Our analyses focus on wild-born individuals born between 1988 and 2006, which follows the period of initial establishment of the population.

Genetic material was obtained for 703 individuals and genotypes were collected at 18 microsatellite loci with an average heterozygosity of 0.65 (Adams 2006). To assign parents to an individual we used a maximum likelihood approach as implemented in the program CERVUS 2.0 (Marshall et al. 1998; Adams 2006) as well as field data on known pairings and spatial locations of individuals. When one parent was known, we could successfully assign parentage 95% of the time at the 95% confidence level and 96% of the time at the 80% confidence level. When neither parent was known, we could successfully assign parentage 88% of the time at the 95% confidence level and 99% of the time at the 80% confidence level using these 18 loci (Adams 2006). Using the resulting pedigree, the proportion of a given founder line of an individual was calculated as the average proportion of that founder line in the two parents.

### Founder Line Analysis

A major difficulty in analysing the effects of founder line is that interbreeding among lines inevitably results in the dilution of proportional genetic contribution of any one founder to subsequent cohorts. In our study, this dilution effect was a key issue, as there was an increase in population density as founder lines became more diluted over time, making density a potential confound for our analyses. In other words, any putative relationships between dispersal and founder lines could simply reflect relationships between dispersal and population density, since founder line proportions decreased as population density increased. We dealt

with this difficulty by creating a standardized variable for each founder line, subtracting the mean cohort value for a given founder (i.e. the mean proportion of a given founder line for all individuals born in a given year) from the proportion of that founder found in each individual, and dividing by the standard deviation for that cohort. Thus, for each individual, standardized founder value = (individual founder proportion – mean cohort founder proportion)/(standard deviation of cohort founder proportion). In this way, we were able to assign values for a particular founder for each individual relative to values for that founder in other individuals of the same cohort, regardless of how diluted a given founder line became over time. This method has one drawback in that standardizing by cohort did not allow us to incorporate absolute differences in founder line composition (i.e. comparing individuals with very high versus low founder line composition for a given founder), regardless of the time period in which they lived. However, we initially conducted parallel analyses with both standardized and nonstandardized founder line variables, and the results were consistent (provided that population density was incorporated as a covariate in the latter analyses). Thus, we present the standardized results here, as a more robust density-independent method. Furthermore, the standardized variables tended to be more normally distributed and prevented statistical relationships from being driven by high outlying points associated with individuals with very high untransformed proportions of a given founder.

Ten of the original wild-caught founder lines successfully contributed genetic material into the free-ranging red wolf population: founder numbers 6, 8, 11, 12, 13, 14, 24, 26, 33 and 34. Of these, we identified three major groupings based on pairing of the founders in captivity: (1) descendants of a pairing between founders 6 and 12, as well as descendants of 11, 26 and 34, which paired with descendants of 6 and 12, (2) descendants of a pairing between founders 14 and 33, which paired with descendants of 24 and (3) descendants of a pairing between founders 8 and 13. Although within any given individual in the wild population there can be some disparity in percentage of founder lines within these three groups, due to the reintroduction of descendants of other pairings among the original founders, the founder lines within these groups tended to be strongly correlated. Thus, analyses of the relationships between individual founder lines and life-history traits within these groups were largely redundant (see Table 2). Furthermore, there was a strong negative correlation between groups 1 and 2, which appeared to be attributable to the fact that when they interbred in the wild, individuals with high amounts of group 1 founder lines had low amounts of group 2 founder lines. Thus, results from analyses of individual founder lines within groups 1 and 2 tended to be opposite in sign.

In light of both positive and negative correlations among founder lines, we conducted a principal component analysis (PCA) on nine founder lines to reduce the dimensionality of the data set. There has been some dispute regarding whether it is appropriate to conduct PCA on compositional data (i.e. variables that sum to 1) (reviewed in Jolliffe 2002). However, as variable transformation methods designed to deal with this issue suffer from several methodological limitations and have not been shown to be more effective (Jolliffe 2002), and as our results from analyses conducted on principal component (PC) variables were consistent with univariate analyses (see Table 2), we conducted the PCA on the standardized founder lines in the traditional manner.

