THE ENDANGERED RED WOLF (*CANIS RUFUS*): SPATIAL ECOLOGY OF A CRITICALLY IMPERILED SPECIES IN A HUMAN-DOMINATED LANDSCAPE

by

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ABSTRACT

MELISSA LYNN KARLIN. The endangered red wolf (*Canis rufus*): spatial ecology of a
critically imperiled species in a human-dominated landscape. (Under the direction of DR.
DAVID JOHN CHADWICK)

The purpose of this dissertation research was to analyze the ecology of the reintroduced red wolf (*Canis rufus*) population on the Albemarle Peninsula, NC and determine variables such as intraspecific interactions among red wolves, and how the species has responded to the human-dominated landscape and presence of interspecifics. Specifically, this dissertation research examined interactions between male red wolves utilizing a shared area, quantified red wolf natal dispersal characteristics, and modeled preferred red wolf habitat and its overlap with coyotes and red wolf/coyote hybrids. The results of this research found that adult male red wolf pack members associated less during the pup-rearing season than the non-breeding season, and associated more during nocturnal time periods than diurnal. During the pup-rearing season, the non-breeding male red wolf may have served as a helper at the den. These results documented the first time an unrelated male was accepted into a red wolf social group. Among natal dispersers, I found that yearling/adult red wolves dispersed shorter distances than pups during a period of population stability and decreased their dispersal distances during this period compared to when the population was increasing. Dispersals occurred nearly year round during the period of population stabilization and the peak in pup dispersal timing shifted from December to January. The peak in dispersal timing was later for pups than yearlings/adults during this period as well. Dispersal direction was not random and there was a preference for a westward dispersal direction, attributed to a preference for agricultural habitat. Natal habitat preference was evident in dispersers during the period of population growth, but this preference decreased during the period of population stability to only 35%. Red wolves, coyotes and red wolf/coyote hybrid animals prefer similar resource types based on land use/land cover type, but there was a clear separation between the groups based on road and human population density. Red wolves preferred significantly lower road and human population densities than hybrids or coyotes. Areas of high road and human population density may be the best indicators for targeting coyotes for management, and areas of agriculture with lower road and human population density are where the threat of hybridization between red wolves and coyotes may be greatest. These dissertation results provide baselines for red wolf ecology during periods of population growth and stability, and identify highly suitable red wolf habitat on the Albemarle Peninsula and where coyote management activities should be targeted for the protection of the red wolf species.

DEDICATION

To my parents.

ACKNOWLEDGEMENTS

I would like to thank the U.S. Fish and Wildlife Service red wolf biologists for their many years of dedication to field work and data collection. Without their efforts, this research and that of many others would not be possible and the endangered red wolf might not exist today. I would also like to thank my advisor, Dr. John Chadwick, for his encouragement and guidance during the past several years. My doctoral committee, Ross Meentemeyer, Eric Delmelle, Stan Schneider, and Todd Steck, have also provided helpful comments and suggestions that improved this manuscript. I would also like to thank Tomáš Václavík for his substantial guidance and direction in applying the species distribution model. Lastly, I want to thank my parents for their support and encouragement during all of my academic endeavors, and the love for wildlife and the environment that we share together.

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TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION

The preservation of biodiversity is a top goal for wildlife managers and conservation biologists, but in light of land use changes associated with human development, forestry and agricultural practices, managers are often faced with establishing conservation priorities that incorporate scenarios of altered habitats (Boone and Krohn 2000, Guisan and Zimmermann 2000). The management and protection of large carnivores can be particularly challenging because due to their large space requirements, even the largest protected reserves often cannot accommodate populations, and so they often come into contact with human-dominated land uses which can result in conflicts with humans (Mladenoff et al. 1999, Schadt et al. 2002). Conservation strategies for such species must consider minimum habitat requirements and connectivity of potentially suitable habitat within the framework of a multi-use landscape that is dominated by humans (Schadt et al. 2002). However, because these species are also often most sensitive to fragmented habitat, studying their response to human-induced landscape changes and designing guidelines their conservation or reintroduction may also benefit a host of other species at a greater scale (e.g., regional-scale conservation) (Carroll et al. 2003).

Among mammalian carnivores, wolves represent unique challenges for reintroduction and management due to their status as predators, potential for conflicts with humans, and space requirements. Only 2 species of wolves exist in the United

States, the gray wolf (*Canis lupus*) and the red wolf (*Canis rufus*). Since their protection in 1974, gray wolves have existed in areas of Minnesota and Isle Royale in Lake Superior, and in 1995 were reintroduced to Yellowstone National Park after years of predator control programs eliminated wolves throughout most of the lower 48 states (Bangs and Fritts 1996, Mladenoff and Sickley 1998). This species has been thoroughly studied in the United States (Fuller and Snow 1988, Fuller 1989, Mech 1994a, b, Mech et al. 1995, Mladenoff et al. 1995, Mladenoff and Sickley 1998, Mech 1999, Mladenoff et al. 1999, Fuller et al. 2003, Mech and Boitani 2003) and in other parts of the world, such as Italy (Ciucci et al. 1997) and Poland (Jedrzejewski et al. 2001, Jedrzejewski et al. 2004). Wolf social behavior is highly complex and represent a significant challenge to conservation biologists and resource management because habitat choice and habitat occupancy cannot be explained by simple ecological attributes likes many others species (Massolo and Meriggi 1998, Mladenoff et al. 1999). Wolves colonize new areas as their population increases and individuals disperse, but these dispersal events are influenced by competition over resources (e.g., access to food, mates or denning sites) and populations can only expand into areas with suitable habitat, prey abundance, and minimal anthropogenic pressure (Massolo and Meriggi 1998). While the gray wolf has been successfully restored to areas in Idaho, Montana and Wyoming, the red wolf still faces considerable challenges due to lack of research and a basic understanding of the species requirements, habitat fragmentation and human development throughout its historic range, and competition with interspecifics.

The red wolf was reintroduced in 1987 to the Alligator River National Wildlife Refuge (ARNWR) and Pocosin Lakes National Wildlife Refuge (PLNWR) on the

Albemarle Peninsula in northeastern North Carolina and monitored using VHF radio telemetry collars. The red wolf was extirpated from most of its historic range by the late 1960s (McCarley and Carley 1979), leading to its listing as an endangered species in 1967. The historic range consisted of much of the southeastern United States, from eastern Texas to the Atlantic coast, as far north as Maine and south to the southern tip of Florida (Nowak 2002). In 1973, the United States Fish and Wildlife Service (USFWS) began a formal recovery program for the red wolf (USFWS 1989). Currently, only the 1 wild population reintroduced in 1987 exists in the United States. The population has varied between 114 and 130 individuals during 1997 to 2009 calendar year counts (USFWS 2009). Hybridization with the increasing coyote (*Canis latrans*) population is a primary threat to the persistence of the red wolf population and has become a significant problem since 1994 (Phillips et al. 1995, Kelly et al. 1999). A second reintroduction in the Great Smoky Mountains National Park in 1991 was unsuccessful (Henry 1998, Lucash and Crawford 1998).

Most previous research on the red wolf has addressed its status as a species (Wayne and Jenks 1991, Wilson et al. 2000, Kyle et al. 2006, Murray and Waits 2007). Ecological studies on the reintroduced population have been limited by small sample sizes or duration (Mauney 2005, Hinton 2006, Chadwick et al. 2010, Hinton and Chamberlain 2010) or by VHF telemetry data collection or visual observation that is typically infrequent and limited to daytime observations (Phillips et al. 2003). Studies of other canid species, such as the maned wolf (*Chrysocyon brachyurus*), corsac fox (*Vulpes corsac*), short-eared dog (*Atelocynus microtis*), and Indian fox (*Vulpes bengalensis*) have faced similar limitations (Sillero-Zubiri et al. 2004, Bandeira de Melo et al. 2007, Mendes Coelho et al. 2008). These studies have revealed critical information regarding canid behavior and ecology, however, documenting previously unknown information such as interactions between members of the same pack and habitat use by breeding and non-breeding wolves (Phillips et al. 2003, Bandeira de Melo et al. 2007, Mendes Coelho et al. 2008, Chadwick et al. 2010, Hinton and Chamberlain 2010). The red wolf is listed as critically endangered by the International Union for Conservation of Nature (IUCN) (Kelly et al. 2004) and as an endangered species in the U.S. (USFWS 2007); ecological and behavioral information is needed to effectively monitor and manage this imperiled species and to guide future study objectives.

The purpose of this dissertation research is to analyze the ecology of the reintroduced red wolf population on the Albemarle Peninsula, NC and determine variables such as intraspecific interactions among red wolves, and how the species is responding to the human-dominated landscape and presence of interspecifics. This dissertation research utilizes recent advances in computational capabilities and geospatial technologies to quantify these spatial and temporal attributes of the red wolf population. Each chapter is an independent study presented in publication-style format. Chapter 2 represents one of the first long-term, high temporal and spatial resolution studies of red wolves using GPS radio collar technology. This research project collected five GPS locations four times per day on 2 adult male red wolves for 1 year. Not only is this study one of the first to analyze this species using GPS radio collar technology, it is also the first to document intraspecific interactions of 2 unrelated adult male red wolves using a shared area and the resultant spatial and temporal interactions between them. Red wolf group composition has traditionally been described as the breeding pair, their pups of the year, and offspring from previous years (Phillips et al. 2003). The inclusion of an unrelated, adult male wolf therefore represents a unique group composition. Chapter 2 has been published in the journal Mammal Study.

Chapter 3 encompasses nearly 20 years of VHF radio telemetry data collected since the wolves were reintroduced. This chapter is an analysis of red wolf natal dispersal characteristics as the population increased during the 1990s and leveled off after approximately 1999. This study quantifies basic, undocumented species attributes such as straight-line dispersal distance, duration, timing, age, direction, and evidence of natal habitat preference induction of dispersers. I compared these values during a time when the population was increasing to a period when the numbers had leveled off and stabilized. I test the hypothesis that these attributes have changed in response to the increased population, as natal dispersers face greater challenges trying to find unoccupied territory. This chapter has been accepted for publication by the Journal of Zoology.

Chapter 4 represents some of the most important research objectives and results for red wolf management because of the inclusion of coyote data. In this chapter, I present habitat suitability models for red wolves, coyotes and red wolf/coyote hybrids on the Albemarle Peninsula. This research also relies on the VHF radio telemetry location data, but analyzes locations collected from 1999-2008 when red wolves, coyotes and hybrid animals were all radio collared. Due to the nature of VHF radio telemetry collection and lack of true absence data, I use a presence-only model known as Maximum Entropy (MaxEnt) (Phillips et al. 2006). Using these models and statistical analyses, I identify significant differences between the three species. The results identify a clear separation between red wolf preferred habitat and coyote and hybrid preferred habitat based on road and human population densities, but overlap in their preference for agricultural land cover. These results will prove to be vital for the management issue of red wolf and coyote hybridizations, because it identifies areas within the reintroduction area that are more likely to support coyotes and areas that coyotes are currently avoiding; USFWS red wolf biologists can use this information to target their coyote trapping efforts and manage red wolf preferred habitat. This chapter will be submitted to the journal Biological Conservation.

CHAPTER 2: MEASURES OF SPACE USE AND ASSOCIATION OF TWO UNRELATED MALE RED WOLVES IN A SHARED AREA

Abstract

I applied 3 methods to measure the levels of association between 2 unrelated male red wolves (*Canis rufus*) that occupied the same area over a 12-month study using GPS collar data (five locations/day). One of the males had pups with its mate during the study period and the other was a non-breeder. All three methods reported significant declines in association between the males during the pup-rearing season (April-May) compared to the non-breeding season (June-January). During the non-breeding season, the shared home range area between the males was highest (up to 99%), a coefficient of association (C_A) based on their proximity was highest, and ten-day average distance between the males was smallest (as low as 0.11 km). Levels of association were generally highest during nocturnal observations. During the pup-rearing season, the non-breeding male's home range area, C_A, and shared home range area declined, and distance between the males increased. These results represent the first long-term study using GPS radio telemetry in the red wolf population and the first analysis of spatial and temporal interactions between red wolves. Also, this study documents for the first time a red wolf social group that is composed of unrelated males.

Introduction

Most research on the red wolf has addressed its status as a species (Wayne and Jenks 1991, Wilson et al. 2000, Kyle et al. 2006, Murray and Waits 2007). Ecological studies have been limited by small sample sizes or duration (Mauney 2005, Hinton 2006, Chadwick et al. 2010, Hinton and Chamberlain 2010) or by VHF telemetry data collection that is infrequent and limited to daytime observations (Phillips et al. 2003). Although GPS and VHF radio collars are used to monitor the population, intra-group spatial relationships are largely undocumented. Red wolves form groups consisting of the breeding pair and their sexually immature offspring (Phillips et al. 2003) and groups may include helpers at the den (Sparkman et al. 2010), which are mainly offspring from previous years.

In this study, 2 unrelated male red wolves using a shared area (Chadwick et al. 2010) were monitored 5 times per day for 12 months using GPS collars. The purpose was to determine if the non-breeding male was a member of the group composed of the breeding male and an uncollared female. I hypothesized that association between the males would be high if the non-breeder was a member of the group, whereas there would be no significant association if the non-breeder was simply using the same area. If the unrelated non-breeder was a group member, this represents a unique pack composition that has not been studied in this species.

Methods

The red wolf reintroduction area encompassed approximately 688,000 ha in 5 counties on the Albemarle Peninsula in northeastern North Carolina (Figure 2:1). This area includes the ARNWR and Pocosin Lakes National Wildlife Refuges and private lands (USFWS 2007).

Two adult male red wolves (referred to herein as the breeder, 11326M, and the non-breeder, 11373M) were outfitted with Lotek Model 4400S GPS collars (Lotek

Wireless Inc., Ontario, Canada). These collars contain a GPS receiver and VHF and UHF tracking beacons. The VHF signal was used to track the animals and the UHF signal to download the data. The collars collected locations every 4 hours over a 16-hour period: 20:00, 24:00, 04:00, 08:00, and 12:00 (1 hour later during daylight savings time). The 2 wolves were born in 2004 and based on birth and den records, were not related (USFWS unpublished data). However, the non-breeder was the brother of the uncollared female that bred with 11326M (USFWS personal communication). The breeding male and this uncollared female formed a group and produced 3 offspring in 2008 but no offspring in 2007. The 2 males were released on 31 March 2007 and their GPS collars collected simultaneous locations until 23 May 2008. For this study, data prior to 30 May 2007 was not included due to possible short-term effects of capture (Chadwick et al. 2010) and in order to confine the analysis to 1 complete year.

The first measure of association in this study, the shared home range area, was the geometric mean of the ratio of overlap area to home range area (Minta 1992). This analysis produced a percent shared area for each individual wolf. The second measure of association was the mean separation distance. This measure was calculated by time of day and by nocturnal (20:00-04:00) and diurnal (08:00-12:00) time periods. Finally, I calculated a coefficient of association: $C_A = 2AB/(A+B)$ (Cole 1949, de Almeida Jacomo et al. 2009), where A is the total number of times animal A is observed, B total number of times animal B is observed, and AB the total number of times they are observed together. A $C_A > 0.5$ indicates association, and I used a separation distance of < 100 m as the threshold for defining when the 2 wolves were considered together (Demma et al. 2007).

Average C_A value, C_A values by time of day, and nocturnal versus diurnal C_A values were calculated.

For each calculated measure of association between the 2 males, the GPS data were grouped into 6 equal 2-month periods. The unit of measurement for each variable was set at 10 days because this window of time identified short-term spatial and temporal variation, but still maintained the ≥ 30 observations required for accurate fixed kernel home range estimates (Seaman et al. 1999). Therefore, each 2-month period of analysis consisted of 6 10-day windows of data. Home ranges were calculated by fixed kernel density estimate using the Hawth's Tools extension in ArcGIS 9.3 (Beyer 2004) and home ranges were defined by the 95% contour (Powell 2000). For all statistical tests, α was set at 0.05 except for multiple comparisons, when adjusted *P*-values were calculated using the false discovery rate (FDR) (Benjamini and Hochberg 1995).

Results

The total numbers of GPS points collected were 1,569 for the breeder (87.2% observation rate) and 1,562 for the non-breeder (86.8% observation rate), and a total of 1,434 locations were collected simultaneously. Both wolves had similar changes in home range areas, including a decline in home range areas during April-May 2008 and larger home range areas during February-March 2008 relative to most other observation periods (Table 2:1). There was significant variation in home range size during the study (breeder, ANOVA test: $F_{5,30} = 3.7$, $P = 0.01$; non-breeder, ANOVA test: $F_{5,30} = 6.5$, $P = 0.0003$) and post hoc Tukey's HSD comparisons indicated this difference was attributed to multiple observation periods (Table 2:1). Notably, the non-breeder experienced a significant decline in home range area between February-March 2008 (breeding season) and April-May 2008 (pup-rearing season) (Kelly et al. 2004), while the breeder did not. The percent shared home range area between the wolves ranged from nearly 60% to over 80%, but there was no significant variation over the study periods (breeder, Kruskal-Wallis test: $H_{5,30} = 8.0$, $P = 0.15$; non-breeder, Kruskal-Walis test: $H_{5,30} = 3.0$, $P = 0.70$).

The separation distance between the wolves decreased post-release through December 2007-January 2008 when it reached a minimum, and then increased during February-March 2008 and April-May 2008. By time of day, separation distance was consistently largest at 12:00 and at a minimum at 24:00 and 04:00 in December 2007-January 2008. Mean separation distance between the study periods was significantly different (ANOVA test: $F_{5,30}$=3.4, $P = 0.01$) (Figure 2:2a) and post hoc Tukey's HSD comparisons revealed the increase in separation distance between December 2007-January 2008 and February-March 2008 was significant. Mean separation distance by time of day varied significantly at 24:00 (Kruskal-Wallis test: $H_{5,30} = 12.2$, $P = 0.03$) and 04:00 (Kruskal-Wallis test: $H_{5,30} = 15.9$, $P = 0.007$) time periods (Fig 2:2b). Mean nocturnal separation distances were not significantly different from diurnal distances (Mann-Whitney U-test: $Z = 1.67$, $P = 0.09$).

Average C_A values were greater than 0.5 during October-November 2007 and December 2007-January 2008 and for all times of day in only December 2007-January 2008. C_A values were less than 0.5 for all time periods immediately post-release in June-July 2007 and again from February-May 2008. The decrease in average C_A between December 2007-January 2008 and April-May 2008 was significant (ANOVA test: $F_{5,30} = 4.28$, $P = 0.005$). There were also significant changes in C_A values at 20:00, 04:00, and 08:00 (20:00, Kruskal-Wallis test: $H_{5,30} = 15.5$, $P = 0.008$; 04:00, Kruskal-Wallis test:

$H_{5,30}$ = 20.5, $P = 0.001$; 08:00, Kruskal-Wallis test $H_{5,30}$ = 14.5, $P = 0.0125$) (Figure 2:3) (Table 2:3a). C_A values during nocturnal time periods were greater than 0.5 more often than during the diurnal time periods (Mann-Whitney *U*-test: $Z = 4.24$, $P < 0.0001$) (Table 2:3b).

Discussion

This is the first red wolf study that compares the annual spatial and temporal association of 2 non-kin male red wolves. Based on these analyses, it appears that the non-breeding male wolf is a member of the group consisting of the breeding male and uncollared female. This conclusion is based on the extensively overlapping home range areas, similar pattern of home range area change, close proximity of the wolves during the majority of the study and high C_A values during most of the non-breeding season (August – January) (Kelly et al. 2004). As previously reported, wolf 11373M is related to the uncollared female that bred with 11326M, which likely explains why he was accepted into this group. This group structure is supported by other canid pack studies (Girman et al. 1997, Mech and Boitani 2003, Grewal et al. 2004).

Both males remained in close proximity and used the same area during the entire study period. The non-breeder did not attempt to disperse, form a separate home range area, or expand into neighboring regions. There were other wolf groups to the south of the study group and barriers also existed to the north east. The western boundary consisted of managed timber, which is less preferred red wolf habitat (Hinton 2006) and did not contain red wolf groups. These barriers may have inhibited the non-breeder from leaving the study area. However, the GPS data did not show any extraterritorial movements, dispersal events, or prolonged separation between the wolves to suggest that the non-breeder attempted to leave the area. This further supports his inclusion as a member of the family group.

The home range areas of the wolves overlapped extensively for most of the study periods. The reduction in home range size and shared area for both wolves in April-May 2008 can be attributed to the birth of the pups on 14 April 2008. Only the non-breeder had a significant decline in home range area during the pup-rearing season and he restricted his movements to the den area during this time period. The breeder, although his home range area declined in relation to other periods, did not appear to restrict his movements to the den. Studies of gray wolf pup attendance support restricted movement by non-breeding group members that remain closer to the den (Jedrzejewski et al. 2001) and red wolf groups can contain helpers (Sparkman et al. 2010). Based on these results, the non-breeder may have been a helper at the den.

The separation distance and C_A values support a significant decline in association beginning with the breeding season (February 2008) and continuing through the pup-rearing season (April-May 2008). However, the home range areas and percent shared areas do not reflect this decline in association; this suggests that although the wolves are still using the same areas, they are not together as often compared to August 2007-January 2008. The decrease in association can be attributed to the non-breeding male’s decreased mobility, while the breeder remained relatively active within his average annual home range area.

