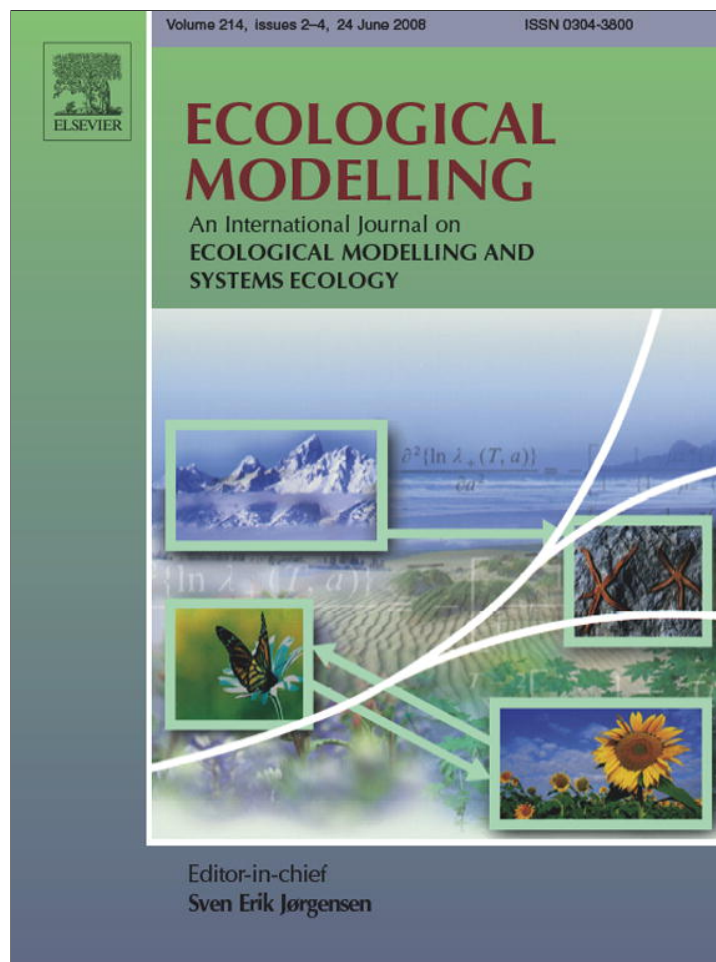


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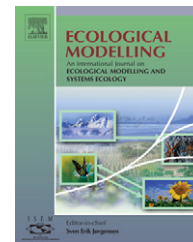
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Spatial dynamics of sympatric canids: Modeling the impact of coyotes on red wolf recovery

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ABSTRACT

Interspecific competition can have a substantial impact on sympatric carnivore populations and may threaten reintroduction attempts of threatened or endangered species. Coyotes (*Canis latrans*) are the primary threat to recovery of red wolves (*C. rufus*) in the wild, through hybridization and loss of the red wolf genotype and habitat occupancy that reduces space available for wolf occupation. We built a stochastic simulation model (using data collected from a recovering red wolf population in northeastern North Carolina as well as from the literature) to examine spatial dynamics of sympatric red wolves and coyotes (independent of habitat influences) and to elucidate the potential role of coyotes on wolf recovery and reintroduction success. Survival of juvenile and adult wolves had the greatest impact on wolf population size and likelihood of extinction. Introducing coyotes to the model had a substantial negative impact on wolf numbers, and the model was highly sensitive to the estimates of the competitive impact of coyotes on red wolves, through declines in wolf productivity. We simulated coyote management from either removal (lower coyote survival) or surgical sterilization (lower coyote reproductive rates) and found that both management strategies increased viability of red wolf populations, especially during initial colonization. Our results suggest that coyotes can inhibit red wolf reintroduction success through competitive interactions, but that management of coyote populations can improve the probability of successful wolf recovery. Additional information on spatial dynamics and dietary overlap between coyotes and wolves in the recovery area is needed to further elucidate the current and potential competitive impact of coyotes on red wolf populations.

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1. Introduction

Interspecific competition is a powerful force shaping species assemblages and community structure. Potential competitors may interact indirectly through exploitation of common resources or directly through intraguild predation or spatial displacement, thereby altering the habitat use of the competitor (Polis et al., 1989; Palomares and Caro, 1999; Fedriani et al., 2000; Kamler et al., 2003). Such interactions can threaten the

success of reintroduction of endangered species to their native range (Moruzzi et al., 2003).

Reviews of sympatry in canids have examined how resources and space are partitioned among competing species (Johnson et al., 1996; Crabtree and Sheldon, 1999). Dynamic changes in distribution and abundance of canids, combined with reintroductions and removal efforts, have provided opportunities to assess how changes in canid assemblages affect the use of space and other resources among coexist-

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ing carnivores (Carbyn, 1982; Dekker, 1983, 1989; Harrison et al., 1989; Arjo and Pletscher, 1999). In general, these studies reveal that species with larger body size are dominant over smaller species, although a numerical advantage in the smaller species can override benefits of larger body size. Smaller canids tend to avoid larger ones by spatial and temporal habitat partitioning, which may not decrease dietary overlap but may reduce agonistic (and potentially lethal) interactions with the dominant competitor (Dekker, 1989; Arjo and Pletscher, 1999; Tannerfeldt et al., 2002). These competitive effects can be most easily detected between species that are closest in size (Peterson, 1995).

The red wolf (*Canis rufus*) is an endangered species that currently is found in the wild in a single carefully managed population in eastern North Carolina (Phillips et al., 2003). Red wolves were extirpated from the wild in the 1960s, when the last remaining individuals were translocated to a captive facility and propagated through a captive breeding program that continues to this day (Phillips et al., 2003). Red wolves were reintroduced to North Carolina starting in 1987, and the wild population has continued to expand during the last 20 years (Stoskopf et al., 2005). Historically, red wolves ranged throughout the southeastern United States and had little contact with coyotes (*C. latrans*), which evolved in the central plains (Parker, 1995; Nowak, 2002). However, following eradication of both red wolves and gray wolves (*C. lupus*) throughout much of their range, coyotes expanded their distribution to encompass most of the North American continent (Parker, 1995), including much of the former range of red wolves. Coyotes currently occupy portions of the red wolf recovery area, and hybridization with coyotes is considered a serious threat to the recovery effort (Miller et al., 2003; Phillips et al., 2003; Fredrickson and Hedrick, 2006). However, coyotes also are potential competitors with red wolves, being of comparable body size, feeding on similar prey, and having comparable habitat and space requirements as red wolves. Indeed, because aggressive interactions have been observed between red wolves and coyotes in areas where wolves have been reintroduced (Henry, 1995, 1998), interference competition likely plays an important role in the dynamics of these species where they co-occur. Therefore, an understanding of the potential effects of interspecific competition on red wolf space use and population trends is important from the perspective of successful reintroduction of the species.

We investigated the competitive interactions between sympatric red wolves and coyotes using a spatially explicit stochastic simulation model. Stochastic simulation models can be valuable for addressing conservation problems when available data are scant and our understanding of the problem is incomplete (Starfield and Bleloch, 1991). Such models can help clarify fundamental interactions and identify which data are most critical to collect, and can serve to evaluate benefits of various management scenarios even in the absence of apparently crucial data (Starfield et al., 1995).

2. Background biology

Model structure and parameters were derived from information gathered by the red wolf restoration program in

northeastern North Carolina (Phillips et al., 2003; U.S. Fish and Wildlife Service, *unpublished data*) and from other published information on coyotes, red wolves, gray wolves, and interactions among these species. In this section we review the relevant background biology upon which the model was based.

Wolf and coyote groups usually consist of an adult breeding pair, their pups, and non-breeding subadults that are offspring from the previous year (Mech, 1970; Nowak, 1999). These family groups typically share a home range and defend an area within that home range (Crabtree and Sheldon, 1999; Phillips et al., 2003). Territory sizes of wolves and coyotes vary greatly across large geographical areas and are most influenced by local prey abundance and wolf or coyote density (Fuller and Murray, 1998; Crabtree and Sheldon, 1999). In gray wolves, home range size increases with pack size (Ballard et al., 1987; Peterson et al., 1984). Regression analyses of data from gray wolves in south-central Alaska found that each additional pack member required a 17% increase in space over that required by the breeding pair (Ballard et al., 1987).

