ABSTRACT

BECK, KAREN BOKENY. Epidemiology of coyote introgression into the red wolf genome. (Under the direction of Michael Stoskopf and Laurel Degernes)

Extensive predator control programs and habitat alterations reduced red wolves, once native to the southeastern United States, to a remnant population found in only a small portion of their historic range by the late 1960's. Coyotes expanded their range into territories previously occupied by red wolves. As wolves became scarce, they began to breed with the more prevalent coyote. Introgression threatened the continued existence of the genetic integrity of the red wolf. The U.S. Fish and Wildlife Service, following a planned extirpation and institution of a captive breeding program, reintroduced red wolves to northeastern North Carolina in 1987. Though surveys had shown no evidence of coyotes in the reintroduction area, coyotes expanded their range eastward and a small red wolf population again interfaced with an increasing coyote population. The movement of introgression within the red wolf population is akin to the movement of an infectious disease. Identification of "infected" and "non-infected" individuals is accomplished at an early age in this population through pup assessments in the den. Intervention is accomplished through the use of sterilized coyotes and coyote-wolf hybrids to prevent the spread of the "disease" to "susceptible" individuals. Understanding how the "disease" moves through the population by describing movement rates and the potential for contact between "infected" and "susceptible" individuals is accomplished through the analysis of telemetry locations of radiocollared individuals. The model for this "disease" is also presented and evaluated to determine the effectiveness of intervention strategies in controlling the spread of this "disease".

Epidemiology of coyote introgression into the red wolf genome

by

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DEDICATION

For my husband, Brady, who believed in me and stood by me through it all.

BIOGRAPHY

I'm one of those people who will tell you they always knew they wanted to be a vet. In fact, my inspiration to be a vet was a beautiful black cat named Malcolm that belonged to some friends of mine. When he was diagnosed with feline leukemia, I decided then and there at the age of 11 that I was going to vet school. It wasn't until I got to college that I realized I might just be able to combine my love for animals and the outdoors into the best of both worlds. As an undergraduate, I was once required to write a paper on how my intended career would impact our natural resources. I tried in that paper to explain to my professor the idea of wildlife medicine and how a veterinarian could contribute to wildlife conservation. Based on her comments, I don't think I did a very convincing job conveying a concept that was still forming in my head.

I was fortunate to be accepted to vet school at North Carolina State University, home to one of the nation's leading programs in zoological medicine. I took advantage of every opportunity to learn as much as I could about zoo and wildlife medicine and was fortunate enough to be mentored by some very supportive faculty members and residents. Thanks to them, I had the opportunity to learn about river otter anesthesia and trap wound management, collect blood from pelican and osprey nestlings, help implant radiotransmitters in black ducks, and assist with surgery on a fish, to name a few. I knew I was living right when my first case as a senior vet student was an impressive dromedary named Jamie.

After graduating from vet school, I looked for a way to enhance my veterinary education with knowledge and experience in wildlife biology and management. That's how I came back to NCSU for this doctoral program in population medicine. This field, no longer synonymous with production medicine, looks at ways to maintain healthy populations whether they be herds of cattle or herds of bison.

I feel that veterinarians can contribute to the world of wildlife management by offering insight from a fresh perspective. Hopefully, this dissertation will give you an idea of what I and others like me have in mind. So, no, I don't intend to open my own practice when I graduate. Instead, I hope to find a way that I can contribute to the field of ecosystem health.

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I thank my graduate committee members, Laurel Degernes, Brian Kelly, Mike Loomis, Chris Lucash, Roger Powell, and Michael Stoskopf for their participation in my education.

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I thank my friends Kerry Brust, Susan Campbell, Dr. Pam Dennis, Susan Miller, Lisa Richman, and Bill and Margaret Toburen, all of whom provided a shoulder to lean on and words of encouragement.

I thank my family who have all supported me throughout this and other educational endeavors. I feel so fortunate to have them in my corner. I am grateful to my mom, my dad, my sister and her family, my extended family of grandmas, aunts and uncles, and to all the Becks, who took me in as one of their own.

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INTRODUCTION

Red wolves (*Canis rufus)* were once native to the southeast, but extensive predator control programs and habitat alterations reduced the species to a small fragment of its range by the 1960s. With this reduction in wolf range, the ever-adaptable coyote (*Canis latrans*) expanded its range into once occupied wolf territories (McCarley 1959, 1962; Paradiso and Nowak 1971). Wolves looking for mates were more likely to find a coyote than a wolf, and hybridization soon became a very grave threat to the continued existence of the red wolf in the wild (Carley 1975, Nowak 1979). Hybridization resulted in the production of fertile offspring capable of breeding with red wolves and, therefore, the introduction of coyote genes into the red wolf genome. Left unchecked, this introgression would soon have led to the extinction of the red wolf.

Pure red wolves were thought to exist in southeast Texas and southwest Louisiana with extensive hybridization occurring where red wolves still existed outside this area (Carley 1975, Paradiso and Nowak 1971). Canids from this area were thought to have a higher probability of being a wolf than those canids elsewhere because of lower coyote population densities. As part of a plan to save the red wolf from this "hybrid swarm", the United States Fish and Wildlife Service (USFWS) deliberately extirpated red wolves in the wild by trapping and removing canids from southeastern Texas and southwestern Louisiana, their last stronghold, in the late 1960s and early 1970s (U.S. Fish and Wildlife Service 1989).

Captive propagation efforts

The canids brought into captivity during the extensive trapping efforts were evaluated based on morphology, genetic analysis, vocalizations, area where caught, and knowledge of canids from that area as well as breeding trials to determine which canids were pure red wolves (Parker 1988). Morphological criteria were established for skull length, zygomatic breadth, weight, total length, hind foot length, ear length, shoulder height, and brain/skull ratio (U.S. Fish and Wildlife Service 1989). Genetic analysis at the time was limited to "electrophoretic and chromosomal analysis", with one researcher describing the difference in the frequency of alleles that control the enzyme glucose phosphate isomerase (Shaw 1975, U.S. Fish and Wildlife Service 1989: 11). Vocalizations of red wolves were described by McCarley (1978) as a flat howl that is longer and of lower frequency than that of coyotes.

From fall 1973 to July 1980, biologists captured and evaluated more than 400 canids. Forty-three putative red wolves were bred in captivity and their offspring evaluated before those wolves were admitted to the captive breeding program (U.S. Fish and Wildlife Service 1989). Of the wolves admitted to the captive breeding program, 14 eventually became the founders from which all red wolves today are descended. These wolves were managed through the captive breeding program, administered by Point Defiance Zoological Park in Tacoma, Washington, to maintain the genetic integrity of the species until a suitable restoration area could be found (U.S. Fish and Wildlife Service 1989).

The long-term success of the red wolf captive breeding program was enhanced in 1984 by the acceptance of the red wolf into the Species Survival Program (SSP) of the American Association of Zoological Parks and Aquariums (U.S. Fish and Wildlife Service 1989). This program develops management strategies that are designed to maintain long-term genetic diversity and demographic stability for individual species (http://www.aza.org/ConScience/ConScienceSSPFact/ accessed 7 March 2005). The captive breeding program was so successful that expanding the program to include other zoos was necessary to provide enough holding space for the captive population (Parker 1987a). By 1988, six other zoos were participating in the SSP, with a total captive population size of 72 (Parker 1988).

Restoring red wolves to the wild

The results of the captive breeding program prompted managers to begin the formulation of a strategy to restore red wolves to the wild (U.S. Fish and Wildlife Service 1989). Two different pairs of red wolves, both originally wild caught, were released on Bulls Island, Cape Romain National Wildlife Refuge, on two separate occasions, once in 1976 and once in 1977 (U.S. Fish and Wildlife Service 1989). This release was planned to provide information to the USFWS on how captive animals would fare when returned to the wild (U.S. Fish and Wildlife Service 1989). Though these pairs both wandered extensively, both releases were deemed successful and the animals were returned to captivity (U.S. Fish and Wildlife Service 1989). Several mainland sites were considered as the next step in the reintroduction process, including sites in Florida and Georgia as well as one that spanned the Kentucky and Tennessee border (U.S. Fish and Wildlife Service 1989). Following careful evaluation of the site over several years, a proposal to reintroduce red wolves to the Land Between the Lakes in Kentucky and Tennessee was published (U.S. Fish and Wildlife Service 1989). This plan met with extensive public opposition from many different groups and was withdrawn by the USFWS following the rejection of the proposal by both the Kentucky and Tennessee state wildlife agencies (U.S. Fish and Wildlife Service 1989).

While considering alternate sites for the restoration effort, the Prudential Life Insurance Company donated approximately 480 km^2 to the USFWS that became the

Alligator River National Wildlife Refuge (ARNWR) (U.S. Fish and Wildlife Service 1989). This new refuge provided the USFWS with a large area of federal land in the historic range of the red wolf with the added advantages that no coyotes, feral dogs, or livestock operations were found in this area of low human population density (U.S. Fish and Wildlife Service 1989). In September of 1987, after an extensive public relations campaign, the USFWS released a breeding pair of red wolves on ARNWR under the experimental, nonessential designation (Parker 1989, U.S. Fish and Wildlife Service 1989). This designation reduces the protection the population is afforded under Sections 7 and 9 of the Endangered Species Act, gives managers increased flexibility to address issues as they arise, and was essential to allaying public fears over restrictions the reintroduced population would place upon local hunters, trappers, and residents (Parker 1989).

For the restoration program to be successful, captive animals would have to learn to survive in the wild. Efforts to instill these skills needed for survival proved to be a time intensive process for the USFWS (Parker 1987b). Initial releases of captive animals on ARNWR resulted in poor survival and an unacceptable tolerance for humans in some cases (Henry and Lucash 2000). An innovative solution to this problem was to release wolves onto selected islands and allow them to raise their offspring in a wild yet somewhat controlled environment (Parker 1987b). These island propagation projects have successfully addressed these concerns, providing wolves with survival skills and precluding the development of human tolerant behavior (Parker 1990).

Following the initial success of the reintroduction effort in northeastern North Carolina, the USFWS looked to identify potential sites within the historic range of the red wolf that could prove suitable for a second reintroduction site (Parker 1990). Great Smoky

Mountains National Park (GSMNP) was identified as a suitable site, in part because of its size, the availability of extensive biological studies, and the proximity of other federal lands to the park. Coyotes were known to exist in the park and the USFWS viewed this as an opportunity to examine interactions between the two in a carefully designed way (Parker 1990). Lessons learned from the ARNWR reintroduction were heeded when preparing for release of wolves into GSMNP including the use of the experimental, nonessential designation (Parker 1990). Two adult pairs were released in April of 1991 following an approximately three month acclimation period (Lucash and Crawford 1993). Two of these wolves exhibited behavior indicative of tolerance of humans and one was subsequently removed (Lucash and Crawford 1993). Several suspected depredation incidents were reported involving one chicken, three domestic turkeys, and a calf (Lucash and Crawford 1993).

From 1991-1998, a total of 37 red wolves were released in GSMNP but these wolves were unable to establish home ranges within the park itself (Henry and Lucash 2000). Natural recruitment into the population did not occur because none of 33 known pups born in the wild are known to have survived other than five that were captured and removed from the wild between 6-10 months of age (Henry and Lucash 2000). As a result, the USFWS terminated the GSMNP project in 1998 and redirected resources to the restoration effort underway at ARNWR (Henry and Lucash 2000).

Population and habitat viability assessment and an adaptive management plan

The restoration area around the ARNWR includes five counties in northeastern North Carolina: Beaufort, Dare, Hyde, Tyrrell, and Washington counties. Since the restoration effort began, red wolves expanded their range to include all five counties, totaling more than 6,650 km^2. During this same time period, coyotes expanded their range into the area and introgression again became a major concern of the red wolf recovery effort.

In April of 1999, the USFWS sponsored a Population and Habitat Viability Assessment (PHVA) that brought together experts from many different fields including canid biology, genetics, population modeling, and veterinary medicine to review data from the red wolf program and to discuss the challenges of maintaining a viable population (Kelly et al. 1999). The agenda was reflected in the focus of each of five small working groups: 1) coyote hybridization and genetic consequences, 2) wild population monitoring, 3) new population site selection, 4) captive population management, and 5) risk assessment modeling (Kelly et al. 1999). All of these issues were important to implementing red wolf recovery; a consensus from early in this meeting, however, was that introgression was the primary threat to recovery (Kelly et al. 1999). Accordingly, the groups were restructured such that addressing this threat became the primary focus of the workshop (Kelly et al. 1999). The discussion at this meeting was the foundation for the development of an adaptive management plan to address the threat of introgression (Kelly 2000).

Adaptive management is a paradigm that allows the integration of research and management such that management strategies are continually refined based on the implementation and evaluation of previous strategies and information (Walters 1986). By implementing management in an experimental context, researchers gain knowledge of the structure and function of the system while providing managers with valuable, evidence based information to refine management strategies (Lancia et al. 1996). Advocates of this type of management paradigm encourage the use of hypothesis driven research with minimal modification of traditional research design principles (MacNab 1983, Nichols 1991, Pimm 1993, and Schmiegelow and Hannon 1993). The adaptive management plan developed for the red wolf indeed lists hypotheses to test the effectiveness of implementation of the plan in achieving the desired result, abating introgression (Kelly 2000).

A principal component of the red wolf adaptive management plan involved the surgical sterilization of non-wolf canids (coyotes and coyote-wolf hybrids) within the recovery area (Kelly 2000). For this technique to be most effective, the behavior of sterilized canids should not be affected (Asa and Porton 1991, Asa 1995, DeLiberto et al. 1998). If a sterilized canid stayed hormonally intact yet was reproductively inviable, it could maintain territorial behavior and pair bonds (Till and Knowlton 1983, Asa 1995, Zemlicka 1995). By excluding other canids from its territory, it would, in theory, make that territory secure from hybridization and allow managers to focus their limited resources on other, unsecured areas.

Previous research with both coyotes and wolves suggests that this desired result was, indeed, achievable (Mech and Fritts 1993, Mech et al. 1996, Spence et al. 1999, Bromley and Gese 2001*a, b*). Tubally-ligated and vasectomized coyotes maintain territories and pair bonds just as their intact counterparts do (Bromley and Gese 2001b). When coyotes were sterilized for one study, a decrease in predation on domestic sheep was documented (Bromley and Gese 2001a). With no pups to provision, adult coyotes are less likely to be involved in depredation (Bromley and Gese 2001a, Tillman and Knowlton 1983). Thus, sterilization might be an effective tool to limit depredation by coyotes (Bromley and Gese 2001a).

Sterilization of gray wolves (*Canis lupus*) has been used for a different purpose. In some areas, gray wolves are considered so numerous that population control may be needed

(Mech et al. 1996). Vasectomized male gray wolves in one study maintained their social status in all cases for the duration of the study, up to 7 years for one individual (Mech et al. 1996).

Sterile, non-wolf canids were the driving principle behind the development and application of the red wolf adaptive management plan (Kelly et al. 1999, Kelly 2000). These animals would be used to buffer red wolves in the eastern part of the recovery area from coyotes and hybrids coming in from the west. The plan called for the establishment of a coyote and hybrid-free zone on ARNWR, a peninsula surrounded on three sides by water (Kelly 2000). All terrestrial access to this zone (zone 1) would require transit through a zone 2, where coyotes and hybrids were sterilized to meet management objectives. A third zone was thought to be beyond the capacity for intensive management, given available resources.

By design, the sterilized non-wolves would maintain territories yet be unable to reproduce (Bromley and Gese 2001b). To facilitate the establishment of new wolf groups, these sterilized animals were subject to removal if a dispersing wolf was available to occupy that space. As the plan was implemented, fewer non-wolves would be found in the population, as a result of the sterilization effort and later removal; therefore, an increase in wolves filling breeding vacancies and more wolf breeding pairs should be seen (Kelly 2000).

Identification of red wolves

Several morphologic features were used early on to distinguish red wolves from coyotes, including the longer legs and larger ears typical of red wolves (Riley and McBride 1972). Today, morphologic measurements are still used in conjunction with genetic testing, location of capture, and knowledge of pedigree when establishing the identity of unknown canids (Kelly 2000).

Identifying canids in northeastern North Carolina as wolf, coyote, or hybrid, and, therefore, which canids are candidates for sterilization, is very easy in some cases and more challenging in others. A microsatellite test first using 8 loci, then 18 (Miller et al. 2003, Wilson et al. 2000) distinguishes red wolves from hybrids. This refinement in genetic testing, combined with pedigree information when available, allows canids to be classified as wolf or non-wolf and can include an estimate of the percentage of an individual's ancestry that is attributable to red wolves (Kelly 2000, Miller et al. 2003). The research laboratory running this test can get results back to the biologists in about a week if the results are considered urgent. The development of these techniques and synthesis of information gives managers the most detailed information available to make informed decisions on the disposition of unknown canids.