When the C_A values were greater than 0.5, the wolves showed a preference for interacting during the overnight hours. These results and the separation distance results confirm that red wolves are nocturnal (Kelly et al. 2004, Hinton and Chamberlain 2010), and indicate that the wolves spend more time less than 100 m apart and associate more often during nocturnal time periods. During these times, the wolves may be engaged in activities together, such as maintaining their home range boundaries or hunting, and multiple wolves operating together as a group or coalition may be beneficial for these activities (USFWS unpublished). Estimates of gray wolf kills suggest most prey were killed within 3 hours of sunrise and sunset (Theuerkauf et al. 2003). No direct observations of the wolves in this study exist during these time periods to confirm activities.

The observations documented in this study are the first to provide details on a red wolf group that includes a non-kin member and evidence that this group composition exists for red wolves. However, additional data is needed from the red wolf population to determine if varying group compositions exist elsewhere or if shared home range areas and group members other than offspring are common throughout the population.

Tables and Figures

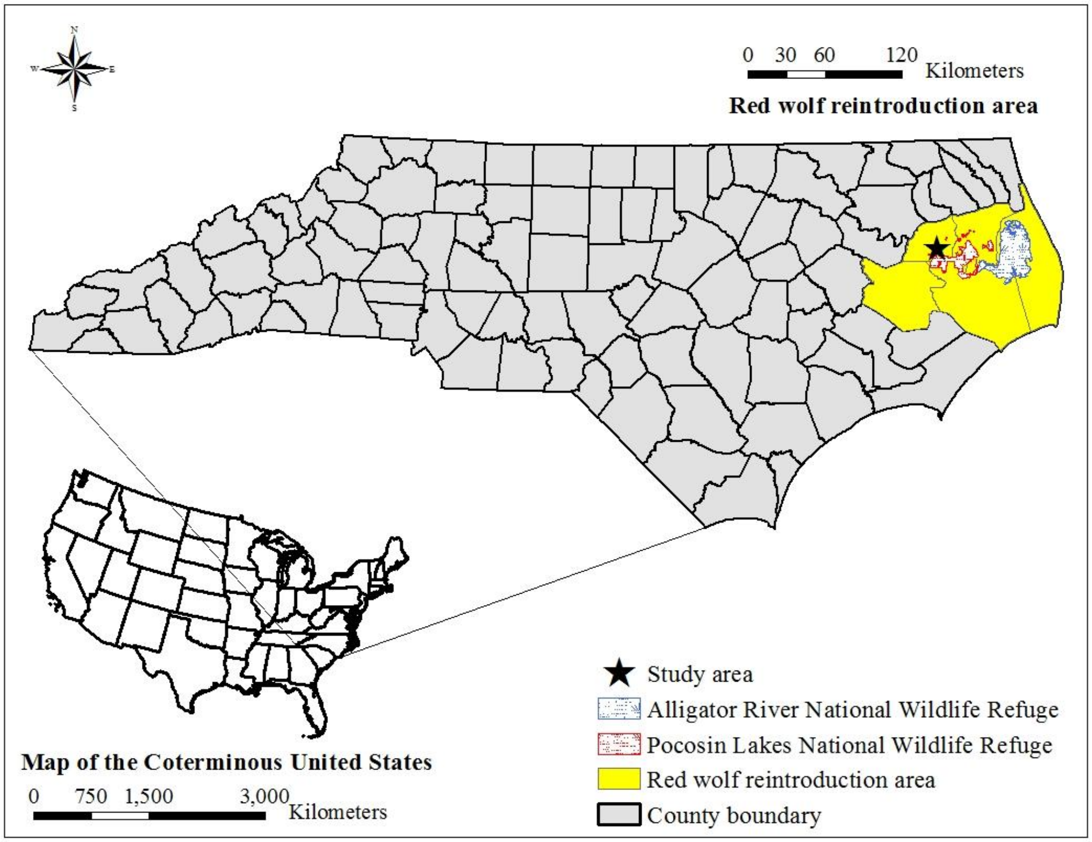


Fig 2:1. Red wolf (*Canis rufus*) reintroduction area on the Albemarle Peninsula in eastern North Carolina, U.S.A. The original reintroduction sites included the Alligator River (ARNWR) and Pocosin Lakes (PLNWR) National Wildlife Refuges. The location of the 2 GPS collared adult male red wolves in this study is indicated by the black star.

Table 2:1. Average 2-month home range size (km^2 ± SD) of 2 male red wolves (*Canis rufus*) on the Albemarle Peninsula, NC, USA, from June 2007 - May 2008.

Wolf	Jun-Jul 2007	Aug-Sep 2007	Oct-Nov 2007	Dec 2007-Jan 2008	Feb-Mar 2008	Apr-May 2008
11326M	55.3 ± 19.3*, **	70.1 ± 30.0	102.2 ± 23.2*	80.0 ± 21.4	108.1 ± 22.6**	68.3 ± 36.8
11373M	44.3 ± $14.9^{1,2}$	73.7 ± 20.4	103.5 ± $24.1^{1,3}$	80.7 ± 25.6	98.2 ± $15.5^{2,4}$	57.1 ± $28.2^{3,4}$

*P = 0.04, **P = 0.02

^1P = 0.0008, ^2P = 0.003, ^3P = 0.01, ^4P = 0.03

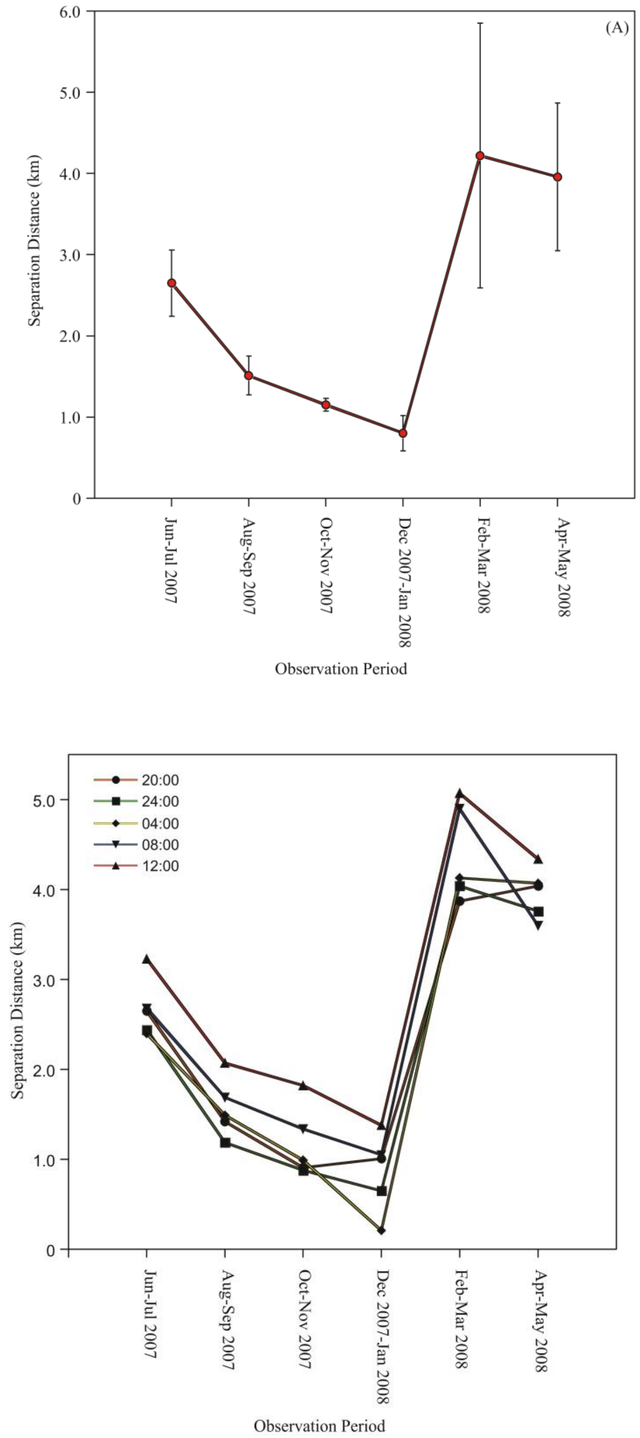


Figure 2:2. Mean separation distance (km) between the 2 male red wolves (*Canis rufus*) (A) during each 2-month observation period from June 2007 - May 2008 and (B) by time of day during each 2-month observation period from June 2007 - May 2008 on the Albemarle Peninsula, NC.

Table 2:2. Significant average 2-month separation distances (km) by time of day between 2 male red wolves (*Canis rufus*) on the Albemarle Peninsula, NC, USA, from June 2007 - May 2008.

Time	Jun-Jul 2007	Aug-Sep 2007	Oct-Nov 2007	Dec 2007-Jan 2008	Feb-Mar 2008	Apr-May 2008
24:00	2.44 ± 0.36*, **	1.19 ± 0.31	0.88 ± 0.20*	0.65 ± 0.26**, ***	4.04 ± 1.70	3.76 ± 0.92***
04:00	2.40 ± 0.50^{1}	1.49 ± 0.42	0.99 ± 0.17^{2}	0.21 ± $0.09^{1,2,3}$	4.13 ± 1.72	4.07 ± 0.94^{3}

**P* = 0.006, ***P* = 0.006, ****P* = 0.02; significant at adjusted *P*-value < 0.03

$^{1}P = 0.01$, $^{2}P = 0.01$, $^{3}P = 0.004$; significant at adjusted *P*-value < 0.0125

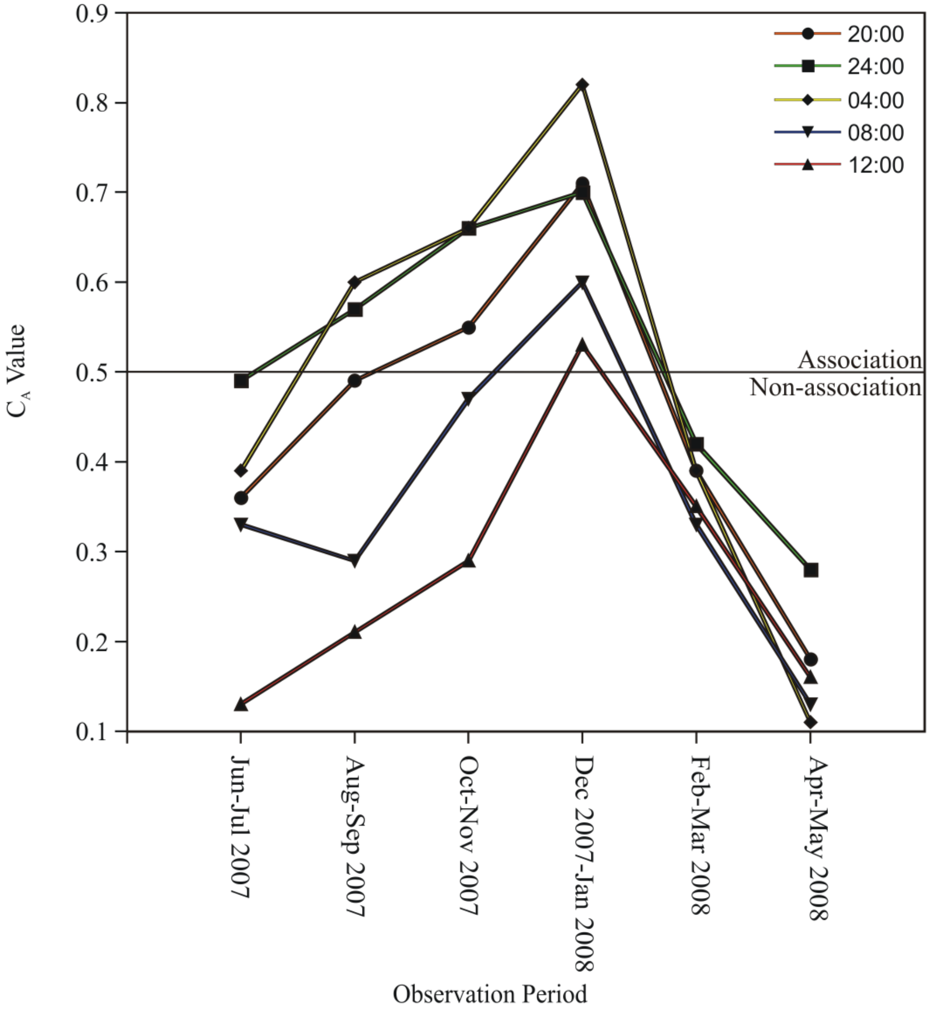


Figure 2:3. Mean C_A values by time of day for 2 male red wolves (*Canis rufus*) on the Albemarle Peninsula, NC, USA, from June 2007 - May 2008.

Table 2:3a. Significant average C_A values by time of day between 2 male red wolves (*Canis rufus*) on the Albemarle Peninsula, NC, USA, from June 2007 - May 2008.

Time	Jun-Jul 2007	Aug-Sep 2007	Oct-Nov 2007	Dec 2007-Jan 2008	Feb-Mar 2008	Apr-May 2008
20:00	$0.36 \pm 0.13^{*}$	0.49 ± 0.09	0.55 ± 0.08	$0.71 \pm 0.11^{*, **}$	0.39 ± 0.42	$0.18 \pm 0.24^{**}$
04:00	0.39 ± 0.11^{1}	0.60 ± 0.11^{2}	0.66 ± 0.12^{3}	$0.82 \pm 0.17^{1,4}$	0.39 ± 0.41	$0.11 \pm 0.17^{2,3,4}$
08:00	0.33 ± 0.35	$0.29 \pm 0.08^{\circ}$	0.47 ± 0.14	$0.60 \pm 0.11^{\circ, \circ\circ}$	0.33 ± 0.38	$0.13 \pm 0.20^{\circ\circ}$

$^{*}P = 0.006$, $^{**}P = 0.008$; significant at adjusted P-value < 0.0125

$^{1}P = 0.004$, $^{2}P = 0.004$, $^{3}P = 0.004$, $^{4}P = 0.004$; significant at adjusted P-value < 0.005

$^{\circ}P = 0.004$, $^{\circ\circ}P = 0.006$; significant at adjusted P-value < 0.0125

Table 2:3b. Percentage of average C_A values between 2 male red wolves (*Canis rufus*) on the Albemarle Peninsula, NC, USA, from June 2007 - May 2008 during nocturnal and diurnal time periods that were greater than 0.50, indicating positive association.

	Jun-Jul 2007	Aug-Sep 2007	Oct-Nov 2007	Dec 2007-Jan 2008	Feb-Mar 2008	Apr-May 2008
Nocturnal	22.2%	50.0%	72.2%	100.0%	38.9%	16.7%
Diurnal	5.6%	0.0%	16.7%	44.4%	16.7%	0.0%

CHAPTER 3: RED WOLF NATAL DISPERSAL CHARACTERISTICS: COMPARING PERIODS OF POPULATION INCREASE AND STABILITY

Abstract

I analyzed natal dispersal characteristics for 79 red wolves in the first long-term dispersal analysis for this species. Variables analyzed included straight-line dispersal distance, duration, timing, age, direction, and evidence of natal habitat preference induction of dispersers. I compared these values during a time when the population was increasing (1990-1998) to a period when the numbers had leveled off (1999-2007) and stabilized. I found no difference in average dispersal distance, duration, or age between the 2 periods, and no gender bias in these characteristics. Yearlings/adults dispersed shorter distances (29.5 km) than pups (42.5 km) from 1999-2007 and decreased their dispersal distances during this period. After 1999, dispersals occurred 11 months of the year (compared to 7 months in 1990-1998) and the peak in pup dispersal timing shifted from December to January. The peak in dispersal timing was also significantly later for pups than yearlings/adults in 1999-2007. Dispersal direction was not random and there was a preference for a westward dispersal direction, attributed to a preference for agricultural habitat. Natal habitat preference was evident in dispersers from 1990-1998, with 78% of dispersers selecting areas with habitat similar to their natal range. From 1999-2007, this decreased to only 35%.

Introduction

The United States Fish and Wildlife Service (USFWS) listed the red wolf (*Canis rufus*) as an endangered species in 1967 and a formal recovery program for the species began in 1973 (USFWS 1989). By that time, however, the wolf had already been extirpated from most of its range (McCarley and Carley 1979). Only 1 wild population of red wolves currently exists, reintroduced in 1987 to the Alligator River National Wildlife Refuge (ARNWR) and Pocosin Lakes National Wildlife Refuge (PLNWR) on the Albemarle Peninsula in northeastern North Carolina (Figure 3:1). The population has varied between 114 and 130 individuals during 1997-2009 calendar year counts (USFWS 2009).

In wolf populations, dispersal is the primary means by which the population expands its range (Blanco and Cortes 2007). Wolf dispersal is influenced by a variety of factors, including social organization (Hamilton 1964, Greenwood 1980) or colonization opportunities (Fritts and Mech 1981) and is a response to competition for food and mates (Boyd and Pletscher 1999). Two types of dispersal are recognized in wolves. Natal dispersal is the movement of an individual from its natal group to its first breeding group, while breeding dispersal is movement between consecutive breeding groups by an adult breeder (Gese and Mech 1991, Boyd and Pletscher 1999, Blanco and Cortes 2007). Factors affecting dispersal in yearling gray wolves include density of intraspecific competitors, access to mates and access to resources (Boyd and Pletscher 1999). There is also evidence that dispersing canids are influenced by their natal habitat type and settle in areas with similar habitat types (Geffen et al. 2004, Pilot et al. 2006, Musiani et al. 2007, Sacks et al. 2008), known as natal habitat preference induction (NHPI) (Davis and Stamps 2004).

Only 1 prior study has been conducted regarding dispersal behavior in red wolves; Phillips et al. (2003) examined 18 dispersing red wolves from 1987-1994 during the first eight years of the reintroduction. This small study revealed a lack of sex bias among dispersers and an average dispersal age of 27 ± 9 months for males and 23 ± 10 months for females. The study documented early dispersal of pups following the disruption of social bonds between the adults and the pups. Red wolf dispersals occurred from September – March, peaking between November – February. Dispersal duration averaged nine days (range = 1-44 days) and average dispersal distance was 36 ± 22 km for males and 45 ± 58 km for females. Most of the wolves dispersed in southward or westward directions and settled new, unoccupied areas.

The purpose of this study was to determine red wolf natal dispersal distance, duration, timing, age, direction, and evidence of natal habitat preference for 79 dispersers using VHF collar location data collected by the USFWS from 1990-2007. This study is the first long-term analysis of red wolf natal dispersal and establishes dispersal characteristics for red wolves. There is evidence that after growing steadily since 1987, the population stabilized after 1999 (Sparkman et al. 2010) and the red wolf management area has reached its functional carrying capacity (USFWS 2007). I divided this study into 2 periods (1990-1998 and 1999-2007), reflecting these different stages (Sparkman et al. 2010). I hypothesized that average dispersal distance, duration, and age would be greater during 1999-2007 compared to 1990-1998 due to the increased population and fewer unoccupied areas available to settle. I hypothesized that timing of dispersal would match the results reported in Phillips et al. (2003) and be similar to results for the more thoroughly studied gray wolves, since this variable is related to factors associated with the mating season (Mech and Boitani 2003) and not change with population size. I hypothesized that dispersal direction would be random since there were few barriers immediately adjacent to the established wolf groups that would prohibit dispersal. In accordance with other canid studies and NHPI, I hypothesized that land use/land cover (LULC) type in a disperser's natal home range would be similar to the LULC in the settled home range.

Methods

The red wolf management area encompassed approximately 688,000 ha in five counties on the Albemarle Peninsula in northeastern North Carolina (Figure 3:1). This area includes the ARNWR and PLNWR and private lands (USFWS 2007). LULC type was determined for each year of the study (1999-2008) using cloud-free Landsat TM satellite images acquired from U.S. Geological Survey (USGS 2011) and classified into 5 categories using heads-up digitizing. I based the LULC groups on and used for comparison purposes the 1992, 2001 and 2006 National Land Cover Database (NLCD) (USGS 2006) and grouped LULC types into urban, forest, scrub/shrub, agriculture, and wetlands.

I also analyzed habitat conditions for the red wolves in the study area based on area in agriculture and white-tailed deer population estimates. Agriculture is a preferred LULC type of red wolves (Hinton and Chamberlain 2010, Karlin and Chadwick in preparation) and white-tailed deer are a primary prey of the wolves (Phillips et al. 2003). I determined acreage of the study area in agriculture in five year estimates from 1987-

2007 using the United States Department of Agriculture, Census of Agriculture (USDA 2010) and used the number of white-tailed deer harvested in the study area from the North Carolina Wildlife Resources Commission (NCWRC) Deer Harvest Statistics by County (NCWRC 2010) as a rough approximation for the relative deer population (Evans et al. 1999). The agriculture census data showed little change in agricultural area from 1987-1997, an increase of 15% from 1997-2002, and then a decrease of 18% from 2002-2007 to below 1987 levels. The number of white-tailed deer harvested in the study area was stable during the study, averaging 6,754/year from 1990-1998 and 6,986/year from 1999-2007; regulations regarding hunting of antlered and antlerless deer were also relatively consistent since the early 1990's (NCWRC 2010). While a red wolf habitat suitability study is necessary to characterize conditions on the Albemarle Peninsula, these 2 relative measurements suggest conditions were similar between the 2 periods.