Home ranges of 30 red wolf packs in northeastern North Carolina averaged 111 km² (range: 27–255 km²) in the early 2000s, compared to 99 km² (range: 22–360 km²) in the early 1990s (T. Steury, *unpublished data*; home ranges were based on the 95% isopleth of the pack utilization distributions estimated using the kernel density method with a fixed kernel size and a root-n bandwidth estimator; Worton, 1989; Wu and Tsai, 2004; Hemson et al., 2005). Coyote home ranges typically range between 2 and 20 km² (Crabtree and Sheldon, 1999) and often exhibit overlap at the outer edges, but territorial core areas generally do not show any overlap (Crabtree and Sheldon, 1999; Chamberlain et al., 2000). Likewise, sympatric coyotes and gray wolves, or red foxes and coyotes, may have partial home range overlap even though core areas generally are exclusive (Carbyn, 1982; Harrison et al., 1989; Arjo and Pletscher, 1999; but see Paquet, 1991).

Coyotes and red wolves are monestrous, with a single litter usually being produced per social group (Crabtree and Sheldon, 1999; Phillips et al., 2003). The reproductive rate (probability of a given pack producing a litter) of red wolf packs in northeastern North Carolina averaged 53% from 1988 to 2004, and litter sizes averaged 3.92 ($n=105$), ranging from 1 to 10 (U.S. Fish and Wildlife Service, *unpublished data*). Coyote reproductive rates are slightly higher, given that up to 80% of adult female eastern coyotes may breed and bear young each year (Parker, 1995). Coyote litter size at birth averages about 6 pups/year, with an even sex ratio (Beckoff, 1977; Sacks, 2005) and appears to be relatively insensitive to changes in prey abundance (Crabtree and Sheldon, 1999).

Because only one pair breeds within a wolf or coyote pack, the incentive for other group members to disperse and establish their own territory is high. In coyotes, delayed dispersal (until the second year) is more common in saturated populations where available territories may be few (Parker, 1995), and therefore in low-density populations most individuals may disperse during their first year. In gray wolves where the population is expanding, young wolves rarely remain with their parental pack past breeding age (22 mo; Fritts and Mech, 1981). Extra-territorial excursions beyond the established pack home range prior to dispersal are common in gray wolves (Messier,

1985; Fuller, 1989), and dispersing gray wolves may occasionally join a neighboring pack (Stahler et al., 2002).

Annual survival rates calculated from 408 radio-collared red wolves in northeastern North Carolina (1987–2001) were 0.678, 0.793, and 0.806 for pups, yearlings, and adults, respectively (D. Murray, unpublished data). Since pups were born in spring and not collared until fall, early pup mortalities were not included in this calculation, resulting in an overestimate of pup survival. Survival of non-resident wolves is less than half that of residents (D. Murray, unpublished data). For coyotes, pup survival varies with human exploitation and may be 20–60% in populations with low human-related mortality (Crabtree and Sheldon, 1999). Adult mortality in unexploited coyote populations can range from 9 to 10% (Crabtree and Sheldon, 1999) to 40% (Knowlton, 1972).

Intraspecific strife is the most common natural cause of death for red wolves (U.S. Fish and Wildlife Service, 2005). Interspecific aggression between similar-sized sympatric canids also is common, and larger-bodied canids can be an important source of mortality for smaller canid species in the same area (Carbyn, 1982; Dekker, 1983, 1989; Arjo and Pletscher, 1999). Such dynamics can affect space use patterns, social structure, and population size. Aggressive interactions observed between red wolves and coyotes (Henry, 1995, 1998) indicate that interference competition may influence dynamics of these species where they co-occur.

Coyotes are about 2/3 the size of red wolves; body mass ranges from 9 to 20 kg for coyotes and 20 to 36 kg for red wolves (Beckoff, 1977; Nowak, 1999). Little is known about the diet of either species in the area of sympatry in North Carolina, although coyotes are known to have very diverse food habits (Beckoff, 1977; Phillips et al., 2003).

3. Model description and assumptions

3.1. Purpose

The purpose of our model was to investigate factors that could potentially affect red wolf space use patterns and success of the recovery program, including presence of coyotes and potential management activities designed to control coyote populations. We also evaluated which model parameters and assumptions had the largest effect on reintroduction success to help guide future field data collection efforts.

3.2. State variables, scales, and scheduling

The model assumed a landscape of continuous space and homogeneous habitat (initially 50 km × 50 km). Territories were modeled as a circle because in such a homogeneous landscape, a circular territory would be the most economically defensible (smallest perimeter/area ratio). The basic unit of analysis in the model was the pack; pack members shared a home range and defended a core area within it (Fig. 1). For each pack, the model tracked group size and numbers in each age class, but not individual animals. Thus, the state variables (per group) included the species (wolf or coyote), number of individuals in each age class (pups 0–1 years, yearlings 1–2

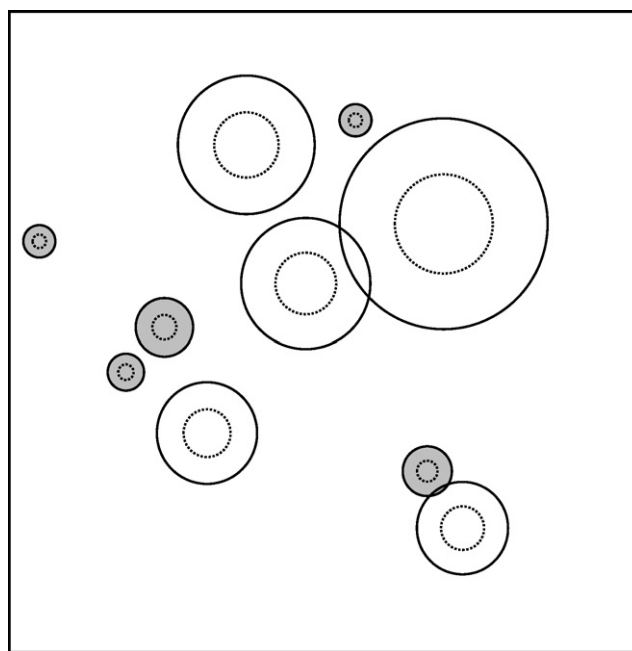


Fig. 1 – Simulated landscape of red wolf (open circles) and coyote (shaded circles) territories in a homogeneous habitat. Inner core areas (dotted lines) are defended.

years, adults >2 years), the territory center (x, y coordinate) and radius.

We assumed an even sex ratio and explicitly included only females in the model (as is customary for models of animal populations, since only females produce offspring). The time step of the model was one year, and the annual sequence of events was reproduction, mortality, inter-pack conflict, dispersal, and maturation (Fig. 2), based on the annual timing of these events in wild populations (U.S. Fish and Wildlife Service, unpublished data). Each of these processes is described more fully below. Exploitative (resource) competition was implemented as a density-dependent effect on reproduction. Interference competition between adjacent groups occurred through expansion of territory size with an increase in group size. Most simulations ran for 50 years.