Current field practices

Morphological criteria for differentiating wolf from non-wolf neonates have not been defined; applying genetic criteria to pups while still in a den, however, would give managers a tool to address introgression more effectively. That is, if a litter can be identified as non-wolf while that litter is still in the den, managers could remove the litter and be reasonably sure to remove the entire litter at once. If those pups are not identified as non-wolf until after they leave the den, managers must dedicate a significant portion of time to identifying the number of pups thought to be living in a given area and to trapping and removing them. This identification process involves both collecting a small blood sample for genetic analysis as well as implanting a passive integrated transponder (PIT tag) to allow for individual identification.

The benefit of handling neonatal pups to identify their genetic composition must be carefully weighed against the costs in terms of pup survival. Canid dens have been considered susceptible to abandonment as a result of human disturbance (Chapman 1979, Smith 1998). Because red wolves are endangered, any management action that could affect reproductive output must be carefully scrutinized.

Identifying neonatal pups means those pups are then known individuals when caught at later dates. Known wolves, whether caught for the first time outside the den as pups, juveniles, or adults, can be processed (weighed, measured, vaccinated, and fitted with a radio-collar) and returned to the site of capture without having to be held pending results of genetic testing. A canid of unknown origin may be held for more than two weeks while waiting for genetic results and the determination of whether to release the animal intact, sterilize it, or euthanize it.

All sterilized animals, as well as all red wolves, are also fitted with radio-collars. Managers can, therefore, monitor movements of both wolves and sterilized non-wolf canids in the recovery area. Understanding patterns of movement of these two types of canids could give us insight into patterns of contact and pairing and, therefore, introgression. For example, in many areas where gray wolves and coyotes exist, wolves have large home ranges and coyotes have smaller home ranges. If this is the case in the red wolf recovery area, it may be possible that coyotes exist in the interstitial spaces between wolf territories. When determining the availability of breeding territories within the recovery area, managers must consider the potential for coyotes to occupy territories unsuitable for red wolves. These territories could be a source of non-wolves that could hybridize with wolves.

Introgression as a disease

Understanding how introgression may be moving through the red wolf population is akin to understanding how an infectious disease moves through a population. Infectious disease epidemiology is a branch of epidemiology that focuses on diseases with the potential for transmission from one host to another (Halloran 1998). Infectiousness, contact patterns, transmission probability, the basic reproductive number, and the impact of different methods of intervention are a few of the concepts that make this branch of epidemiology unique (Halloran 1998).

The dynamics of infectiousness describe the process whereby an individual goes from susceptible to the disease to a noninfectious state (Halloran 1998). Once a susceptible individual is infected, a latent period, the time between infection and when an individual becomes infectious to others, follows. Following the infectious period, the final phase is the noninfectious period where the individual has recovered, become immune, died, or been removed from the population. In the case of introgression, a hybrid animal could be considered infected at birth. The affected animal then goes through a latent period until it reaches sexual maturity, and reaches noninfectious status either through sterilization or removal from the population.

Contact patterns influence which individuals are likely to be exposed to a disease (Halloran 1998). If a red wolf does not come in contact with a coyote or hybrid, then it cannot be exposed to the possibility of a hybridizing. Red wolves that maintain strong pair bonds and defend territories from other canids should be less at risk for hybridization while those red wolves that are dispersing and in search of establishing a territory are at higher risk due to increased chance of contact with non-wolves. Also, if more red wolves live in a geographic area than non-wolves, the potential for hybridization is lower than for wolves living in areas where non-wolves are numerous.

All individuals who are exposed to an infectious disease do not necessarily develop the disease. This concept is referred to as transmission probability (Halloran 1998). When red wolves and non-wolves come in contact with each other, multiple outcomes are possible. Red wolves may kill non-wolves and thus render those non-wolves noninfectious. Red wolves may pair with a non-wolf and thus the disease will likely be transmitted to a new generation. It is also conceivable that the two may part ways without pairing or killing each other. The outcome may be dependent upon density, season, or sex. If red wolves are more likely to find another wolf than a non-wolf, then the possibility of contact and transmission is less. If contact occurs during the pair bonding season or during breeding season, two canids that may otherwise have had no interest in each other may pair and produce a litter.

The basic reproductive number for a disease (R_o), as applied to this example, is a function of contact, transmission probability, and the duration of infectiousness. Essentially, R_o is a measure of how likely a disease is to spread within a population and quantifies the number of new individuals likely to become infected by one infectious individual (Halloran 1998). An $R_o < 1$ will die out whereas an $R_o > 1$ is likely to spread. Managers may be able to slow or eliminate the spread of introgression by targeting one of the aforementioned parameters that affect R_o.

The concept of surgical sterilization offers a method of intervention to decrease the spread of introgression and can be viewed as an intervention meant to decrease the infectiousness of an individual. Surgically sterilized animals may, therefore act as a buffer between wolves on one side and fertile non-wolves on the other. This type of intervention could result in a long-lasting effect that could be applied strategically across the landscape. By maintaining hormonally-driven behavior, tubally ligated and vasectomized animals have been documented to defend their territories to the exclusion of other canids and to maintain pair bonds (Bromley and Gese 2001b, Mech et al 1996). In contrast, euthanasia, another method to render an animal non-infectious, would open a breeding territory and allow another canid to move in that may or may not be infected. If infected, it too would have to be removed. Thus, the sterilization strategy provides a longer-term and more time-efficient solution than euthanasia.

Preview of chapters to follow

This dissertation addresses several of these epidemiologic issues through a wildlife management perspective. First, I describe the challenges and approaches to the management of a very large and complex historical data set being supplemented at a very high rate using the advantages offered by GIS referencing data. This is followed by an evaluation of GPS collars for monitoring canid movements in the red wolf recovery area. Next, I present the model of introgression as a disease. The following three chapters each address parameters from this model. In the first of these chapters, I discuss the results of den work that has been done since April of 2000 and its effect on short-term survival of red wolf pups. The processing and identification of pups while in the den is an important management tool for the red wolf recovery program and knowing how it impacts pup survival will guide its application in the wild. I then describe the use of sterile non-wolf canids to buffer red wolves from introgression. Then, I describe movement patterns of wolves and non-wolves elucidated from following individuals outfitted with radio-telemetry collars. Finally, I insert into the model values for parameters derived from field data.

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BUILDING A GIS TO ANALYZE RED WOLF DATA FROM NORTHEASTERN NORTH CAROLINA

A large amount of historical data of varying quality and detail exists for the red wolf program. Combining current data with historical data allows biologists the advantage of looking at trends and the results of management strategies. For biologists to be most effective in managing this population, they need to review field data in a timely, accurate, and detailed manner. Indeed, this review of data is vital to the effective implementation of an adaptive management plan that refines management strategies based on the analysis of the impact of previous ones.

The red wolf program has stored much of its data in a relational database. Location estimates for individuals since the beginning of the restoration effort are kept in multiple tables within this database and were recorded with varying degrees of precision. Events such as births, deaths, and captures are also tracked in a separate table. One of the most efficient ways to manage such a collection of data is by integrating a database with a geographic information system (GIS). A GIS is a collection of software, hardware, and procedures that are used for the management, analysis, and display of spatial data (modified from http://www.gis.com/whatisgis/whatisgis.pdf, accessed March 1, 2004).

Spatial data are data that can be associated with a physical location, such as the red wolf telemetry data. GIS allows the user to tie data to the landscape in such a way that any analysis of patterns can include how the data relate to each other spatially. The spatial component is critical to any analysis of introgression. That is, what is important is not just if introgression is occurring, but also where it occurs on the landscape. For example, does it occur in the heart of the red wolf management area or on the periphery? The implications for management actions designed to address introgression could be very different, depending on the location of these events.

Examples of spatial data relevant to our discussion here include telemetry location estimates, den locations, and mortality locations that have been kept by the recovery program since the inception of the restoration effort. Such data include not only which animal, what date, and notes about what the animal may have been doing, but also Universal Transverse Mercator coordinates (UTMs) for each of these locations. That is, spatial reference information is assigned to each event. By using these coordinates and plotting these locations on a map, one can visualize how these events are distributed across the recovery area and one can look for patterns.

Other spatial data are necessary to put a set of coordinates in perspective. I assembled data for the five county restoration area in northeastern North Carolina primarily from the NCSU libraries' geodata collection, available to NCSU users at http://www.lib.ncsu.edu/stacks/gis. This website provides users with geographic data from many sources, including the North Carolina Center for Geographic Information and Analysis (CGIA), a primary source for much of the data I used.

I performed most of the analyses using shapefiles, a proprietary data model of Environmental Systems Research Institute (ESRI). Shapefiles are a way of representing spatial data as points, lines, or polygons in a computing environment. ESRI's desktop GIS software ArcView 3.3 was the first program I used for spatial analysis and display. This version has limited though extremely respectable capabilities. Once available, their next generation of GIS software, ArcGIS 8.3, soon became the program of choice. Extensive or intricate data generation, modification, and analysis were accomplished through ArcInfo

Workstation 6, a command line interface that lacks the user friendly graphical user interface found in ArcView. Much of this functionality became available in ArcGIS 8.3 through a new interface, ArcToolbox. With ArcGIS 8.3, ESRI began promoting the use of geodatabases, a new data model based on either Microsoft Access or other commercial database software designed to handle datasets larger than 2 gigabytes (e.g., Oracle). The red wolf data were already stored in a relational database, facilitating the importation of the tabular data into a spatial format. Late in 2004, ArcGIS 9.0 was released and subsequently became the software used for all data analysis, generation, and display. This version maintains the user interface that was introduced with 8.3 but offers improved functionality.

For analyzing red wolf data, I routinely used shapefiles of North Carolina's county boundaries, major hydrology, roads (TIGER® line files), and 1998 color infrared digital orthophotograph quarter-quadrangles, all obtained through NCCGIA. I also used a quad, block, square (QBS) grid, generated by Doug Howell of the North Carolina Wildlife Resources Commission, for reference purposes. I generated shapefiles of management zone boundaries as defined in the red wolf adaptive management plan. These boundaries were digitized on screen and reviewed by recovery program personnel for accuracy.

After converting tables of locations with UTMs to shapefiles and later to a geodatabases feature class, I was able to plot all telemetry location estimates, deaths, den locations, and captures. These data were then reprojected from UTM to North Carolina state plane, 1983 meters. By plotting these locations with respect to other data such as hydrology and county boundaries, I was able to identify and correct outliers where, for example, digits had been transposed during data entry. Because the entry for each location usually included a verbal description of the location, I was able to match the coordinates to the location and confirm the coordinates were correct. These two steps were crucial in improving the accuracy of the location estimates and home ranges generated from them.

The individual locations could be symbolized on a map by the type of event (for example, birth, death, disappearance, or transponder placement), the type of animal, the year, management zone, sex of the individual, or a combination of these things. Data could then be summarized by type of animal and management zone within which the event occurred and then analyzed for trends. For example, the number of wolves caught for the first time could be displayed for each management zone over time. Using ArcView 3.3, the Spatial Analyst extension, and the animal movement extension written by Phil Hooge and Bill Eichenlaub of the U.S. Geological Survey's Alaska Science Center (http://www.absc.usgs.gov/glba/gistools/), I generated home range estimates from telemetry location estimates.

Recovery program personnel also record data on trap effort and sign surveys and assign QBS grid coordinates to each trap line or survey area. These data are summarized in a table so that the total number of trap nights or minutes of survey in a grid square can be calculated. I take these data and join them to a georeferenced QBS grid to display the effort (trap nights or minutes of survey) that went into looking for animals in a given area.

These data are used for parts of my dissertation but are also a subset of the data presented twice a year at Recovery Implementation Team meetings. By having the data generated, extracted, and formatted, we are able to view the results of implementation of the red wolf adaptive management plan not only in numbers but as a reflection of how they play out across the landscape.

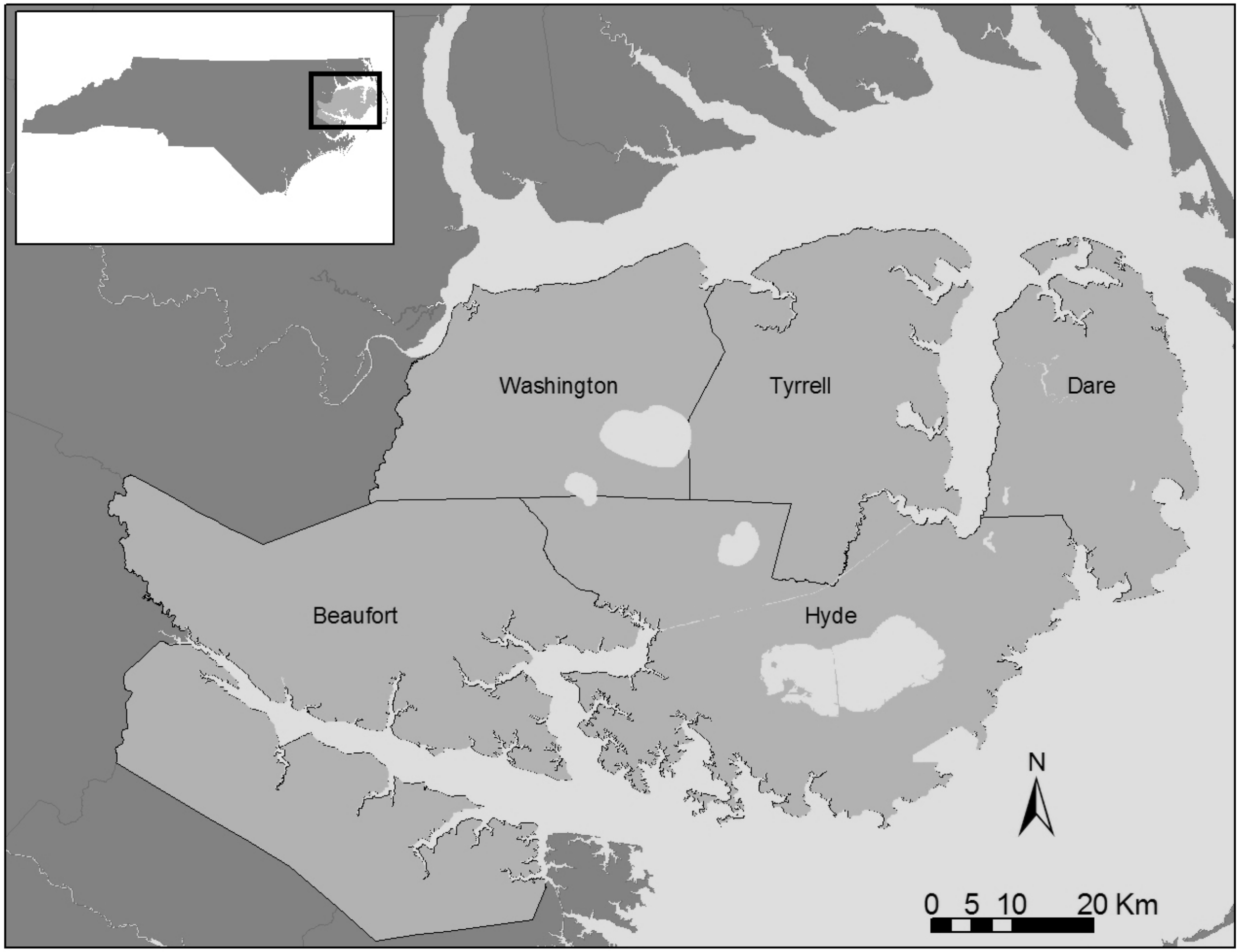

Figure 1. The red wolf recovery area in northeastern North Carolina. This figure was generated using county boundary and hydrology data.