We excluded founder 26 from the PCA, since it appeared to exert effects that were independent from any other founders in group (1) (see Table 2). Note, however, that our findings were the same even when founder 26 was included. We obtained two PC variables that clearly represented our founder line groups: PC1 ( $\lambda_1 = 4.56$ ;

explained 51% of variation), which carried negative loadings for group 1 founders (range 0.36, 0.39) and positive loadings for group 2 founders (range –0.28, –0.40), as well as PC2 ( $\lambda_2 = 1.86$ ; explained 21% of variation), which carried strong positive loadings for group 3 founders (range 0.60, 0.61).

In summary, we tested for effects of founder lines by (1) calculating the proportion of ancestry of each of the 10 original founders for each individual, (2) standardizing this proportion for each founder by cohort to eliminate confounds with population density and (3) conducting a PCA on standardized values from all 10 founder lines to assign principal components scores to each individual. The two resulting principal component variables, founder PC1 and founder PC2, represented the relative genetic contribution of the three main groups of founder lines to each individual.

We restricted our analysis to wild-born individuals, as reintroduced captive-born individuals tended to be larger (A. M. Sparkman, unpublished data), and were reintroduced at a range of ages, making age at first reproduction a dubious measure. Most importantly, as these individuals were not born in the wild, they did not have a dispersal age from their natal pack. We also excluded all coyote hybrids (i.e. less than an estimated 100% red wolf; see Adams et al. 2007) from this analysis, since dilution of founder line effects by a large number of unknown coyote lineages could obscure any patterns manifest within the red wolf species itself. Since 50% or more of our sample for each life-history trait came from litters with only one or fewer individuals per sex represented, we were unable to introduce litter as a random effect to control for potential nonindependence among littermates. Instead, we conducted all analyses on mean values for each sex of a given litter. Note, however, that in each case we obtained similar results with and without averaging over litters.

Dispersal age, body mass and age at first reproduction were analysed in a stepwise fashion with respect to founder PC1, founder PC2, sex, natal population density, natal home range size, litter size at 6 months (the earliest age at which adequate data was available), litter sex ratio and all two-way interactions. Population density ranged from very low numbers steeply increasing over the first 10 years of study, to a high and relatively stable level over the last 8 years (USFWS 2007). Home range size was calculated from the 95% isopleths of utilization distributions, as estimated using kernel density estimators with fixed bandwidth estimated using the root- $n$  bandwidth estimator (T. D. Steury, K. Beck, A. Beyer & D. L. Murray, unpublished data). Relationships were considered significant at an  $\alpha$  level of 0.05, and all effects with  $P > 0.1$  were dropped from the final model. As an alternative to the stepwise method, model comparisons using Akaike's Information Criterion adjusted for small samples (AICc) were also performed to assess which models provided the best fit (Burnham & Anderson 2002). However, as our results were entirely consistent for both methodologies, we do not present the AICc results here (A. M. Sparkman, unpublished data). All analyses were conducted using SAS 9.2 (SAS Institute, Cary, NC, U.S.A.).

We focus primarily on results from analyses involving founder PC scores rather than individual founder line variables, as the former constitutes the most robust method for dealing with correlated variables. However, we also conducted parallel analyses with each standardized founder variable separately to discern whether the aggregated analysis obscured any individual founder effects. We incorporate the results from these parallel analyses into our Discussion, and provide the statistical details in a supplementary table (Table S1).

#### Age at first dispersal

Age at first dispersal 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 radiocollared animals were monitored for survival and movements twice weekly, dispersal age and timing was known with sufficient precision ( $\pm 14$  days) to be treated as a continuous variable with age in months. Those individuals that died prior to dispersal ( $N = 46$ , mean  $\pm$  SE age =  $1.49 \pm 0.83$  years) or did not disperse from their natal pack prior to breeding ( $N = 6$ ) were excluded from all analyses, as were those whose pack dissolved at an early age due to the death of a parent ( $N = 4$ ). After removal of individuals for whom precise founder line information was not known ( $N = 4$ ), the final sample size was composed of 70 individuals from 23 litters containing females and 30 litters containing males. Dispersal age was log transformed to achieve normality.

#### Body mass

Adult body mass (kg) was derived from measures of free-ranging wolves taken at any age over 18 months, the age at which growth appears to cease in red wolves (A. M. Sparkman, unpublished data). Where more than one adult measure was available for an individual, the average was used instead. Body mass was normally distributed among 93 individuals from 26 litters containing females and 26 litters containing males.

#### Age at first reproduction

Age at first reproduction in years was known for 50 individuals from 21 litters containing females and 20 litters containing males that had been monitored since they were pups, and was analysed as a normally distributed continuous variable.