3.3. Initialization, home range and territory size

At the beginning of each simulation a home range size and location was determined for each member of the initial population (first red wolves, then coyotes). The radius of each new wolf territory was randomly chosen between a minimum and maximum corresponding to territory size of 25–255 km². Coyote territory sizes were determined similarly between 2 and 20 km². Initial territory locations were determined randomly, with the caveat that no territory could be partly or fully off the available landscape. Territory locations were further constrained such that no core area could overlap with any part of any other territory. Core area was defined as a smaller concentric circle within the territory, initially set at 22% of the area of the territory (the 50% kernel) for red wolves and 18% for coyotes (Chamberlain et al., 2000; Steury et al., unpublished data). Thus, some territorial overlap could occur,

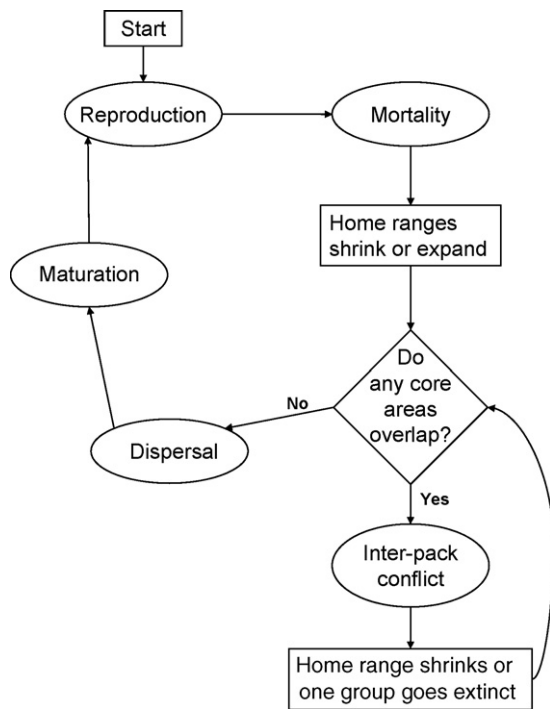


Fig. 2 – Annual sequence of events in model.

but core areas were held exclusively by the resident group (Fig. 1). Core overlap occurred if the centers of two territories were closer than the minimum of two distances, d_1 and d_2 , where $d_1 = r_1 + c_2$, $d_2 = r_2 + c_1$, r_i is the radius of territory i , and c_i is the radius of the core area of territory i . If core overlap occurred between the new territory and any previously established territory, a new size and location were randomly chosen and tested for core overlap with all other groups. Founding individuals were considered adults. After 40 failed attempts to establish a territory without any overlap of core areas (twice the dispersal endurance, defined below), the individual joined a previously established group of same species as a yearling.

3.4. Reproduction and survival

We used a model derived from reproduction data collected from free-ranging red wolves in northeastern North Carolina to calculate the probability of a given pack producing a litter each year. Pack reproduction was not a function of pack size (logistic regression, effect of pack size: $\chi^2_1 = 0.99$, $P = 0.32$), but was affected by population size. Pack reproduction decreased with increasing wolf population size according to the following model (T. Steury, unpublished data): $\ln(p/(1-p)) = 1.107 - 0.017 \times N$, where p is the probability a pack will successfully produce a litter that year and N is the population size (logistic regression; effect of population size: $\chi^2_1 = 4.24$, $P = 0.039$; $n = 198$ pack-years; Fig. 3a). With this model, the maximum pack reproductive rate is 75.2%. We modeled coyote reproduction using the same function used for red wolves but with a maximum reproductive rate of 80% and a more slowly decreasing response to increasing population size ($\ln(p/(1-p)) = 1.386 - 0.013 \times N$; Fig. 3a), since their

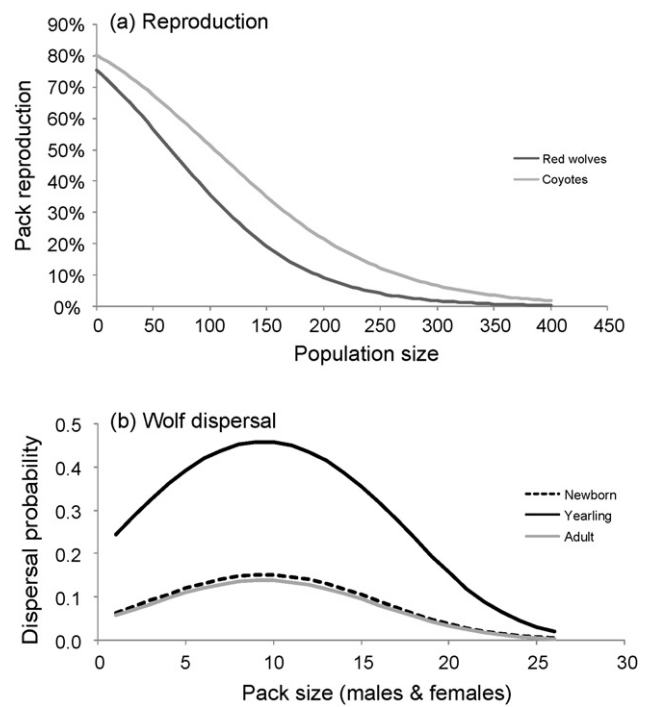


Fig. 3 – Probability of (a) pack reproduction and (b) wolf dispersal.

smaller body size and correspondingly lower resource requirements suggest that each additional coyote should have a lesser density-dependent impact on reproduction.

If red wolves and coyotes overlap in resource use, the population size used in this equation should actually be a function of both species. We assumed that the competitive impact of coyotes on red wolves was determined by a competition coefficient ($\alpha < 1$; Gotelli, 2001) such that $N = 2(N_w + \alpha N_c)$, where N is the population size used in the pack reproduction equation, N_w is the number of female red wolves in the model, and N_c is the number of female coyotes. To parameterize the competition coefficient we considered only the impact of resource exploitation, as overt conflict (interference competition) was included elsewhere in the model. If diet overlap between species were 100% and energy requirements per unit biomass were similar for both species, then α should be ~ 0.66 based on relative body size. Since dietary overlap is unknown, the model initially assumed $\alpha = 0.3$. Although red wolves may compete with coyotes for food or space, wolves also may supplement coyote populations by providing carrion (Paquet, 1992; Wilmers et al., 2003). Therefore, we assumed that the net competitive effect of red wolves on coyotes through resource exploitation was 0.

For packs in the model that successfully reproduced, litter size (of females) at birth was randomly chosen between 1 and 5 for wolves and 1 and 6 for coyotes. Following reproduction, all individuals were subjected to a survival probability. The model assumed wolf survival rates of 0.5 for pups and 0.8 for yearlings and adults. Coyote pup survival was similar to that of red wolves (0.5), and each yearling and adult coyote in the model was initially given a 0.7 survival probability (Windberg, 1995).

3.5. Inter-group aggression

We modeled intraspecific and interspecific aggression through expansion and contraction of territory size with changes in group size. Our model assumed that each individual (female) added to a group would increase territory size by up to 17% of the area required by a single female (the actual increase for each individual was chosen randomly between 0 and 17%). Likewise, losses due to dispersal or mortality decreased territory size by a similar amount.

If increases in territory size caused core overlap (as defined above) between adjacent groups, the model assumed aggression between those groups and resulted in the death of at least one individual. Aggression occurred prior to dispersal, when group sizes were at a maximum and offspring would have neared adult size. We simulated intraspecific as well as interspecific conflict. The larger body size of red wolves should give them an advantage in conflicts with coyotes, so the relative biomass of overlapping groups was used to determine the outcome of the conflict in the model. Body mass ranges from 9 to 20 kg for coyotes and 20 to 36 kg for red wolves (Beckoff, 1977; Nowak, 1999), so the model randomly assigned a mass between those ranges for each adult or yearling member of interacting groups, and the sum total biomass of each group (ignoring pups) determined the winner of the conflict (if the biomass was equal, the group that recently expanded lost). This same mechanism was used for adjacent groups of the same species as well as different species. Losing groups suffered the loss of one individual, and the territory size of that group decreased by 9–17% of the territory size. If core areas of the neighboring groups still overlapped, relative biomass was again calculated, another mortality occurred, and territory size of the losing group decreased correspondingly. This interaction continued until the core areas no longer overlapped or all members of one group were killed.

3.6. Dispersal

We assumed that all members of a group, except one adult female, potentially could disperse. We calculated red wolf dispersal probability using a model derived from data collected in northeastern North Carolina (U.S. Fish and Wildlife Service, unpublished data). The best logistic model, as determined using AIC, was a function of age class, sex, pack size, and pack size² (AIC = 740.03, $n = 1041$ wolves per year across 17 years; ΔAIC for all other models > 9.69). This best model (Fig. 3b) describing the probability that female of age class a dispersed (p_a) was $\ln(p_a/(1 - p_a)) = C_a + 0.25768G - 0.01369G^2$, where G is the group size and C_a is a constant for that age class (pups = -2.936 , yearlings = -1.379 , adults = -3.051). Therefore, to determine potential dispersers in each simulation this probability was calculated for every wolf except one adult female per group.

For coyote dispersal, we used a function derived by Pitt et al. (2003) based on several observations that group size affects the probability a coyote will disperse: $p_d = 0.05 \times G^2$, where G is total group size (males + females) and p_d is the probability that an individual disperses. Thus, assuming an even sex ratio, for packs with > 2 females the dispersal probability was 100% for all but one resident. For packs with exactly two females, one female had an 80% chance of dispersal and the other remained

in the current territory. In a group with one female there was no dispersal.