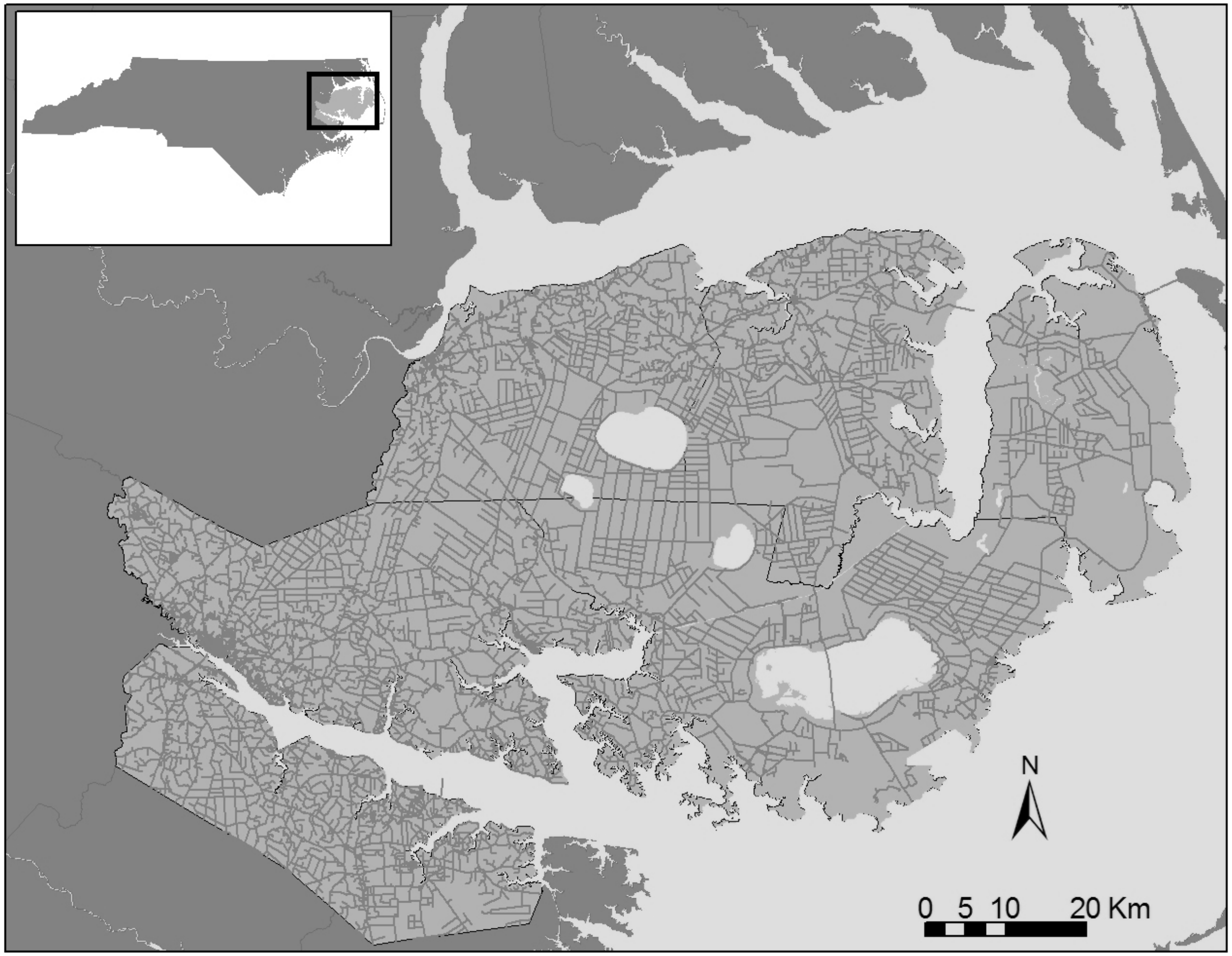

Figure 2. Roads in the red wolf recovery area. This figure was generated by adding TIGER® road files and clipping them to the recovery area (i.e., displaying only those roads within and no roads outside the 5 counties).

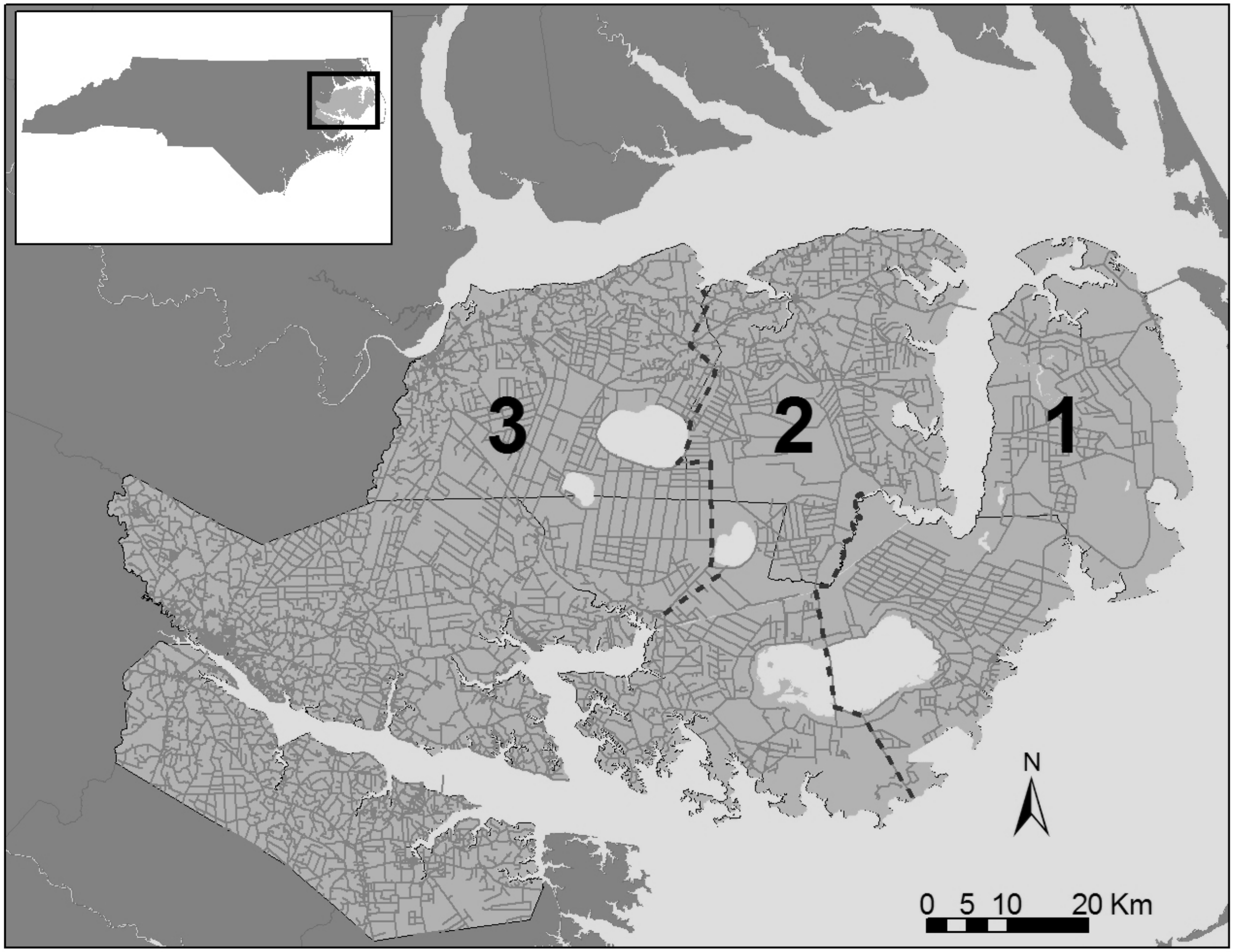

Figure 3. Management zones within the red wolf recovery area. This figure was generated by displaying the digitized boundaries between the management zones.

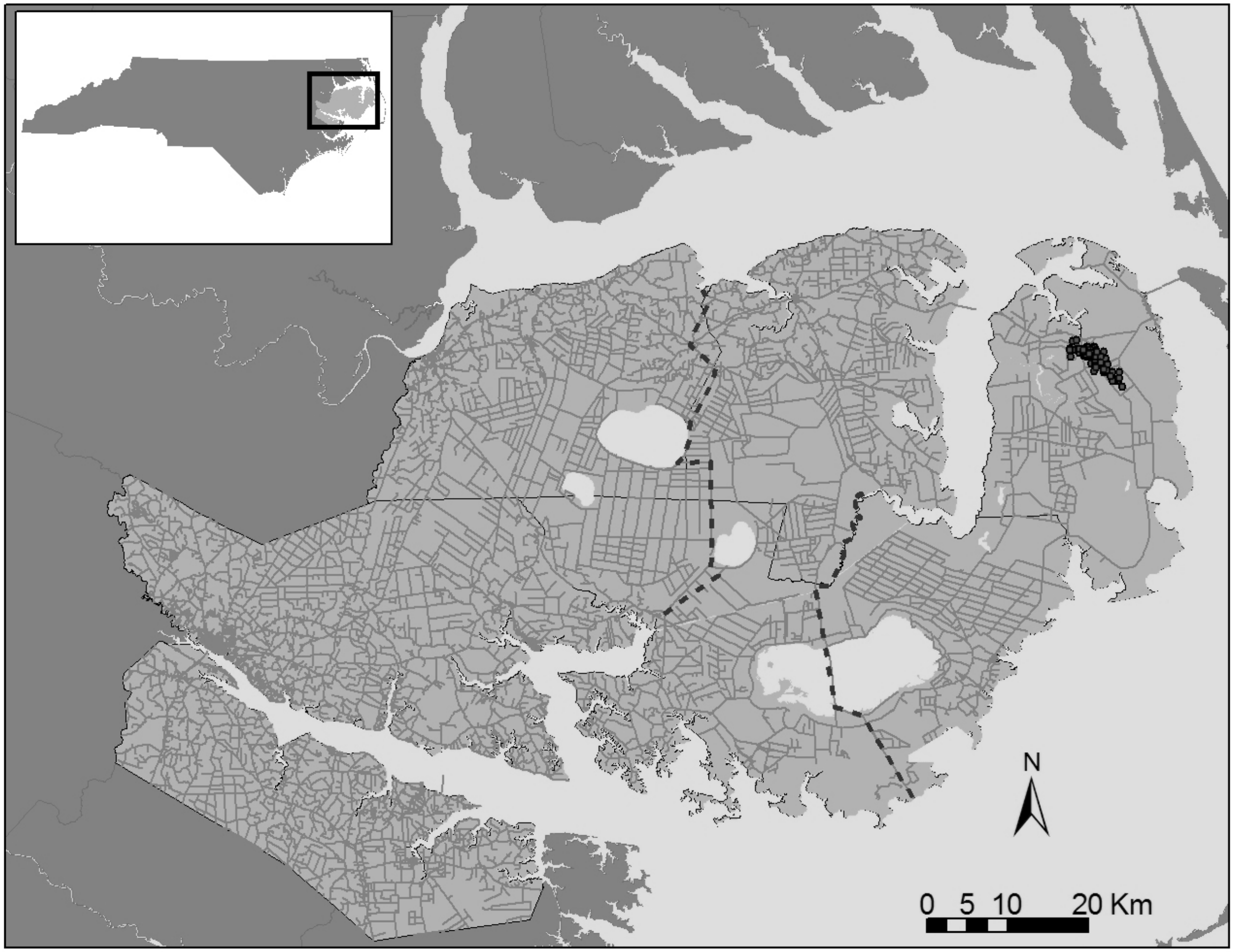

Figure 4. Telemetry locations of a single animal. This figure was generated by displaying the coordinates from telemetry location estimates for 1 wolf over the course of a year.

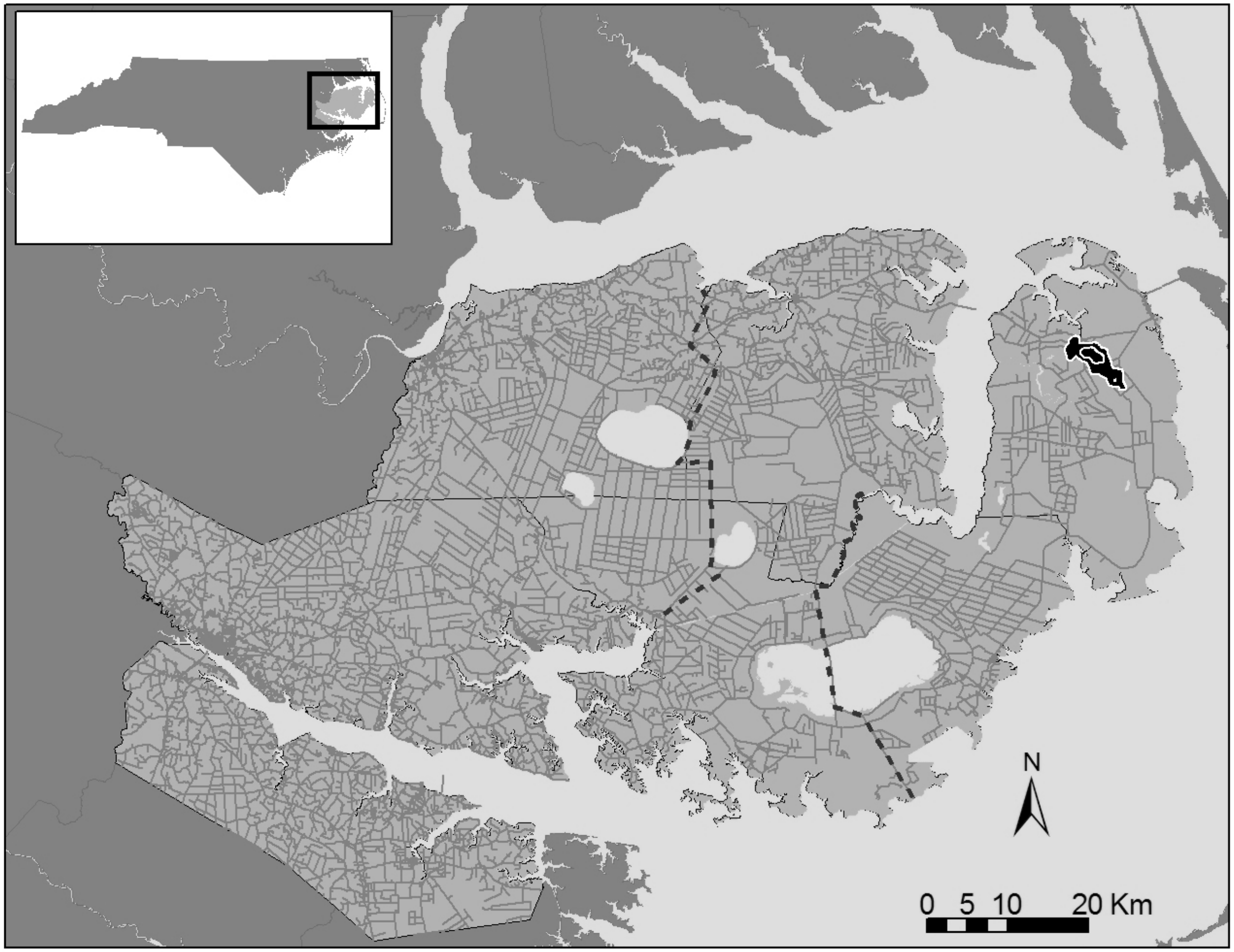

Figure 5. Home range estimation. Using the Animal Movement Extension for ArcView 3.3, the telemetry locations from Figure 4 were used to generate the estimate of home range size depicted here (50 and 95% contours).

EVALUATION OF GPS COLLARS FOR USE IN TRACKING CANIDS IN THE RED WOLF RECOVERY AREA

INTRODUCTION

Researchers have used radiotelemetry to study wildlife ecology for more than 40 years, answering questions on topics ranging from patterns of animal movements to estimation of survival rates (e.g., Gese et al. 1990, Kolenosky and Johnston 1967, Laundre et al. 1987, Mech 1983, Pollock et al 1989, and Trent and Rongstad 1974). When studying elusive carnivores, the importance of remote techniques to monitor movement and survival is clear. These techniques offer the opportunity to collect data with minimal disturbance of an animal or influence on behavior after the transmitter is applied.

Radiotelemetry is an important tool for studying wildlife but the accuracy and precision of location estimates can limit its usefulness. Errors of relocation estimates may be hundreds of meters and depend on factors such as equipment, observer experience, the skill of pilots used in aerial surveys, and landscape characteristics (Hoskinson 1976, Mills and Knowlton 1989, Saltz and Alkon 1985).

The development of radiotelemetry collars that incorporate the Global Positioning System (GPS) offered a new way to study wildlife movement and habitat use (Rempel et al 1995, Rodgers and Anson 1994). GPS relies on communication between receivers on the ground and 24 satellites orbiting the earth to estimate locations (Hurn 1989). When a receiver is in contact with four or more satellites, the receiver can calculate a position to determine latitude, longitude, and elevation (3D fix). If the receiver is only able to communicate with three satellites, a position is calculated to determine latitude and longitude (2D fix), and elevation must be specified or is assumed to be that of the last 3D fix. Two-dimensional positions are often less precise due to errors of inferring elevation. An error of 10 m in elevation, for example, may result in horizontal error of more than 50 m (Trimble Navigation Ltd 1994).

Selective availability, the deliberate degradation of GPS signals by the United States government, was once the main influence on positional accuracy and precision and was responsible for location errors of up to 100 m (Trimble Navigation Ltd 1994). A process known as differential correction allowed post-processing of data or real-time correction to account for system-wide errors including selective availability. With differential correction, users were able to reduce errors to less than 5 m (Trimble Navigation Ltd 1994). On 1 May 2000, selective availability was turned off, thereby decreasing average error in position estimation by a factor of 10 even without differential correction.

The precision in locations offered by GPS collars may delineate habitat preferences and movement patterns not discernable from VHF telemetry, thus researchers have begun studying the utility of GPS collars for following animal movement and habitat use (Dussault et al 1999, Moen et al 1996, Moen et al 1997, Rempel and Rodgers 1997, Rempel et al 1995). A major factor limiting the widespread deployment of GPS equipment is the expense as compared to VHF equipment. A single GPS collar may cost as much as 20 VHF collars, and receivers and remote data download options bring added costs. This technology, though, does offer advantages such as the potential for more precise location estimates and location estimates in all types of weather (Dussault et al

1999, Moen et al 1997). Perhaps the biggest advantage is that one gets location estimates even when VHF cannot locate the animal because of where the animal is. For example, an animal may be in an unexpected place, have moved a long distance, or be in a place where topography blocks the signal. Because the time of each relocation attempt is programmed into a collar prior to placement on an animal, each collar can record a location estimate for each animal simultaneously, without a biologist present, and thus increase the utility of these collars for studying interactions between collared individuals. This savings in personnel time along with the quantity and quality of data that can be obtained may, in the long run, offset the initial cost of the equipment.