#### Sire–Offspring Regressions

Mean log dispersal age for offspring from a given sire was regressed against sire log(dispersal age) ( $N = 7$  sires for 16 males;  $N = 6$  sires for 13 females). We conducted regressions by sex to obtain sex-specific heritability scores. Regression involving dam and/or midparent (i.e. average of dam and sire) values were not feasible, given small sample sizes ( $N = 3$  females, 3 males). Heritability was estimated as the slope of the regression of offspring on sire dispersal age.

We also estimated heritability in the same manner for adult body mass, with the exception that we were able to use midparent values ( $N = 17$  parents for 64 males;  $N = 18$  parents for 59 females). Sample sizes were too low to conduct a meaningful heritability analysis for age at first reproduction.

#### Hybrid Analysis

Hybrids were defined as individuals descended from coyote–red wolf pairings, and coyote composition ranged from 2 to 50% (see Adams 2006). As for the founder line analysis, this analysis was conducted with mean litter log(dispersal age) as the response variable. Hybrid status (yes/no) and sex were introduced as main effects, as well as natal population density as a covariate and all two-way interactions. Similar analyses were also conducted with mean litter age at first reproduction as the response variable. We were unable to conduct a robust analysis comparing hybrid and red wolf body mass, as population density and hybrid status were confounded. That is, as the recovering population grew over time, body mass became smaller in red wolves as the incidence of hybrids increased, making it difficult to discern whether hybrids were smaller because of density-dependent or genetic effects. We can say, however, that coyote–red wolf hybrids have previously been reported to be smaller than red wolves (Phillips et al. 2003).

#### Ethical Note

The field work on red wolves was conducted solely by the U.S. Fish and Wildlife Service and all work and procedures conformed to national standards for wildlife handling (Gannon et al. 2011).

## RESULTS

#### Founder Line Analysis

##### Age at first dispersal

No relationship between founder PC1 and dispersal age was evident for females, but males showed a strong negative relationship, where individuals with high PC1 for a given cohort (high proportion of founders 14–24–33, low proportion of founders 6–11–12–34) dispersed earlier than those with low PC1 (Tables 1, 2, Fig. 1). This relationship remained significant even when excluding the two individuals with the very high PC1/low dispersal age from the analysis. Analyses of individual standardized founder lines provided consistent results and suggest that descendents from the pairing of founders 6 and 12 (which included descendents of founders 11 and 34) were largely responsible for this trend (Tables 2, S1). In other words, individuals with a greater genetic contribution from founders 6 and 12 had later dispersal age. There was no relationship between dispersal age and founder PC2 (founders 8 and 13), litter size, litter sex ratio, natal population density or natal home range size. Note that since population density increased over the study period, the lack of a relationship between dispersal age and density also reflects lack of a temporal trend in dispersal age. Furthermore, as previously reported (Sparkman et al. 2011b), dispersal age did not differ significantly between the sexes, with mean  $\pm$  SE dispersal age being  $18.7 \pm 8.0$  months of age for females and  $19.2 \pm 8.6$  months of age for males.

##### Body mass

Founder PC1 showed a sex-specific relationship to adult body mass (Table 1). While there was no relationship between PC1 and body mass in males, females showed a strong positive relationship. In other words, females high in founders 14–24–33 and low in founders 6–11–12–34 tended to be larger. There was also a positive effect of founder PC2 for both sexes, demonstrating that individuals high in founders 8 and 13 tended to be larger (Table 2). Body mass was also significantly higher in males, and decreased with increasing density (Table 1). There were no significant effects of litter size, litter sex ratio or home range size. Analyses of individual founder lines were largely consistent with these results, with the exception of founder 13, which showed no relationship with male body mass, and founder 6, which showed no significant interaction between sex and body mass, indicative of a weak negative trend in males (Tables 2, S1).