Red wolves have been monitored since their reintroduction in 1987 using VHF radio telemetry collars by USFWS biologists (USFWS 2007). VHF telemetry location data was available for a total of 347 individual wolves from 1990-2007 and I examined these data for natal dispersal events. I classified a wolf as a natal disperser if it permanently left its natal group (Boyd and Pletscher 1999). I only included successful dispersers and not wolves that died or lost radio contact while dispersing, since either event may have resulted in biased smaller estimates. The available data showed no dispersal events from 1987-1989. The natal dispersers were categorized in 2 groups for analysis: pups (< 12 months old) or yearlings/adults (≥12 months old) (Blanco and Cortes 2007); yearlings and adults were combined due to small sample sizes in the adult category (n = 3).

The management area has been monitored weekly from the ground or aircraft using standard triangulation or homing techniques (Mech 1983) with a location accuracy of approximately 100-200 m for aerial tracking (Samuel and Fuller 1996), but not every wolf was located during each monitoring session. Monitoring frequency was based on management needs, such as re-capturing a particular wolf to service a collar (USFWS personal communication). The average time interval between red wolf locations was 16.1 days from 1990-2007; from 1990-1998, location frequency averaged 8.4 days and 25.8 days from 1999-2007. For dispersal distance, timing, age, direction, and natal habitat preference, I further subset the data based on sampling interval and included wolves with intervals greater than 30 days only if the subsequent location obtained revealed that the wolf was still in its natal group and dispersal had not occurred.

I calculated dispersal distance as the straight-line distance between the center of the natal home range to the center of the settled home range or where the disperser exhibited site fidelity (Boyd and Pletscher 1999, Maehr et al. 2002, Blanco and Cortes 2007). The dispersers originated from 14 natal groups and home ranges for each group were calculated every breeding year using the minimum convex polygon (MCP) estimate (Powell 2000). There is no established minimum number of points necessary for calculating a MCP (Seaman et al. 1999), but the estimated area may stabilize with sample sizes greater than 40 (Arthur and Schwartz 1999). I included groups with at least 10 points (mean = 48, range 11-139) because I was not calculating home range area using MCP but simply using this method to estimate the center of home ranges. All home ranges, centroids of the home ranges (Figure 3:1), and distances between points were calculated using the Hawth’s Tools Extension in ArcGIS 9.3 (Beyer 2004).

Dispersal duration is the length of time over which the dispersal event and settlement occurred (Blanco and Cortes 2007) and 31 wolves were excluded from this calculation because they were not located at least every 30 days after dispersal from their natal group. The average sampling intervals for the 48 remaining wolves was 4.1 days and 9.4 days during 1990-1998 and 1999-2007, respectively. Timing of dispersal was calculated as the month when the dispersal occurred. Age at dispersal was calculated as the halfway point between the date the wolf was last located in its natal home range and the date it was first permanently located away from its natal range (Boyd and Pletscher 1999). Direction of dispersal was estimated by measuring the azimuth formed between the center of the natal home range and the center of the settled area, grouped into four directional categories: (1) north = 315° – 44°, (2) east = 45° – 134°, (3) south = 135° – 224°, and (4) west = 225° – 314° (Boyd and Pletscher 1999). I quantified the percentage of each LULC type within the home ranges to determine if the wolves were selecting to settle in habitat similar to their natal ranges.

The data was analyzed in JMP 8.0 statistical software using Mann-Whitney *U* test for quantitative group comparisons, Chi-square test for categorical observations, and when applicable, a *Z*-test to compare my results to the 1987-*1994* study (Phillips et al. 2003). A *P*-value of < 0.05 was considered statistically significant.

Results

A total of 79 natal dispersal events were recorded (41 males, 38 females) (Table 3:1). Straight-line natal dispersal distance averaged 41.0 ± 17.5 km from 1990-1998 and 34.4 ± 21.6 km from 1999-2007 and this difference was not significant (Tables 3:1 and 3:2). I identified a significant decrease in yearling/adult dispersal distances in 1999-2007 compared to 1990-1998 (Tables 3:1 and 3:2) and found from 1999-2007, yearlings/adults were dispersing shorter distances than pups. I found no gender bias in dispersal distance during either time period and no change in average straight-line dispersal distance for either gender between the periods. Dispersal distances from 1990-2007 were also similar to the results obtained from 1987-1994 (Phillips et al. 2003) (Tables 3:1 and 3:2).

Dispersal duration averaged 35.5 ± 25.4 days from 1990-1998 and 37.1 ± 33.3 days from 1999-2007 but this increase was not significant (Tables 3:1 and 3:2). I found no significant change in pup or yearling/adult dispersal durations between the 2 periods or between groups within each time period. I found no gender bias in duration and no significant change in average duration for either gender between the 2 periods. Durations calculated during both time periods were significantly greater than the results from 1987-1994 (Phillips et al. 2003) (Tables 3:1 and 3:2).

Dispersals occurred seven months of the year (September – April) during 1990-1998 and increased to 11 months (August – June) during 1999-2007 (Figure 3:2a). I compared number of dispersals occurring from September-March (Phillips et al. 2003) and there was a decline in the proportion of dispersal events during this period between the 2 periods (Tables 3:1 and 3:2). I also found a significant change in pup dispersal timing between 1990-1998 and 1999-2007 and in between pups and yearling/adults during 1999-2007. During 1990-1998, the peak of pup dispersal occurred in December and in 1999-2007, shifted to January. From 1999-2007, pups dispersed mostly during January-March, while yearlings dispersed mainly in December-January (Figure 3:2a). As seen in Table 3:1, the results obtained from 1990-1998 are relatively consistent with the estimates from the earlier study (Phillips et al. 2003); however, the proportion of dispersers from September-March in 1999-2007 was significantly less than the results from 1987-1994 (Table 3:2).

Dispersal age averaged 15.9 ± 7.3 months old from 1990-1998 and 15.3 ± 5.0 months old from 1999-2007 (Tables 3:1 and 3:2). I found a significant increase in pup dispersal age but not in yearling/adult dispersal age between the 2 periods. I found no gender bias and no significant change in average dispersal age for either gender between the periods. Average dispersal ages calculated during both periods for males, but only from 1999-2007 for females, were significantly younger than the 1987-1994 results (Phillips et al. 2003) (Tables 3:1 and 3:2). Dispersal age had a bimodal distribution for both time periods, with a peak in dispersers aged 8-9 months and 16-17 months during 1990-1998 and a peak ages 8-9 months and 20-21 months during 1999-2007 (Figure 3:2b).

The direction of dispersal was not random during either time period. From 1990-1998, there was a strong preference for westward dispersal (77.8%) and there were no eastward dispersals. From 1999-2007, the majority of dispersers still traveled westward (52.5%), but dispersers also traveled in all other directions (Table 3:3). Only 2 wolves dispersed to the west beyond the five county management area (Figure 3:3).

The major (comprising >50%) LULC type of natal and settled home ranges was agriculture during 1990-1998 (Table 3:4) and 78% of wolves (71% of pups and 82% of yearling/adults) settled an area dominated by the same LULC type as their natal home range. Of these, 61% were dispersers from agricultural areas that settled in agricultural areas. During 1999-2007, this trend weakened. Although the majority (55%) of natal home ranges was dominated by agriculture, only 44% of the settled areas were dominated by agriculture. Wetlands (20%) and agriculture/wetland mixes (16%) comprised the other major LULC types of the settled areas (Table 3:4). Also, only 38% of dispersers (39% of pups and 37% of yearling/adults) settled in areas with a LULC type similar to their natal home range, and only 30% of these dispersers were from agricultural areas and settled in agricultural areas.

Discussion

The red wolf population increased during the 1990s following the reintroduction of 63 wolves from 1987-1994 (Phillips et al. 2003) and leveled off after approximately 1999 (Sparkman et al. 2010). Although there was no significant change in average dispersal distances between the 2 periods for all wolves, yearlings/adults decreased their dispersal distances and were dispersing significantly shorter distances than pups in 1999-2007. The decrease may be attributed to the older dispersers familiarity with the local area and ability to perceive local opportunities (Mech and Boitani 2003). This may have been particularly true if areas with LULC similar to the natal sites were unavailable, and wolves had to settle in new LULC types, as in 1999-2007. The older dispersers may have more quickly accepted these local opportunities of new LULC types, leading to a decrease in dispersal distances, if they were more familiar with them due to extraterritorial forays with group members. In gray wolves, younger dispersers often travel greater distances than older dispersers, due to their unfamiliarity with the local area or feeling less secure after leaving their natal group (Mech and Boitani 2003). This same effect may be evident in the red wolf.

Dispersal duration was similar among all groups and to results obtained for gray wolves in high wolf density and agricultural areas (Fritts and Mech 1981, Gese and Mech

1991, Blanco and Cortes 2007), but much greater than the ranges reported by Phillips et al. (2003). I suspect the 1987-1994 population results give insight into the earliest conditions of the population during a unique and very low density period. As the population increased, unoccupied areas became less available and the time required for dispersers to settle changed accordingly (Fritts and Mech 1981, Messier 1985, Gese and Mech 1991). Dispersal duration did not change after the population stabilized, suggesting these values represent dispersal duration for red wolves in high density populations and potentially saturated habitat (USFWS 2007).

The timing of dispersal shifted between the 2 periods, although the sampling frequency must be considered for this variable. Dispersal events increased from 7 to 11 months of the year between the 2 periods. The increase may be due to the saturated conditions in the management area (USFWS 2007), which could lead to increased aggression over food year round (Mech and Boitani 2003), increased social group disruption events (e.g. displacement of a parent by an unrelated wolf (Phillips et al. 2003)), or increased social aggression related to breeding opportunities (Mech and Boitani 2003). If the trend of nearly year-round dispersals continues, this supports that the area is saturated, leading to competition for resources. Also, the timing of the greatest percentage of pup dispersal shifted from December to January. The sampling frequency from 1999-2007, however, was greater than during 1990-1998 which could have caused lower accuracy in the dispersal date and therefore dispersal timing. While the population was increasing, pups and yearlings/adults dispersed at similar times, but after the population stabilized, most pup dispersals occurred later than the yearlings/adults. Studies of gray wolves have found that while dispersal occurs throughout the year, pups dispersing in their first year primarily disperse from January-May and adults and yearlings disperse in the autumn and early spring (Gese and Mech 1991, Mech and Boitani 2003). These are periods of increased aggression in wolves, due to social competition related to breeding and food resources (Mech and Boitani 2003). The change in pups and yearlings/adults dispersal timing in 1999-2007 may indicate that as resources were less available and social competition increased, the yearling and adult wolves still with their natal group are the first to disperse, while the pups are allowed to remain for a few more months. Without direct observations or a significant number of corresponding observations of group members, I cannot determine if the yearlings/adults received more aggression from their group and therefore dispersed earlier, or selected to disperse and maximize their own opportunities.

Average dispersal age was similar during the study, but the age at which pups dispersed increased in 1999-2007. Dispersal age is influenced by many of the same factors as timing, mainly food abundance and competition within packs (Boyd and Pletscher 1999, Mech and Boitani 2003). When food is more abundant, gray wolves may delay dispersal (Ballard et al. 1997) leading to an increase in dispersal age. I determined that amount of area in agriculture from 1987-1992 was fairly consistent and since the red wolf population was low and food availability presumably high, this led to delayed dispersal and the older ages in the early study (Phillips et al. 2003). As agriculture decreased (2002-2007) (USDA 2010), abundance and distribution of prey likely changed. Although the white-tailed deer harvest estimates were stable, the decrease in agriculture may have caused other prey items such as raccoons, rabbits and rodents in the agricultural areas (Lee et al. 1982, Phillips et al. 2003) to change in abundance and distribution. These changes during a time of increasing wolf population may have caused the earlier dispersal ages in my study. As with dispersal duration, my results may represent average red wolf dispersal age under current stable population conditions, unlike during the first few years of the reintroduction (Phillips et al. 2003). There was no gender bias in dispersal age, similar to many gray wolf studies (Ballard et al. 1987, Boyd et al. 1995, Mech and Boitani 2003, Blanco and Cortes 2007).

I hypothesized that dispersal direction would be random because unoccupied areas were present in all directions on the Peninsula. Although the management area is bounded by water, dispersal distances and the locations of natal groups were such that wolves should not have been influenced to travel west due simply to the presence of water. Other than the wolves on the ARNWR which were constrained to initially disperse south (Figure 3:1), most dispersers could travel in any direction. My results identify a strong preference for westward dispersal which may be explained by presence of agriculture in the western part of the management area, in addition to the water barriers in the other directions (Figure 3:1). This is supported by my finding that in 1990-1998, the majority of natal home ranges and settled home ranges contained agriculture as the dominant LULC type. Wetlands and forest are considered less preferred red wolf habitat (Hinton and Chamberlain 2010) and prey availability is scarce in the managed timber areas but higher in agriculture (Lee et al. 1982, Noffsinger et al. 1984 *in* Phillips et al. 2003). Therefore, the availability of higher quality habitat with sufficient prey to the west may have been influencing dispersal direction, particularly from 1990-1998. This westward preference decreased slightly in 1999-2007, likely due to an increased number of established wolf packs to the west. The preference for agriculture in home ranges also declined during 1999-2007, with only 30% of dispersers leaving and settling in an agricultural area. In 15% of the remaining cases, the natal home range was dominated by agriculture but the dispersers settled in an agricultural mix (e.g., 50% agriculture and 50% wetland). Since a group's home range can shift based on location points used or number of group members, LULC composition of home ranges varies as well. The increase in mixed LULC types seen in the home ranges from 1999-2007 compared to 1990-1998 (Table 3:4) suggests that as the population increased, wolves were using areas with multiple LULC types due possibly to increased competition over access to preferred resources such as agriculture. The wolves may have stopped at the western boundary of the management area because large areas of wetlands and managed timber are found in this area, as well as major roads and developed areas (Figure 3:1). Studies of gray wolf dispersal show that direction is influenced by habitat type, topography, wolf density, and human density (Mech and Boitani 2003). In my study, wolf dispersal direction seemed to be influenced by habitat type and a preference for agricultural lands.

This study offers the first long-term, comprehensive analysis of red wolf natal dispersal characteristics. While the favorable habitat on the Albemarle Peninsula may be saturated (USFWS 2007), average dispersal age and distance are not significantly changing in response. The most notable changes in natal dispersal characteristics were the decrease in yearlings/adults dispersal distance, the shift in dispersal timing, and the apparent decrease in natal habitat preference from 1999-2007 which all occurred after the population stabilized. It is important to note that my results provide an understanding of red wolf natal dispersal characteristics during a period of changing conditions. The results from 1999-2007 may show dispersal characteristics in a stable, established red wolf population, which has never been possible due to the eradication of red wolves in the wild by the 1970s prior to any long-term scientific studies (McCarley and Carley 1979).

Tables and Figures

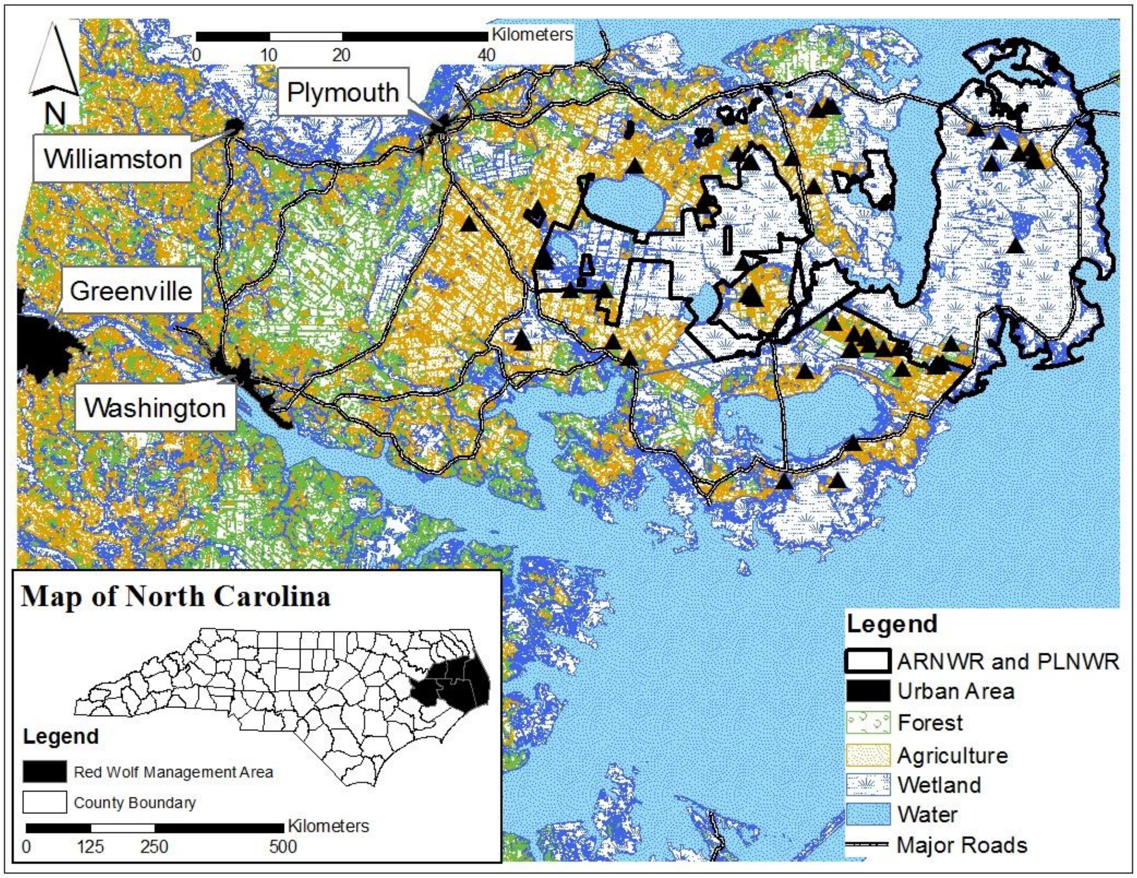


Figure 3:1. Red wolf management area on the Albemarle Peninsula, North Carolina. Black triangles represent locations of natal home ranges for dispersers from 1990-2007.

Table 3:1. Average dispersal distance, duration, timing, and age of natal red wolf dispersers on the Albemarle Peninsula, NC from 1990-2007

	Average straight-line natal dispersal distance (km)		
	1987-1994 (n=18) (Phillips et al. 2003)	1990-1998	1999-2007
Pups	n/a	35.4 + 17.4 (n=7)	42.5 + 27.1 (n=23)
Yearlings/adults	n/a	44.6 + 17.3 (n=11)	29.5 + 16.0 (n=38)
Male	36 ± 22	43.8 + 21.3 (n=11)	36.6 + 27.0 (n=30)
Female	45 ± 58	36.7 + 8.4 (n=7)	32.3 + 14.9 (n=31)
All wolves	n/a	41.0 + 17.5 (n=18)	34.4 + 21.6 (n=61)
	Dispersal duration (days)		
	1987-1994 (n=12) (Phillips et al. 2003)	1990-1998	1999-2007
Pups	n/a	52.0 + 26.4 (n=5)	54.5 + 50.3 (n=11)
Yearlings/adults	n/a	21.8 + 15.3 (n=6)	29.8 + 20.0 (n=26)
Male	n/a	38.2 + 29.2 (n=5)	29.0 + 19.0 (n=20)
Female	n/a	33.3 +24.4 (n=6)	48.4 + 44.4 (n=16)
All wolves	9 ± 13	35.5 + 25.4 (n=11)	37.1 +33.3 (n=37)
Range: all wolves	1-44	7-75	6-193
	Timing of dispersals		
Months	1987-1994 (n=18) (Phillips et al. 2003)	1990-1998	1999-2007
September - March	100%	94.4% (n=17)	75.4% (n=46)
November - February	72%	61.1% (n=11)	55.7% (n=34)
	Average dispersal age (months)		
	1987-1994 (n=18) (Phillips et al. 2003)	1990-1998	1999-2007
Pups	n/a	8.6 + 1.4 (n=7)	9.9 + 1.1 (n=23)
Yearlings/adults	n/a	20.5 + 5.4 (n=11)	18.5 + 3.4 (n=38)
Male	27 ± 8	16.2 + 7.3 (n=11)	15.4 + 5.1 (n=29)
Female	23 ± 10	15.4 + 8.0 (n=7)	15.0 + 5.1 (n=31)
All wolves	n/a	15.9 + 7.3 (n=18)	15.3 +5.0 (n=61)

Table 3:2. Statistical Results of Average Dispersal Distance, Duration, Timing, and Age of Natal Dispersers on the Albemarle Peninsula, NC from 1990-2007. Bolded entries indicate significant comparisons.