We imposed an additional mortality rate on dispersers. Disperser survival was 0.5 for red wolves and 0.6 for coyotes (F. Knowlton, U.S. Department of Agriculture, personal communication). We randomly determined the order of dispersal among all surviving dispersers of each species in all groups, to prevent bias in the amount of space available to a potential disperser of either species or any group.

A dispersal attempt occurred as follows: direction of dispersal was chosen randomly; size of the disperser's new territory was determined randomly between the minimum and maximum for that species; initial dispersal distance was chosen randomly between the minimum possible distance (old territory radius plus the radius of the new core area) and an additional distance past that minimum equal to the diameter of the new territory. If no core overlap occurred between the new territory and any existing territory of either species, the territory became established at that location. If overlap of core areas did occur, the disperser could not settle there and had to seek a new unoccupied area. The only exception was if the core area overlap occurred between a dispersing wolf and a single coyote. Then, the coyote was usurped by the wolf and the coyote became nomadic. Otherwise, a new random direction and distance were chosen from the current location (or from the natal territory if the location was off the edge of the available habitat) and the new location was again compared with occupied territories. This process continued until the disperser either colonized a new territory or exhausted its endurance (i.e., the number of new locations tested exceeded some maximum, initially set at 20). Thus, the disperser could travel a long distance from the natal territory. This dispersal strategy created a neighborhood effect such that areas nearest the natal territory would be colonized first, if possible. This method also effectively allowed dispersal, dispersal distance, and group size to become density-dependent. A disperser that was unable to find an unoccupied area before exhausting its endurance was added to a pre-existing group (of same species) at random.

After dispersal, any coyotes forced to become nomadic by dispersing red wolves were subjected to an additional mortality factor equivalent to dispersal mortality. For simulations including immigration by coyotes, a predetermined number of immigrants were added to the nomads. The model attempted to find a new territory for these nomads using the same procedure as for dispersers. If an unoccupied area was not found after a predetermined number of attempts (twice dispersal endurance), the nomad joined another coyote group at random.

3.7. Model simulations

Each simulation (a particular combination of parameter values) was replicated 1000 times. The aggregated variables calculated for each species at the end of each replicate included population size, number of groups, mean group size, mean territory size, year the population reached 50 females (if it did), and year of extinction (if extinct). Since the model included females only, actual population size and group size would be approximately double what is reported

below. Additional aggregated variables calculated each year of each replicate included average dispersal rate (number of dispersers per pack), dispersal distance, and deaths due to agonistic interactions.

We initially explored the model with only red wolves present to ensure that it conformed with known dynamics and space use patterns of red wolves. We explored the effect of several parameters in the model to determine which assumptions had the greatest impact on model outcomes. Simulating all possible combinations of values for each parameter would involve a parameter space much too large for a systematic investigation, so we chose several values of each parameter of interest to represent plausible scenarios based on our understanding of canid biology.

We then investigated the impact of coyotes on red wolf populations under two scenarios; in the first case we started with a small founding wolf population of five females and tracked its likelihood of becoming established in the presence of coyotes; in the second we assumed 50 female wolves became established in the absence of coyotes and we investigated the impact of coyotes immigration and settlement into the area. Since adding a second species to the model has a multiplicative effect on the parameters that could be investigated, we restricted our analysis to a select number of parameters to explore plausible scenarios under which canids may interact. These decisions about plausible parameter values and scenarios to investigate were based on the literature, our own experience, and discussions with and feedback from the red wolf recovery team (Stoskopf et al., 2005).

4. Results

4.1. Single-species simulations

We ran the model using the default parameter set (Table 1) for 5, 10, 20, 30, 50, and 100 years to illustrate the relationships among the output variables (Fig. 4). As wolf numbers increased, habitat became saturated and thereby decreased mean home range size, as dispersers seeking large territories became less likely to find sufficient space than those seek-

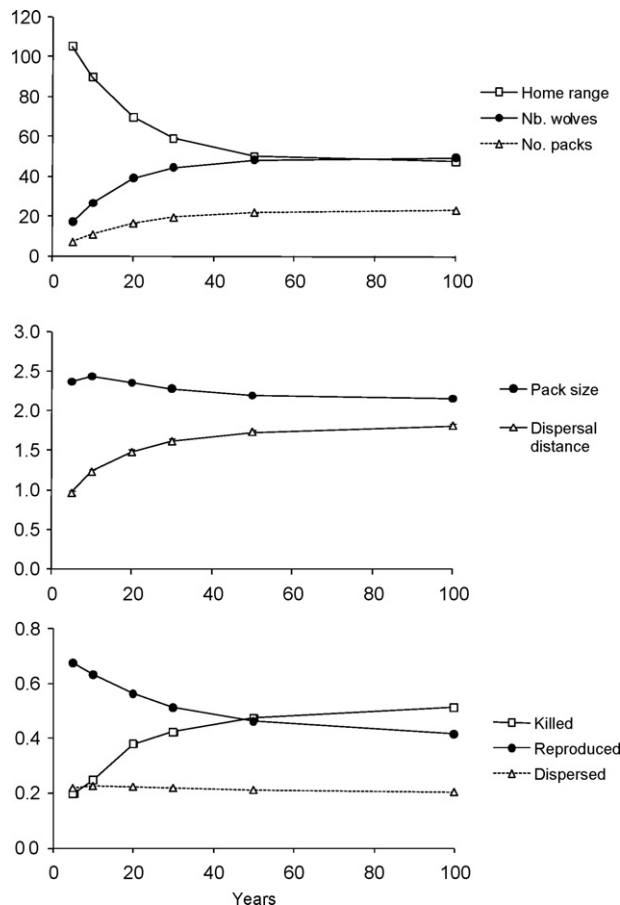


Fig. 4 – Simulation output using default parameter values in Table 1. Each point is the mean of 1000 replicates; error bars are 1 SE (rarely visible). Home range is in km² and dispersal distance in km. The number of wolves killed per pack by agonistic interactions (killed), the proportion of packs that reproduced (reproduced), and the number of dispersers per pack (dispersed) are averaged over all years for all 1000 replicates.

Table 1 – Initial (default) parameter set used in simulations; 2500 km² habitat available, 50 years

Parameter	Type ^a	Wolf value	Coyote value
Range of territory sizes (km ²)	Random	25–255	2–20
Core area (% of territory)	Fixed	22	18
Per capita change in home range size (%)	Random	0–17	0–17
Initial population size (females)	Fixed	5	5
Maximum probability of producing a successful litter	Fixed	0.71	0.8
Range of litter sizes (female pups only)	Random	1–5	1–6
Pup survival	Probability	0.5	0.5
Adult/yearling survival	Probability	0.8	0.7
Disperser survival	Probability	0.5	0.6
Maximum dispersal attempts before joining another group	Fixed	20	20
Body mass (kg)	Random	9–20	20–36

^a Random = the value was determined randomly between a minimum and maximum; fixed = value remained constant throughout a given simulation; probability = parameter interpreted as a probability.