**Table 1**

ANCOVAs of age at first dispersal (AFD), body mass (Mass) and age at first reproduction (AFR) in red wolves

	Effect	df	F	P
AFD	Founders PC1	1, 49	4.13	0.05
	Sex	1, 49	0.00	0.99
	Founders PC1*sex	1, 49	5.07	0.03
Mass	Founders PC1	1, 46	12.11	0.001
	Founders PC2	1, 46	3.88	0.06
	Sex	1, 46	33.77	<0.0001
	Founders PC1*sex	1, 46	10.73	0.002
	Population density	1, 46	16.56	0.0002
	AFR	Founders PC2	1, 38	3.29
	Sex	1, 38	2.53	0.12

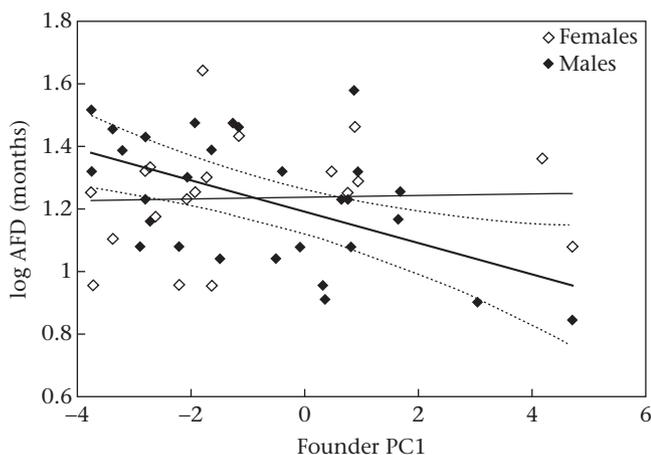
**Table 2**  
Relationships between founder lines and age at first dispersal (AFD), adult body mass (Mass) and age at first reproduction (AFR) in red wolves

	AFD		Mass		AFR	
	Female	Male	Female	Male	Female	Male
<b>Founder PC1</b>	<b>None</b>	<b>Neg</b>	<b>Pos</b>	<b>None</b>	<b>None</b>	<b>None</b>
14	None	None	Pos	None	None	None
24	None	None	Pos	None	None	None
33	None	None	Pos	None	None	None
6	None	Pos	Neg	None	Pos*	Pos*
11	None	Pos	Neg	None	None	None
12	None	Pos	Neg	None	None	None
34	None	Pos	Neg	None	None	None
<b>Founder PC2</b>	<b>None</b>	<b>None</b>	<b>Pos</b>	<b>Pos</b>	<b>Pos</b>	<b>Pos</b>
18	None	None	None	None	None	None
13	None	None	Pos	None	Pos	Pos
26	None	None	Pos	Neg	None	None

Results from analyses conducted on principal components scores (Founder PC1 and PC2), as well as results from analyses conducted for each founder line individually (see Table S1) are given. Note that founders 14–24–33 loaded positively (Pos) and founders 6–11–12–34 loaded negatively (Neg) onto Founder PC1. Founders 8–13 loaded positively onto Founder PC2. Asterisks for age at first reproduction for founder 6 indicate that these relationships were driven by two outlying points representing very late breeders with very high levels of that founder.

**Age at first reproduction**

There was no relationship between age at first reproduction and PC1 (founders 14–24–33/founders 6–11–12–34), litter size, litter sex ratio, natal population density or natal home range size. Although not significant ( $P = 0.0778$ ), there was a positive relationship between founder PC2 and age at first reproduction in both sexes, suggesting that individuals with higher founders 8 and 13 may began breeding at later ages (Tables 1, 2). Results from individual standardized founder lines differed somewhat from these results (Tables 2, S1). Only founder 13, and not founder 8, showed a positive relationship with age at first reproduction. There was also some evidence of a positive relationship between age at first reproduction and founder 6, not present in the PC1 analysis. The relationship was driven entirely by the same two individuals as above that did not commence breeding until 7 years of age, suggesting that if there were an effect of founder line 6, it was not very strong, and may have been primarily an artefact of interbreeding with lines 8 and 13.



**Figure 1.** Log-transformed age at first dispersal (AFD) in relation to the first principal component (PC1) of red wolf founder lines. Heavy and light regressions lines represent male and female trends, respectively; 95% confidence intervals (dashed lines) are shown for males.