<table>
<tr><th colspan="3">Average red wolf straight-line natal dispersal distance</th></tr>
<tr><th></th><th>1990-1998</th><th>1999-2007</th></tr>
<tr><td>Pups</td><td colspan="2">$U = 0.59$, $P = 0.56$</td></tr>
<tr><td>Yearlings/Adults</td><td colspan="2">$U = 2.62$, $P = 0.009$</td></tr>
<tr><td>Pups vs. Yearlings/Adults</td><td>$U = 1.27$, $P = 0.20$</td><td>$U = 2.16$, $P = 0.03$</td></tr>
<tr><td>Male</td><td colspan="2">$U = 1.18$, $P = 0.24$</td></tr>
<tr><td>Female</td><td colspan="2">$U = 1.09$, $P = 0.27$</td></tr>
<tr><td>Male vs. Female</td><td>$U = 0.45$, $P = 0.65$</td><td>$U = 0.27$, $P = 0.79$</td></tr>
<tr><td>Male vs. Phillips et al. (2003)</td><td>$Z = 0.78$, $P = 0.45$</td><td>$Z = 0.07$, $P = 0.95$</td></tr>
<tr><td>Female vs. Phillips et al. (2003)</td><td>$Z = 0.37$, $P = 0.71$</td><td>$Z = 1.14$, $P = 0.26$</td></tr>
<tr><td>All Wolves</td><td colspan="2">$U = 1.75$, $P = 0.08$</td></tr>
<tr><th colspan="3">Dispersal Duration</th></tr>
<tr><th></th><th>1990-1998</th><th>1999-2007</th></tr>
<tr><td>Pups</td><td colspan="2">$U = 0.45$, $P = 0.61$</td></tr>
<tr><td>Yearlings/Adults</td><td colspan="2">$U = 0.82$, $P = 0.41$</td></tr>
<tr><td>Pups vs. Yearlings/Adults</td><td>$U = 1.83$, $P = 0.07$</td><td>$U = 1.81$, $P = 0.07$</td></tr>
<tr><td>Male</td><td colspan="2">$U = 0.61$, $P = 0.54$</td></tr>
<tr><td>Female</td><td colspan="2">$U = 0.70$, $P = 0.48$</td></tr>
<tr><td>Male vs. Female</td><td>$U = 0.0$, $P = 1.0$</td><td>$U = 1.64$, $P = 0.10$</td></tr>
<tr><td>All Wolves</td><td colspan="2">$U = 0.0$, $P = 1.0$</td></tr>
<tr><td>All Wolves vs. Phillips et al. (2003)</td><td>$U = 3.2$, $P = 0.004$</td><td>$U = 2.8$, $P = 0.007$</td></tr>
<tr><th colspan="3">Timing of dispersals</th></tr>
<tr><th></th><th>1990-1998</th><th>1999-2007</th></tr>
<tr><td>Pups</td><td colspan="2">$\chi^2 = 21.0$, $P = 0.0008$</td></tr>
<tr><td>Yearlings/Adults</td><td colspan="2">$\chi^2 =10.9$, $P = 0.37$</td></tr>
<tr><td>Pups vs. Yearlings/Adults</td><td>$\chi^2 = 12.5$, $P = 0.05$</td><td>$\chi^2 = 28.4$, $P = 0.002$</td></tr>
<tr><td>Male</td><td colspan="2">$\chi^2 = 8.6$, $P =0.38$</td></tr>
<tr><td>Female</td><td colspan="2">$\chi^2 = 11.9$, $P = 0.22$</td></tr>
<tr><td>Male vs. Female</td><td>$\chi^2 = 5.2$, $P = 0.51$</td><td>$\chi^2 = 11.4$, $P = 0.33$</td></tr>
<tr><td>All Wolves</td><td colspan="2">$\chi^2 = 17.4$, $P = 0.07$</td></tr>
</table>

Table 3:2 (continued)

September-March		Z = 1.8, P = 0.04	
September-March vs. Phillips et al. (2003)	Z = 1.0, P = 0.16		Z = 1.6, P = 0.01
November-February		Z = 0.40, P = 0.34	
November-February vs. Phillips et al. (2003)	Z = 0.71, P = 0.24		Z = 1.3, P = 0.11
	Average red wolf natal dispersal age		
	1990-1998		1999-2007
Pups		U = 2.4, P = 0.02	
Yearlings/Adults		U = 0.13, P = 0.90	
Male		U = 0.26, P = 0.80	
Female		U = 0.68, P = 0.50	
Male vs. Female	U = 0.32, P = 0.75		U = 0.27, P = 0.78
Male vs. Phillips et al. (2003)	U = 2.9, P = 0.01		U = 4.8, P = 0.0003
Female vs. Phillips et al. (2003)	U = 1.7, P = 0.12		U = 3.4, P = 0.002
All Wolves		U = 0.58, P = 0.56	

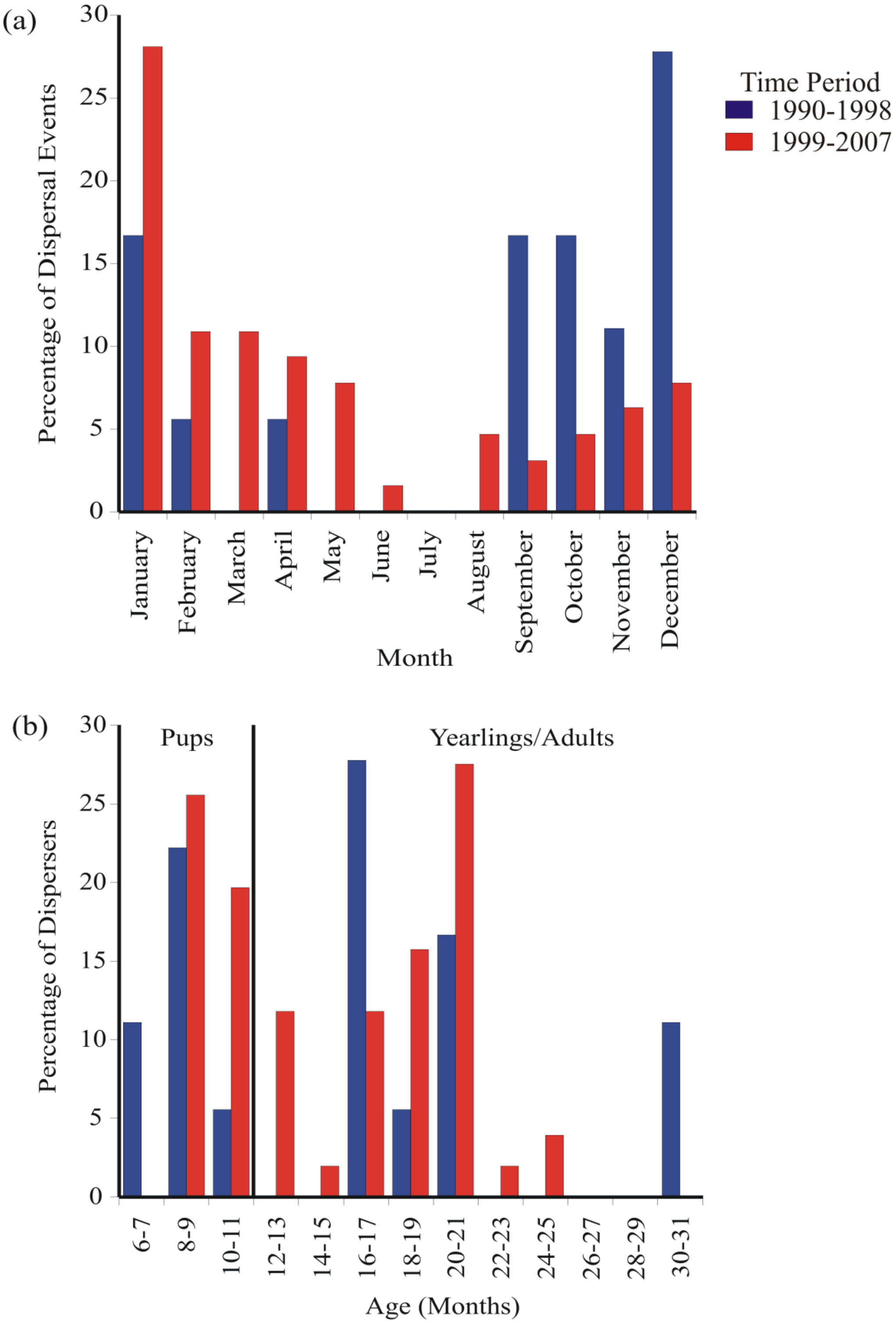


Figure 3:2 (a) Percentage of dispersing red wolves grouped by month showing the increase in number of months dispersals occurred during 1999-2007; and (b) Percentage of dispersing red wolves grouped by age showing a shift in peak dispersal age during 1999-2007 for multiple age groups

Table 3:3. Direction traveled by red wolf natal dispersers on the Albemarle Peninsula, NC from 1990-2007. Bolded entries indicate significant comparisons.

	Dispersal Direction			
1990-1998	N	S	E	W
Male	18.2% (n=2)	18.2% (n=2)	0% (n=0)	63.6% (n=7)
Female	0% (n=0)	0% (n=0)	0% (n=0)	100% (n=7)
All Wolves	11.1% (n=2)	11.1% (n=2)	0% (n=0)	77.8% (n=14)*, ***
1999-2007	N	S	E	W
Male	23.3% (n=7)	20.0% (n=6)	6.7% (n=2)	50.0% (n=15)
Female	16.1% (n=5)	25.8% (n=8)	3.2% (n=1)	54.8% (n=17)
All Wolves	19.7% (n=12)	23.0% (n=14)	4.9% (n=3)	52.5% (n=32)**,***
1990-2007	N	S	E	W
Male	22.0% (n=9)	19.5% (n=8)	4.9% (n=2)	53.7% (n=22)
Female	13.2% (n=5)	21.1% (n=8)	2.6% (n=1)	63.2% (n=24)
All Wolves	17.7% (n=14)	20.3% (n=16)	3.8% (n=3)	58.2% (n=46)

*$\chi^2 = 16.0$, $P < 0.001$; **$\chi^2 = 29.0$, $P < 0.0001$, ***1990-1998 compared to 1999-2007: $\chi2 = 4.0$, $P = 0.27$

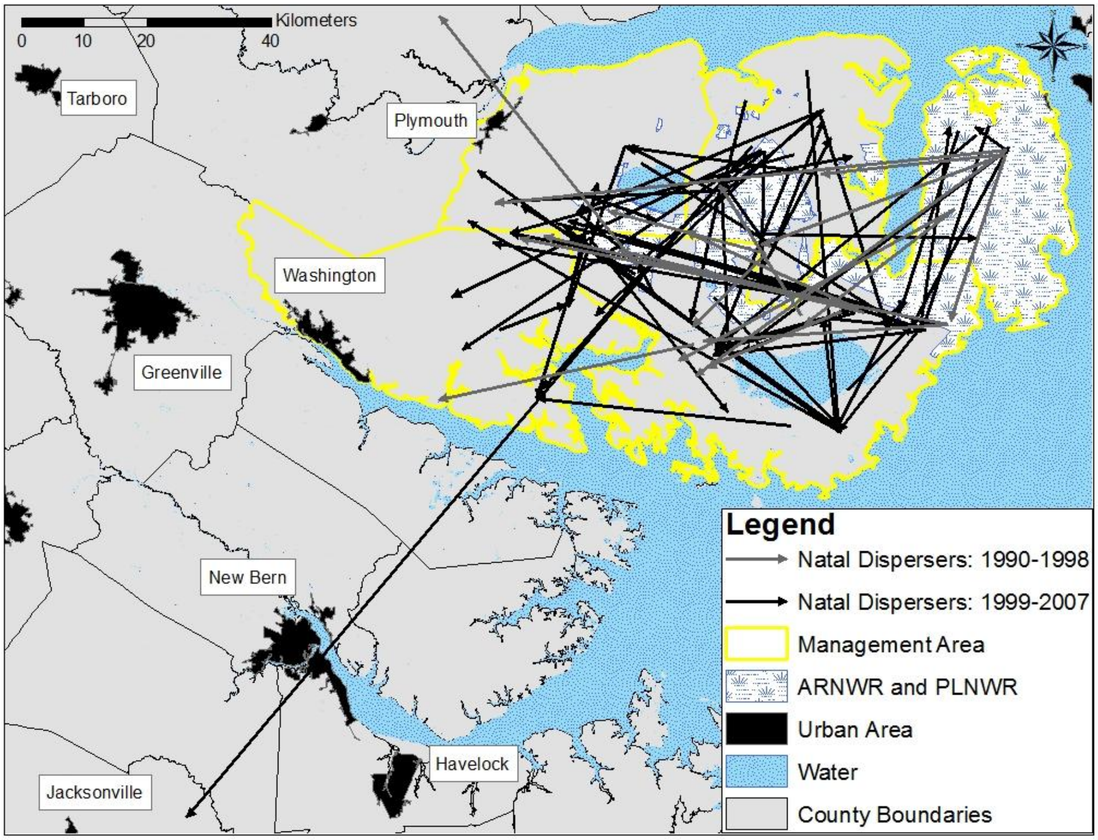


Figure 3:3. Red wolf straight-line dispersal paths on the Albemarle Peninsula, North Carolina. Gray lines and arrows represent dispersers from 1990-1998 and black lines and arrows represent dispersers from 1999-2007.

Table 3:4. Percentage of natal dispersers home range areas dominated by each LULC type on the Albemarle Peninsula, NC from 1990-2007

	1990-1998	
LULC Type	Natal Home Range	Settled Home Range
Urban	0.0	0.0
Forest	5.6	11.1
Scrub/Shrub	0.0	0.0
Agriculture	61.1	55.6
Wetland	22.2	27.8
Agriculture/Wetland Mix	11.1	5.6
Agriculture/Wetland/Forest Mix	0.0	0.0
Agriculture/Forest Mix	0.0	0.0
Wetland/Forest Mix	0.0	0.0
	1999-2007	
LULC Type	Natal Home Range	Settled Home Range
Urban	0.0	0.0
Forest	0.0	3.3
Scrub/Shrub	0.0	0.0
Agriculture	54.8	44.3
Wetland	18.0	19.7
Agriculture/Wetland Mix	21.3	16.4
Agriculture/Wetland/Forest Mix	4.9	8.2
Agriculture/Forest Mix	0.0	6.6
Wetland/Forest Mix	0.0	1.6

CHAPTER 4: PREFERRED HABITAT AND SPATIAL OVERLAP OF RED WOLVES, COYOTES, AND RED WOLF/COYOTE HYBRIDS ON THE ALBEMARLE PENINSULA, NC

Abstract

Loss of contiguous tracts of forest considered ideal for wolf (*Canis lupus* and *rufus*) populations and the increase in agricultural lands throughout the 1900s has led to decreases in wolf populations and increases in coyote (*Canis latrans*) populations. This shift has increased contact between the 2 species, and for the endangered red wolf (*Canis rufus*) has led to hybridization events. In order to provide decision-support material for red wolf conservation and establish a baseline for red wolf preferred habitat, I evaluated habitat selection by red wolves, coyotes and hybrids on the Albemarle Peninsula, NC from 1999-2008 using the species distribution modeling method maximum entropy and statistical analyses based on more than 6,000 VHF radio telemetry locations. My objectives were to measure habitat preferences of each group, identify where red wolf and coyote suitable habitat overlap occurred, and characterize the predictor variables that supported overlap between these species. I also identified overlap between red wolves and hybrids in order to determine if the hybrids select habitat similar to red wolves, coyotes, or neither. The results indicate that there is similarity in preferred resource types between these three groups based on land use/land cover, but a clear separation between red wolves and the other groups based on road and human population density. Red wolves preferred significantly lower road (average 0.18 km/km^2) and human population

densities (average 1.67 people/km^2) than hybrids or coyotes. Hybrids were tolerant of higher road densities (mean 0.30 km/km^2) and human population densities (average 4.06 people/km^2) than red wolves, while coyotes were tolerant of the highest road density of the three groups (average 0.34 km/km^2) and human population densities higher than red wolves and similar to hybrids (average 3.92 people/km^2). All groups except hybrid non-breeders preferred agricultural lands, and all groups except red wolf non-breeders and hybrid yearlings avoided wetland areas. There was 505 km^2 of overlap between red wolf and coyote suitable habitat, which represented 33% of total red wolf suitable habitat, and the majority of overlap was composed of agriculture (72%). There was 659 km^2 of overlap between red wolf and hybrid suitable habitat, which represented 43% of total red wolf suitable habitat. The majority of this overlap also occurred in agriculture and in the western part of the study area. My results suggest areas of high road and human population density may be the best indicators for targeting coyotes for management, and areas of agriculture with lower road and human population density are where the threat of hybridization between red wolves and coyotes may be greatest. Also, I characterized the habitat preferences of hybrids and determined they are tolerant of higher levels of human disturbance, as indicated by road and human population density, and are selecting habitat similar to coyotes in this study area.

Introduction

Human settlement and conversion of natural lands to agriculture resulted in a decline in wolf populations since the settlement of North America (Lehman et al. 1991, Ballard et al. 2003, Thiel 2010). Predator control programs also had a heavy hand in reducing wolf numbers in the early 1900s, but efforts since the 1980s to restore wolf populations have been faced with the remaining negative effects of habitat loss. Identifying large, contiguous areas of suitable habitat capable of supporting wild wolf populations is difficult to find in North America; the restoration of the gray wolf (*Canis lupus*) in Yellowstone National Park in 1995 is one of the great success stories of the reintroduction of native large carnivore by the United States Fish and Wildlife Service (USFWS) and National Park Service (NPS). However, with the decline of wolf populations throughout the lower 48 states for many decades and the increase in agricultural area, coyote (*Canis latrans*) populations have exploded (Bekoff and Gese 2003). While for some gray wolf populations established coyote populations may not be of great concern because gray wolves are dominant to coyotes and will reduce their numbers or competitively exclude them from access to resources (Berger and Gese 2007), for other species such as the red wolf (*Canis rufus*), habitat fragmentation and frequent contact with coyotes can lead to hybridization events, jeopardizing the genetic integrity and protection of the species (USFWS 1989, Kelly et al. 1999, USFWS 2007). In cases such as these, intense management efforts are required to sustain the population (Phillips et al. 2003, USFWS 2007).

To combat spatial and temporal interactions between interspecifics in a managed system, we need to understand the habitat preferences and resource use of each species. Focusing management and monitoring efforts on particular resources that are indicative of species presence, such as a specific land use/land cover (LULC) types, road density, or proximity to features such as urban development, can reduce time and resources spent in the field. VHF radio telemetry collars or GPS radio collars are often employed in managed wildlife populations (Bangs and Fritts 1996, Schadt et al. 2002, Phillips et al.

2003) and these technologies provide an abundance of location data to then create habitat suitability models and address management issues.

Habitat suitability for a species is based on understanding what factors contribute to its occurrence at a particular location, and identifying locations with similar habitat conditions. These models are based on hypotheses regarding relationships between the species distribution and environmental communities, and they link information on species occurrences to environmental variables present in the community (Guisan and Zimmermann 2000, Austin 2002, Guisan and Thuiller 2005, Hirzel and Le Lay 2008, Elith and Leathwick 2009). Habitat suitability models have been created for a wide range of species with a suite of environmental constraints, using presence-only, presence/absence, or presence/pseudo-absence occurrence data. VHF radio telemetry data is commonly used as the presence data for animal locations. In these situations, there are an infinite number of points in the study area that may have been used by the animal but not recorded during a sampling event; therefore, these areas cannot be defined as unused by the animal (Boyce et al. 2002). In these situations, a presence-only method for assessing habitat suitability is most appropriate.

The red wolf represents such a situation, reintroduced in 1987 to the Alligator River National Wildlife Refuge (ARNWR) and Pocosin Lakes National Wildlife Refuge (PLNWR) on the Albemarle Peninsula in northeastern North Carolina and monitored using VHF radio telemetry collars. The red wolf was extirpated from most of its historic range by the late 1960s (McCarley and Carley 1979), leading to its listing as an endangered species in 1967. The historic range consisted of much of the southeastern United States, from eastern Texas to the Atlantic coast, as far north as Maine and south to the southern tip of Florida (Nowak 2002). In 1973, the United States Fish and Wildlife Service (USFWS) began a formal recovery program for the red wolf (USFWS 1989). Currently, only the 1 wild population reintroduced in 1987 exists in the United States. The population has varied between 114 and 130 individuals during 1997 to 2009 calendar year counts (USFWS 2009). A second reintroduction in the Great Smoky Mountains National Park in 1991 was unsuccessful (Henry 1998, Lucash and Crawford 1998).

Hybridization with the increasing coyote population is a primary threat to the persistence of the red wolf population and has become a significant problem since 1994 (Phillips et al. 1995, Kelly et al. 1999). To combat hybridization, in 2000 the USFWS and the Red Wolf Recovery Implementation Team (RWRIT) created an adaptive management plan for the species, which included dividing the red wolf reintroduction area into three zones associated with non-wolf canid presence and specific management objectives (Stoskopf et al. 2005). The zones are numbered 1-3 (Figure 4:1) from east to west and management actions vary in each zone; zone 1 receives the highest level of protection in terms of management actions, which include sterilization and use of the non-wolf canid as a ‘place-holder’ until it is displaced by a red wolf, or euthanasia of the animal (Stoskopf et al. 2005, USFWS 2007).

In addition to the threat of hybridization, the level of competition for prey and habitat between red wolves and coyotes, and between red wolves and red wolf/coyote hybrid animals (herein referred to as hybrids), is unknown (Kelly et al. 2004). Red wolves are dominant to coyotes; from 1993-2007, USFWS biologists documented 32 events in which a red wolf killed or displaced a coyote or hybrid, but not one instance in which a red wolf was killed by a coyote or hybrid (USFWS 2007). Direct and indirect competition has been documented between coyotes and gray wolves, in which coyotes have been killed by wolves or avoid using certain areas or habitat types because of the presence of wolves (Peterson 1995). The degree of spatial overlap or competition for resources between red wolves and coyotes on the Albemarle Peninsula, however, has not been studied. We also have no information on the current hybrid animals, such as habitat suitability and preferred resources, which may lead to a better understanding of why red wolves and coyotes are hybridizing. Studies of habitat selection and resource use by red wolves, hybrids and coyotes are imperative in order to understand if the groups are competing spatially for particular resources and if so, to use this information for management purposes such as targeting areas for increased coyote management, or improving or increasing areas of preferred red wolf habitat. Additionally, information on resource use and habitat selection can be used to predict other areas of suitable red wolf habitat in its historic range, which is a prerequisite for additional populations to be reintroduced (van Manen et al. 2000, USFWS 2007).