VHF radiotelemetry has been used for monitoring red wolves in northeastern North Carolina (NE NC) since red wolves were reintroduced to the area in 1987 (Phillips et al. 1995). Relocations of collared red wolves have typically been done from aerial telemetry flights because red wolves range over more than 6,000 km^2 and often use areas inaccessible for reasons such as lack of a road network or nearly impassable habitat. These telemetry flights, however, are typically done at the same time of day due to limitations in airspace availability over the Navy and Air Force bombing ranges in Dare County. Little information, therefore, had been collected on temporal variation in movement and home range utilization by red wolves. GPS radiotelemetry offers numerous advantages to the biologists tracking red wolves including precise locations at any time of day in inaccessible areas and decreasing the need for expensive telemetry flights. The potential utility of GPS collars given the habitat found in N ENC needs to be determined before collars are placed on wolves.

Habitat characteristics can play an important role in the utility of GPS for tracking animal movement. Habitat characteristics such as canopy closure and basal area influence the chances of successfully obtaining a location estimate and the precision of the estimate because GPS collars often have difficulty locating themselves in dense habitats (Dussault et al 1999, Moen et al 1996, Rempel et al 1995).

Numerous habitat types were present within the study area in NE NC. Predominant habitat types were 1) non-riverine swamp forests, 2) pocosin, and 3) open areas that include farm fields and bombing ranges. Non-riverine swamp forests were characterized by bald cypress (*Taxodium distichum*), swamp black gum (*Nyssa aquatica*), blackgum (*Nyssa sylvatica*), Atlantic white cedar (*Champaecyparis thyoides*), and loblolly pine (*Pinus taeda*) while scattered pond pine (*Pinus serotina*) and low evergreen shrubs characterized pocosins (Parker 1987).

The thick vegetation, both overstory and understory, found in swamp forests and pocosins may interfere with the ability of a GPS receiver to acquire satellite signals. Successful location attempts, those attempts where a location estimate is obtained, may be less likely in these habitats as compared to open habitats and may be more likely to result in a 2-D location estimate, requiring communication with only 3 satellites, than a 3-D location estimate, requiring communication with at least 4 satellites. Since 2-D estimates are usually less precise than 3-D estimates, I expect that location estimates obtained in swamp forests and pocosins will be less precise than those estimates obtained in open locations.

This experiment evaluated the reliability, precision, and optimal signal search time for GPS collars in the major habitat types found in the red wolf recovery area. I hypothesized that 1) collars would not differ in their ability to successfully obtain location estimates, 2) increasing the amount of time a collar attempts to obtain a location estimate would increase the probability of success, 3) collars would be more successful in obtaining location estimates in open habitats as compared to dense habitats, and 4) GPS collars would return precise location estimates, even in dense habitat.

MATERIALS AND METHODS

Four GPS collars without differential correction ability were used to evaluate how well GPS collars function in NENC habitat. Because the collars were equipped with active antennas, each collar was placed around a three liter bottle filled with saline and suspended from a tripod at a height of .5m, slightly lower than the height the collar would be on a standing wolf.

Each GPS collar attempted to locate itself at each of five locations in each of three predominant habitat types: swamp forest, pocosin, and open. All collars were tested at each location before the tripod was moved to a new location. Late in this study, I noted that the connection between the GPS collar and the test battery was somewhat fragile and not designed for repeated attachment and detachment. Therefore, the number of open sites used in this study was reduced from 5 to 4 to reduce wear on the connector. Habitat type was identified in the field as a function of composition and density of vegetation. The collars attempted five location estimates for each of four specified times: 60s, 90s, 120s, and 150s in each test location. This time, referred to as maximum search time, represents the maximum amount of time a collar would search for a location before shutting down and trying again at the next specified time. The time between location estimates was 6-minutes. This design allowed for a total of 100 fix attempts per collar for two habitat categories and 80 for the other.

By design, the GPS collars record any 2D location estimate obtained within the specified time period and attempt to obtain a 3D location estimate for 20 seconds after a 2D location estimate is obtained. If a 3D location estimate is obtained, the GPS collar automatically turns off. Data recorded by the GPS collar included the time and date of the position, the dilution of precision (DOP, a measure of precision related to satellite geometry), and the type of location estimate (3D versus 2D).

To determine the coordinates of each location precisely, a Trimble GPS Pathfinder Pro XL was used to collect a minimum of 400 GPS positions at each collar test location. These positions were then subjected to differential correction and averaged to calculate the coordinates of each location for comparison to the GPS collar locations. A non-GPS method was not used to estimate collar location.

Data from these GPS collars can be retrieved remotely through a receiver via a VHF pulse-coded signal or directly by connecting a collar to a personal computer and downloading the data. To test the field retrieval mechanism, three attempts were made in each habitat type to retrieve the data using a truck-mounted antenna. The retrieval experiment was repeated with the receiver operating in a plane during a scheduled telemetry flight.

The manufacturer provided a spreadsheet so that I could try different combinations of those factors that affect battery life including maximum search time, frequency of location estimate attempts, frequency of data transfer via VHF signal, and frequency and duration of a VHF beacon to locate an animal while preparing for data transfer. The goal is to maximize battery life while maintaining the ability to relocate a GPS collared animal on a schedule that meets management or research objectives.

The first three research hypotheses involve a binary outcome, whether or not a collar obtained a location estimate, so logistic regression was used to determine the effect of collar, maximum search time, and site category (open, pocosin, or forest) on success. The third hypothesis involves a continuous variable, distance to the estimate obtained from the Trimble GPS unit, so an analysis of variance was used to assess the influence of collar, site category, maximum search time, and type of location estimate (3D or 2D) on distance to control point. Tukey's method was used to look for significant differences in pairwise comparisons of means.

RESULTS

Collars were tested during the late summer and early fall of 2000. Three of the four collars functioned well, but one collar was returned to the manufacturer for adjustment after it functioned poorly (i.e., obtained estimates for only 38.3% of location attempts) at the first three test sites. This collar was not returned by the manufacturer in time to complete the experiment with this collar. Summary data for the location attempts are presented in tables 1 through 3.

Collar, maximum search time, and site category were all significant in the logistic regression model ($p < 0.000$) of effect on success (Table 4). Collar 1 functioned poorly as compared to collars 2 and 3 (Tables 1 and 4). Increasing maximum search time increased the number of location attempts that were successful, and location attempts in open habitat were more successful than those attempts in swamp forest or pocosin

(Tables 1 and 4). Open habitats had success rates of 90.8% while pocosins and swamp forests had success rates of 63.3% each (Table 1).

Type of location estimate (2D or 3D) and site category were significant predictors of distance to known location ($p = 0.000$, Table 5). Collar and maximum search time were not significant predictors of error distance at $\alpha = .05$ ($p = 0.080$ and 0.777, respectively, Table 5). Average distance error for open test sites was 10.74 m and was significantly less than errors for either pocosin (21.09 m) or swamp forest (25.4 m, Tukey's method, Table 3). Location estimates made using 3D fixes were, on average, closer than those using 2D fixes (Tukey's method, Table 3). Seven of the 590 location estimates (3 at pocosin sites, 4 at swamp forest sites) were > 100 m (range 106 m to 288 m). These location estimates were included in all analyses.

Data were successfully downloaded from the collars using the VHF transmitter. Downloading location estimates via VHF required approximately 6 seconds per location to be transmitted. To maintain a signal strong enough to retrieve the data via ground telemetry, I had to be within approximately 400 m. Signal fluctuation caused the loss of some data during transfer though these data points were stored in the collar and later retrieved directly from the collar. The one attempt to retrieve data via aerial telemetry was successful with minor fluctuations in signal strength. All data were downloaded from each collar by connecting the collar directly to a personal computer.

DISCUSSION

Biologists with the red wolf recovery program affix radiocollars to each wolf they catch and release. Losing track of a collared animal necessitates expanding telemetry effort over a wider area and potentially setting traps to recapture an animal. The time and effort put in to relocating an individual whose collar has failed means fewer resources are available to accomplish other recovery program objectives. Since GPS collars were an emerging technology when this study was conducted, their precision and reliability were the two main questions that needed to be answered before biologists were willing to place them on wild wolves. If this new GPS technology were not reliable, biologists would not consider using it in the field.

Overall, the GPS collars used in this study worked as expected though there was some unexpected variation between collars with respect to the number of successful location attempts. Longer maximum search times were associated with a higher number of successful location attempts than shorter search times. Success was higher in open rather than dense habitats and open sites were associated with more precise location estimates than were dense habitats, a result of the higher percentage of 3D fixes obtained in open rather than dense habitats.

Trying different combinations of maximum search time, frequency of location estimate attempts, frequency of data transfer via VHF signal, and frequency and duration of a VHF beacon resulted in choosing a maximum search time of 120 s with data transfer once every two weeks and a 1 hour VHF beacon prior to scheduled data transfer. The manufacturer had suggested 90 s as a starting point but noted that longer search times may be needed in dense habitats. Increasing maximum search time to 120 s from 90 s would require decreasing the number of location estimates per week from a proposed three to two in order to have the collars functional for approximately two years. This compromise may affect research objectives but may be necessary to balance management effort.

Data retrieval was somewhat challenging, even with a stationary collar. Thus downloading data remotely under field conditions would be even more challenging. Collars made by different companies have different options for data retrieval. The user of these collars is required to program the time of data transfer into the collar before the collar is deployed. If someone is not present to retrieve these data at the scheduled time, the data will be stored and not accessible until the collar is retrieved. Thus, data that is not remotely downloaded is not lost but is not immediately available.

Tuning the receiver to achieve optimum signal strength to avoid loss of data during transfer takes practice. Once a collar is deployed, getting close enough to retrieve data without causing an animal to move, and thus the signal to fluctuate, would require skill, creativity, and patience. Retrieving the data during aerial telemetry flights is possible though it adds time to an already long and, therefore, costly flight.

Newer GPS collars have been developed since this study began and battery life has been extended. Long battery life for a GPS collar is preferred because repeat captures of an individual can be difficult. Newer collars may be more useful than the collars described here for intensive monitoring over a long period of time before the battery would need to be replaced. The collars described in this study do appear to be a useful tool for monitoring canid movements in NENC. Their weight of 550 g, however, means an individual who will wear one of these collars must be at least 18 kg. Though Murray and Fuller (2002) recommended that a collar or other mark not exceed 10% of a mammal's body mass, red wolf biologists have chosen a more conservative cut off of 3%.

Ultimately, the red wolf program made the decision not to deploy these collars due to perceived concerns regarding battery life, reliability of the collar, and remote retrieval of location estimates. The data from this study show that GPS collars can work in the habitat in northeastern North Carolina but the study also shows the importance of testing the collars before deployment. One of these collars did not work well, but that was determined before it would have been deployed. This testing of collars also provided valuable information regarding precision and reliability that will be useful for interpreting results of any study relying on these collars.

The red wolf program did deploy a newer generation GPS collar on a wolf-coyote hybrid in the recovery area. This individual was also implanted with an abdominal VHF transmitter so that it could be followed if the collar failed. No pilot study was conducted on this collar prior to its deployment. Three hundred seventeen of 632 location attempts (50.2%) over a 1 year period were retrieved remotely. Data transfers were scheduled at a time of day that allowed biologists who had done a telemetry flight to communicate the animal's approximate location to the biologist who would be attempting to collect the transferred data. Even then, telemetry flights did not always coincide with pre-scheduled data transfers.

The animal outfitted with the collar did not appear to be settled in a home range and had wide ranging movements that made finding the animal for data downloads somewhat challenging. The data from the GPS collar did include location estimates that were not in areas the animal had been found during telemetry flights, thereby yielding additional information that otherwise may have gone undetected.

The expense of GPS collars may affect their deployment on any large scale. At approximately $2,500 per collar, one GPS collar costs 10 times more than the VHF collars used by the red wolf program. A receiver to retrieve data from this collar is approximately $2,000 whereas a regular VHF receiver that the program currently uses costs only approximately $800. Flight time costs the program approximately $140 per hour. Given an average of 2 flights per week and 3 hours per flight over 52 weeks in a year, the red wolf program would spend $43,680 on flight time and $7,665.84 in salary for a GS 11, step 5 biologist doing the tracking in a year (total = $51,345.84). In contrast, if the same biologist had to spend 3 hours a week and drive 100 miles (at 18 miles per gallon and $3.00 per gallon of gas) each week specifically to get near one animal's location to collect the data download and fly only once per week for 3 hours, the program would spend $21,840 in flight time, $7,665.84 in biologist's salary, and $884.00 in gas (total = $30,389.84). The time and resources spent driving around to retrieve data from multiple animals could be unacceptable, depending on how those collars are distributed across the landscape. To make this second option feasible in terms of acceptability to the red wolf biologists in maintaining a desired level of monitoring, a remote method of data download, such as via satellite, would be required and add an additional cost.

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Table 1. The number of successful attempts and the total number of attempts to obtain a GPS location estimate summarized by maximum search time, site category, and collar. Site categories are swamp forest (SF), pocosin (PO), and open (OP). Since collar 4 performed poorly, it was returned to the manufacturer without completing testing. The 60 locations attempts by this collar are included only in the collar summary data and were excluded from further analyses.

Factor	Level	Successes	Attempts	Percent Successful
Maximum	60	71	210	33.81
Search time	90	150	210	71.43
(seconds)*	120	179	210	85.24
	150	198	210	94.29
		598	840	71.19
Site Category*	SF	190	300	63.33
	PO	190	300	63.33
	OP	218	240	90.83
		598	840	71.19
Collar	1	150	280	53.57
	2	229	280	81.79
	3	219	280	78.21
	4	23	60	38.33
		621	900	69.00

* Does not include data for collar 4

Table 2. For successful location attempts, the number of 2D and 3D fixes summarized by maximum search time, site category, and collar. Site categories are swamp forest (SF), pocosin (PO), and open (OP). Since collar 4 performed poorly, it was returned to the manufacturer without completing testing. The 23 locations estimates by this collar are included only in the collar summary data and were excluded from further analyses.

Factor	Level	2D fixes	3D fixes	Total Successful Attempts	% 3D fixes
Maximum Search Time (seconds)*	60	24	47	71	66.20
	90	65	85	150	56.67
	120	81	98	179	54.75
	150	95	103	198	52.02
		265	333	598	55.69
Site Category*	SF	116	74	190	38.95
	PO	128	62	190	32.63
	OP	21	197	218	90.37
		265	333	598	55.69
Collar	1	71	79	150	52.67
	2	116	113	229	49.34
	3	78	141	219	64.38
	4	15	8	23	34.78
		280	341	621	54.91

* Does not include data for collar 4

Table 3. Distance (in meters) to a known point for successful location attempts, summarized by maximum search time, site category, collar, and type of fix. Site categories are swamp forest (SF), pocosin (PO), and open (OP). A minimum of 0 represents at least one successful position fix with 0 m error in each category. Since collar 4 performed poorly, it was returned to the manufacturer without completing testing and is not summarized in the data below.

Factor	Level	n	Mean	SE	Minimum	Maximum
Maximum Search Time (seconds)	60	71	14.68	1.94	0	126.13
	90	150	19.47	2.42	0	288.61
	120	179	18.18	1.30	0	130.13
	150	198	19.24	1.26	0	113.78
Site Category	SF	190	25.4	2.13	0	288.61
	PO	190	21.09	1.39	0	130.13
	OP	218	10.74	0.44	0	34.49
Collar	1	150	18.41	1.34	0	112.41
	2	229	16.99	1.36	0	189.48
	3	219	19.98	1.65	0	288.61
Type of Location Estimate	2D	265	25.49	1.74	0	288.61
	3D	333	12.83	0.53	0	63.31

Table 4. Logistic regression model for influence of collar, maximum search time, and site category on success. Site categories are swamp forest (SF), pocosin (PO), and open (OP).

						95 % CI	
Predictor	**Coefficient**	**Std Error**	**z**	**p**	**Odds Ratio**	**Lower Bound**	**Upper Bound**
Constant	-0.37	0.31	-1.23	0.22			
Collar (Collar 1 is reference value)							
2	2.39	0.28	8.39	0.00	10.89	6.23	19.01
3	2.00	0.27	7.47	0.00	7.39	4.37	12.49
Maximum Search Time (60 s in reference value)							
90	2.33	0.27	8.48	0.00	10.29	6.00	17.63
120	3.47	0.32	10.82	0.00	32.17	17.15	60.35
150	4.71	0.40	11.70	0.00	110.91	50.39	244.11
Site (OP is reference value)							
PO	-2.83	0.34	-8.22	0.00	0.06	0.03	0.12
SF	-2.86	0.34	-8.41	0.00	0.06	0.03	0.11

Test that all slopes are zero: G=424.097, df = 7, p-value = 0.00

Table 5. Analysis of variance table for effect of collar, type of fix , maximum search time, and site category on success of a location attempt. Three individual collars were tested. Type of fix was recorded as 2D or 3D. Maximum search time was 60 s, 90 s, 120 s, or 150 s. Site categories were swamp forest, pocosin, and open.