Table 2 – Sensitivity of model output (red wolves only) to several parameter estimates

Parameter ^a	Value	Population ^b	Home range ^b	Packs ^b	Pack size ^b	Dispersers ^c	Distance ^c	Killed ^c	Extinctions
Initial size of population	5	47.9	50.5	22.0	2.2	0.21	17.3	0.48	0
	10	48.5	49.4	22.4	2.2	0.21	18.3	0.55	0
	20	48.6	49.1	22.5	2.2	0.20	19.1	0.63	0
	50	49.0	48.2	22.8	2.2	0.20	19.7	0.66	0
	100	49.0	47.9	22.9	2.2	0.20	19.7	0.56	0
Area (km ²)	900	31.3	37.2	10.8	2.9	0.25	9.5	0.30	0
	1600	41.2	43.3	16.8	2.5	0.23	13.9	0.41	0
	2500	47.9	50.5	22.0	2.2	0.21	17.3	0.48	0
	3600	52.0	58.7	26.0	2.0	0.20	19.3	0.49	0
	6400	56.4	75.6	30.4	1.9	0.20	20.0	0.43	0
	10000	58.1	88.1	32.1	1.8	0.20	19.1	0.34	0
Home range minimum	15	52.0	40.0	25.6	2.0	0.21	16.5	0.48	0
	25	48.1	50.4	22.1	2.2	0.21	17.4	0.47	1
	50	40.4	74.8	16.1	2.5	0.22	17.6	0.43	1
Per capita change in home range	0%	49.6	56.8	22.4	2.2	0.21	17.7	0.00	1
	8%	48.3	54.9	21.9	2.2	0.21	17.6	0.26	1
	17%	47.9	50.5	22.0	2.2	0.21	17.3	0.48	0
	25%	47.7	47.1	22.2	2.2	0.21	17.1	0.65	0
	34%	46.8	45.0	21.9	2.1	0.21	16.8	0.79	0
	50%	45.9	42.4	21.5	2.1	0.21	16.3	1.01	1
Pup survival	0.2	6.5	62.8	3.9	1.2	0.09	4.9	0.04	295
	0.3	26.1	65.5	13.9	1.9	0.12	11.4	0.17	23
	0.4	39.5	55.5	19.4	2.1	0.20	15.4	0.34	2
	0.5	47.9	50.5	22.0	2.2	0.21	10.4	0.48	0
	0.6	53.9	47.9	23.6	2.3	0.22	19.5	0.59	1
	0.7	59.0	46.0	24.8	2.4	0.24	54.1	0.71	0
Adult/yearling survival	0.5	6.6	54.6	3.3	1.3	0.19	6.6	0.08	363
	0.6	19.5	70.9	9.4	2.0	0.21	10.9	0.18	61
	0.7	33.7	59.9	16.1	2.1	0.21	14.6	0.34	5
	0.8	47.9	50.5	22.0	2.2	0.21	17.3	0.48	0
	0.9	66.1	44.1	28.4	2.3	0.21	19.3	0.55	0
Disperser survival	0.25	35.3	64.0	14.9	2.4	0.12	10.8	0.29	1
	0.50	48.1	50.4	22.1	2.2	0.21	17.4	0.47	1
	0.75	55.8	44.8	26.5	2.1	0.30	19.5	0.57	0
Dispersal attempts (max)	1	30.4	57.5	10.1	3.1	0.25	12.9	0.11	2
	5	40.7	54.7	16.2	2.5	0.23	15.4	0.26	1
	10	44.8	52.3	19.2	2.4	0.22	16.4	0.36	1
	20	47.9	50.5	22.0	2.2	0.21	17.3	0.48	0
	40	50.8	49.1	24.8	2.1	0.21	18.0	0.60	0
	100	53.3	47.4	27.7	1.9	0.20	18.6	0.74	1

^a Values of other parameters listed in Table 1. Default values in bold.

^b Mean of 1000 replicates at the end of 50 years. Home range is km².

^c The number of dispersers per pack, dispersal distance (km), and number of wolves killed by intraspecific aggression are averaged over each year in all replicates. Extinctions are the number of replicates in which the population went extinct.

ing smaller territories. Pack reproductive rates also decreased as the population grew, and dispersal distance and intraspecific agonistic interactions increased. Extinctions were highly unlikely, occurring in <0.1% of the simulations using the default parameter set.

We examined the relationship between output variables by correlating 50-year simulations using our default parameter set. All outputs were correlated ($p < 0.0001$). At the end of 50 years, population size was positively correlated with number of groups (Pearson $r = 0.602$) and group size ($r = 0.526$), but number of groups and group size were negatively correlated with each other ($r = -0.352$). Home range size was negatively corre-

lated with population size ($r = -0.211$) and number of groups ($r = -0.571$), as a smaller mean territory size allowed more groups to fit the landscape, but home range size was positively correlated with group size ($r = 0.365$). Thus, we concluded that basic model dynamics followed general patterns observed among free-ranging canid populations.

We next explored model sensitivity to changes in several parameter values (Table 2). Increasing founding population size from 5 up to 100 (over twice what could be supported in the habitat) had little effect on output after 50 years other than increasing mean dispersal distance by up to 1.4 km, increasing number of wolves killed by intraspecific aggression

by up to 37% (but still <1 per year), and slightly increasing population size (Table 2). Increasing habitat availability and decreasing space requirements (minimum home range size) had similar qualitative effects on the wolf population; number of wolves, packs, and wolves killed annually by intraspecific aggression all increased, while pack size decreased (Table 2). However, a >10 -fold increase in available habitat (from 900 to 10,000 km²) less than doubled wolf numbers, with the increase in wolf numbers after 50 years leveling off for the largest areas. Home range and dispersal distance increased with amount of habitat available, but decreased with lessened space requirements. Larger amounts of additional space required for each individual added to the pack (per capita change in home range) had the greatest effect on number of wolves killed by intraspecific aggression (Table 2), with the increased aggression between adjacent packs resulting in smaller populations (up to 4 fewer wolves) with smaller mean home ranges (>14 km² smaller).

Final population sizes were most strongly affected by changes in survival. Increased survival of pups, adults, and dispersers all increased the number of wolves and packs, up to a nearly 10-fold increase across the range of survival rates examined, thereby decreasing home range size (Table 2). Pack size increased with survival of pups and adults (doubling over the range of pup survival rates examined), but decreased with increasing disperser survival (Table 2). Extinctions were much more common with low pup and adult survival, with a 36% extinction rate at the lowest adult survival examined (50%). No changes in other demographic parameters had a substantive effect on the extinction probability of the wolf population (Table 2).

Dispersal persistence (maximum number of new locations each disperser tested for overlap with existing core territories) was the parameter for which the least empirical evidence exists in the single-species simulations. As dispersal persistence increased, dispersers moved farther from the natal range (up to 6 km) and wolf numbers increased by up to 75%. Thus, habitat became increasingly saturated as dispersers were more likely to find vacant habitat to colonize. The increased colonization success reduced the mean pack size from >3 females to <2 females across the range of values examined and reduced territory size by ~ 10 km² (Table 2).

4.2. Two-species simulations

We investigated the impact of coyotes on red wolf populations under two scenarios; in the first case we started with a small founding wolf population of 5 females and tracked its likelihood of becoming established in the presence of coyotes; in the second we assumed 50 female wolves became established in the absence of coyotes and we investigated the impact of coyotes immigration and settlement into the area. Since adding a second species to the model has a multiplicative effect on the parameters that could be investigated, we restricted our analysis to a select number of parameters to explore plausible scenarios under which canids may interact.

Coyotes had a marked effect on red wolves in both a small founding population and a large established population.

Adding coyotes lowered the number of wolves and wolf packs by $>40\%$ and increased mean wolf home range size by 9–12% (Table 3). The effect of coyotes on small and large wolf populations differed very little, although red wolf extinction rates were slightly higher with a small founding wolf population, especially with high coyote numbers (up to 0.8%). However, further increases in the number of coyotes had little effect on model output for either species (Table 3). Increasing the amount of available habitat increased the number and home range size of wolves, with wolf numbers nearly doubling as available habitat increased from 900 to 3600 km² and then leveling off with additional increases in area (Table 3). Coyote numbers and home range also increased with available habitat, but to a lesser degree. With only small areas of habitat available, extinction rate of wolves increased in the presence of coyotes (up to 1.4%).

The simulation results were quite sensitive to assumptions of the competitive impact of coyotes on red wolves (Table 3). As coyotes competed more strongly with wolves (α increased up to 0.6), wolf numbers declined to 18% of the population size assuming no competition ($\alpha = 0$) and probability of extinction increased to nearly 15%. Coyote immigration also affected wolf populations (Table 3). As the annual number of coyote immigrants increased from 0 to 20, numbers of wolves decreased linearly (by 4–5 wolves with every 10 additional coyotes) and the wolf extinction rate increased to 3.4% in small founding populations. Wolf populations that were already large prior to the influx of coyotes were less susceptible to extinction due to coyote immigration, although their numbers still declined. Coyote numbers increased with additional immigrants at the same rate regardless of initial number of wolves (Table 3).

4.3. Coyote management

We investigated how coyote populations could be manipulated to enhance red wolf reintroduction by evaluating the efficacy of management options. To enhance the need for management, we included immigration of 5 coyotes per year and increased the competitive impact of coyotes on red wolves to 0.4.