**Sire–Offspring Regressions**

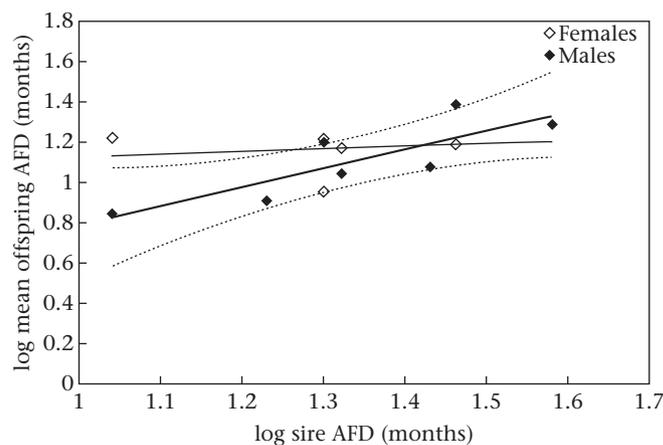
There was a significant positive relationship between male offspring and sire dispersal age, with a slope of 0.95 (SE 0.28) ( $F_{1,5} = 11.51, P = 0.0194$ ; note that sample size was small). Traditionally, estimates of heritability are derived from a doubling of the slope of the regression of offspring on a single parent (Falconer & Mackay 1996). According to this definition, the heritability of dispersal age is 1.9 (2 SE 0.56). However, as heritability ranges by definition from 0 to 1, we can consider the heritability no greater than 1.0. The low sample size may be responsible at least in part for such high heritability. There was no significant relationship between female offspring and sire dispersal age ( $F_{1,4} = 0.20, P = 0.679$ ; Fig. 2).

There was a significant positive relationship between female offspring adult body mass and midparent adult body mass, with a slope of  $0.88 \pm 0.27$  ( $F_{1,16} = 10.31, P = 0.005$ ). There was no significant relationship between male offspring adult body mass and midparent adult body mass ( $F_{1,17} = 1.15, P = 0.301$ ).

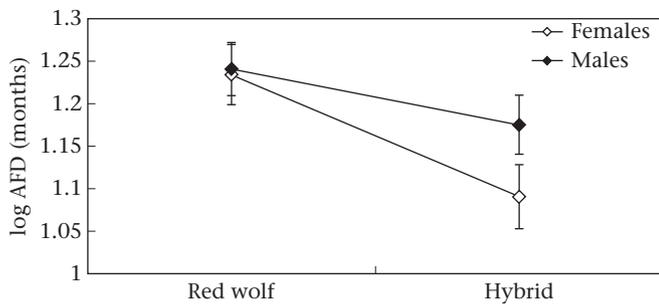
**Hybrid Analysis**

The comparative analysis of dispersal age was conducted on 147 individuals from 45 litters containing females and 56 litters containing males, similarly distributed across both hybrids and non-hybrids. Coyote hybrids had significantly earlier dispersal age than nonhybrids ( $F_{1,99} = 8.525, P = 0.0043$ ), with red wolves dispersing at a mean  $\pm$  SE of  $19.08 \pm 0.96$  months and hybrids dispersing at a mean of  $14.28 \pm 1.04$  months (Fig. 3). Only 3% ( $N = 73$ ) of hybrids dispersed at 2 years of age, and none later, in contrast to 20% ( $N = 74$ ) of red wolves dispersing at 2–3 years of age. Population density did not significantly affect dispersal age. There was no sex\*hybrid status interaction; however, the significant difference between groups appeared to be primarily driven by females, as analyses conducted by sex showed no significant difference between males ( $F_{1,54} = 1.753, P = 0.191$ ).

The comparative analysis of age at first reproduction was conducted on 89 individuals from 32 litters containing females and 30 litters containing males, evenly distributed across both hybrids and nonhybrids. Coyote hybrids had significantly earlier age at first reproduction than nonhybrids ( $F_{1,60} = 14.493, P = 0.0003$ ), with nonhybrids commencing at a mean  $\pm$  SE of  $3.51 \pm 0.018$  years of age and hybrids commencing at a mean of  $2.43 \pm 0.023$  years of



**Figure 2.** Log-transformed mean offspring age at first dispersal (AFD) regressed against log-transformed sire dispersal age. Heavy and light regressions lines represent male and female trends, respectively; 95% confidence intervals (dashed lines) are shown for males.



**Figure 3.** Least square means of red wolf and coyote–red wolf hybrid log-transformed age at first dispersal (AFD).

age. Only 8% ( $N = 36$ ) of hybrids commenced reproduction after 3 years of age, with a maximum age of 5 years, in contrast to 35% ( $N = 54$ ) of red wolves commencing at 3 years or later, with a maximum age of 8 years. There was no effect of sex, population density, or any two-way interactions on age at first reproduction.