In this study, I evaluated habitat selection by red wolves, hybrids, and coyotes in order to assess habitat suitability and quantify spatial overlap between the groups. Because VHF radio telemetry data was used and true absence data was not available, I used a presence-only method. My goals were (1) to identify preferred habitat of red wolves, hybrids and coyotes on the Albemarle Peninsula; (2) to model habitat suitability for each group using a presence-only method; and (3) to identify the spatial overlap in resource use by coyotes and hybrids with red wolves. Although overlap between red wolf and hybrid suitable habitat is less of a management concern than overlap with coyotes, I analyzed this variable because if red wolf and hybrid overlap was significant, this may indicate if hybrids are selecting habitat like red wolves or more like coyotes.

I analyzed the results by management zone to determine if greater areas of habitat suitability and therefore potential conflict areas varied by zone. I hypothesized that coyotes would be tolerant of areas with greater human presence and therefore use areas of higher road and human population densities because they are habitat generalists and can adapt to most environments (Gese and Bekoff 2004), while hybrids and red wolves would prefer areas with relatively lower road and human population densities. I hypothesized that the preferred LULC type and the greatest areas of both suitable habitat and spatial overlap between the groups would be in agriculture, because smaller prey density (e.g., rodents and rabbits) should be higher in this LULC type (Phillips et al. 2003, Atwood et al. 2004, Brinkman et al. 2004) and it may be a preferred red wolf LULC type (Chadwick et al. 2010, Hinton and Chamberlain 2010).

Study System

The red wolf management area encompasses approximately 688,000 ha in five counties on the Albemarle Peninsula (referred to herein as Peninsula) in northeastern North Carolina (Figure 4:1). The Peninsula is characterized by areas of generally low road density and human population density, with agriculture and wetlands representing the major LULC types (Figure 4:2). Average road density in both the agriculture and wetland areas on the Peninsula was 0.23 km/km^2 in 2008, and average human population density was 9.07 $people/km^2$ and 4.13 $people/km^2$ in agriculture and wetlands, respectively, as of the 2000 census data (US Department of Commerce 2000). The Peninsula includes the ARNWR and PLNWR and private lands (USFWS 2007). Land cover in the refuges is predominately wetlands, such as pocosin wetlands, hardwood and Atlantic white cedar swamps, and marshes. Surrounding private lands consisted of agriculture, managed timber and rural development. White-tailed deer (*Odocoileus virginianus*) use forest and wetland areas for cover, while the agriculture and wetland areas provide them a food source (Fleming et al. 2004). The agriculture areas also provide cover to a variety of smaller animals, such as rodents and rabbits (Phillips et al. 2003).

I analyzed habitat suitability for red wolves, hybrids and coyotes by management zone to complement management actions and decisions in these respective zones. Also, because the study area is a Peninsula, coyotes entering the red wolf management area will come from the west and enter zone 3, while zone 1 will be the furthest east in the management area that the coyotes could penetrate. Therefore, the amount of suitable habitat overlap between the groups may be influenced by the fact that the study area is a peninsula. The proportion of LULC types found in each zone also varies considerably: zone 1 includes the ARNWR and consists mostly of wetlands; zone 2 includes portions of both the ARNWR and PLNWR and major LULC includes wetlands and agriculture; and zone 3 includes a portion of the PLNWR and the main LULC types area agriculture, wetlands, and forest.

Methods

Data Collection

Species Data

Red wolves, hybrids and coyotes were captured by the USFWS biologists using padded No. 3 foot-hold traps and fitted with mortality-sensitive VHF radio telemetry collars (Telonics, Inc., Mesa, AZ) for monitoring and to meet red wolf management objectives (USFWS personal communication). Animals were monitored from the ground or aircraft using standard triangulation or homing techniques (Mech 1983) with a location accuracy of approximately 100-200 m for aerial tracking (Samuel and Fuller 1996). Monitoring frequency for each animal was based on management needs, such as re-capturing a particular individual to service a collar; therefore, every animal was not located during each monitoring event (USFWS personal communication). Red wolves have been monitored since 1987 and hybrids and coyotes have been monitored since 1999 (USFWS unpublished data); in this study, I included data from 1999-2008. The sampling interval during the study period was 6 days for red wolves, 8 days for hybrids, and 18 days for coyotes.

I divided red wolves, hybrids and coyotes into groups based on social class, which were determined by USFWS biologists collecting the location data (USFWS unpublished data). Red wolves were grouped into four social classes: breeders (>24 months old), non-breeders (>24 months old), yearlings (12-24 months old), and pups (< 12 months old) (Kelly et al. 2004). Hybrids were grouped into four social classes: breeders, non-breeders, unknown and yearlings, while coyotes were only identified as belonging to 2 possible classes: breeders or unknown. The unknown social class refers to an animal that cannot be accurately described as a breeder or non-breeder, based on observations recorded by USFWS biologists. In terms of canid hierarchy, breeders are adults that are paired with another breeder and in some literature are referred to as the alpha group members (Packard 2003). Non-breeders are adults that have not paired with another wolf; these may be considered as subordinate members in terms of a pack’s social status (Packard

2003), or may be adults that are not members of a social group. Because red wolf pups are not radio collared until they are at least 9 months old due to safety concerns (Hinton and Chamberlain 2010), the results in this study are only applicable to red wolf pups aged 9-11 months. Through these procedures a total of 6,618 VHF telemetry locations were collected for 279 red wolves, 77 hybrids and 39 coyotes from 1999-2008 (Table 4:1).

Red wolves on the Peninsula prey largely on white-tailed deer, raccoon, and rabbits, and exhibit resource partitioning within packs (Phillips et al. 2003). In general, wolves do not prefer a specific type of landcover; as long as prey and cover is sufficient, they may use an area (Fuller et al. 2003). The last red wolves removed from the wild in Texas and Louisiana in the 1980s were captured in what was considered marginal habitat, mainly wetland areas (Phillips et al. 2003). Red wolves are likely habitat generalists, needing areas with suitable cover and prey and minimal human disturbance (Kelly et al. 2004). Coyotes are habitat generalists, utilizing almost all available habitats including some urban areas (Gese and Bekoff 2004). They are also opportunistic, generalist predators, eating human-related items, fruit, insects, carrion and small mammals depending on availability (Gese and Bekoff 2004). There is evidence that the agricultural practices which resulted in loss of forest cover created favorable habitat for coyotes; this also created opportunities for increased contact between coyotes and wolves, and therefore potential for hybridization (Ballard et al. 2003, Thiel 2010). Based on the large areas of agriculture on the Peninsula, a high degree of habitat and prey species overlap may be expected between red wolves and coyotes in this system.

Predictor Variables

Predictor variables used to measure habitat selection included five categories of LULC type, road density, and human population density. LULC type was determined for each year of the study (1999-2008) using cloud-free Landsat TM satellite images acquired from U.S. Geological Survey (USGS 2011) and classified into 5 categories using heads-up digitizing. I based the LULC groups on and used for comparison purposes the 1992, 2001 and 2006 National Land Cover Database (NLCD) (USGS 2006) and grouped LULC types into urban, forest, scrub/shrub, agriculture, and wetlands. I created a binary raster file of each LULC type to determine the contribution of each in the habitat suitability models. Therefore, I had 5 categorical LULC layers (Figure 4:2a).

Road density was also determined for each year of the study. I overlaid an existing 2008 road layer (NCDOT 2010) on the Landsat TM satellite image for each year to determine which roads were present in each respective year. I then created a road density layer (total distance of roads/km^2) for each year using the kernel density function in ArcGIS 10.0 (ESRI 2011) and a 3 km search radius (Belongie 2008) (Figure 4:2b).

Finally, human population density was based on the 2000 census block (US Department of Commerce 2000) data. The total number of people reported per census block and the area of the census block were used to calculate the population density, reported as people/km^2 (Figure 4:2c). The spatial resolution of all predictor variables was 30 m. The boundary of the three management zones were digitally created in ArcGIS 10.0 based on the boundaries described in Stoskopf et al. (2005) (Figure 4:1).

Statistical Analysis of Habitat Selection

I conducted a statistical analysis of road and human population density preferences for each group by comparing the VHF telemetry points as the presence points with 20,000 random values generated in ArcGIS 10.0 (ESRI 2011) as the background points. I masked out water from the LULC images so that random background points would not be selected from these areas. I partitioned the 20,000 random background points for each group throughout the entire study period based on the number of presence points for the given species/social class and year in order to keep the prevalence, the ratio between presence and background points, the same for all groups. For example, if 15% of presence points for red wolf breeders from 1999-2008 were from 1999, I generated 3,000 (i.e., 15% of 20,000) background points for red wolf breeders in 1999. Because the presence data were not normally distributed, I used the non-parametric Mann-Whitney *U* test for comparisons of presence values versus random background values and the Kruskal-Wallis Test for comparisons between groups. I used JMP 8.0 (SAS 2009) for all statistical analyses and considered $p < 0.05$ as significant. For LULC type selection, I used the Bonferroni confidence intervals to determine LULC type preference, avoidance, or random use (White and Garrott 1990), based on the proportion of locations in each LULC type and the available proportion of each LULC type on the Peninsula.

Habitat Suitability Models

Calibration

I evaluated habitat suitability using the maximum entropy (MaxEnt) method (Phillips et al. 2006). MaxEnt is a machine-learning method that estimates species' distributions by finding the probability distribution that is closest to uniform, based on a set of constraints. These constraints represent some information that is known about the species, and are features such as environmental variables or functions of environmental variables (e.g., soil, elevation, vegetation type). The constraints in MaxEnt are that the expected value of each feature included in the model should match the average value for a set of sample points taken from the species of study (Phillips et al. 2006, Phillips and Dudik 2008, Elith et al. 2011). In this study, features were measured at both the VHF telemetry location data collected for the red wolves, hybrids and coyotes (i.e., the presence data) and at the 20,000 random background values (i.e. the background, or available data) generated in ArcGIS 10.0 (ESRI 2011) and used in the statistical analyses.

I first created MaxEnt models using all the VHF telemetry locations for a given group to evaluate overall species habitat suitability, 1 model each for red wolves, hybrids and coyotes. I then subdivided the species data into social classes and created habitat suitability models for each social class. I extracted the values of the seven predictor variables (five LULC categories, road density, and population density) at each location and random background point for the corresponding year.

The presence data and accompanying predictor variable values and the random background data and accompanying predictor variable values were input into the MaxEnt model as the sample file and background data, respectively. I calculated the probability distribution as the sum of each weighted variable divided by a scaling constant to ensure the output range was between 0 and 1. Using the MaxEnt software version 3.3.3, I selected 500 iterations for model convergence and employed the regularization procedure to prevent overfitting (Phillips and Dudik 2008). The habitat suitability model outputs were projected onto year 2008 LULC, road density, and human population density layers in order to assess the suitability of the Peninsula in the most recent time period.

Validation

MaxEnt model accuracy was evaluated using the area under the curve (AUC) of the receiver operating characteristic (ROC). The AUC of the ROC is a measure of the ability of the model to discriminate between sites where the species is present and absent, and is expressed as the probability that a randomly selected presence site is ranked above a randomly selected absence site (Phillips and Dudik 2008). When absence data is not used, as in MaxEnt, the AUC is instead calculated using randomly selected background data. Therefore, the AUC is a measure of the probability that a randomly chosen presence location is ranked above a random background site (Phillips et al. 2006, Phillips and Dudik 2008). A subset (25%) of the VHF telemetry points were withheld from the model for validation. A random ranking has an AUC value of 0.5 and AUC >0.70 is considered acceptable (Hosmer and Lemeshow 2000). Although a perfect ranking using presence/absence data would receive an AUC of 1.0, this is not possible with presence-only data. Using presence-only data, the species' distribution covers a fraction a of the pixels, and the maximum achievable AUC is $1-a/2$. Since a is often unknown, the maximum achievable AUC in a presence-only model is also unknown (Wiley et al. 2003).

In order to determine which predictor variable(s) contributed the most to predicting habitat suitability, I conducted a jackknife estimation of relative importance for each predictor variable included in the model. This estimation excludes each variable 1 at a time and creates a model with the remaining variables, and also creates a model using only 1 variable at a time. These results indicate the relative contribution of each variable to the model results and the AUC plot of the jackknife tests identifies the effectiveness of each variable for predicting the distribution of the occurrence data used (Phillips et al. 2006).

Application

The MaxEnt habitat suitability models are expressed as a probability of occurrence, ranked from 0 to 1. To express the results in terms of habitat suitability, I first grouped the model outputs into 2 categories (suitable and unsuitable habitat) using the maximum training sensitivity plus specificity logistic threshold for each model as the division between suitable and unsuitable habitat (Liu et al. 2005). This approach minimizes both false negatives and false positives. I then equally subdivided these categories: unsuitable habitat was divided into poor suitability and marginal suitability; and suitable habitat was divided into suitable and high suitability. For each of the suitable categories, I measured the predicted area for each model and the amount of overlap of habitat between red wolves and coyotes and red wolves and hybrids, to determine if resource competition may exist between the species or resource partitioning within the social classes.

Results

Statistical Analyses

Red wolves used areas of lower road and human population density than hybrids and coyotes, and all red wolf, hybrid and coyote groups used areas of lower road and human population density compared to random, although the difference was not significant for all groups (Table 4:2). The average road density for locations used by all red wolves was 0.18 km/km^2, compared to the 0.30 km/km^2 and 0.34 km/km^2 road density used by all hybrids and coyotes, respectively. A similar trend was observed for human population density, which averaged 1.67 people/km^2 for all red wolf preferred areas but 4.06 people/km^2 and 3.92 people/km^2 for all hybrid and coyote preferred areas, respectively.

Each red wolf social class consistently used significantly lower road and human population density areas on the Peninsula. The all hybrids group, hybrid breeders and hybrid unknown social classes used areas of significantly lower road density than random, and only the hybrid unknown social class used areas of population density significantly lower than random (Table 4:2). Of the coyote groups, only the coyote unknown social class used areas of significantly lower road density than random (Table 4:2).

I found that each group except hybrid non-breeders preferred the agricultural LULC type and all groups except red wolf non-breeders and hybrid yearlings avoided wetlands (Table 4:3). All groups also avoided urban areas or exhibited random use of this LULC type, and all red wolf groups except red wolf pups avoided scrub/shrub areas. The hybrids and coyotes showed random use of scrub/shrub and forest areas, while red wolves tended to avoid or exhibit random use of these LULC types.

I found consistent differences between the road and human population densities preferred by each species/social class. All red wolves, analyzed without respect to social class, preferred significantly lower road and human population densities than all hybrids and all coyotes, but the same was not true comparing hybrids and coyotes (Table 4:4). Analyzing the groups by social class, red wolf breeders preferred lower road and human population densities than hybrid and coyote breeders, and hybrid breeders preferred significantly lower road densities than coyote breeders. Red wolf non-breeders preferred areas of lower road density than the unknown coyote group. Between red wolf social classes, red wolf breeders preferred areas of higher road density than red wolf yearlings, and red wolf breeders, yearlings and pups all preferred areas of higher road and human population density than red wolf non-breeders (Table 4:4).

Habitat Suitability Models

Overall, habitat suitability model accuracies as measured by the AUC statistics (range 0.70 – 0.74) were acceptable and showed a greater area predicted suitable for all hybrids and coyotes than red wolves (Table 4:5). In general, high suitability areas corresponded with agricultural areas and poor suitability areas corresponded with the urban areas and wetland areas surrounding rivers (Figs. 4:3, 4:4, and 4:5).

Variable Contributions

The variable that most contributed to predicting species occurrence varied between the models, as did the functional response of the species to the variable – positive or negative (Table 4:6). I considered the top three variables that contributed most (>75%) to each model. I identified a preference by all red wolves for low road density, followed by agricultural areas and low human population density, while for all hybrids, road density was most important, followed by avoidance of wetlands. In the coyote model, a preference for agriculture was most important, followed by an avoidance of wetlands and preference for lower road densities.

Examining these results by social class, I found that red wolf breeders and non-breeders had a preference for low road density and low human population density, while a preference for agriculture was most dominant for yearlings and pups. For the hybrids, the variables that contributed most varied for each social class. The breeders' avoidance of wetland areas contributed most to the models, while the non-breeders preference for low road density, unknown's preference for agriculture and yearling's preference for low human population density were most important. The most important variable for both coyote social classes, both breeders and unknown, was a preference for agriculture and avoidance of wetlands. Overall, the model including all red wolves exhibited a constant negative response to increase road density, while the model including all hybrid and hybrid breeder data showed a varying functional response (Figure 4:6a and 4:6b). These results show a preference for low road density by red wolves, but the all hybrid model and hybrid breeder model show a preference mainly for low road density (<0.75 km/km^2) but then an increase in probability of presence at higher road densities above 1.5 km/km^2. The results of the response to population density are consistent for all groups and social classes, which exhibit a preference for lower population densities.

Suitable and High Suitability LULC types

LULC type in areas predicted suitable for all red wolves included a mix of agriculture and wetlands (Table 4:7). The area predicted suitable for hybrids also included mainly agriculture and wetlands, but also forested and scrub/shrub areas, while the areas suitable for coyotes were agriculture and forest. Red wolf breeder and non-breeder suitable habitat was composed mainly of wetlands, while agriculture was the major LULC type predicted suitable for red wolf yearlings and pups, hybrid breeders and yearlings, and the unknown coyote class (Table 4:7). Forest and scrub/shrub composed a larger percentage of suitable area for red wolf pups compared to the other red wolf social classes, which may be related to red wolf pup presence consolidated near den/home site locations. Red wolf dens or home sites have been found in forest stands or brushy areas adjacent to agricultural fields (Phillips et al. 2003, Hinton and Chamberlain 2010).

The preference for agricultural LULC dominates the high suitability habitat for all groups, although wetlands compose over a third of the hybrid yearling high suitability habitat (Table 4:7).

Spatial Overlap

There was 355 km^2 and 150 km^2 of overlap in suitable and high suitability area, respectively, between red wolf and coyote habitat (Table 4:8). In each model, agriculture composed the largest percentage of this overlap, 62% of suitable area and 98% of high suitability. I found the most overlap of suitable area in zone 3 (272 km^2), which composed 45.5% of the area of red wolf suitable habitat in zone 3, and the least in zone 1 (5 km^2) (5% of the area of red wolf suitable habitat in zone 1), which is the zone with the most strict management actions for coyotes (Figure 4:7a).

The overlap of high suitability habitat was similar in zones 2 (56 km^2) and 3 (89 km^2), composing 24% and 29% of the area of red wolf high suitability habitat in zones 2 and 3, respectively, and only 5 km^2 overlap in zone 1 (5.3% of the area of red wolf high suitability habitat) (Figure 4:7b).

Overlap of suitable habitat between red wolves and hybrids was greater than red wolves and coyotes in all zones, but the same was not true for the high suitability habitat analysis (Table 4:8). The greatest overlap of suitable area occurred in zone 3 (489 km^2), which composed 81.7% of the area of red wolf suitable habitat, and the least in zone 1 (8.9 km^2) (9% of the area of red wolf suitable habitat in zone 1) (Figure 4:8a).

The overlap of high suitability habitat was also greatest in zone 3 (19.6 km^2), composing 6.4% of the area of red wolf high suitability habitat, and 10.1 km^2 in zone 2, which was 3.5% of the area of red wolf high suitability habitat (Figure 4:8b). There was no overlap of high suitability habitat between red wolves and hybrids in zone 1.

Discussion

The use and application of models to predict occurrence or habitat suitability for a species can be a first step in the management of a critically imperiled and poorly understudied species, such as the red wolf, and can be used to guide future conservation planning (Schadt et al. 2002). Measuring preferred habitat indices and modeling suitable habitat of red wolves, hybrids and coyotes provides a first glimpse of how the reintroduced red wolf is acclimating to a human-influenced landscape and to the presence of interspecifics competing for similar resources. Studies such as this offer an understanding of overall wolf ecology, which is critical to the continued management and preservation of this species in the face of hybridization.

Preferred Habitat

In the statistical analyses, I found that red wolves consistently preferred lower road and human population densities compared to both the random background values and hybrids or coyotes. Compared to what was available at random on the Peninsula, red wolves selected areas with very low road and human population densities. These results are similar to studies analyzing potential gray wolf habitat in the upper Midwest (Mladenoff et al. 1995, Mladenoff et al. 1999). In that area, suitable habitat included areas of road density < 0.23 km/km^2 in the core wolf territory and human population density < 1.52 $people/km^2$. The jackknife estimation of variable importance supports that low road density was the most important indicator for red wolf presence. Road density was also most important for hybrids, although they used areas of much higher road density than red wolves. In general, hybrids and coyotes did not show consistent preferences for lower road and human population densities and were tolerant of densities much greater than red wolves. In the analysis by social class, I also found that hybrid breeders preferred lower road densities than coyote breeders, and were therefore intermediate to red wolves in terms of road density preferences. This higher tolerance supports the established fact that coyotes are habitat generalists that can adapt to most environments (Gese and Bekoff 2004). This suggests areas of higher road and population density should be targeted for the management of coyotes, and should be the areas where red wolves are least likely to be captured. The explanation for this selection may be two-fold: (1) red wolves are dominant to coyotes and therefore may be selecting the best available resources, leaving coyotes to use the less desirable areas of higher road and human population density; and (2) coyotes are habitat generalists (Gese and Bekoff 2004) and therefore may simply be better equipped to adjust to and flourish in less desirable conditions than red wolves. If the latter is true, then this represents a threat to the red wolf population in terms of hybridization, because if red wolves are unable to inhabit the areas of higher road and human population density but coyotes can, these areas may be a continued source of coyotes on the Peninsula.