Source	df	Seq SS	Adj SS	Adj MS	F	p
Collar	2	945.4	1988.6	994.3	2.53	0.08
Type of Fix	1	25420.5	8480.5	8480.5	21.61	0.00
Maximum Search Time	3	620.9	432.2	144.1	0.37	0.77
Site Category	2	8847.3	8847.3	4423.7	11.27	0.00
Error	589	231154.7	231154.7	392.5		
Total	597	266988.8				

MODELING INTROGRESSION AS AN INFECTIOUS DISEASE

Anderson and May (1979) proposed that parasites may affect size of host populations much as predators influence prey population sizes. They define parasitic disease broadly to include viral, bacterial, and protozoal diseases as well as those caused by helminths and arthropods. Previously, the medical community treated population size as a constant when modeling parasitic diseases while ecological researchers had routinely looked at the effects that parasites have on growth rates of host populations.

I propose that the impact that introgression of coyote genes into the red wolf population is similar to the impact that parasites have on their host. Genetic introgression certainly could affect the size of the red wolf population if, over time, wolf-coyote hybrid pups were to replace wolf pups. By building a model of introgression as a disease, we can predict where changes in management strategies can have the greatest influence on outcome.

Figure 1 is a modification of a classic model for directly transmitted infections (adapted from Anderson and May 1979). The notation is a combination of traditional epidemiologic terms and several biological terms for which analogous epidemiologic terms do not exist (Table 1). Assumptions made in this model are that 1) a pair bond remains intact until a member of the pair dies or is displaced, 2) bonded pairs are monogamous, 3) coyotes and coyote-wolf hybrids function similarly in all aspects of the model and are referred to as one group, non-wolves, 4) males and females function similarly in all aspects of the model and are combined, and 5) the probability of encounter between a wolf and non-wolf depends on population densities and not geographic location.

Non-wolves are considered infectious individuals and are diagramed in the model below the dotted line (I). Susceptible individuals (X) are unpaired, breeding age red wolves. Red wolves that find and pair with red wolves move directly from the susceptible (X) compartment to the immune (Z) compartment. The rate at which this happens (b) is determined by a variety of factors, including wolf density. Knowledge of how red wolves choose mates is very limited and the subject of current research. Red wolves that are unpaired are susceptible to hybridizing with non-wolves. Infected individuals (Y) are those red wolves who are paired with a reproductively intact non-wolf.

For a wolf to pair with a mate, it obviously must first come in contact with that individual. Contact patterns between infectious non-wolves and at risk wolves play an important role in the transmission of any disease. For a disease that requires direct transmission to spread, there is no chance the disease will be transmitted if a susceptible individual never comes in contact with an infectious individual. On the other hand, contact between an infected individual and a susceptible individual does not guarantee disease transmission.

Understanding how infectious individuals move through the population is important to estimating rates related to contact patterns and transmission probabilities. The probability of whether or not the disease is transmitted (β) depends on a variety of factors. In our study population, contact that occurs outside the breeding season, for example, may not result in pair formation. Contact may also result in conflict and possibly the death of the infectious individual. The rate of contact between wolf and non-wolf is expected to be at least somewhat density dependent and, therefore, could vary geographically. An analysis of data related to movement patterns was the focus of the third chapter in this dissertation.

Once infected, a wolf could stay paired with an infectious animal and thus remain infected. Alternatively, an infectious animal mated with a wolf could die (c_n) or be removed from the population by managers (c_m). Thus the wolf again becomes susceptible to infection. The other possibility is for the wolf to move to the immune compartment. This recovery rate (ν) has two components.

First, a dispersing red wolf could move into an occupied territory and displace or kill an infectious individual (ν_d). Now paired with a red wolf, the resident wolf is no longer at risk of hybridization (Z_w). Displacement of non-wolves by red wolves has been seen in the recovery area as has interspecific aggression resulting in the death of non-wolves by wolves. These situations are both desirable and necessary for the long-term viability of the recovery program. Otherwise, intensive management to maintain the population may be difficult to justify.

Second, the non-wolf of the pair could be surgically sterilized, such that it maintains hormonally-driven behaviors, and then returned to its territory (ν_s). Because it remains hormonally intact, it will defend its territory from other, likely intact, non-wolves and could maintain its status in a non-breeding pair for multiple years (see sterilization chapter in this volume). Having been sterilized, there is no chance of hybrid pups from this individual. Thus, its wolf mate could be considered immune (Z_h). Immunity in this model is not life-long. The death of a mate means that a previously immune red wolf is again susceptible to hybridization, as shown by inclusion of the rate of loss of immunity (γ). This loss of immunity is either natural (γ_n) or a result of management (γ_m).

Only immune groups that are composed of two red wolves (Z_w) produce offspring (a_w) that will become new susceptible individuals (X). Infected individuals, however, are capable of producing offspring that are infectious to susceptible individuals (a_h). That is, hybrid pups from an infected individual can grow to become infectious to a susceptible red wolf. It is also possible for non-wolves to breed with non-wolves and thereby produce offspring that are infectious for a red wolf (a_n).

Intervention in the course of an infectious disease can be important to limit its impact. In our population, we have several tools available for intervention, and all are related to decreasing the number of infectious individuals or the duration of infectiousness for an infected individual.

First, we can trap and remove any non-wolf from the recovery area (μ_m). This method is very time and labor intensive. Capturing individuals takes a lot of skill and a bit of art. This strategy of trap and removal would have to be continually applied and could become a time sink for the biologists implementing the strategy. Removing one animal simply creates a hole for another animal to move in and fill.

Alternatively, having a captured individual stay and defend its territory but be unable to reproduce is a valuable management strategy. Surgical sterilization by tubal ligation or vasectomy is a method to implement this strategy. In our model, surgical sterilization of a non-wolf canid would move its mate from the infected compartment to the immune compartment (Z_h). Having done so, the territory occupied by such a pair is considered immune or secure and management efforts can be focused elsewhere.

Sterilized individuals are subject to removal if a wolf becomes available to fill a space occupied by a sterile individual (γ_m). This strategy is the subject of the sixth chapter of this dissertation.

A third strategy for intervention to prevent the spread of introgression is removal of hybrid litters. To accomplish this effectively, biologists need to be able to identify and remove hybrid litters when entire litters are accessible. The most efficient way to remove these litters is when pups are in a den and relatively immobile. Implementing this strategy would be unacceptable if red wolf litters were negatively affected during the process. The need to evaluate impacts of handling neonatal wolf pups drove the work outlined in the fifth chapter of this dissertation.

Every model should be developed with a realistic purpose in mind. This model was developed to explain how introgression can function as an infectious disease and to determine the effect that management strategies have on the spread of the disease. Management goals are aimed at increasing the number of immune red wolves while decreasing the number of infectious individuals in the recovery area.

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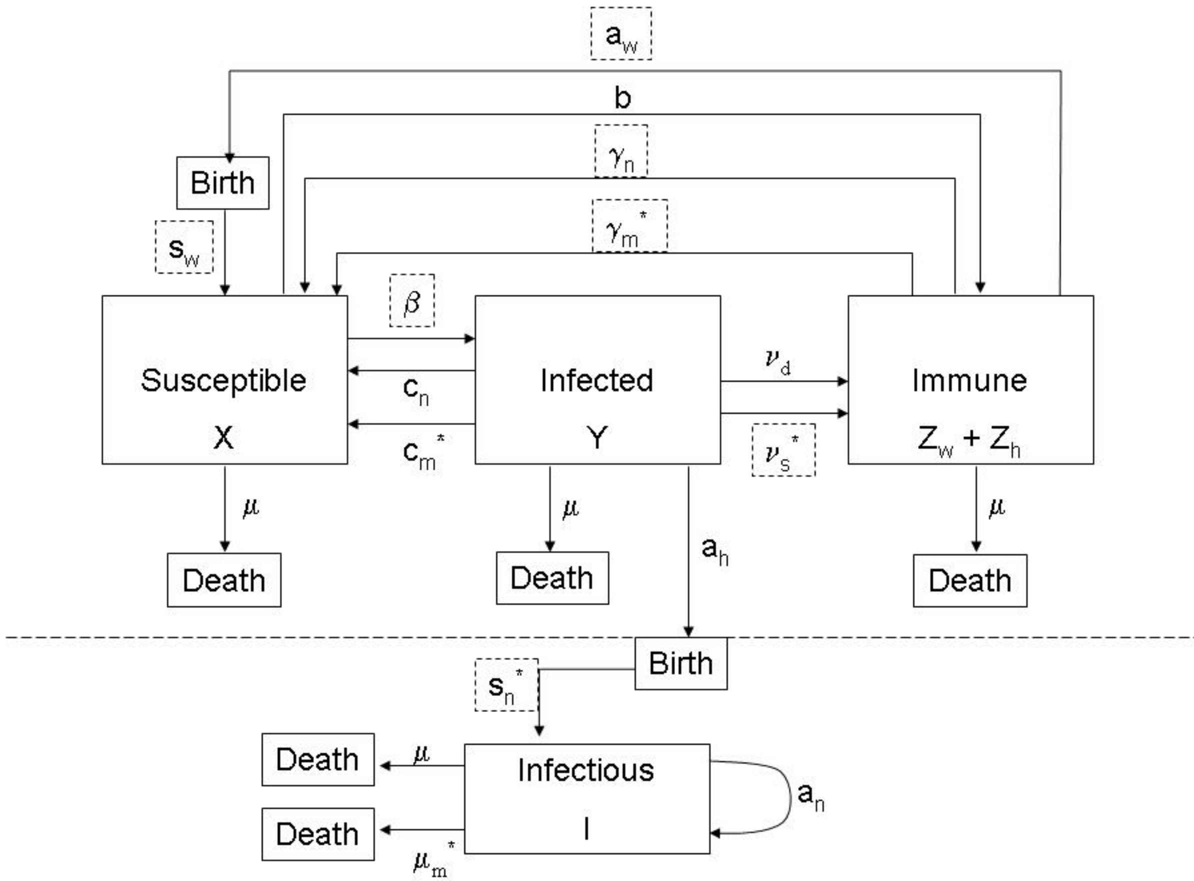

Figure 1. Diagram of the introgression as a disease model. Parameters outlined in dotted lines represent those rates specifically addressed in other chapters of this dissertation. Parameters marked with an asterisk represent potential intervention opportunities. Notation is defined in Table 1.

Table 1. Parameters used in the model and their abbreviations.

Parameter	Abbreviation
Birth rate for red wolves	a_w
Birth rate for hybrids	a_h
Birth rate for non-wolves	a_n
Rate of red wolf pair formation	b
Natural mortality rate of infectious mate	c_n
Management removal rate of infectious mate	c_m
Survival rate of wolf pups to reproductive age	s_w
Survival rate of non-wolf pups to reproductive age	s_n
Susceptible (unpaired red wolf)	X
Infected (red wolf paired with intact non-wolf)	Y
Immune (red wolf paired with red wolf)	Z_w
Immune (red wolf paired with sterilized non-wolf)	Z_h
Infectious (non-wolves)	I
Loss of immunity (loss of mate due to natural cause)	γ_n
Loss of immunity (loss of mate due to management action)	γ_m
Natural mortality	μ
Mortality due to management	μ_m
Recovery rate due to displacement	ν_d
Recovery rate due to sterilization	ν_s

LACK OF IMPACT OF DEN DISTURBANCE ON NEONATAL RED WOLVES

Relationship to Infectious Disease Model

This chapter discusses the impact that handling neonatal red wolves has on their short-term survival, up to 6 months of age. Handling pups provides data for estimating parameters a_w (red wolf birth rate) and s_w (survival rate of red wolf pups to reproductive age). If red wolf and non-wolf litter sizes are assumed to be equal, then we also get an estimate for a_h (hybrid birth rate) and a_n (birth rate for non-wolves). Because genetic composition of a litter may not be known with confidence prior to handling a litter, biologists need to be able to handle red wolf litters without affecting survival and non-wolf litters to identify opportunities for intervention in the spread of the disease, namely affecting survival rate of non-wolf pups to reproductive age (s_n).

ABSTRACT

Biologists handled red wolf (*Canis rufus*) pups from 12 wild litters over three years to determine the effect of den disturbance and handling on neonatal survival. Litters were handled on one of two den visits approximately 14 days apart. Median pup age at first visit was 5 days and the median age at the second visit was 19 days. No biologically important difference in the proportion of pups surviving was seen between pups handled on the first visit and those not handled. Dams moved eleven of twelve litters between visits. Handling, blood collection, and transponder placement in neonatal pups did not have a significant effect on pup survival.

Key Words: *Canis rufus*, den disturbance, handling, neonate, pup, red wolf

INTRODUCTION

Handling neonatal wild mammals provides researchers and managers the opportunity to collect data necessary for population monitoring and population modeling. With individuals of a known age and location, one can estimate growth rates, dispersal patterns, and age structure of a population. Marking individuals also facilitates the collection of data on rates, timing, and causes of mortality. The benefits of marking neonates must be weighed against potential risks. Risks inherent in handling neonates vary by species and include injury, exposure to predators, or altered maternal behavior. Research addresses the impact of handling on neonatal survival in some mammals (Dorney and Rusch 1953, White et al. 1972, Henderson and Johanos 1988, Franklin and Johnson 1994, Byers 1997) but anecdotal information only guides management decisions related to handling neonates in many species, including many canids. Because human disturbance may affect maternal behavior and, therefore, pup survival, wolf dens in areas where wolves are threatened or endangered have traditionally been considered inviolable.

Coyote pups (*Canis latrans*) under 6 weeks of age, and in some cases less than 10 days of age, have been handled (Andelt et al 1979, Andelt 1985, and Harrison and Gilbert 1985). Andelt et al (1979) reported that pups were moved to secondary den sites on each of 4 occasions that researchers visited natal dens. Harrison and Gilbert (1985) reported that one group of coyotes moved their pups 6 times while another group moved their pups 3 times. Five of these 9 moves occurred within 48 hours of researchers visiting dens. These researchers also noted four occasions when coyotes moved their dens unrelated to ongoing research. Andelt (1985) handled and marked coyote pups less than six weeks of age. Parent coyotes in Andelt's study made approximately the same number of trips during the nursing season to visit pups before and after radiotransmitters were attached to the pups. Thus, Andelt concluded the disturbance and fitting of transmitters did not affect adult behavior toward the pups.

Gray wolves (*Canis lupus*) may move pups in response to inadvertent human disturbance (Chapman 1979, Smith 1998), yet Thiel et al (1998) documented gray wolf tolerance of noninvasive human activity near dens close to centers of human activity. Mech (1970) recounted several incidents of gray wolves moving pups to new dens, apparently unrelated to human activity near the dens, but also noted that one wolf pack reused a den following human disturbance and removal of one pup.

Introgression of coyote genes has been and continues to be the primary obstacle to red wolf (*Canis rufus*) recovery (Kelly 2000, Kelly et al 1999, U.S. Fish and Wildlife Service 1989). Early identification of hybrid litters would allow biologists managing the recovery effort to remove hybrid animals from the population before those animals reach reproductive age and with less effort than trapping each individual at a later time. If handling and taking blood samples from neonatal red wolf pups can be done without affecting survival, biologists could use this technique as an effective tool to manage introgression. In this chapter, I describe the results of a study to determine whether handling wild neonatal red wolves results in den abandonment, affects proximate pup survival, or affects survival to age six months.

STUDY AREA

The red wolf recovery area consists of five counties (Beaufort, Dare, Hyde, Tyrrell, and Washington) in northeastern North Carolina comprising more than 6,650 km^2 (Figure 1). This area contains three national wildlife refuges as well as a Navy and an Air Force bombing range. Major land cover types in this area are agricultural (29%), pine (mostly *Pinus taeda*) plantation (15%), pocosin (13%, consisting of *Pinus serotina* and evergreen shrubs), and non-riverine swamp forests (10%, consisting of *Pinus taeda*, *Nyssa sp.*, and *Champaecyparis thyoides*). Open water covers about 5% of the area with minor land cover types comprising the remaining 28% of the area. Mean temperatures range from 5.3ºC in January to 26ºC in July. Annual rainfall averages 126 cm, and elevation ranges from sea level to 50 m.