One management option is to remove coyotes from the reintroduction area. Although the success of coyote removal attempts in North America has been limited (Parker, 1995), increased coyote mortality through human intervention could limit numbers and thereby allow a red wolf population increase. We simulated human-related coyote mortality by decreasing survival of adult and yearling coyotes, starting with a population of either 5 or 50 females of each species. Decreasing coyote survival to 10% decreased coyote numbers to 40% of the pre-management population size, which more than doubled wolf numbers (Table 4). The impact on red wolves was even greater when a small founding population was simulated, with a 2.3-fold increase in numbers and a drop in the extinction probability from 3.2% to nearly zero (Table 4). Coyote extinctions were prevented in these simulations by the annual influx of new immigrants.

Surgical sterilization of coyotes has also been used as a management tool for coyote populations (Bromley and Gese,

Table 3 – Model output^a with coyotes included

Parameter ^b	Value	Red wolves				Coyotes			
		Population size	Home range	Packs	Extinctions	Population size	Home range	Packs	Extinctions
Initial coyote population size (5 wolves)	0	48.1	50.4	22.1	1	0.0			
	5	27.1	55.7	13.5	2	80.4	6.8	66.0	0
	10	27.2	56.0	13.4	0	80.0	6.9	65.7	0
	20	26.5	56.2	13.3	6	80.2	6.9	65.8	0
	50	26.6	56.0	13.3	8	80.6	6.9	66.0	0
Initial coyote population size (50 wolves)	0	48.9	48.3	22.8	0	0.0			
	5	28.8	53.0	14.4	0	79.6	6.8	65.1	6
	10	28.3	52.7	14.3	0	79.7	6.9	65.4	0
	20	28.6	52.7	14.4	0	80.5	6.9	66.0	0
	50	28.3	53.2	14.2	0	80.1	6.8	65.8	0
Area available (km ²)	900	15.5	38.0	6.0	14	73.8	5.0	56.3	3
	1600	22.9	46.2	10.3	5	77.5	6.1	62.0	2
	2500	27.3	55.5	13.6	1	79.9	6.9	65.5	0
	3600	29.7	65.3	15.7	0	81.5	7.3	67.8	0
	6400	31.8	82.7	17.6	1	84.1	7.8	70.2	0
	10000	31.6	92.7	17.6	3	85.4	8.0	71.8	0
Competition coefficient	0	46.4	46.8	20.7	1	77.2	6.5	62.2	3
	0.1	39.8	48.9	18.4	2	77.9	6.6	63.1	1
	0.2	33.6	51.8	16.1	1	78.9	6.8	64.3	3
	0.3	27.1	55.7	13.5	2	80.4	6.8	66.0	0
	0.4	20.9	59.8	10.8	10	81.0	7.0	66.8	2
	0.5	14.1	62.7	7.6	32	82.5	7.2	68.5	1
	0.6	8.1	57.5	4.5	149	83.8	7.2	70.2	2
Coyote immigrants/year (5 wolves)	0	27.1	55.7	13.5	2	80.4	6.8	66.0	0
	1	26.7	55.7	13.3	1	83.2	6.9	68.8	0
	5	24.1	57.2	12.2	6	92.3	7.0	78.7	0
	10	21.7	58.7	11.2	11	102.5	7.0	89.9	0
	20	16.4	63.2	8.7	34	121.8	6.9	111.5	0
Coyote immigrants/year (50 wolves)	0	28.5	52.3	14.3	0	80.0	6.9	65.6	4
	1	27.7	53.0	14.0	0	82.6	6.9	68.2	0
	5	25.5	55.0	13.0	0	92.2	7.0	78.5	0
	10	23.1	56.4	12.0	1	102.2	6.9	89.4	0
	20	18.8	61.8	10.0	2	121.5	6.8	110.9	0

^a Population size, home range, and number of packs are the mean of 1000 replicates of the model run for 50 years. Extinctions are the number of replicates in which the population went extinct.

^b Default values in bold.

2001a,b), and has been used opportunistically in the context of reducing introgression of coyote genes in the North Carolina red wolf population (U.S. Fish and Wildlife Service, unpublished data; Stoskopf et al., 2005). We simulated sterilization by reducing maximum reproductive rate of coyotes from our default value of 0.8. Starting with populations of either 5 or 50 of each species, we decreased maximum coyote reproductive rate (probability of producing a litter) every year for 50 years. The impact of coyote sterilization was similar to that of coyote removal (Table 4). Dropping the maximum coyote reproductive rate to 20% decreased coyote numbers to 27% of their pre-management levels in both small and large initial populations, which increased wolf numbers 2.5- and 2.3-fold in small and large initial populations, respectively (Table 4). Red wolf extinction risk was again highest (3.1%) in small populations with high coyote reproductive maxima, but decreased to zero with sufficient decrease in coyote reproduction (Table 4).

5. Discussion

Under the assumptions of these models, the mere presence of coyotes on the landscape reduced red wolf population viability. However, the strength of the coyote impact on red wolves was particularly sensitive to assumptions of the degree of resource exploitation (i.e., competition coefficient) between the two species. In our model, the degree to which coyotes usurp resources used by red wolves determined their effect on red wolf reproduction, and therefore population growth. We assumed that resource competition was the mechanism by which coyotes would have the greatest impact on wolf reproduction, and simulated this impact using a simple competition coefficient similar to that used in several other competition models (e.g., Gotelli, 2001).

The competition coefficient represents per capita effect of one species on another's population growth rate (Gotelli, 2001).

Table 4 – Effect of management^a, simulated by adjusting coyote survival and reproductive rates

Parameter ^b	Value	Red wolves				Coyotes			
		Population size	Home range	Packs	Extinctions	Population size	Home range	Packs	Extinctions
Adult survival (5 wolves, 5 coyotes)	0.1	35.8	53.5	17.3	1	37.0	8.0	29.5	0
	0.3	31.1	55.0	15.3	0	49.2	7.8	39.4	0
	0.5	25.0	57.4	12.6	7	67.0	7.6	54.8	0
	0.7	15.5	60.8	8.2	32	94.2	7.2	81.0	0
Adult survival (50 wolves, 50 coyotes)	0.1	36.2	51.4	17.6	0	37.2	8.0	29.7	0
	0.3	32.0	52.4	15.8	0	49.7	7.8	39.7	0
	0.5	26.2	55.0	13.3	0	67.2	7.5	55.0	0
	0.7	17.9	60.3	9.5	3	93.6	7.2	80.1	0
Max reproductive rate (5 wolves, 5 coyotes)	0.2	40.0	53.8	19.1	0	24.9	8.0	23.2	0
	0.4	34.8	55.6	17.0	2	40.3	7.7	36.0	0
	0.6	27.4	58.9	13.7	3	61.5	7.4	53.5	0
	0.8	15.9	62.2	8.5	31	93.9	7.2	80.7	0
Max reproductive rate (50 wolves, 50 coyotes)	0.2	40.9	51.6	19.8	0	25.1	8.0	23.4	0
	0.4	35.7	53.2	17.7	0	40.6	7.7	36.2	0
	0.6	28.0	55.9	14.2	0	61.5	7.5	53.5	0
	0.8	17.8	60.0	9.5	5	93.2	7.2	79.9	0

^a Each output is the mean of 1000 replicates of the model run for 50 years, with $\alpha = 0.4$ and 5 coyote immigrants per year. Extinctions are the number of replicates in which the population went extinct (initial population sizes in parentheses).

^b Default values in bold.

Competition coefficients have been estimated in the field based on dietary overlap alone (MacArthur and Levins, 1967) or including feeding rates and relative availability of food types in the environment (Schoener, 1983; Spiller, 1986). These methods of estimating competition coefficients reflect consumptive competition, which occurs when food is limited and individuals reduce another's intake of food via exploitation (Schoener, 1983). Interaction coefficients between species have also been estimated using regression models based on either census of population sizes at one point in time over many sites (static models) or population changes over time (dynamic models) to examine whether per capita changes in one species are associated with the abundance of other species (Pfister, 1995; Shenbrot and Krasnov, 2002). The dynamic approach may indicate exploitative competition, whereas the static approach could reflect negative interspecific spatial association (interference; Shenbrot and Krasnov, 2002). Coyotes could affect red wolf populations through both mechanisms of competition, either through consuming limited food sources or by occupying space and thwarting the establishment of territories by dispersing red wolves. However, very few field data are available for determining the strength of either mechanism and the resulting impact of coyotes on red wolf populations.