From my analysis of hybrid preferences, this group appears to be more coyote-like in its tolerance for higher road and human population densities. Although hybrids preferred lower road densities than coyotes, they were still tolerant of higher densities than red wolves and used areas of much greater human population densities than even coyotes in many cases. Therefore, they may also be better able to adapt to less than ideal conditions like coyotes. Targeting areas for management of these animals should be similar to actions taken for coyotes.

I was also interested in establishing a baseline for red wolf preferred habitat and differences between social classes for this critical species. I found that low road and human population density was most important for predicting preference by adult red wolves (breeders and non-breeders), while presence of agriculture was most important for the younger red wolves (yearlings and pups). Red wolf non-breeders appear to be the social class that deviates from the rest of the group, using areas of lower road and human population density than red wolf breeders, yearlings and pups. This can be partially explained by the red wolf non-breeders higher use of wetland areas, which have lower road and human density population than many of the other LULC types.

Areas of agriculture, wetlands, forest and scrub/shrub composed the suitable LULC types all red wolves based on the MaxEnt model results. These results are supported by what knowledge we do have of red wolves. Agriculture and wetlands are home to a variety of red wolf prey items (Phillips et al. 2003) and forested and scrub/shrub areas provide cover for red wolves when agriculture is harvested and are often associated with den sites (Chadwick et al. 2010, Hinton and Chamberlain 2010). The jackknife estimation of variable contribution and Bonferroni analysis, however, do not support a preference for any LULC type except agriculture. The red wolves exhibit avoidance or random use of wetlands, forest and scrub/shrub areas based on the Bonferroni analysis. In the jackknife estimation of variable contribution analysis, wetlands were not a significant variable in predicting red wolf presence. The Bonferroni analysis, however, considers only the proportion of presence locations and proportion of each LULC type available on the Peninsula. The MaxEnt model considers the LULC type, road, and human population densities at each presence location, and estimates habitat suitability considering all these variables combined. Therefore, the Bonferroni confidence intervals may not be as useful in predicting preferred LULC in light of the modeling results and wide range of road and human population densities present in each LULC type. The jackknife estimation of variable importance suggests that although wetlands are not a preferred LULC type, the low road and human population densities found in the wetland areas are very significant for red wolf use, making wetlands a suitable habitat.

For each red wolf species class, the major suitable LULC type varied. This may be related to different needs for each age group. Wetlands composed the majority of red wolf breeders and non-breeders suitable habitat, in addition to agriculture (Table 4:3). Phillips et al. (2003) found that red wolves in wetland areas preyed on larger prey, such as white-tailed deer and raccoons. Therefore, the adult red wolves may have been more capable of preying on the larger prey found in the wetlands. Yearlings, on the other hand, had a larger percentage of agricultural area in their suitable habitat. In this LULC type, smaller prey items are more abundant (Phillips et al. 2003). Finally, suitable habitat for pups was a combination of agriculture, forest, and scrub/shrub. This may be related again to the smaller prey items in agricultural areas, and to the location of dens or home site areas in the brushy scrub/shrub and forest edges (Phillips et al. 2003, Hinton and Chamberlain 2010).

The overall hybrid model and the hybrid breeder model indicated a preference for agriculture, while the hybrid non-breeder preferred wetlands; the unknown preferred a mix of forest, scrub/shrub and forest, and the yearling preferred agriculture. These results, analyzed with respect to red wolf preference and coyote preference, indicate that hybrid LULC preference may similar to red wolf groups. Overall, red wolves and hybrids had a similar amount of forest and scrub/shrub predicted suitable, and hybrids had a larger percentage of agriculture predicted suitable than red wolves, but less than coyotes. The overall coyote model indicated that agriculture composed the largest percentage of suitable habitat, but the coyote breeder model indicated that forest was the main LULC type predicted suitable. Looking at each model by species class, I found that red wolf yearlings and hybrid yearlings had similar amounts of each LULC type predicted suitable, and red wolf non-breeders and hybrid non-breeders shared a higher percentage of wetlands as predicted suitable. While hybrids may be tolerant of road and human population densities higher than red wolves and similar to coyotes, many of their LULC preferences appear similar to red wolves, based on the MaxEnt results. However, as previously indicated, wolves and coyotes do not generally have a preference for a particular LULC type. An area with suitable prey and cover, and little human disturbance in the case of wolves, may support canid populations regardless of whether the LULC type is forest, agriculture or wetland.

The jackknife estimation of variable importance for all hybrid models except yearlings and all coyote models included wetlands as a major predictor variable, and the response was always negative. This response may in fact be due to the presence of red wolves in the wetland areas on the ARNWR and PLNWR (primarily zones 1 and 2), which were the original red wolf reintroduction sites and still contain a number of red wolf groups (USFWS unpublished data). Also, as coyotes began moving on to the Peninsula from the west, they first encountered more forest, agriculture, and scrub/shrub in the western area (zone 3) (Figure 4:2) and subsequently settled those areas to a greater degree than wetlands. This is also evident in the percentage of each LULC type found in the suitable habitat for hybrids and coyotes, which included larger amounts of forest in the case of coyotes and forest and scrub/shrub in the case of hybrids, compared to red wolves. The hybrids currently found on the Peninsula may have also originated in the agricultural areas found predominately in zones 2 and 3, which may explain their avoidance of wetland areas on the refuges. Studies of hybridization events between gray wolves and coyotes suggest that agricultural areas provide favorable habitat for coyotes, and as forested areas where wolves live are converted to agriculture, there is an increase in wolf and coyote contact which favors hybridization (Lehman et al. 1991, Ballard et al. 2003). On the Peninsula, coyotes are entering from the west into zone 3 and encountering agricultural, a preferred habitat, and a recent analysis of red wolf natal dispersal characteristics indicated a preference for westward dispersal of red wolves to agricultural areas (Karlin and Chadwick In review). Therefore, dispersing red wolves are likely encountering coyotes in these western agricultural areas, leading to hybridization events.

The Bonferroni confidence interval analysis of LULC type preferences showed an overwhelming trend towards selection of agriculture, which is supported by the high suitability model results for each species and social class. Agricultural areas are prime habitats for coyotes (Ballard et al. 2003, Thiel 2010), offering an abundance of smaller prey (Phillips et al. 2003) and cover when crops are in (Gosselink et al. 2003). During winter when corn and soybean crops have been harvested, many areas are planted with winter wheat (personal observation), which still provides cover and access to prey. Agricultural areas also support populations of white-tailed deer, a main prey of red wolves, although the abundance may be less than in the wetland habitats based on red wolf scat analysis (Phillips et al. 2003). Coyotes are about 2/3 the size of red wolves (Roth et al. 2008) and hybrids are intermediate to coyotes and red wolves (Phillips et al. 2003). Other studies of wolf and hybrids habitat type and prey selection indicates that these medium to small sized canids (hybrids and coyotes), prey on small to medium sized prey compared to the larger prey (e.g., white-tailed deer) consumed by larger canids (e.g. wolves) (Sears et al. 2003). Therefore, the shared high suitability preference for agricultural areas may indicate that there is resource partitioning between the three groups: red wolves preying on white-tailed deer and smaller animals when deer are scarce, while hybrids and coyotes prey on smaller animals such as rodents and rabbits, and on deer carcasses left by red wolves. Studies of gray wolf and coyote interspecific competition indicate in one study that resident coyote home range areas were completely subsumed within gray wolf packs, and differential use of areas between these 2 species allowed the coyotes to remain in these wolf areas (Berger and Gese 2007). Coyotes may have remained in these areas because of the potential energetic benefits associated with scavenging wolf kills (Paquet 1992). Analyses on prey items by coyotes and hybrids on the Peninsula would indicate if resource partitioning of prey is occurring, and this would support the overlapping preference for agriculture by all three species.

Spatial Overlap

I identified only 611.8 km^2, 91.1 km^2, and 323.3 km^2 of high suitability habitat for red wolves, hybrids, and coyotes, respectively, which represents only 11.2%, 1.7%, and 5.9% of the total area of the Peninsula, respectively. These low values, particularly for the hybrids and coyotes, are likely because they are habitat generalists and the model could not identify a strong trend or preference for a specific combination of habitat conditions. There was 354.6 km^2 of overlap of suitable areas between the model results for all red wolves and all coyotes, and this overlap occurred predominantly (61.8%) in agriculture and in zone 3, confirming that this LULC type is preferred by both groups and is likely the area where the greatest competition for resources may occur. Overlap of high suitability habitat between red wolves and coyotes followed similar trends in LULC type and zone. The minimal overlap of suitable and high suitability area between red wolves and coyotes in zone 1 suggests that coyote presence is lowest in this zone, which may be a result of both USFWS management actions such as the removal of coyotes captured in this area (Stoskopf et al. 2005) and the location of zone 1 – in the easternmost area of the Peninsula. The VHF telemetry location data support the idea that coyote presence is lowest in this zone, with only 17.7% of the coyote location points occurring in zone 1, followed by 23.0% in zone 2 and 59.3% in zone 3. Suitable habitat overlap also occurs in the scrub/shrub areas (34%), which are used by red wolves during the winter when the agricultural crops are harvested and may be used for den or home sites (Chadwick et al. 2010, Hinton and Chamberlain 2010). This overlap of scrub/shrub areas may identify where potential resource competition between red wolves and coyotes exists when the agricultural fields are harvested and both groups have to move to different LULC types for prey and cover.

Red wolf and hybrid suitable habitat overlap totaled 629.5 km^2 and overlap of high suitability habitat was only 29.7 km^2. The overlap of suitable habitat was greater for this comparison than the red wolf and coyote comparison, and red wolf and hybrid overlap included a greater diversity of LULC types. Agriculture, forest and scrub/shrub areas were included in the suitable habitat overlap, which as previously mentioned suggested hybrids are selecting LULC types similar to red wolves.

Conclusions

Addressing the threat of hybridization with coyotes and identifying habitat needs of the red wolves are vital to the management and persistence of the red wolf in the wild. Because coyotes are now present in every area of the red wolf's historic range (Phillips et al. 2003), identifying suitable areas for future red wolf reintroductions will have to take into account coyotes. The abundance of agriculture habitat fragmentation throughout most of North America (Thiel 2010) and specifically the red wolf historic range also indicates that total coyote eradication from an area may not be feasible. Based on the results of my study, I suggest that areas of agriculture where road and human population density are highest should be targeted for increased coyote management based on the habitat suitability results and preferred resource selection by coyotes. Red wolves dispersing to the west are likely encountering more coyotes than red wolves, leading to hybridization events. Studies of gray wolf and coyote hybridization events suggest that female wolves and male coyotes are more likely to mate because they are more closely matched in size (Lehman et al. 1991). Whether male or female red wolves are more likely to mate with coyotes was not analyzed in this study, but the main factor may be abundance of coyotes and abundance of red wolves. Until dispersing red wolf come into contact with more red wolves of the opposite gender than coyotes, pairings between red wolves and coyotes and potential hybridization events will be difficult to control. Careful management of the current red wolf population has led to decreased hybridization events, however, by capturing and sterilizing coyotes and hybrids and returning them as place-holders until red wolves can become established in the area (USFWS 2007). Backcrossing has been rare in the red wolf population, which has helped to reduce the negative effects of hybridization (USFWS 2007).

My study establishes a baseline for red wolf habitat suitability and preferred resources, evaluated by social class, on the Peninsula and is the first assessment of coyote and hybrid habitat suitability on the Peninsula and resource competition between these groups. The results suggest that critical habitat for the red wolf is not LULC specific; rather, low road and human population density are most important (Sears et al. 2003), and, on the Peninsula, lead to a preference for agricultural and wetland habitats, which both support red wolf prey.

Tables and Figures

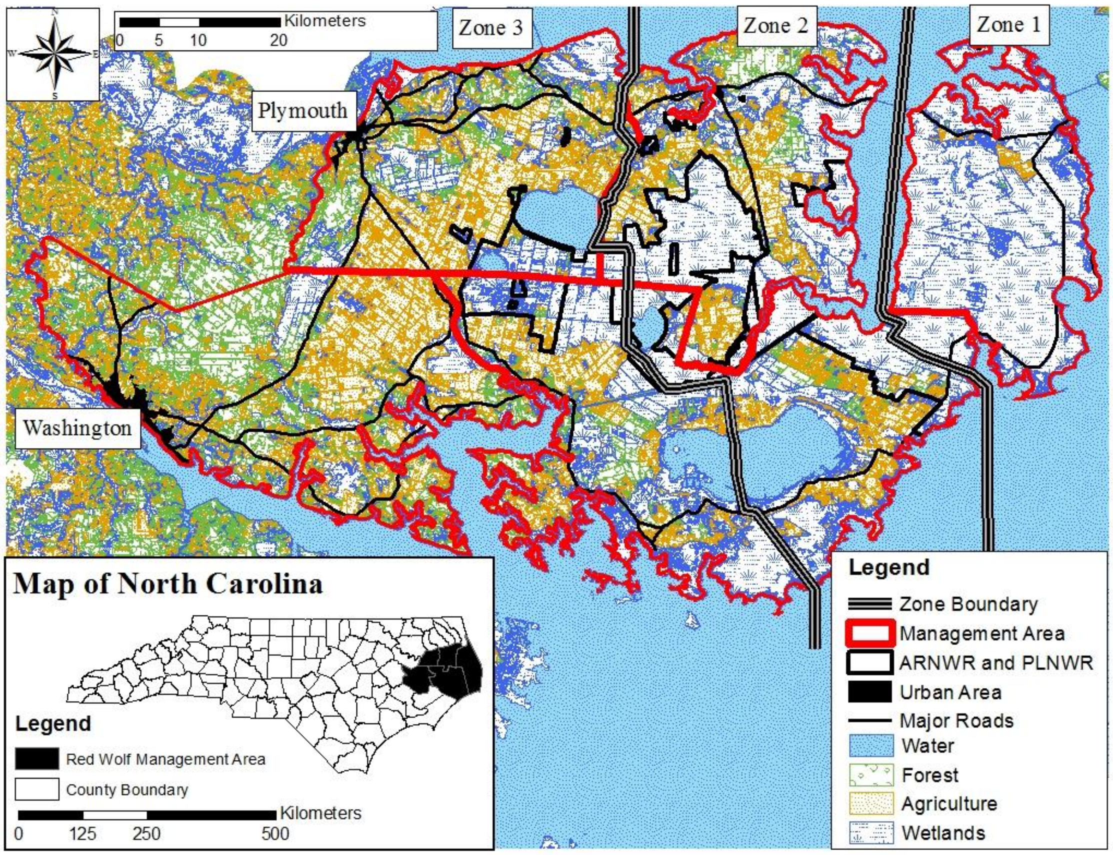


Figure 4:1. The study area is known as the Albemarle Peninsula and encompasses the red wolf management area, which also includes the ARNWR and PLNWR wildlife refuges. The Peninsula is divided into management zones for red wolf, coyote, and red wolf/coyote hybrid management.

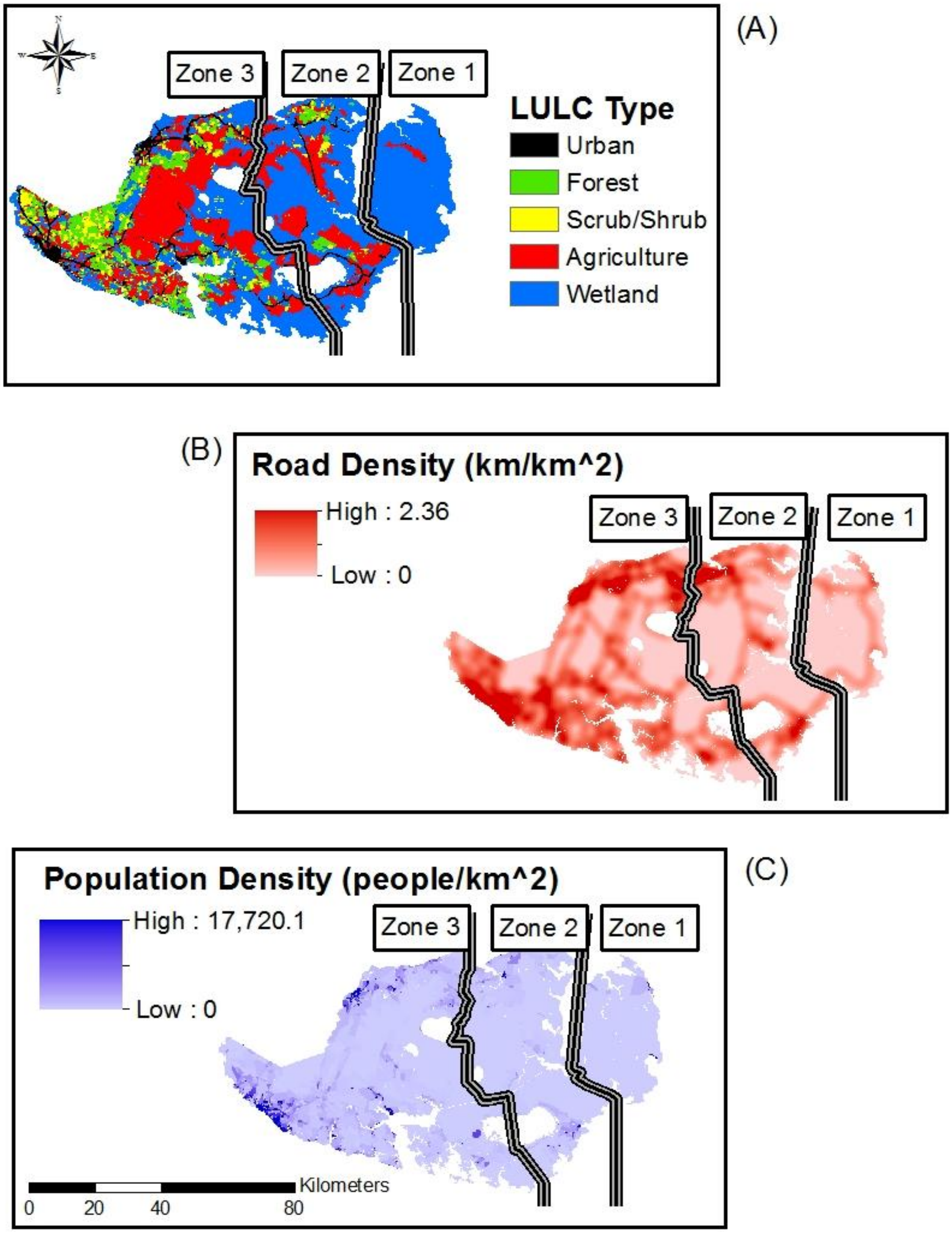


Figure 4:2. Explanatory variables used in the habitat suitability models for red wolves, hybrids and coyotes on the Albemarle Peninsula, NC in 2008. (A) illustrates the five LULC types as of 2008; (B) indicates the road density of the study area as of 2008; and (C) indicates the human population density in the study area based on the 2000 Census data.

Table 4:1. Number of animals (N) and VHF telemetry location points (n) for each group and social class analyzed for preferred habitat selection on the Albemarle Peninsula, NC from 1999-2008

	Breeders		Non-breeders		Unknown		Yearlings		Pups	
	N	n	N	n	N	n	N	n	N	n
Red wolves	177	4,191	67	367	n/a		130	778	110	397
Coyotes	20	99	n/a		19	109	n/a		n/a	
Hybrids	39	345	12	32	30	278	5	22	n/a	

Table 4:2. Comparative analysis of road (Rd) density and Population (Pop) density at used and random background locations of red wolf (RW), hybrid (H) and coyote (C) groups from 1999-2008 on the Albemarle Peninsula, NC. Comparisons were conducted using Mann-Whitney *U* Test.