## DISCUSSION

In this study, we provide evidence of a genetic basis for age at first dispersal in a reintroduced population of red wolves, such that males more closely related to the founder lines 6 and 12 (i.e. low PC1) tended to disperse at later ages than those less closely related (Table 2, Fig. 1). Similarly, sire–offspring regressions demonstrated a high heritability for dispersal age in males but not in females (Fig. 2). Furthermore, we present evidence for an effect of hybridization on dispersal behaviour, with coyote–red wolf hybrids dispersing at earlier, more ‘coyote-like’ ages. Surprisingly, although body mass declined with natal population density, there was no evidence of an effect of density on dispersal age, indicating that numbers of individuals may not be a major factor in determining dispersal age in this system. Similarly, neither litter size nor sex ratio explained significant variation in dispersal age, suggesting that if social factors such as these do influence dispersal strategy, they do so in a complex manner that we were unable to detect.

Identifying a multigenerational family resemblance in dispersal age is not conclusive evidence of a genetic basis for dispersal, as common environmental factors may be sufficient to create a misleading resemblance among closely related individuals. Although our small sample size precluded our ability to use the animal model to analyse dispersal age (Wilson et al. 2009), we did confirm that neither natal population density nor natal home range size explained significant variation in dispersal age. However, while all pups in our analyses dispersed from their natal pack prior to reproduction, some may have settled in nearby home ranges relatively similar in habitat composition to that of their natal pack (Lehman et al. 1992). It is also possible that pups actively selected habitat types that were similar to those in which they were born (e.g. Olson & Van Horne 1998; Sacks et al. 2004). In both cases, if home range composition influenced dispersal age, an artificial genetic relationship among closely related individuals could be simulated. In a series of independent analyses (not presented here) we tested for confounding effects of natal home range vegetational composition, but found no significant relationships with dispersal age, leaving a genetic basis still a powerful interpretation of our results. However, as pack home ranges may vary based on the diversity and abundance of prey, (Phillips et al. 2003), we were unable to completely rule out the possibility of some degree of environmental confound. Nevertheless, as all the three major founder lines examined were spread broadly throughout the red

wolf recovery area, including home ranges of a variety of compositions, and exhibited high levels of interbreeding, it seems unlikely that common environmental effects would be strong enough to produce the multigenerational family resemblance we present here.

Age at first dispersal is a difficult trait to pin down mechanistically, as it has been variously linked to other traits such as body size, sexual maturation and social dominance in a variety of species (Gese et al. 1996; Koopman et al. 2000; Ekman et al. 2002; Zedrosser et al. 2007), but has sometimes not been found to be clearly associated with any of these (e.g. Gese & Mech 1991; Soulsbury et al. 2008). Red wolf male pups dispersing in their second year tend to be smaller than those dispersing in their first or third year (A. M. Sparkman, unpublished data), but it is unknown how larger pups decide to leave or to delay dispersal, especially as early dispersal does not translate to early age at first reproduction (Sparkman et al. 2011b). In this study, we show that effects of founder line on dispersal age, body mass and age at first reproduction tend to be uncoupled in red wolves (Table 2), providing further evidence that these traits either are not strongly linked, or may interact in a complex manner with a variety of genetic, social and environmental factors. The finding that coyote–red wolf hybrids and red wolves differ in both dispersal age and age at first reproduction, however, leaves open the possibility that these traits are more strongly linked on an interspecific level, with physiological and behavioural changes associated with earlier sexual maturation as the major triggers for earlier dispersal in coyotes.

It is also possible that dispersal age is more directly linked to genetic variation in behavioural traits, such as aggression or risk-taking behaviours, than other life-history traits. There is strong evidence in rhesus macaques, for instance, that allelic differences in a serotonin transporter gene are related to differences in dispersal age in males (Trefilov et al. 2000). Since serotonin is a highly conserved gene among vertebrates associated with impulsive behaviour and risk taking, it is not unlikely that it is involved in dispersal behaviour in a wide range of species. Future work should examine this possibility, and other target genes (such as those coding for key metabolic and reproductive hormones) in species exhibiting delayed dispersal, to test whether genetic regulation of dispersal is conserved across diverse groups.