Understanding the impact of coyotes on red wolves through resource exploitation, and therefore effectively parameterizing the competition coefficient in our models, requires information on the diet of each species in the recovery area. Studies of the diets of sympatric carnivores often detect appreciable dietary overlap, with varying degrees of

dietary partitioning (Dibello et al., 1990; Kitchen et al., 1999; Neale and Sacks, 2001; Thornton et al., 2004; Azevedo et al., 2006; but see Thurber et al., 1992). Available data on red wolf diets in the recovery area indicate that deer, raccoons, and rabbits are consumed primarily, although food habits vary with wolf age and habitat (Phillips et al., 2003). Information on coyote diets in the area is lacking, but coyotes are considered to be opportunistic, generalist predators that typically consume a wide variety of food sources, including small mammals (rodents and lagomorphs), ungulates, and fruits (Beckoff, 1977). Their use of these various food sources varies seasonally and spatially with changes in food abundance (Andelt et al., 1987; Neale and Sacks, 2001) and may also change with age or group size (Gese et al., 1988, 1996). As such, coyotes may exploit a wider range of resources than other sympatric carnivores (Fedriani et al., 2000). Although canid biologists usually concentrate on determining levels of interference between sympatric canids, exploitation competition underlies the evolution of interference behavior (Peterson, 1995) and likely continues to be important for coexisting species. Thus, diet estimation of red wolves and coyotes in areas of sympatry, as well as allopatric populations in similar habitats, deserves close attention. Such estimates could be derived through a combination of fecal analysis and measurements of stable isotope ratios of hair from captured wolves, coyotes, and their prey (Urton and Hobson, 2005).

Our model assumed that dispersing wolves could always usurp a territory held by a single (female) coyote. However, coyote group sizes averaged around 1.2 females, indicating that

wolves were prevented from occupying space held by some coyote groups. The model also assumed that an expanding coyote group could usurp a neighboring red wolf pack of a single female if coyote numerical advantage outweighed wolf size advantage. Lowering coyote dispersal likely would have increased coyote group sizes in the model and exacerbated their impact on wolf populations through both of these mechanisms. Information on the dominance interactions between coyotes and red wolves and how often individuals of one species are displaced by the other is imperative for better understanding the importance of interference competition by coyotes on red wolves. Specific field data that are needed include home range overlap between the two species, patterns of colonization of vacant areas, and the impact of territorial coyotes on dispersing wolves.

Although our model assumed a homogeneous habitat, habitat heterogeneity can affect territory size, space use, and density of wolves and coyotes (Gese et al., 1988; Fuller and Murray, 1998; Phillips et al., 2003). Habitat heterogeneity can also induce density-dependent reproduction because poorer-quality territories are occupied as population size increases (Dhondt et al., 1992). The impact of coyotes on red wolf populations may be lower if the larger red wolves can exclude coyotes from the highest quality habitats, at least prior to the habitat becoming saturated. Indeed, the ability of a larger-bodied species to exclude a smaller competitor, which is usually assumed to exploit resources more efficiently, from resource patches is thought to enable coexistence of competitors that differ in body size (Basset and DeAngelis, 2007). However, in a landscape already fully colonized by coyotes, newly reintroduced red wolves may have greater difficulty securing the highest quality habitats, and habitat heterogeneity could exacerbate the effects of coyotes on reintroduction success.

The relationship between territory size and population size detected in the model is consistent with field observations of gray wolves. To accommodate future reproduction, a wolf pair must either establish a territory much larger than they require to sustain themselves or else later expand their territory to accommodate increased energy demands (Peterson et al., 1984; Mech and Boitani, 2003). Wolf pairs colonizing unoccupied habitat could establish a large territory and maintain it as the pack grew, whereas those trying to establish territories in a saturated landscape must start with a smaller area and expand as needed (Mech and Boitani, 2003). Several examples exist of large, new wolf territories being established in areas of low density and thereafter remaining at a constant size as the pack grew or later declined (see Mech and Boitani, 2003). However, as space is filled and habitat becomes saturated, individual pack territories can shrink by 17–68% (Fritts and Mech, 1981). Although we did not find a relationship between pack size and territory size in the field data from the red wolf recovery area (U.S. Fish and Wildlife Service, unpublished data), most of those data were obtained from an expanding population. Thus, the production of smaller home ranges with high populations and many packs observed in the model seems consistent with patterns detected among free-ranging wolves described in the literature.

Despite uncertainties in some of our parameter estimates, red wolves always responded negatively to the presence of

coyotes in our simulations. We assumed no hybridization occurred between red wolves and coyotes, but given that body size of hybrids is closer to that of wolves, the impact of non-wolf competition may be aggravated in an environment where hybridization is possible. Our results suggest that management of coyotes by removal (lower survival) or sterilization (lower fecundity) could aid in red wolf recovery, but further elucidating the competitive interactions between wolves and coyotes in the removal area will help refine management activities to improve their effectiveness. Since competitive impacts could include resource exploitation or territorial exclusion, information on diet and behavioral interactions between the two species appears most critical.

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REFERENCES

- Andelt, W.F., Kie, J.G., Knowlton, F.F., Cardwell, K., 1987. Variation in coyote diets associated with season and successional changes in vegetation. *J. Wildl. Manage.* 51, 273–277.
- Arjo, W.M., Pletscher, D.H., 1999. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. *Can. J. Zool.* 77, 1919–1927.
- Azevedo, F.C.C., Lester, V., Gorsuch, W., Lariviere, S., Wirsing, A.J., Murray, D.L., 2006. Dietary breadth and overlap among five sympatric prairie carnivores. *J. Zool.* 269, 127–135.
- Ballard, W.B., Whitman, J.S., Gardner, C.L., 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildl. Monogr.* 98, 1–54.
- Basset, A., DeAngelis, D.L., 2007. Body size mediated coexistence of consumers competing for resources in space. *Oikos* 116, 1363–1377.
- Beckoff, M., 1977. *Canis latrans*. *Mamm. Species* 79, 1–9.
- Bromley, C., Gese, E.M., 2001a. Surgical sterilization as a method of reducing coyote predation on domestic sheep. *J. Wildl. Manage.* 65, 510–519.
- Bromley, C., Gese, E.M., 2001b. Effects of sterilization on territory fidelity and maintenance, pair bonds, and survival rates of free-ranging coyotes. *Can. J. Zool.* 79, 386–392.
- Carbyn, L.N., 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. *Can. Field Nat.* 96, 176–183.
- Chamberlain, M.J., Lovell, C.D., Leopold, B.D., 2000. Spatial-use patterns, movements, and interactions among adult coyotes in central Mississippi. *Can. J. Zool.* 78, 2087–2095.
- Crabtree, R.L., Sheldon, J.W., 1999. Coyotes and canid coexistence in Yellowstone. In: Clark, T.W., Churlee, A.P., Minta, S.C., Kareiva, P.M. (Eds.), *Carnivores in Ecosystems: The Yellowstone Experience*. Yale University Press, New Haven, CT, pp. 127–163.
- Dekker, D., 1983. Denning and foraging habits of red foxes, *Vulpes vulpes*, and their interactions with coyotes, *Canis latrans*, in central Alberta, 1972–1981. *Can. Field Nat.* 97, 303–306.
- Dekker, D., 1989. Population fluctuations and spatial relationships among wolves, *Canis lupus*, coyotes, *Canis latrans*, and red foxes, *Vulpes vulpes*, in Jasper National Park, Alberta. *Can. Field Nat.* 103, 261–264.