Model	Variable	Background (mean (SE))	Presence (mean (SE))
All RW (n=5,733)	Rd density (rd/km^2)**	0.38 (0.003)	0.18 (0.003)
	Pop density (people/km^2)**	11.0 (0.57)	1.67 (0.09)
RW breeders (n=4,191)	Rd density (rd/km^2)**	0.38 (0.003)	0.17 (0.003)
	Pop density (people/km^2)**	9.99 (0.47)	1.67 (0.12)
RW non-breeders (n=367)	Rd density (rd/km^2)**	0.38 (0.003)	0.15 (0.01)
	Pop density (people/km^2)**	11.01 (0.57)	1.18 (0.24)
RW yearlings (n= 778)	Rd density (rd/km^2)**	0.38 (0.003)	0.20 (0.009)
	Pop density (people/km^2)**	11.0 (0.90)	1.51 (0.18)
RW pups (n=397)	Rd density (rd/km^2)**	0.38 (0.003)	0.19 (0.01)
	Pop density (people/km^2)**	9.31 (0.43)	1.59 (0.26)
H All (n=677)	Rd density (rd/km^2)**	0.38 (0.003)	0.30 (0.01)
	Pop density (people/km^2)	9.99 (0.47)	4.06 (0.42)
H Breeder (n=345)	Rd density (rd/km^2)**	0.38 (0.003)	0.29 (0.02)
	Pop density (people/km^2)	9.99 (0.47)	4.88 (0.72)
H Non-breeder (n=32)	Rd density (rd/km^2)	0.38 (0.003)	0.26 (0.04)
	Pop density (people/km^2)	11.01 (0.57)	3.25 (1.47)
H Unknown (n=278)	Rd density (rd/km^2)**	0.38 (0.003)	0.31 (0.02)
	Pop density (people/km^2)*	10.66 (0.77)	2.99 (0.44)
H Yearling (n=22)	Rd density (rd/km^2)	0.38 (0.003)	0.36 (0.05)
	Pop density (people/km^2)	11.0 (0.90)	5.92 (1.34)
C All (n=208)	Rd density (rd/km^2)	0.38 (0.003)	0.34 (0.02)

Table 4:2 (continued)

	Pop density (people/km^2)	10.29 (0.54)	3.92 (0.46)
C Breeder (n=99)	Rd density (rd/km^2)	0.38 (0.003)	0.40 (0.03)
	Pop density (people/km^2)	10.29 (0.54)	4.80 (0.72)
C Unknown (n=109)	Rd density (rd/km^2)*	0.38 (0.003)	0.29 (0.03)
	Pop density (people/km^2)	10.66 (0.77)	3.11 (0.58)

*Significant at $p < 0.05$

**Significant at $p<0.01$

n=20,000 for background points

Table 4:3. Bonferroni confidence intervals for the proportion of red wolf (RW), hybrid (H) and coyote (C) locations found in each LULC type on the Albemarle Peninsula, NC pooled from 1999-2008. Grayed selections indicate LULC type preference, bolded selections indicate LULC type avoidance, and non-bolded/non-grayed selections indicate random use.

	Proportion of LULC Type Available				
	Urban	Forest	Scrub/Shrub	Agriculture	Wetland
	0.04	0.11	0.07	0.31	0.47

	CI urban	CI forest	CI scrub/shrub	CI agriculture	CI wetland
All RW	$0.02 \le P \le 0.13$	$0.09 \le P \le 0.10$	$0.05 \le P \le 0.06$	$0.47 \le P \le 0.50$	$0.34 \le P \le 0.36$
RW breeder	$0.01 \le P \le 0.02$	$0.09 \le P \le 0.11$	$0.05 \le P \le 0.06$	$0.47 \le P \le 0.50$	$0.33 \le P \le 0.36$
RW non-breeder	$0.009 \le P \le 0.04$	$0.04 \le P \le 0.09$	$0.01 \le P \le 0.05$	$0.36 \le P \le 0.46$	$0.41 \le P \le 0.52$
RW yearling	$0.008 \le P \le 0.03$	$0.07 \le P \le 0.12$	$0.02 \le P \le 0.05$	$0.50 \le P \le 0.57$	$0.29 \le \mathrm{P} \le 0.35$
RW pup	$0.005 \le P \le 0.03$	$0.05 \le P \le 0.10$	$0.03 \le P \le 0.07$	$0.44 \le P \le 0.54$	$0.32 \le P \le 0.41$
All H	$0.007 \le P \le 0.03$	$0.11 \le P \le 0.16$	$0.05 \le P \le 0.08$	$0.49 \le P \le 0.56$	$0.23 \le P \le 0.30$
H breeder	$0.002 \le P \le 0.03$	$0.10 \le P \le 0.18$	$0.05 \le P \le 0.10$	$0.46 \le P \le 0.57$	$0.21 \le P \le 0.31$
H non-breeder	n/a	$0.05 \le P \le 0.32$	$0 \le P \le 0.19$	$0.30 \le P \le 0.64$	$0.10 \le P \le 0.40$
H unknown	$0.002 \le P \le 0.03$	$0.08 \le P \le 0.16$	$0.03 \le P \le 0.08$	$0.48 \le P \le 0.60$	$0.21 \le P \le 0.31$
Hybrid yearling	$0 \le P \le 0.13$	$0 \le P \le 0.20$	n/a	$0.32 \le P \le 0.73$	$0.15 \le P \le 0.54$
All C	$0.003 \le P \le 0.04$	$0.05 \le P \le 0.13$	$0.03 \le P \le 0.09$	$0.60 \le P \le 0.73$	$0.11 \le P \le 0.21$
C breeder	$0 \le P \le 0.03$	$0.04 \le P \le 0.16$	$0.002 \le P \le 0.08$	$0.61 \le P \le 0.79$	$0.08 \le P \le 0.22$
C unknown	$0.001 \le P \le 0.07$	$0.03 \le P \le 0.13$	$0.02 \le P \le 0.12$	$0.55 \le P \le 0.73$	$0.10 \le P \le 0.23$

Table 4:4. Comparison of explanatory variables at red wolf (RW), hybrid (H) and coyote (C) presence locations collected from 1999-2008 on the Albemarle Peninsula, NC using Kruskal Wallis Test (*p* < 0.05 considered significant). Entries indicate significant difference between the respective groups: p < 0.05*, p < 0.01**, p < 0.001***, and p < 0.0001****.

Road Density										
	RW non-breeder	RW yearling	RW pup	All H	H breeder	H non-breeder	H unknown	All C	C breeder	C unknown
All RW				****				****		
RW breeder	**	***			****		****		****	****
RW non-breeder		*	****							****
H breeder									**	

Population Density										
	RW non-breeder	RW yearling	RW pup	All H	H breeder	H non-breeder	H unknown	All C	C breeder	C unknown
All RW				****				**		
RW breeder	**				****				**	
RW non-breeder		**	****							

Table 4:5. Results of MaxEnt habitat suitability model assessments expressed as area under the curve (AUC), the threshold that maximized specificity and sensitivity of the models, and the total area predicted as suitable or high suitability for red wolves, hybrids and coyotes on the Albemarle Peninsula, NC from 1999-2008

Model	AUC	Threshold	Area Predicted Suitable (km^2)	Area Predicted Highly Suitable (km^2)
RW All	0.72	0.43	933.70	611.80
RW Breeder	0.74	0.40	1,887.30	612.30
RW Non-Breeder	0.74	0.48	1,480.60	535.40
RW Yearling	0.72	0.42	1,256.30	663.30
RW Pup	0.70	0.47	538.10	799.90
Hybrid All	0.72	0.40	2,067.00	91.10
Hybrid Breeder	0.74	0.40	1,929.00	143.68
Hybrid Non-Breeder	0.71	0.39	1,913.87	1,236.64
Hybrid Unknown	0.82	0.32	811.68	1,103.69
Hybrid Yearling	0.73	0.43	1,371.41	766.92
Coyote All	0.78	0.42	1,339.45	323.28
Coyote Breeder	0.77	0.34	756.14	1,386.22
Coyote Unknown	0.77	0.42	1,049.03	751.26

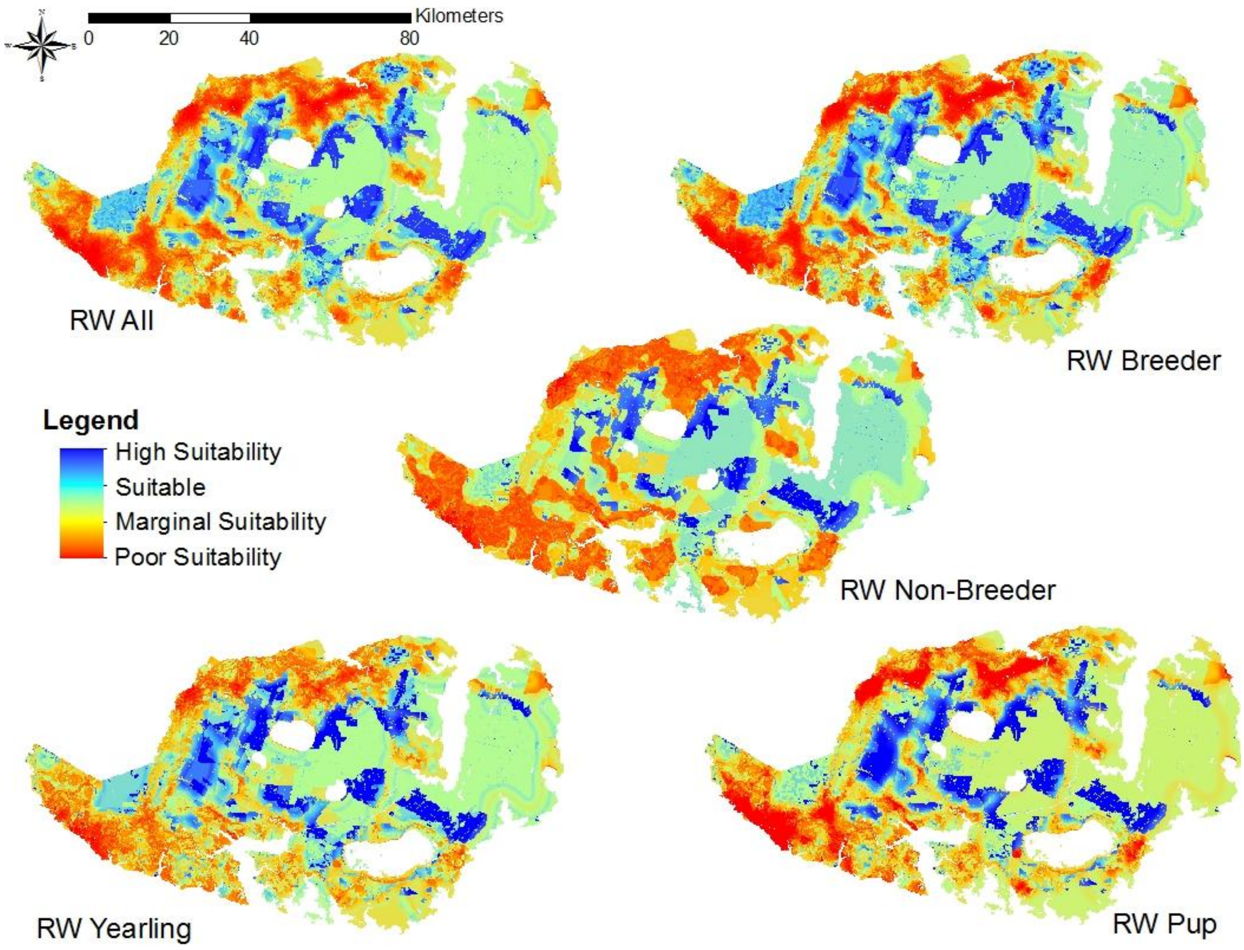


Figure 4:3. MaxEnt habitat suitability for each red wolf (RW) group on the Albemarle Peninsula, NC in 2008, expressed as categories of suitability.

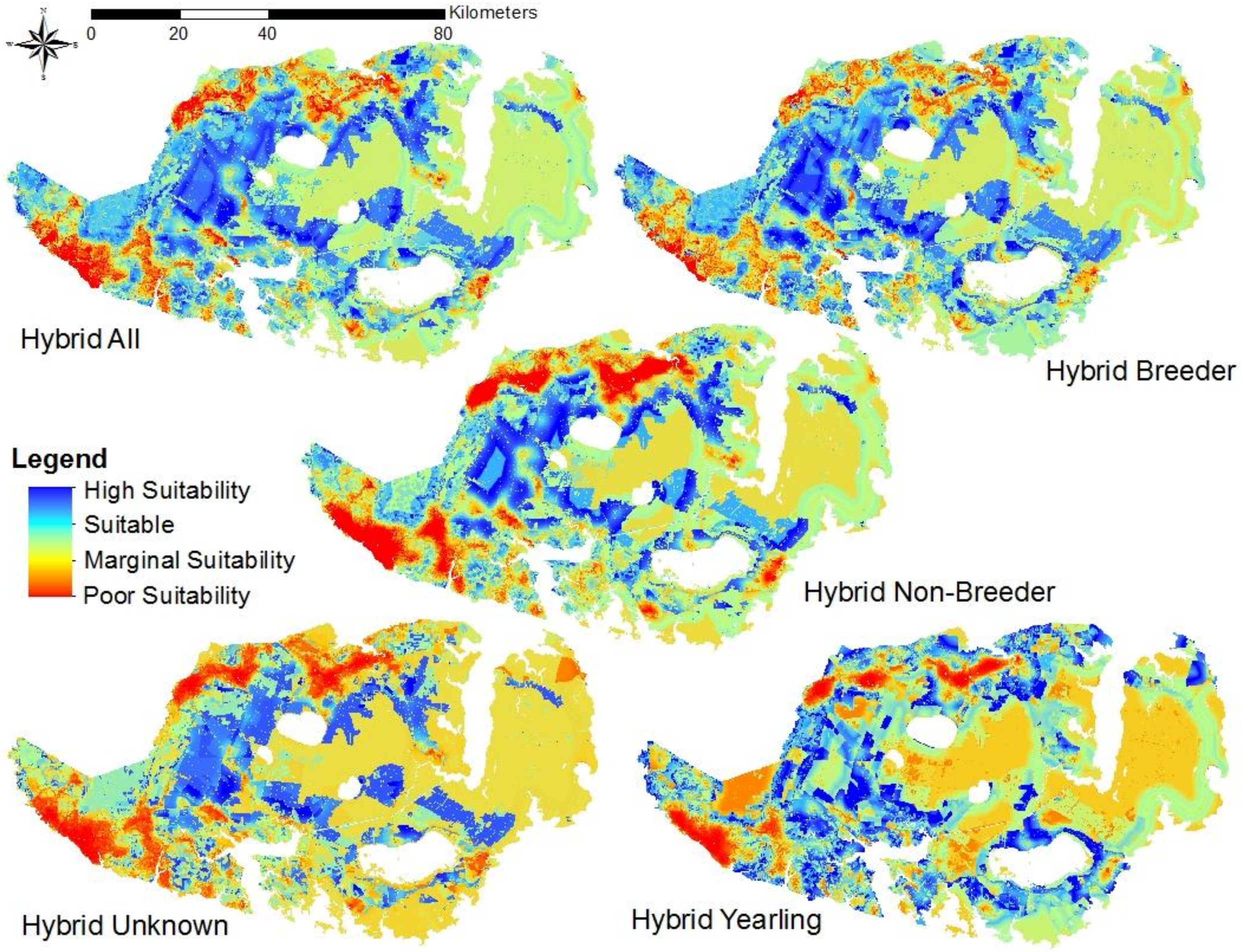


Figure 4:4. MaxEnt habitat suitability for each hybrid group on the Albemarle Peninsula, NC in 2008, expressed as categories of suitability.

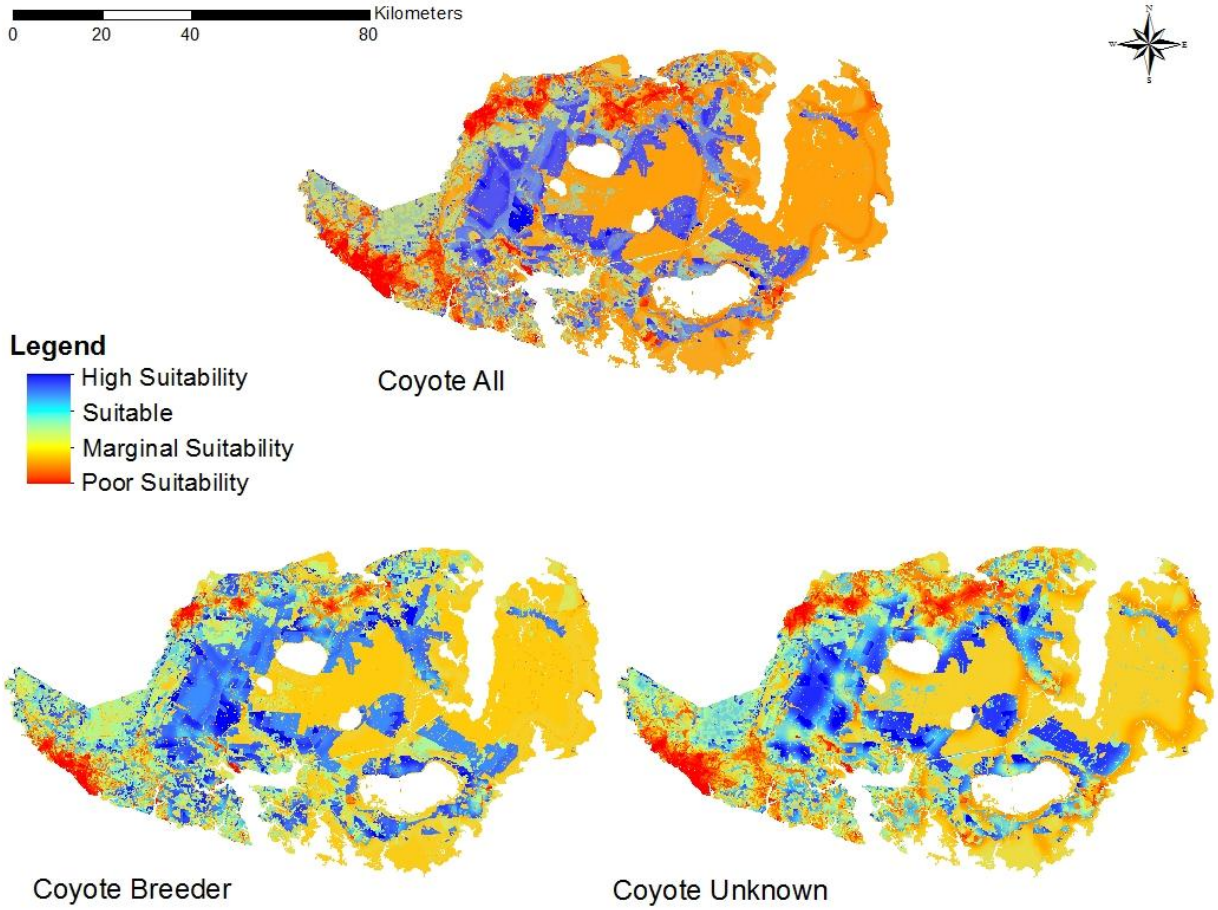
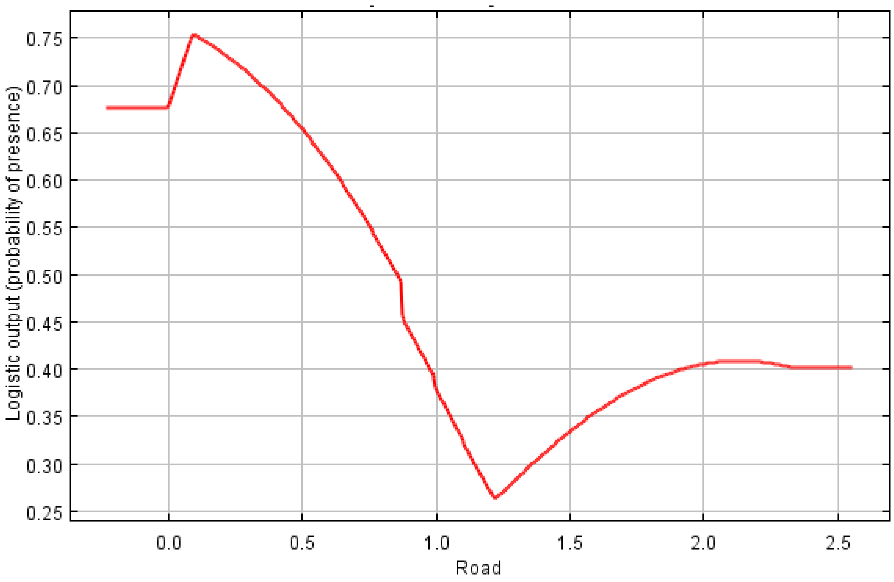


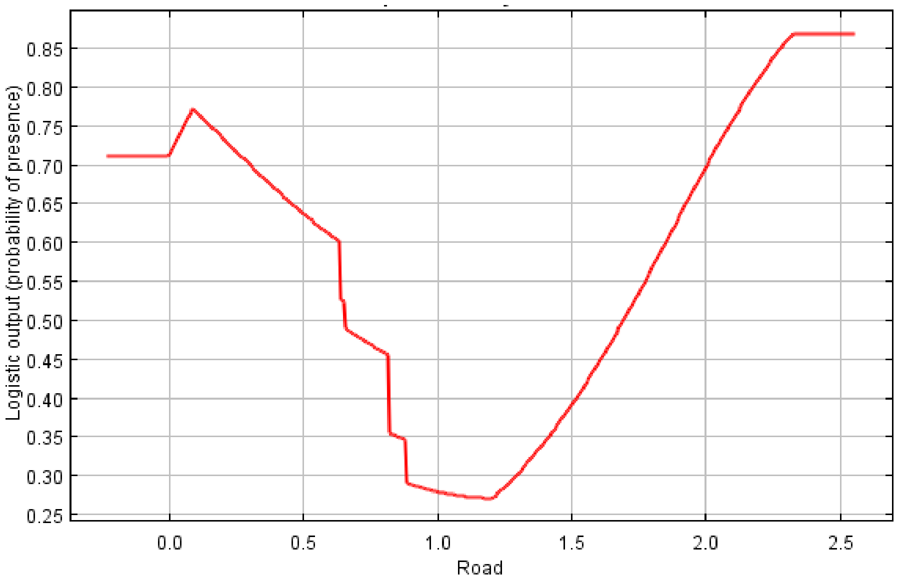
Figure 4:5. MaxEnt habitat suitability for each coyote group on the Albemarle Peninsula, NC in 2008, expressed as categories of suitability.