Our finding that both founder line and regression methods showed evidence for a genetic basis for dispersal age in males but not in females, just as both methods attest to a genetic basis for adult body mass in females but not in males, is intriguing, and suggests that female dispersal age may be more plastic than that of males, and may vary to a greater degree in response to social and environmental factors. Indeed, females, which tend to be smaller in general, and show evidence of being more vulnerable to competition with older siblings (Sparkman et al. 2011a), may have dispersal decisions more often foisted upon them via limited food availability and/or intrapack aggression (Christian 1970; but see Harris & White 1992). Interestingly, while there was no evidence of intraspecific genetic variation in dispersal age in female red wolves, interspecific differences in dispersal age between coyote hybrids and red wolves suggest that genetic differences between female coyotes and red wolves are more pronounced than differences between males (Fig. 3). Sex differences in philopatry and dispersal distance are widespread throughout the fox and fox-like canids, which are basal to the canid phylogeny (Agnarsson et al. 2010). Thus, it is not surprising that the degree to which dispersal-related traits are heritable, and vary across species, differs between the sexes. Sex differences in philopatry or dispersal distance do not appear to be pronounced in the *Canis* genus (Mech & Boitani 2003). However, in the light of our findings in red wolves, we propose that while the sexes may behave similarly, the underlying genetic and

environmental mechanisms involved in dispersal decisions may differ profoundly.

Our results revealed strong genetic divergence between hybrids and red wolves for female dispersal age (Fig. 3) but no evidence of genetic variation in female dispersal age in nonhybrid red wolves (Figs 1, 2), raising the question of how variation may have been maintained in male, but not in female, wolves. Since dispersal age is linked to fitness in males (Sparkman et al. 2011b), one might predict that variation for this trait would be eroded by selection. Among the several existing hypotheses regarding maintenance of genetic variation in traits closely related to fitness, one hypothesis predicts that variation will be maintained when there is significant negative covariance among traits, either within or across the sexes (Roff 1992; Rice & Holland 1997). In our case, it may be that certain genes involved in male dispersal age covary with certain genes involved in female body size, as we found that individuals with higher levels of founder lines 6–11–12–34 had both later-dispersing males and smaller females (Table 2). Thus, selection for delayed dispersal in males may be constrained in so far as very small females may be less fit, incurring an intersexual trade-off. However, this hypothesis is weakened by the fact that female body mass and male dispersal age did not appear to be linked in founder lines 8 and 13, indicating that although it is possible that an intersexual trade-off is only present in the context of certain alleles not present in these lines, such a trade-off is not inevitable. Thus, it may be that other mechanisms, such as frequency-dependent selection or environmental heterogeneity contribute more to the maintenance of genetic variation in males (Roff 1992).

An alternative, although not mutually exclusive, explanation for apparent sex differences in genetic variation for dispersal age involves sex-specific selection. As female dispersal decisions appear to be more variable across the canid phylogeny (ranging from a high degree of philopatry to dispersal rates greater than or equal to those of males), it may be that selection has acted (either directly or indirectly) primarily on female dispersal age, resulting in a gradual erosion of genetic variation. In red wolves, dispersal age does not appear to be associated with any major direct fitness costs or benefits in females, as it is for males (Sparkman et al. 2011b). However, females (but not males) with older siblings that have delayed dispersal (i.e. 'helpers') show higher lifetime reproductive success, which may indicate selection for delayed dispersal through intergenerational benefits (Sparkman et al. 2011a). To determine the relevance of these patterns in red wolves to the history of selection for delayed dispersal across the canid phylogeny, it will be of interest to explore further what extended tenure in the natal pack and involvement in pup rearing contribute to female fitness in other species.

### Conclusion

Although we provide novel evidence of an intermediate or more coyote-like phenotype for dispersal age in hybrids that is indicative of interspecific genetic variation, we were unable to determine whether this behavioural difference was driven by correlated differences in body mass and sexual maturation. However, evidence from intraspecific analyses in the red wolf suggest that quantitative genetic variation for dispersal age, at least in males, may be more directly linked to behavioural traits than other life-history traits per se. Future work should examine whether differences in dispersal age among species within the two major canid lineages are generally linked to differences in body mass and/or sexual maturation, or whether exceptions occur that might provide insight into at least partially independent regulation. Furthermore, it will be of interest to determine whether sex differences in genetic variation in dispersal age are widespread among the canids. Both

inter- and intraspecific studies are needed to provide even greater insight into how and why some individuals, and some species, delay dispersal to a greater extent than others, providing a foundation for multigenerational family bonds and the evolution of cooperative breeding.

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### Supplementary Material

Supplementary material for this article is available in the online version, at [doi:10.1016/j.anbehav.2012.01.041](https://doi.org/10.1016/j.anbehav.2012.01.041).

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