MATERIALS AND METHODS

Denning season for red wolves is approximately 15 March to 1 June. During this period, biologists with the United States Fish and Wildlife Service monitor breeding-age females using aerial and ground-based radio-telemetry to detect localized movements suggestive of denning behavior. Locating a female in the same location in two or more consecutive attempts is considered indicative of whelping and leads to a ground search for the den approximately one week later. As many as three biologists, using prior telemetry locations and direct pursuit of a female wolf's radio-telemetry signal, participate in each den search effort.

From 2000 to 2002, dens were included in this study, at the discretion of the USFWS biologists, based on pedigree of suspected parents and the location of the den with respect to accessibility and defined management areas. These factors also influenced to which of two treatment groups (early disturbance or delayed disturbance) each litter was assigned. That is, dens where one or both of the parents were unknown or suspected to be hybrid were high priority for den work and thus included in the early disturbance group.

The protocol for processing pups included collection of a blood sample for testing to determine genetic composition of each pup; therefore, early test results were obtained for highly suspect individuals. Biologists then had the opportunity to remove an entire litter when hybrid individuals were identified. If a litter were located near an area where biologists had limited access, either for den work or during trapping season, due to habitat or landowner constraints, then that litter was also a high priority for testing. This strategy of assigning litters to treatment groups, admittedly less than random, was necessary from a program management perspective to allow the biologists to test and to identify pups individually before they left their dens and moved to inaccessible areas.

Human disturbance at a den site may have as much, if not more, effect on maternal response to processing pups than the actual handling of the pups. Without some degree of interference, however small, it is not possible to know how many pups are present at a den. For example, even if the location of a den were correctly identified prior to whelping, remote viewing equipment could not be placed without some degree of disturbance. Therefore, it is virtually impossible to control for interference in an experimental design. Instead, we chose to vary the degree and timing of interference for dens included in the study.

Pups in dens assigned to the delayed disturbance group (n=8) were not handled on the first visit. Observers only counted the number of pups by looking in the den and without removing the pups from the den. We tried using a Peeper Video Probe, obtained through a grant from Sandpiper Technologies, as a way to count pups in the den without handling them. The logistics of carrying this equipment across canals and through pocosins limited its usefulness. In some dens in the delayed disturbance group, a biologist crawled into the den with a flash light to view the pups. Approximately two weeks later, observers returned to these den sites or located the new den site and followed the same procedures used for dens in the early interference group as described below. Only those dens where two visits were made have been included in this study. A third check of dens in the delayed handling group would have allowed evaluation of the pups for reactions to transponder placement and a better assessment of pup loss but was not feasible because of the mobility of the older pups. We tried to minimize the effects of den disturbance by taking as few people as necessary to locate and handle pups, by handling pups efficiently, by spending minimal time at the den, and by avoiding handling pups during cool temperatures or rain.

For dens assigned to the early interference group (n=4), pups were removed from the den on the first visit and given a physical examination to look for any signs of illness, injury, or congenital defects. Wearing latex gloves, a biologist used a sterile 25-gauge needle to draw approximately 0.2 mL of blood from a cephalic vein for DNA testing. An area of approximately 6 cm^2 along the dorsal midline between the shoulder blades was lightly moistened with a cotton ball and 70% isopropyl alcohol to clean away any gross contamination, and a passive integrated transponder (PIT) tag (Trovan®) was injected subcutaneously through a sterile 12-gauge needle. Once the transponder was placed, the injection site was sealed with a drop of cyanoacrylate (Nexaband®). All pups were then replaced in their den. Approximately two weeks later, observers returned to the den to count the pups present and to note any reactions such as swelling or drainage at the site of transponder injection.

As pups become mobile, verifying the number of pups in a litter becomes more difficult and after 4 weeks of age, further follow-up by den visitation is not practical. Observations at rendezvous sites, a common technique in gray wolf studies, are not feasible in the red wolf restoration area. There is little elevation change in the restoration area, thick pocosins and forests are common, and much of the land in the restoration area is privately owned. Finding a viewpoint from which one can watch animals without disturbing them is extremely difficult; therefore, fall trapping season has been used as the standard to evaluate red wolf pup production. Consequently, we used the number of pups caught in the fall trapping season to evaluate the impact of pup handling. This choice is imprecise with regard to the absolute impacts of pup handling (but not relative impacts) because many potential causes of mortality in that interval would be unrelated to the initial disturbance events.

Approximately five to nine months following the denning season, biologists tried to trap pups to determine survival. Biologists routinely trap pups of this age to identify the number of pups in each litter, to evaluate their health, and to attach radio-collars. I reviewed data for the program to determine the number of wolf pups known to have survived to at least 150 days of age since the restoration effort began. This age represents an approximate elapsed time between the beginning of whelping season and the beginning of fall trapping season and, thus, is an estimate of fall litter sizes. When an unmarked animal was caught and presumed to be a pup, based on morphology and tooth wear, it was designated as offspring of the pair occupying the area where it was caught. From these data, I estimated litter sizes for those years when den site visits were not done.

The number of pups caught in the fall was compared to the number of pups present at the second visit for the 12 dens in this study using a z-test for two binomial samples. A one-sided t-test with unequal variances was used to compare fall litter sizes with and without den disturbance. The distance a den was moved was compared for the early versus delayed interference group with a Mann-Whitney test.

RESULTS

Table 1 lists for each den the number of pups present at each visit and the number of those pups that were caught during the fall trapping season. Mean age at time of the first visit was estimated at 5 days (range = 2 to 8) for early interference dens and 4 days (range = 2 to 7) for delayed interference dens. Mean time between visits was approximately 14 days with a range of 5 to 19 days.

There was no difference in the proportion of pups surviving to fall for early versus delayed interference dens ($z=-0.75$, $p=.45$). Seven of the 12 dens had the same number of pups present at two successive visits ($n=3$ early interference, $n=4$ delayed interference). One early and two delayed interference dens had one fewer pup present at the second visit. One delayed interference den had more pups present at the second visit, perhaps as a result of difficulty seeing pups in the den on the first visit. Another delayed interference den had only one of two pups present at the second visit, but biologists caught what appeared, based on morphology and tooth eruption and wear, to be the second pup from that litter later that fall. It is possible that the dam was moving her pups to a new den during the first visit by biologists. One litter was not represented by pups caught in the fall.

Of the 12 litters included in the study, 11 were moved by the dam to new den sites between visits. The one litter not moved belonged to the early interference group. Median relocation distance was 124 m for the early disturbance group and 582 m for the delayed interference group, but this difference was not statistically significant ($W=8$, $p=.0682$).

Table 2 contains summary data for fall litter sizes estimated as the number of pups at least 150 days old captured in each territory since the beginning of the restoration effort. Fall litter sizes did not differ for disturbed versus undisturbed dens ($t=-1.32$, $p=.193$).

Only 2 pups, siblings, showed reactions at the site of transponder injection. An attempt was made to drain the putative abscesses by puncturing a small hole in the dependent portion of each abscess with a scalpel blade. These 2 pups were not subsequently captured though 2 of their siblings were.

DISCUSSION

Handling neonatal pups did not appear to affect neonatal survival (Table 1, Table 2). Dams moved dens after human disturbance, a behavior documented for other canids including gray wolves and coyotes (Andelt et al 1979, Chapman 1979, and Harrison and Gilbert 1985). Such movement could potentially put pups at risk during transit or if they are moved to a suboptimal location, making them more vulnerable to predators or environmental conditions; however, movement of dens may be a normal behavior that occurs in response to factors other than human interference. Dams may, in fact, be moving pups to safer locations. Female coyotes may prepare multiple dens prior to whelping (Harrison and Gilbert 1985) and thereby are able to move their pups quickly to satisfactory dens when needed. While searching for the dens included in our study, we found many recently-excavated dens, some of them recently used. Red wolves may also prepare in advance for den movement, regardless of human disturbance.

The two-week interval between visits was long enough to allow negative impacts directly attributable to the pup handling protocols to be readily apparent. These potential impacts include infections from transponder placement or starvation due to abandonment or reduction of dam attentiveness. Pups were sometimes hard to count unless handled due to the shape or structure of the den. Dens that are in old piles of logs, for example, offer pups hiding places where they may go undetected.

Thirty-four of the 59 pups (56%) seen at the second visit were caught in the fall. Sixteen pups (6 males, 10 females) from these litters have since been documented to be members of territorial pairs and 6 (2 males, 4 females) of them have produced litters. Causes of mortality for pups included in this study were largely undetermined because of the limitations of carcass retrieval for animals without telemetry transmitters. At least two pups from one litter died in a fire. Suspected causes of mortality for pups include starvation, inter- and intraspecific aggression, trauma from vehicles or farm equipment, other human associated activities, and parasitic and viral diseases.

That 11 of 12 litters in this study had pups caught in the fall suggests that the risk of dam abandonment of a litter as a result of handling of pups under our protocol was low. The fate of the remaining litter is unknown. The dam of this litter had raised 2 of 5 pups that had been handled in the den in a previous year. However, no evidence of pups was found in the preceding two years that the same territory was occupied by a different pair of wolves, and there is no documentation of a breeding pair in this territory prior to that time. This territory may not be suitable for raising pups, due to factors such as prey base, diseases, or anthropogenic causes or there may have been pups in this territory that went undetected.

The ability to handle neonates without affecting survival negatively provides a valuable management tool. Once marked, wolves can be processed and released quickly when recaptured. Individuals without some sort of identifying mark, such as a passive transponder or radiocollar, must be kept in captivity until genetic test results are known. If pups are implanted with transponders in dens, their identities and origins are known as long as the transponder can be found.

The number of litters available for inclusion in this study was not large enough to detect small differences between the two treatments. Visual inspection of the raw numbers (Table 1) for the two visits clearly shows little if any impact of the disturbance, marking, or sample collection. Other morbidity and mortality factors, such as diseases or anthropogenic impacts, likely have more of an impact on population growth rates than any degree of impact of handling neonates seen in this study. The number of pups trapped each fall following den season work was consistent with previous years where den interference was not a factor (Table 2).

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Table 1. Number and ages of red wolf pups at successive den visits, the number of pups caught in the fall, and the distance dens were moved between visits.

		# Pups			Proportion	Age (days)		Visit	Distance
Year	Type	Visit 1	Visit 2	Fall Captures	Surviving to Fall	Visit 1	Visit 2	Interval (days)	Moved (meters)
2000	Early	5	5	1	0.2	2	9	7	0
2000	Early	8	8	8	1.0	5	10	5	No Data[a]
2001	Early	3	3	2	0.7	8	22	14	124
2001	Early	10	9	2	0.2	No Data	No Data	14	185
Mean		**6.5**	**6.3**	**3.3**	**0.52**	**5**			
Std Dev		**3.1**	**2.8**	**3.2**	**0.4**	3			
2001	Delayed	4	6	6	1.0	2	16	14	No Data[a]
2001	Delayed	6	5	2	0.4	2	19	17	211
2001	Delayed	2	2	2	1.0	5	22	17	1143
2002	Delayed	2	2	2	1.0	2	9	7	683
2002	Delayed	8	8	0	0.0	5	20	15	94
2002	Delayed	2	1	2 [b]	1.0	7	21	14	240
2002	Delayed	4	3	2	0.7	5	21	16	1022
2002	Delayed	7	7	5	0.7	3	17	14	582
Mean		**4.4**	**4.3**	**2.6**	**0.7**	**3.9**			
Std Dev		**2.4**	**2.6**	**1.9**	**0.4**	1.9			

[a]Den was moved but distance was not recorded.

[b]Biologists trapped in the Fall what was thought to have been the second pup from this litter seen only at the first visit.

Table 2. Comparison of fall litter sizes for groups where pups were not handled in the den and groups where pups were handled in the den.

Year	Number of Litters (No Den Visits)	Average Fall Litter Size	Number of Litters (Den Visits)	Average Fall Litter Size
1988	2	1.00		
1990	1	3.00		
1991	3	4.00		
1992	2	2.00		
1993	5	2.80		
1994	8	2.88		
1995	5	2.20		
1996	7	1.86		
1997	4	2.25	1	7.00
1998	1	1.00		
1999	4	2.50	4	1.75
2000	1	4.00	3	4.00
2001	1	1.00	5	2.80
2002	1	4.00	5	3.00
2003	3	1.67	4	3.00
2004	1	2.00	8	2.63
Total	49	2.41	30	2.93
Standard Deviation		1.29		1.93

PROTECTING RED WOLVES FROM HYBRIDIZATION USING STERILIZED COYOTES AND COYOTE-WOLF HYBRIDS

Relationship to Infectious Disease Model

This chapter discusses the use of sterilized but hormonally intact non-wolves as a means of controlling the spread of hybridization. From these data, we can obtain estimates for v_s *(recovery rate due to sterilization) as well as* γ_m *(loss of immunity due to management action). To estimate these rates, we need to first know how effective sterilized animals are at immunizing red wolves against hybridization (*Z_h*).*

ABSTRACT

The red wolf (*Canis rufus*), an endangered species deliberately extirpated from the wild, was reintroduced to the wild in northeastern North Carolina in 1987. A Population and Habitat Viability Assessment (PHVA) conducted in 1999 identified the major obstacle to recovery of the red wolf in the wild to be introgression of coyote (*C. latrans*) genes into the red wolf population. A result of the PHVA was the design and implementation of an adaptive management plan using sterilized animals as a spatial buffer to prevent introgression of genes from coyotes and non-wolf canids into the red wolf population. Geographic zones of gradated management intensity were developed to mitigate the impact of coyote/red wolf interactions. The objective for the most intensively managed zone (Zone 1) was to maintain the zone free of coyotes or hybrids through active removal. All terrestrial access to this core zone would require transit through a research zone (Zone 2) where tubally ligated and vasectomized non-wolf canids (coyotes and coyote-wolf hybrids) served as space holding buffers in areas not occupied by red wolves. The outer-most area (Zone 3) represented the region considered beyond the capacity of intensive management. Trapping and radiocollaring of animals and genetic analysis of captured individuals and scats from surveys were among the tools used to assess the genomic integrity of the management zones from 1999 to 2004. Since implementation of the adaptive management plan, the number of non-wolf canids and the number of hybrid litters have been successfully reduced in the 2 primary zones of wolf occupancy (Zones 1 and 2). The use of sterile, hormonally intact non-wolf canids proved to be a useful management tool to control introgression of coyote genes into the red wolf population.

***Key Words**:* adaptive management, *Canis latrans*, *Canis rufus*, coyote, introgression, red wolf, sterilization

INTRODUCTION

The red wolf (*Canis rufus*) is an endangered species that once occupied the southeastern United States (U.S. Fish and Wildlife Service 1989). The United States Fish and Wildlife Service (USFWS) began restoring red wolves to the wild in 1987, almost twenty years after their deliberate extirpation in the late 1960's. Decades of habitat alterations and active predator control efforts by humans resulted in the last wild red wolves persisting in only a small fragment of their once broad eastern North American range by the late 1960's (McCarley 1959, 1962; Riley and McBride 1972). As the range of the red wolf contracted, the more adaptable coyote (*C. latrans*) expanded into formerly wolf-occupied areas, including the southeastern United States (McCarley 1959, 1962; Paradiso and Nowak 1971). This overlap of ranges and alterations in population sizes led to the breakdown of normal reproductive isolation between the two species and produced what was termed "a hybrid swarm" (Nowak 1979).

Capturing the remaining wild red wolves to begin a captive breeding program was the foundation of a plan to protect the species from genetic swamping that could lead to extinction through hybridization (USFWS 1989). A set of morphologic and genetic criteria were established to differentiate red wolf from non-wolf (USFWS 1989). Offspring from individuals who met those criteria were also compared to those criteria prior to admitting an animal to the captive breeding program (USFWS 1989). Once the number of wolves in captivity increased, the USFWS began efforts to restore the species to the wild. These efforts included the release of red wolves on Alligator River National Wildlife Refuge, North Carolina in 1987 (Phillips 1994). This site was chosen, in part, because surveys had failed to find coyotes in the area (Parker 1987).

Since the beginning of the restoration program, coyotes have expanded their range into northeastern North Carolina and hybridization again became a serious threat to the continued existence of the red wolf in the wild (Kelly et al. 1999). During a Population and Habitat Viability Assessment (PHVA) in April of 1999, an adaptive management plan was outlined to prevent introgression of coyote genes into the red wolf population (Kelly et al. 1999).

A principal component of the adaptive management plan for red wolves involved tubal ligations and vasectomies of non-wolf canids (coyotes and coyote-wolf hybrids) in parts of the recovery area to form a spatial buffer against dispersing non-wolf canids from outside the recovery zones (Kelly 2000). Ideally, sterilized animals would maintain pair bonds and territorial behavior but not reproduce (Till and Knowlton 1983, Asa 1995, Zemlicka 1995). The preferred method of sterilization, therefore, should have little or no impact on the social behavior of such highly social species (Asa and Porton 1991, Asa 1995, DeLiberto et al. 1998).