Table 4:6. Percent contribution of top 3 variables to habitat suitability models for red wolves (RW), hybrids (H) and coyotes (C) on the Albemarle Peninsula, NC from 1999-2008

Model	Variable	% Contribution	Model	Variable	% Contribution
RW All	Rd Density (-)	41.08	RW Breeder	Rd Density (-)	38.5
	Agriculture (+)	25.86		Pop Density (-)	27.4
	Pop Density (-)	25.29		Agriculture (+)	24.1
Model	Variable	% Contribution	Model	Variable	% Contribution
RW Non-Breeder	RD Density (-)	45.2	RW Yearling	Agriculture (+)	41.4
	Pop Density (-)	36.3		Pop Density (-)	38.7
	Agriculture (+)	17.9		Rd Density (-)	15.4
Model	Variable	% Contribution	Model	Variable	% Contribution
RW Pup	Agriculture (+)	38.1	H All	Rd Density (-/+)	34.50
	Rd Density (-)	35.8		Wetland (-)	31.56
	Pop Density (-)	22.7		Agriculture (+)	21.18
Model	Variable	% Contribution	Model	Variable	% Contribution
H Breeder	Wetland (-)	37.0	H Non-Breeder	Rd Density (-)	53.5
	Rd Density (-/+)	34.9		Agriculture (+)	31.2
	Pop Density (-)	14.0		Wetland (-)	13.7
Model	Variable	% Contribution	Model	Variable	% Contribution
H Unknown	Agriculture (+)	42.3	H Yearling	Pop Density (-)	50.04
	Wetland (-)	20.4		Rd Density (-)	29.98
	Rd Density (-)	19.0		Agriculture (+)	13.01
Model	Variable	% Contribution	Model	Variable	% Contribution
C All	Agriculture (+)	52.2	C Breeder	Agriculture (+)	66.37
	Wetland (-)	22.7		Wetland (-)	17.85
	Rd Density (-)	17.4		Rd Density (-)	8.51
Model	Variable	% Contribution			
C Unknown	Agriculture (+)	46.1			
	Wetland (-)	27.3			
	Rd Density (-)	21.1			



(a). All hybrids functional response to road density



(b). Hybrid breeder functional response to road density

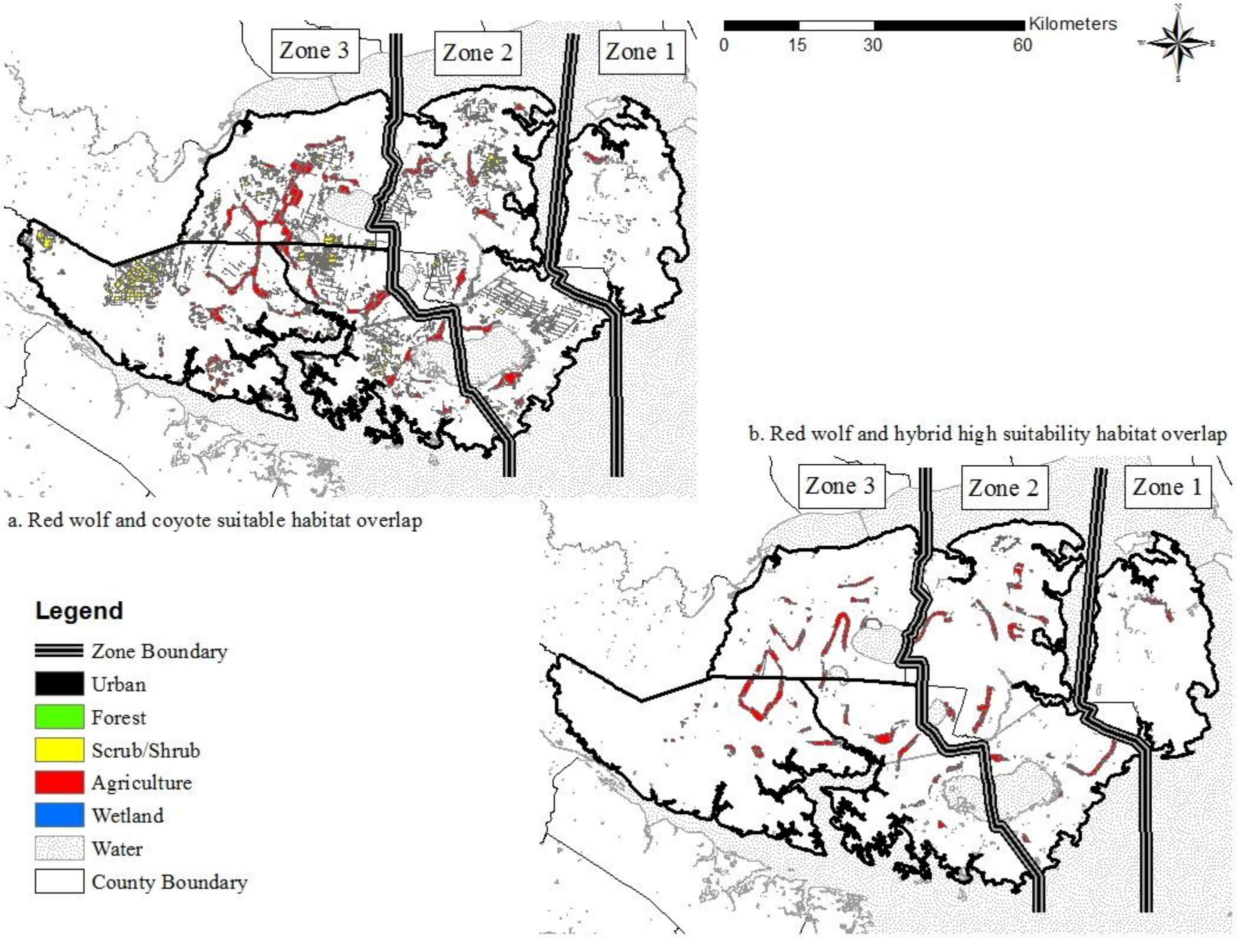
Figure 4:6. Functional response to road density: (a) indicates all hybrids probability of occurrence response to road density, which decreases initially and then increases after densities > 1.25 km/km^2; (b) illustrates the hybrid breeder response, which shows a similar response to the hybrid all, and is likely the social group influencing the results seen in a.

Table 4:7. Percentage LULC in Suitable and High suitability Predicted Areas for red wolves, hybrids, and coyotes on the Albemarle Peninsula, NC from 1999-2008

	Suitable				
	Urban	Forest	Scrub/Shrub	Agriculture	Wetlands
All red wolves	4.05%	20.74%	15.96%	36.19%	23.05%
Red wolf breeder	2.18%	11.92%	8.25%	19.28%	58.37%
Red wolf non-breeder	3.27%	5.24%	6.13%	9.88%	75.47%
Red wolf yearling	3.73%	14.43%	9.07%	53.54%	19.23%
Red wolf pup	0.99%	28.75%	27.33%	41.92%	1.00%
All hybrids	1.39%	20.06%	13.15%	60.21%	5.19%
Hybrid breeder	1.62%	20.53%	13.54%	57.62%	6.70%
Hybrid non-breeder	3.27%	18.26%	8.55%	15.85%	54.07%
Hybrid unknown	5.26%	39.76%	25.81%	27.62%	1.55%
Hybrid yearling	3.36%	14.05%	7.68%	48.33%	26.59%
All coyotes	1.15%	2.68%	14.60%	80.87%	0.70%
Coyote breeder	0.98%	62.10%	8.49%	27.18%	1.25%
Coyote unknown	5.17%	16.68%	18.01%	58.99%	1.14%
	High suitability				
	Urban	Forest	Scrub/Shrub	Agriculture	Wetlands
All red wolves	1.44%	0.38%	2.30%	95.48%	0.41%
Red wolf breeder	1.13%	0.40%	3.00%	95.18%	0.29%
Red wolf non-breeder	1.24%	0.22%	0.21%	98.08%	0.25%
Red wolf yearling	1.15%	0.20%	0.18%	98.20%	0.26%
Red wolf pup	1.07%	0.20%	0.20%	98.26%	0.27%
All hybrids	0.73%	3.69%	2.05%	92.88%	0.66%
Hybrid breeder	1.01%	3.54%	5.46%	89.20%	0.79%
Hybrid non-breeder	1.07%	4.73%	9.67%	83.99%	0.53%
Hybrid unknown	1.08%	0.22%	0.24%	98.14%	0.32%
Hybrid yearling	0.81%	0.54%	0.45%	60.99%	37.21%
All coyotes	0.90%	0.38%	0.53%	97.87%	0.32%
Coyote breeder	1.11%	0.27%	0.29%	97.95%	0.38%
Coyote unknown	1.04%	0.24%	0.31%	98.08%	0.32%

Table 4:8. Percent overlap of red wolf and coyote Suitable and High suitability habitat by zone, expressed as LULC type

				Suitable				
Zone 1	Urban	1.72	Zone 2	Urban	1.93	Zone 3	Urban	0.94
	Forest	0.41		Forest	2.46		Forest	2.04
	Scrub/Shrub	22.09		Scrub/Shrub	25.54		Scrub/Shrub	36.90
	Agriculture	73.11		Agriculture	69.28		Agriculture	59.47
	Wetlands	2.68		Wetlands	0.79		Wetlands	0.65
% of Zone		0.63			4.41			8.46
% of red wolf suitable habitat in zone		5.21			32.65			45.47
				High suitability				
Zone 1	Urban	1.22	Zone 2	Urban	0.86	Zone 3	Urban	0.56
	Forest	0.00		Forest	0.51		Forest	0.12
	Scrub/Shrub	0.12		Scrub/Shrub	0.81		Scrub/Shrub	0.17
	Agriculture	97.97		Agriculture	97.66		Agriculture	99.02
	Wetlands	0.68		Wetlands	0.17		Wetlands	0.14
% of Zone		0.65			3.22			2.76
% of red wolf suitable habitat in zone		5.31			23.82			29.17



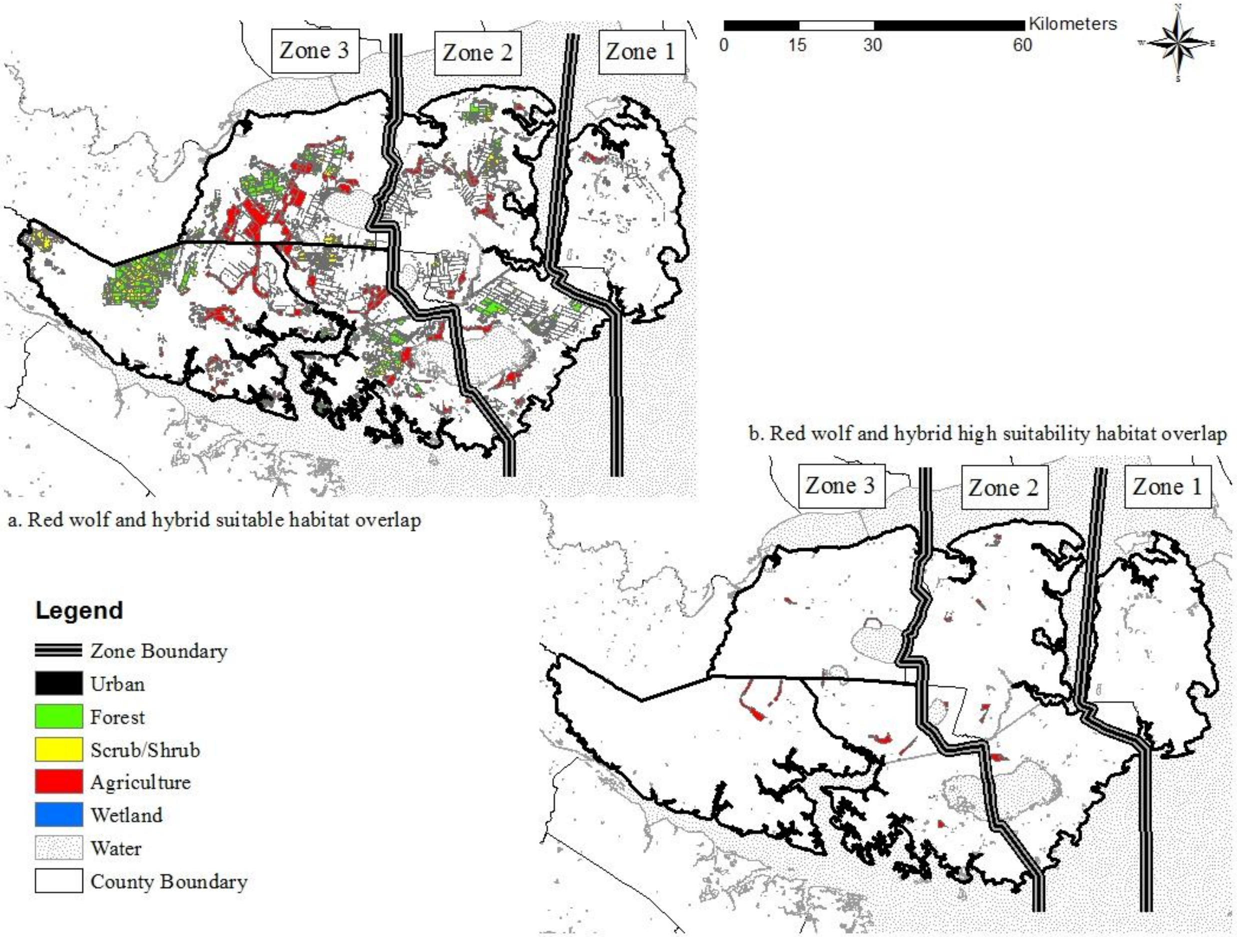
a. Red wolf and coyote suitable habitat overlap

b. Red wolf and hybrid high suitability habitat overlap

Figure 4:7. Spatial overlap of (a) red wolf and coyote suitable habitat and (b) red wolf and coyote high suitability habitat, illustrated by management zone and as LULC type on the Albemarle Peninsula, NC in 2008

Table 4:9. Percent overlap of red wolf and hybrid Suitable and High suitability habitat by zone, expressed as LULC type

				Suitable				
Zone 1	Urban	4.82	Zone 2	Urban	2.13	Zone 3	Urban	1.25
	Forest	25.79		Forest	33.62		Forest	29.26
	Scrub/Shrub	17.36		Scrub/Shrub	19.16		Scrub/Shrub	24.35
	Agriculture	48.19		Agriculture	44.11		Agriculture	44.46
	Wetlands	3.84		Wetlands	0.98		Wetlands	0.68
% of Zone		1.10			7.52			15.20
% of red wolf suitable habitat in zone		9.07			55.68			81.65
				High suitability				
Zone 1	Urban		Zone 2	Urban	0.65	Zone 3	Urban	0.32
	Forest	0.00		Forest	2.64		Forest	0.08
	Scrub/Shrub	0.00		Scrub/Shrub	6.26		Scrub/Shrub	0.08
	Agriculture	0.00		Agriculture	90.05		Agriculture	99.38
	Wetlands	0.00		Wetlands	0.39		Wetlands	0.14
% of Zone		0.00			0.58			0.61
% of red wolf suitable habitat in zone		0			3.48			6.43



a. Red wolf and hybrid suitable habitat overlap

b. Red wolf and hybrid high suitability habitat overlap

Figure 4:8. Spatial overlap of (a) red wolf and hybrid suitable habitat and (b) red wolf and hybrid high suitability habitat, illustrated by management zone and as LULC type on the Albemarle Peninsula, NC in 2008

CHAPTER 5: CONCLUSIONS

The objectives of this dissertation were to gain a better understanding of the critically imperiled red wolf, an endangered species that exists as only 1 small, isolated population in North Carolina. Considering the complexity of wolf social behavior and the ever-changing landscape associated with human development and agriculture, there are inevitably more questions than answers. However, in this dissertation I quantified a variety of red wolf ecological attributes that can aid in the conservation of this species and assist resource managers with taking the next steps towards identifying additional reintroduction sites.

Chapter 2 was a small-scale study that utilized highly accurate GPS radio collars, which up until this study had not been employed for red wolf conservation. This technology, however, offers the best option for studying interactions between red wolves, and between red wolves and coyotes. The programming capability of this technology is such that highly mobile, cryptic, nocturnal animals such as the red wolf can be monitored remotely for extended periods of time while locational data is stored on the collar, an attribute the more traditional VHF radio telemetry collars lack. This feature means that the animals can be left undisturbed for greater periods of time, an asset to both research objectives and the protection of the species. This chapter identified novel information on red wolf group structure by determining that a non-kin adult male red wolf was accepted as a member of the group, consisting of the breeding male and female, and pups during a portion of the study. As previously stated, this group composition has been widely documented in gray wolves (Girman et al. 1997, Mech and Boitani 2003, Grewal et al. 2004) and is often associated with resource availability (i.e., food is abundant) and the acceptance of helpers at the den (Jedrzejewski et al. 2001, Sparkman et al. 2010).

In Chapter 3, I characterized natal dispersal characteristics that were previously poorly understood but have serious implications in reintroduction efforts. Since any reintroduction of additional red wolf populations will likely be in an area of some human development, understanding how far and when red wolves disperse is critical for estimating minimum area requirements and predicting conflicts with humans. Unlike Chapter 2, this chapter utilizes the long-term VHF radio telemetry data. While this data has poorer spatial and temporal accuracy than Chapter 2, the duration of the data collection (19 years) enabled me to assess dispersal conditions as the population increased and then stabilized. These 2 scenarios provide an understanding how the red wolves responded initially to the reintroduction area in terms of LULC types, availability of open (wolf-free) territories, and proximity to human development, and then adjusted in response to the increase in their population and habitat saturation. If the population were to expand naturally or be reintroduced to a new area, the natal dispersal characteristics from 1990-1998 might be expected during the initial years of the expansion or reintroduction, until the population stabilizes.

The results of Chapter 4 have the greatest immediate application to the conservation of the red wolf in the face of hybridization with coyotes. I identified, as many gray wolf researchers before me, that red wolves are not habitat-specific; rather, low road density and minimal human presence are most important for predicting whether or not red wolves will occupy an area. In addition, prey density and sufficient cover are necessary. On the Albemarle Peninsula, the main prey of red wolves (white-tailed deer) can be found in both wetlands and agriculture, and a variety of smaller prey can also be found in these LULC types although they are more abundant in agriculture. Coyotes are habitat generalists and consume smaller prey than red wolves; as such, they were more tolerant of higher road and human population densities and preferred the rodent-rich agricultural lands. On the Albemarle Peninsula, agriculture is a dominant land use and therefore the area is likely a source for coyotes (Bekoff and Gese 2003), which is a threat to the persistence of the red wolf in this area and throughout its historic range.

Coyote management on the Albemarle Peninsula has been effective, based on the displacement of sterile individuals by red wolves and the reduction in coyote numbers, although in 2006 and 2007 USFWS red wolf biologists reported an increase in the number of coyotes trapped (USFWS 2007). Other than hybridization with coyotes, human-caused mortality represents the greatest threat to red wolf survival, with over 50% of deaths attributed directly or indirectly to humans (USFWS 2007). When red wolves are killed, this opens space for coyotes to move in and increases the risk of hybridization events. Due to the high rate of red wolf mortality, the population is struggling to increase to the level that would competitively exclude coyotes, as seen in many gray wolf populations (Berger and Gese 2007) and lead to red wolves encountering more red wolves than coyotes. Chapter 4 identifies specific areas on the Peninsula that are most suitable for coyotes and areas where red wolf and coyote suitable habitat overlap. Intense trapping efforts for coyotes should be directed towards these areas, and if red wolves are released or relocated on the Peninsula in the future, a surge in red wolf numbers should be targeted to these same areas to inhibit coyotes from returning and encourage red wolves to form territories.

The three chapters presented in this dissertation provide three analyses of very different red wolf ecological characteristics. However, connections are apparent between each analysis. Red wolves of all social classes use agricultural areas to a great degree on the Peninsula. Both GPS-collared wolves in Chapter 2 were found in an agricultural area, natal dispersers in Chapter 3 dispersed from and settled in predominantly agricultural areas from 1990-1998, and the results of the habitat suitability model identified agriculture as a highly suitable habitat. This again, however, is probably due to the lower road and human population density in this LULC type, and the abundance of smaller prey in addition to white-tailed deer. The preference for a westward dispersal in Chapter 3 has serious implications when evaluated in light of the results of Chapter 4, which found coyote suitable habitat to be located mainly in the western areas of the Peninsula. These dispersing pups likely encountered more coyotes than red wolves because the red wolf population was so low, especially from 1990-1998. Many of the hybridization events may have occurred because of this fact, and this may also explain why so few wolves dispersed beyond the study area if they paired with coyotes and settled in the agricultural areas.

The red wolf has been and will continue to be a heavily managed species. The continued conflicts with humans and hybridization with coyotes would possibly lead to the demise of the species in the wild without intervention by USFWS and other agencies. However, the future of this species is still promising, and with research such as presented in this dissertation, we can begin to gain a better understanding of how the red wolf is responding to the human-dominated landscape where it was reintroduced. Areas of lower road and human population density in the red wolf’s historic range can still be found in public land –such as in the national forests of western North Carolina and the Big Cypress National Preserve, Everglades National Park and Marjory Stoneman Douglas Wilderness areas in southern Florida. As evident in the Albemarle Peninsula population, however, red wolves know no boundaries, and tolerance or support from surrounding private landowners and the public in general are required for the red wolf to be reintroduced again.

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