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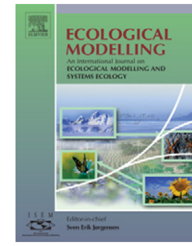

Spatial dynamics of sympatric canids: Modeling the impact of coyotes on red wolf recovery

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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 km^2 (range: 27–255 km^2) in the early 2000s, compared to 99 km^2 (range: 22–360 km^2) 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 km^2 (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,

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