The effects of surgical sterilization on both coyotes and gray wolves (*C. lupus*) have been studied (Mech and Fritts 1993, Mech et al. 1996, Spence et al. 1999, Bromley and Gese 2001*a,b*). Mech et al (1996) followed 5 vasectomized wolves in northern Minnesota and concluded they maintained pair bonds and territories. These male wolves were known to have held territories, in one case for 7 years, until they died or contact was lost with their radio-transmitters. Tubal ligation and vasectomy does not affect the social behavior of captive coyotes (Zemlicka 1995) or wild coyotes (Bromley and Gese 2001*a*). Surgically sterilized coyotes may even prey less on sheep, presumably because sterilized pairs have no pups to provision (Bromley and Gese 2001*b*).

We predicted that sterilization of non-wolf canids would result in a decrease in the number of hybrid litters in the recovery area and, therefore, over time, the percent of reproduction that was non-wolf, the number of non-wolf canids sterilized, and the number of new non-wolf canids captured would decrease.

STUDY AREA

The red wolf recovery area consists of Beaufort, Dare, Hyde, Tyrrell, and Washington counties in northeastern North Carolina comprising almost 6,650 km^2 (Figure 1). This area contains three national wildlife refuges as well as a Navy and an Air Force bombing range. Major land cover types in this area are agricultural (29%), pine (mostly *Pinus taeda*) plantation (15%), pocosin (13%, consisting of *Pinus serotina* and evergreen shrubs), and non-riverine swamp forests (10%, consisting of *Pinus taeda*, *Nyssa sp.*, and *Champaecyparis* *thyoides*). Open water covers about 5% of the area with minor land cover types comprising the remaining 28% of the area. Mean temperatures range from 5.3ºC in January to 26ºC in July. Annual rainfall averages 126 cm. Elevation ranges from sea level to 50 m.

MATERIALS AND METHODS

To implement the adaptive management plan, the red wolf restoration area was divided into three zones with gradated management intensity (Kelly 2000, Figure 1). Physiographic and political boundaries defined the lines between management zones. Zone 1 was the most intensively managed and was designated as a coyote- and hybrid-free zone. Federal land ownership in this zone was extensive and thus facilitated access for management activities. When non-wolf canids were identified in Zone 1, these coyotes or hybrids were trapped and removed. The line demarcating Zone 1 from Zone 2 was the southern portion of Alligator River National Wildlife Refuge, a peninsula buffered on three sides by water. Terrestrial access to Zone 1 was limited to routes crossing through Zone 2 (Figure 1). Zone 2 was designated a research zone where tubally ligated and vasectomized non-wolf canids served as space holding buffers in areas not occupied by red wolves. These non-wolf canids were removed when red wolves became available to replace them, either through acclimation and release or through natural dispersal. Zone 3 was designated as the dispersal zone and represented that part of the recovery area thought to be beyond the capacity of intensive management within the confines of currently available resources and logistical considerations. Modifications to these management zones were made in March 2002 such that the boundaries of Zones 1 and 2 were pushed farther west (Figure 2). All data presented in this paper are summarized based on these modified zones.

Surveys for evidence of canid presence such as scats, tracks, or ground scratching as well as reports of sightings from local residents were used to identify areas to target trapping efforts in all three zones. Howling surveys were also used to search for canids in areas inaccessible by other means (Harrington and Mech 1982, Fuller and Sampson 1988). Wolves, coyotes, and hybrids in the recovery area were trapped with #3 rubber padded leghold traps with offset jaws. Traps were not staked but rather a 2-3 kg drag was attached by a 2-3 m chain to allow the animal the opportunity to get off a road and out of sight of passersby. Newly captured animals were transported to a central processing facility while recaptured animals were often processed on site. Processing included drawing blood, taking morphological measurements, weighing, affixing a transmitter collar, and vaccinating against common canid diseases including canine adenovirus, canine distemper, and rabies. Microsatellite analysis was used to classify animals as wolf, coyote, or hybrid and was expanded from 8 to 18 loci during the study period (Wilson et al. 2000, Miller et al. 2003). Pedigree data and morphologic criteria were also used to refine the classification criteria (Miller et al. 2003, USFWS 2005).

Non-wolves were selected for sterilization rather than euthanasia based on the zone where they were captured, knowledge of other canids in that area, historical use of the area by wolves or non-wolves, availability of dispersing wolves to occupy the area, time of year, and landowner consent for the return of sterilized animals that had been caught on their land. Animals to be sterilized were induced with isoflurane by mask, intubated, and maintained on isoflurane throughout the procedure. Using aseptic technique, females were tubally-ligated through a ventral midline incision. Each fallopian tube was identified, dissected from surrounding tissue, ligated with 3-0 polyglactin 910 (Vicryl®, Ethicon, Inc.) at two points, and the intervening segment removed. The linea alba was closed with 2-0 polyglactin 910 (Vicryl®, Ethicon, Inc.) in a simple interrupted pattern. Subcutaneous and subcuticular layers were closed in simple continuous and horizontal mattress patterns, respectively. All suture material was absorbable and no external skin sutures were placed. Cyanoacrylate (Vetbond™, 3M™) was used to seal the incision. Males were vasectomized through a single pre-scrotal incision. A similar procedure as that described for females was performed on the vas deferens. While anesthetized, each animal was also processed as described in the previous paragraph. An intramuscular injection of butorphanol (Torbugesic®, Fort Dodge) was given to each animal prior to extubation for pain management in the immediate post-operative period. All animals were kept at least 24 hours before being released near the site of capture. While refining this surgical technique, histological examination was used to confirm removal of the appropriate tissue.

Once released, locations of animals were estimated periodically through both ground and aerial telemetry. Sterile, non-breeding, resident pairs were identified as those pairs that were consistently located within a defined territory and where at least one member of the pair was surgically sterilized. When a radiocollar was identified as transmitting in mortality mode (i.e., a change in pulse rate), attempts were made to retrieve the carcass for necropsy.

Spearman's rank correlation coefficient was used to test for trends, within zones, in the number of animals sterilized, the percent of known reproduction that was hybrid, and the number of non-wolf canids captured for the first time.

RESULTS

From April 1999 through July 2004, 49 non-wolf canids (27 males, 22 females) were caught, sterilized, released, and followed via radiotelemetry for 42 to 1798 days (Figure 3). Of these, 16 were later euthanized to open territories for dispersing red wolves or because they had moved to new areas where a private landowner requested their removal. Thirteen animals were alive and still monitored as of 1 August 2004. Of the remaining animals, the causes of mortality were gunshot (n = 8), unknown (n = 3), interspecific aggression (n = 2), mange (n = 1), heartworms (n = 1), and hit by a car (n = 1). Contact was lost with 4 sterilized animals and their fate is unknown. No mortalities resulted during or from the surgical procedure.

Twenty-three of these 49 animals (11 males, 12 females) were identified as members of a resident non-breeding pair during at least one breeding season from 2000 to 2004, and 11 of these animals (4 males, 7 females) maintained their dominance status as a member of a resident pair for 2 to 4 years. Both telemetry and ground surveys for tracks or scats yielded no indication of pups with any of these pairs. Therefore, even without any evidence of reproductive success, sterile pairs maintained social bonds and territories through multiple breeding seasons.

The decrease in the number of non-wolf canids sterilized over time was nearly statistically significant in Zone 2 ($r_s = -0.814$, $r_{s,\ .05} = -0.829$) but not in Zone 3 (Figure 3). The decrease in the percentage of known reproduction that was hybrid was statistically significant only in Zone 3 ($r_s = -0.900$, $r_{s,\ .05} = -0.829$) and reached a plateau in Zones 1 and 2 (Figure 4). Fewer previously unknown canids were caught in Zone 2 over time ($r_s = -0.871$, $r_{s,\ .05} = -0.829$, Figure 5).

Although the management plan allowed for the existence of sterile hybrids to hold space, ideally those sterile pairs would be replaced with reproductive red wolves. Therefore, during the implementation of the plan, the number of hybrid pairs decreased through sterilization and removals, with a corresponding increase in red wolf pairs as they colonized the landscape and even displaced hybrid and sterile animals from territories in the recovery area (Figure 6). The decrease in hybrid pairs was not statistically significant in Zones 1 and 2 but reached statistical significance in Zone 3 ($r_s = -1.00$, $r_{s,\,.05} = -0.829$) if the first two years were removed to correct for a bias in trapping effort. That is, much of the early trapping effort was directed at Zones 1 and 2, so less was known about breeding pairs in Zone 3. Only 3 pairs were identified in Zone 3 in 1999 and 2000, but by 2001, that number had increased to 9. Thus, the trend in the number of hybrid pairs was masked by the trapping effort in the early years the plan was implemented. The increase in the number of wolf pairs was statistically significant in Zone 2 ($r_s = 0.971$, $r_{s,\,.05} = 0.829$) and was nearly significant in Zone 3 ($r_s = 0.800$, $r_{s,\,.05} = 0.829$).

The spatial arrangement of the territorial pairs on the landscape provides additional support for the impact of the management plan (Figures 7 through 12). These figures show the increase in red wolf pairs as it moves from east to west. Note that the hybrid pair in the eastern part of Zone 1 was not designated as such until the refinement of the microsatellite testing allowed detection of a small amount of introgression in the female of this pair, and she was subsequently removed.

DISCUSSION

Surgical sterilization of non-wolf canids began in May 1999 following the recommendations from the PHVA, even though the actual adaptive management plan was not finalized until almost a year later. Because resources were limited, resources and management actions were first focused on establishing a Zone 1 as coyote- and hybrid-free. As Zone 1 was secured, more effort was expended on securing Zone 2 from east to west and on the eastern portion of Zone 3. Trapping efforts were then targeted on new, unsecured territories. In essence, the management actions were based upon securing canid territories similar to pieces in a jigsaw puzzle. Some pieces were red wolf only, others were a mix of red wolf-hybrid, and some were entirely non-wolf. As management proceeded, the main goal was to change all the non-wolf or mixed territories into red wolf territories. As more territories became red wolf only, and the zone became full or saturated with red wolf territories, then the management zone became secure and efforts were expanded into the next zone. Sterilization of non-wolf canids was used to hold a territory to prevent genetic introgression and allowed for insertions of red wolves when logistics allowed. Until that time, the sterile animals maintained space on the landscape and acted as a buffer preventing other reproductively viable non-wolf canids from invading.

The number of sterilized animals increased initially as efforts to capture and identify non-wolf canids began. Three individuals (2 female, 1 male) were sterilized in Zone 1. All 3 were captured in what was originally Zone 2 but is now Zone 1. These females would likely have been removed if they had been captured after March 2002, when the zone boundaries changed. The male was followed briefly to determine who, if anyone, he was associating with and was removed within 4 months of first capture. With more sterile individuals occupying available territories, fewer hybrid litters were produced, fewer non-wolf canids were caught, and therefore, fewer individuals needed to be sterilized in Zone 2.

The number of wolf breeding pairs did not significantly increase in Zone 1, possibly because most of the territories in that zone were already occupied by wolves. In Zone 2, however, there was a trend of an increasing number of wolf pairs. This trend involved a change from an almost equal number of wolf and hybrid pairs in 1999 to more than 80% (8 of 9 in 2003 and 10 of 12 in 2004) wolf pairs. Many sterilized individuals in Zone 2 were removed following the 2002 breeding season to open up more vacancies for dispersing red wolves. Though knowing if red wolves would displace these sterile animals is important for the long-term management of the species, there was an immediate goal of maximizing red wolf breeding potential that overrode the desire for documentation of displacement. That the trend in Zone 3 approached statistical significance may have been biased by the fact that a total of only three pairs were known in the early years and more wolf pairs were found as more effort was expended in Zone 3. The number of wolf pairs in Zone 3 appears to be stable at a lower number, with the exception of the 5 pairs in 2003.

The increase in percent reproduction that was red wolf was not statistically significant over the 6-year period in Zones 1 and 2. The majority of litters in these zones were already red wolf, therefore showing a statistically significant increase in red wolf litters (or a corresponding decrease in hybrid litters) may not be an appropriate metric to evaluate how effective sterilization is at controlling hybridization. An examination of the raw numbers shows only one hybrid litter total in 2003 and 2004 and that was in Zone 3.

The number of previously unknown non-wolf canids caught for the first time decreased only in Zone 2. With mostly wolves and sterilized hybrid pairs occupying territories, there are fewer non-wolves to capture. Because there is no physical barrier to movement between the zones, the source of these newly caught animals is likely from so called Zones of Ignorance, those areas where a territorial pair may exist but one or both members is unknown, in Zone 3 or from outside the recovery area.

Radiotelemetry locations of the tubally-ligated and vasectomized non-wolf canids in our study area showed that they appeared to maintain their social status. Those sterilized animals that did not establish residency as a member of a non-breeding pair may have been dispersing at the time they were caught. Because their status as a resident or non-resident was not known prior to capture, we do not know how long they had been in the area or what their social status had been. A paucity of data exists on the behavior of intact coyotes and hybrids in our study area because these animals were not released reproductively intact. The decrease in hybrid litter production due to the effective use of sterilized animals as a buffer to introgression means that we have fewer opportunities to study the movement of young non-wolf canids.

Bromley and Gese (2001b) showed that surgically sterilized but hormonally intact coyotes maintained territories and pair bonds. This characteristic made this technique ideal for implementation in the red wolf recovery area because sterilized animals maintained their territories but remained reproductively nonviable. Securing one territory, whether it be with a wolf pair or a sterilized hybrid pair, means more effort can be expanded into Zones of Ignorance. Though this strategy is labor intensive, in regards to capturing and sterilizing the animal, it may be more cost effective in both time and money than continually trapping and euthanizing animals.

Adaptive management allows for the integration of research and management and, therefore, was an ideal paradigm for development of a red wolf recovery strategy. The use of surgically sterilized but hormonally intact non-wolf canids remains the foundation upon which this strategy is built and is proving to be an effective means to limit introgression. The success of this technique resulted in the need to redefine the management zone boundaries in March 2002 and extended Zone 1 techniques into part of Zone 2 and expanded Zone 2 strategies into part of Zone 3 (Figure 2). Whether this continued intensive management and sterilization of non-wolf canids is the necessary to limit introgression into the red wolf population remains unknown. Eventually, it is hoped that once the red wolf population reaches a critical mass, they will be self-sustaining and no longer breed with non-wolf canids.

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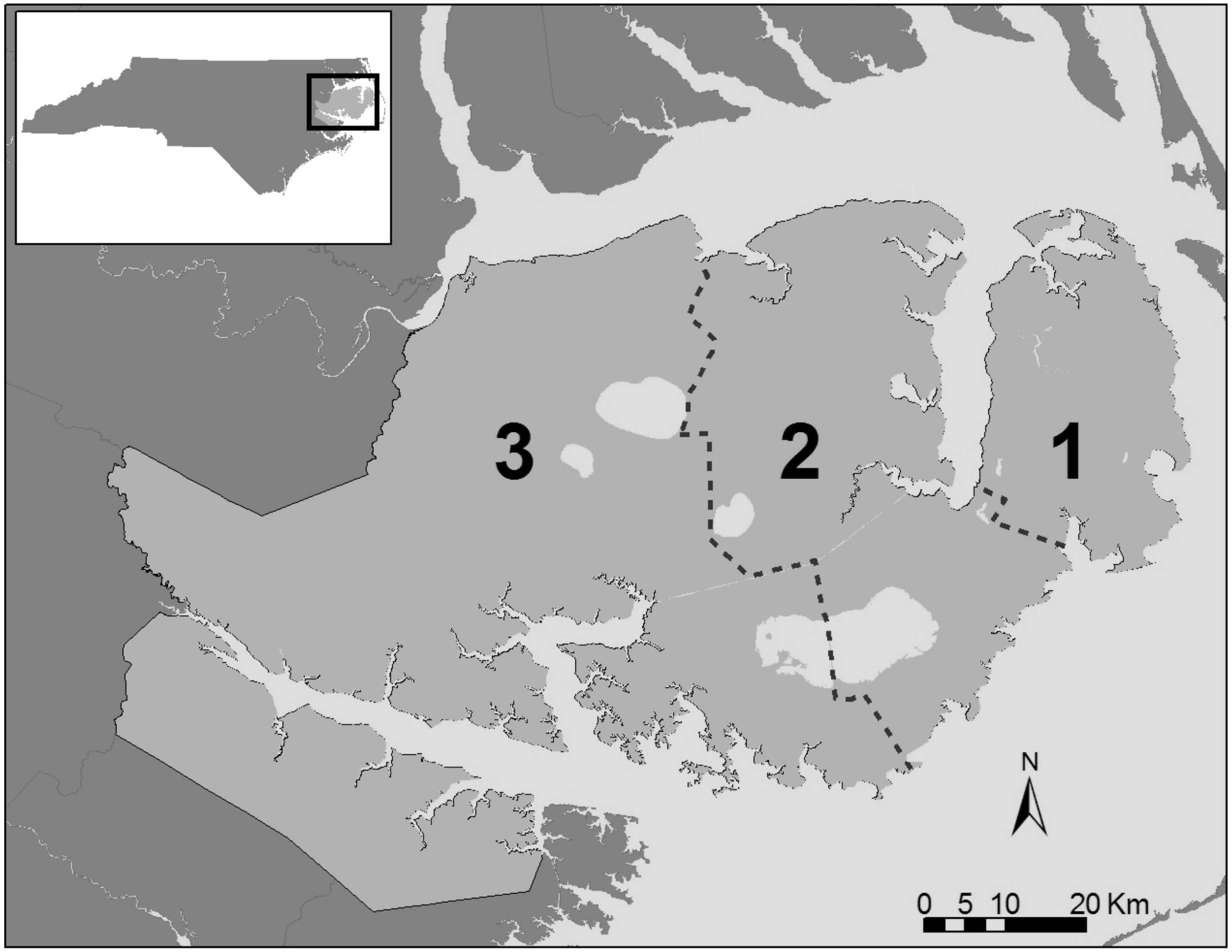

Figure 1. Management zones within the red wolf recovery area as implemented in April 2000. Zone 1 was the hybrid-free zone where all coyotes and coyote-wolf hybrids were removed from the population. Zone 2 was the zone where coyotes and coyote-wolf hybrids were sterilized in accordance with management objectives and landowner consent. Zone 3 was considered to be that part of the recovery area beyond the capacity for intensive management, given resource availability.