- Dhondt, A.A., Kempenaers, B., Adriaensen, F., 1992. Density-dependent clutch size caused by habitat heterogeneity. *J. Anim. Ecol.* 61, 643–648.
- Dibello, F.J., Arthur, S.M., Krohn, W.B., 1990. Food habits of sympatric coyotes, *Canis latrans*, red foxes, *Vulpes vulpes*, and bobcats, *Lynx rufus*, in Maine. *Can. Field Nat.* 104, 403–408.
- Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., York, E.C., 2000. Competition and intraguild predation among three sympatric carnivores. *Oecologia* 125, 258–270.
- Fredrickson, R.J., Hedrick, P.W., 2006. Dynamics of hybridization and introgression in red wolves and coyotes. *Conserv. Biol.* 20, 1272–1283.
- Fritts, S.H., Mech, L.D., 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildl. Monogr.* 80, 6–79.
- Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. *Wildl. Monogr.* 105, 1–41.
- Fuller, T.K., Murray, D.L., 1998. Biological and logistical explanations of variation in wolf population density. *Anim. Cons.* 1, 153–157.
- Gese, E.M., Rongstad, O.J., Mytton, W.R., 1988. Home range and habitat use of coyotes in southeastern Colorado. *J. Wildl. Manage.* 52, 640–646.
- Gese, E.M., Ruff, R.L., Crabtree, R.L., 1996. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. *Can. J. Zool.* 74, 769–783.
- Gotelli, N.J., 2001. *A Primer of Ecology*. Sinauer Associates, Sunderland, Massachusetts, 265 pp.
- Harrison, D.J., Bissonette, J.A., Sherburne, J.A., 1989. Spatial relationships between coyotes and red foxes in eastern Maine. *J. Wildl. Manage.* 53, 181–185.
- Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R., Macdonald, D., 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *J. Anim. Ecol.* 74, 455–463.
- Henry, V.G., 1995. Revision of the special rule for nonessential experimental populations of red wolves in North Carolina and Tennessee. *Fed. Regist.* 60, 18939–18948.
- Henry, V.G., 1998. Notice of termination of the red wolf reintroduction project in the Great Smoky Mountains National Park. *Fed. Regist.* 63, 54151–54153.
- Johnson, W.E., Fuller, T.K., Franklin, W.L., 1996. Sympatry in canids: a review and assessment. In: Gittleman, J.L. (Ed.), *Carnivore Behavior, Ecology and Evolution*. Cornell University Press, Ithaca, pp. 189–218.
- Kamler, J.F., Ballard, W.B., Gilliland, R.L., Mote, K., 2003. Spatial relationships between swift foxes and coyotes in northwestern Texas. *Can. J. Zool.* 81, 168–172.
- Kitchen, A.M., Gese, E.M., Schauster, E.R., 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. *Can. J. Zool.* 77, 1645–1656.
- Knowlton, F.F., 1972. Preliminary interpretations of coyote population mechanics with some management implications. *J. Wildl. Manage.* 36, 369–382.
- MacArthur, R.H., Levins, R., 1967. Limiting similarity convergence and divergence of coexisting species. *Am. Nat.* 101, 377–385.
- Mech, L.D., 1970. *The Wolf: The Ecology and Behavior of an Endangered Species*. University of Minnesota Press, Minneapolis.
- Mech, L.D., Boitani, L., 2003. Wolf social ecology. In: Mech, L.D., Boitani, L. (Eds.), *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press, Chicago, pp. 1–34.
- Messier, F., 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. *Can. J. Zool.* 63, 239–245.
- Miller, C.R., Adams, J.R., Waits, L.P., 2003. Pedigree-based assignment tests for reversing coyote (*Canis latrans*) introgression into the wild red wolf (*Canis rufus*) population. *Mol. Ecol.* 12, 3287–3301.
- Moruzzi, T.L., Royar, K.J., Grove, C., Brooks, R.T., Bernier, C., Thompson, F.L., DeGraaf, R.M., Fuller, T.K., 2003. Assessing an American Marten, *Martes americana*, reintroduction in Vermont. *Can. Field Nat.* 117, 190–195.
- Neale, J.C.C., Sacks, B.N., 2001. Food habits and space use of gray foxes in relation to sympatric coyotes and bobcats. *Can. J. Zool.* 79, 1794–1800.
- Nowak, R.M., 1999. *Walker's Mammals of the World*. Johns Hopkins University Press, Baltimore.
- Nowak, R.M., 2002. The original status of wolves in eastern North America. *Southeast. Nat.* 1, 95–130.
- Palomares, F., Caro, T.M., 1999. Interspecific killing among mammalian carnivores. *Am. Nat.* 153, 492–508.
- Paquet, P.C., 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. *J. Mamm.* 72, 397–401.
- Paquet, P.C., 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *J. Mamm.* 73, 337–343.
- Parker, G., 1995. *Eastern Coyote; the Story of its Success*. Nimbus Publishing, Halifax, 254 pp.
- Peterson, R.O., 1995. Wolves as interspecific competitors in canid ecology. In: Carbyn, L.N., Fritts, S.H., Seip, D.R. (Eds.), *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institutes, Edmonton, pp. 315–323.
- Peterson, R.O., Woolington, J.D., Bailey, T.N., 1984. Wolves of the Kenai Peninsula, Alaska. *Wildl. Monogr.* 88, 1–82.
- Pfister, C.A., 1995. Estimating competition coefficients from census-data – a test with field manipulations of tidepool fishes. *Am. Nat.* 146, 271–291.
- Phillips, M.K., Henry, V.G., Kelly, B.T., 2003. Restoration of the red wolf. In: Mech, L.D., Boitani, L. (Eds.), *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, pp. 272–288.
- Pitt, W.C., Box, P.W., Knowlton, F.F., 2003. An individual-based model of canid populations: modelling territoriality and social structure. *Ecol. Model.* 166, 109–121.
- Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Ann. Rev. Ecol. Syst.* 20, 297–330.
- Sacks, B.N., 2005. Reproduction and body condition of California coyotes (*Canis latrans*). *J. Mamm.* 86, 1036–1041.
- Schoener, T.W., 1983. Field experiments on interspecific competition. *Am. Nat.* 122, 240–285.
- Shenbrot, G., Krasnov, B., 2002. Can interaction coefficients be determined from census data? Testing two estimation methods with Negev Desert rodents. *Oikos* 99, 47–58.
- Spiller, D.A., 1986. Consumptive-competition coefficients: an experimental-analysis with spiders. *Am. Nat.* 127, 604–614.
- Stahler, D.R., Smith, D.W., Landis, R., 2002. The acceptance of a new breeding male into a wild wolf pack. *Can. J. Zool.* 80, 360–365.
- Starfield, A.M., Bleloch, A.L., 1991. *Building Models for Conservation and Wildlife Management*. Burgess International, Edina, MN.
- Starfield, A.M., Roth, J.D., Ralls, K., 1995. Mobbing” in Hawaiian monk seals (*Monachus schauinslandi*): the value of simulation modeling in the absence of apparently crucial data. *Conserv. Biol.* 9, 166–174.
- Stoskopf, M.K., Beck, K., Fazio, B.B., Fuller, T.K., Gese, E.M., Kelly, B.T., Knowlton, F.F., Murray, D.L., Waddell, W., Waits, L., 2005. From the field: Implementing recovery of the red wolf –

- integrating research scientists and managers. *Wildl. Soc. Bull.* 33, 1145–1152.
- Tannerfeldt, M., Elmhagen, B., Angerbjörn, A., 2002. Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* 132, 213–220.
- Thornton, D.H., Sunquist, M.E., Main, M.B., 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in south-central Florida. *J. Mamm.* 85, 973–982.
- Thurber, J.M., Peterson, R.O., Woolington, J.D., Vucetich, J.A., 1992. Coyote coexistence with wolves on the Kenai Peninsula, Alaska. *Can. J. Zool.* 70, 2494–2498.
- Urton, E.J.M., Hobson, K.A., 2005. Intrapopulation variation in gray wolf isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) profiles: implications for the ecology of individuals. *Oecologia* 145, 317–326.
- U.S. Fish and Wildlife Service, 2005. Where do red wolves go when they die? *Red Wolf News* 5, 1–2.
- Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz, W.M., 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *J. Anim. Ecol.* 72, 909–916.
- Windberg, L.A., 1995. Demography of a high-density coyote population. *Can. J. Zool.* 73, 942–954.
- Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164–168.
- Wu, T.J., Tsai, M.H., 2004. Root n bandwidths selectors in multivariate kernel density estimation. *Prob. Theory Related Fields* 129, 537–558.