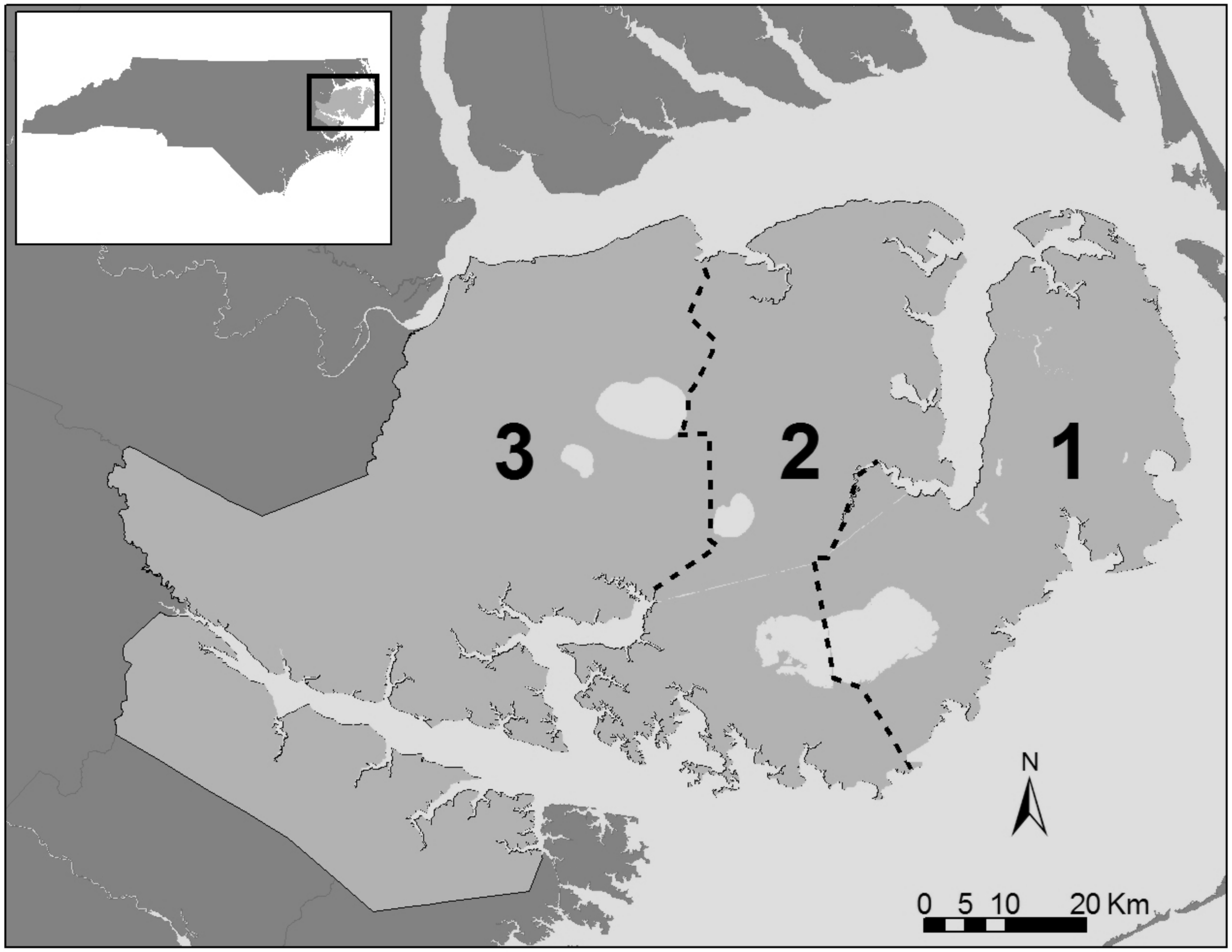

Figure 2. Management zones within the red wolf recovery area as modified in March 2002. All coyotes and coyote-wolf hybrids are removed from zone 1. Surgical sterilization of coyotes and coyote-wolf hybrids is performed in zone 2 when consistent with management objectives and landowner consent. Zone 3 is managed as a modified zone 2 as resources permit.

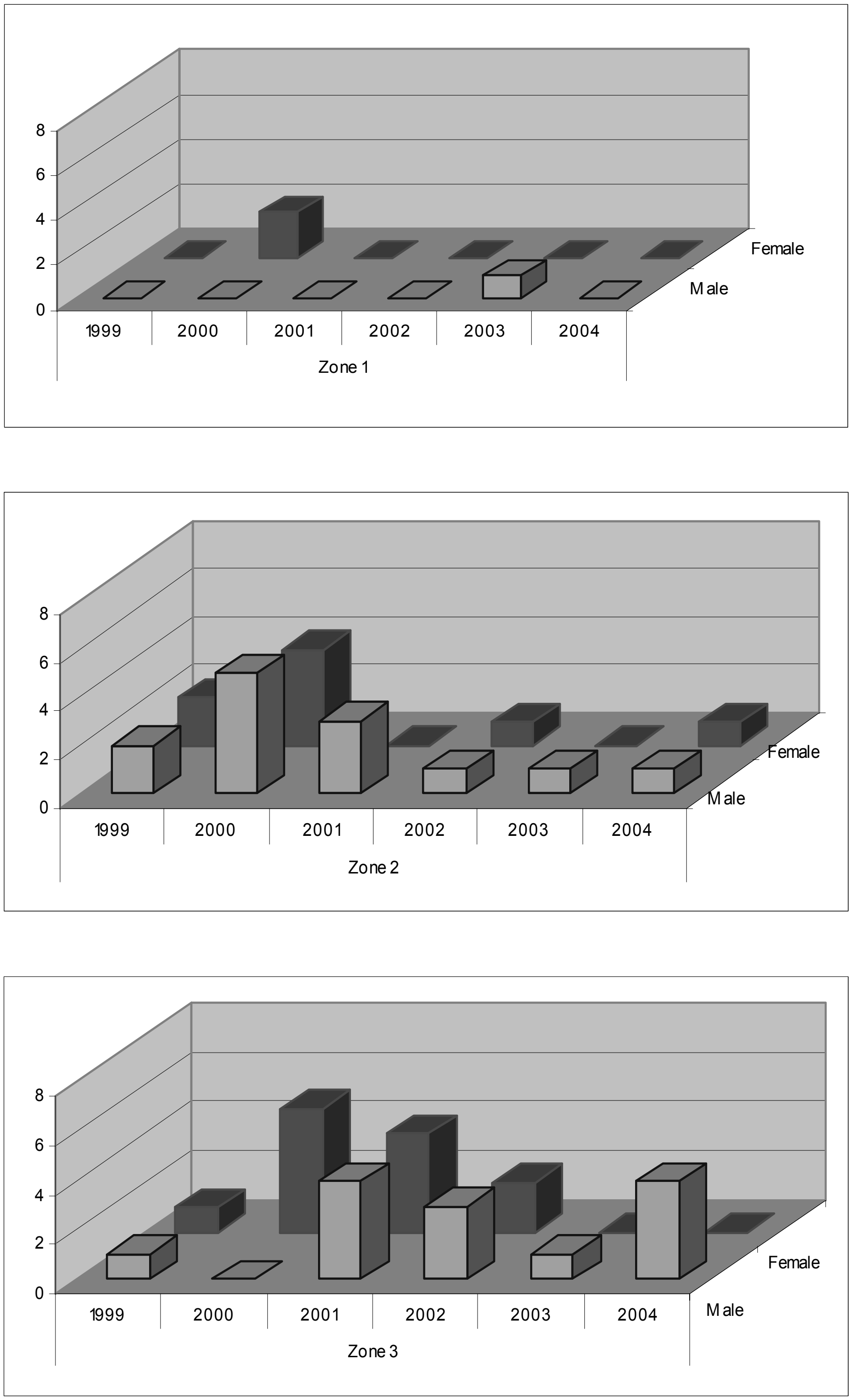

Figure 3. Number of non-wolf canids sterilized in the red wolf recovery area, summarized by current management zone, North Carolina 1999-2004.

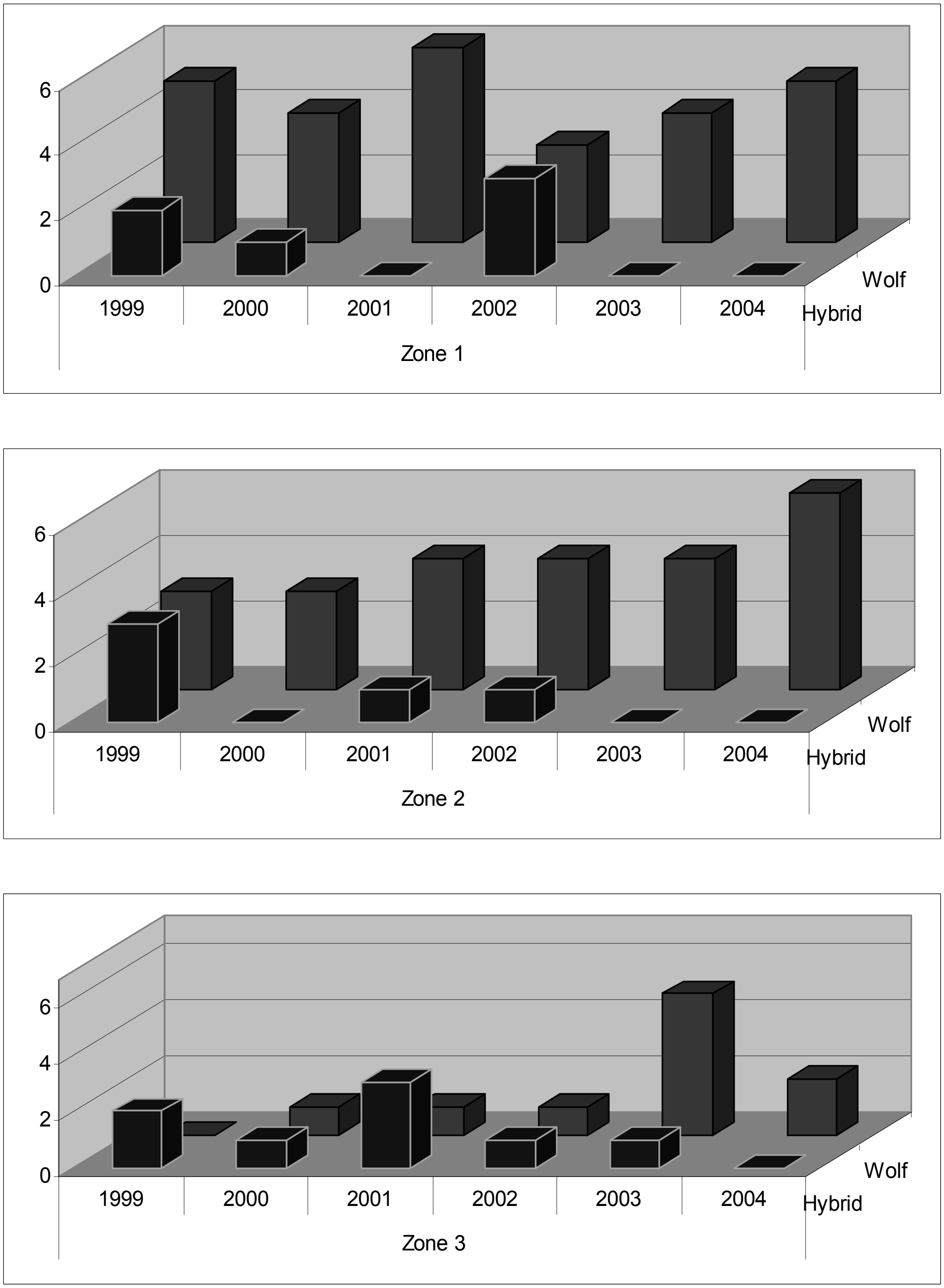

Figure 4. Number and type of canid litters found in the red wolf recovery area, summarized by current management zone, North Carolina 1999-2004.

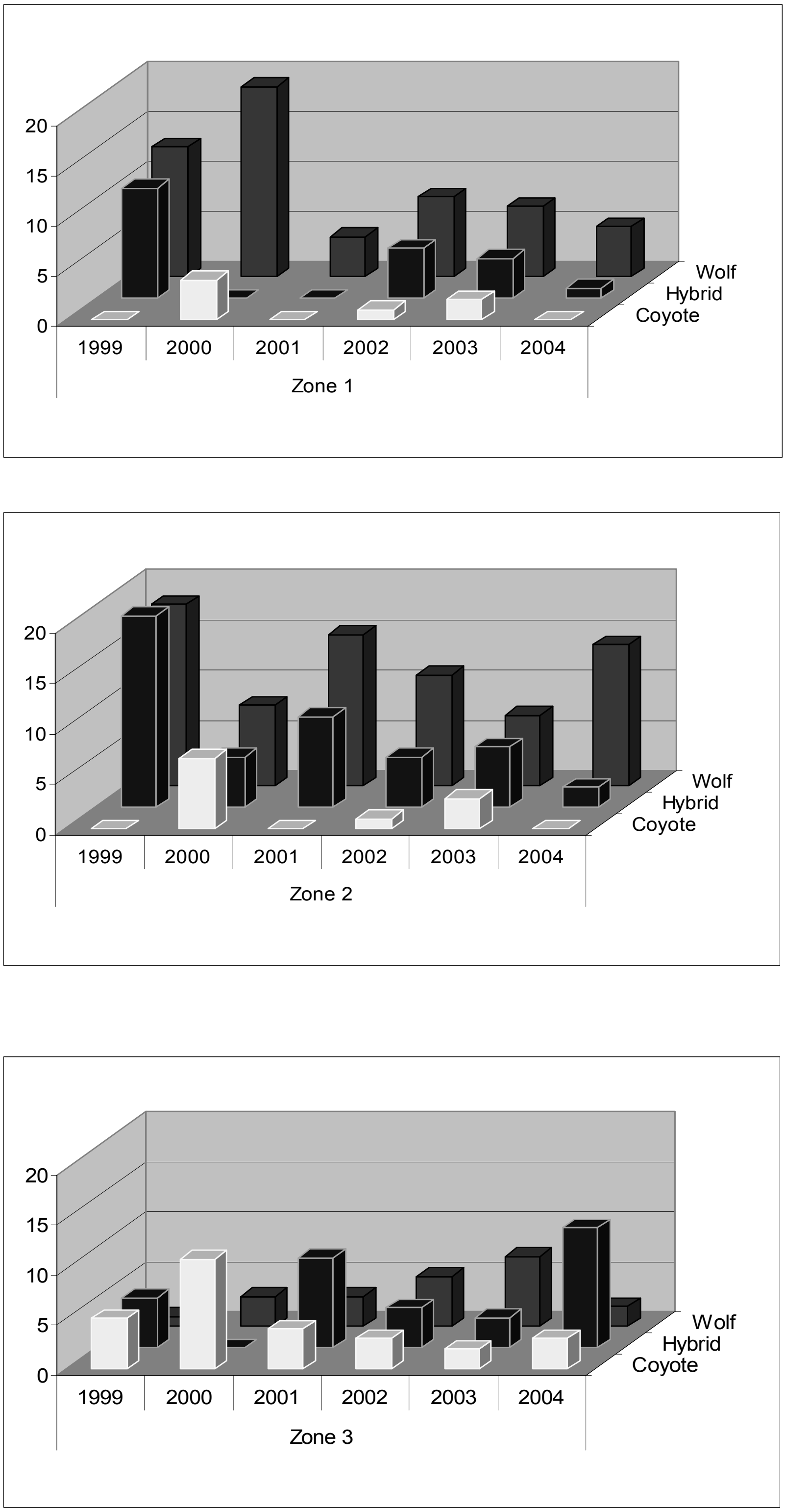

Figure 5. Number and type of canids caught for the first time in the red wolf recovery area, summarized by current management zone, North Carolina 1999-2004.

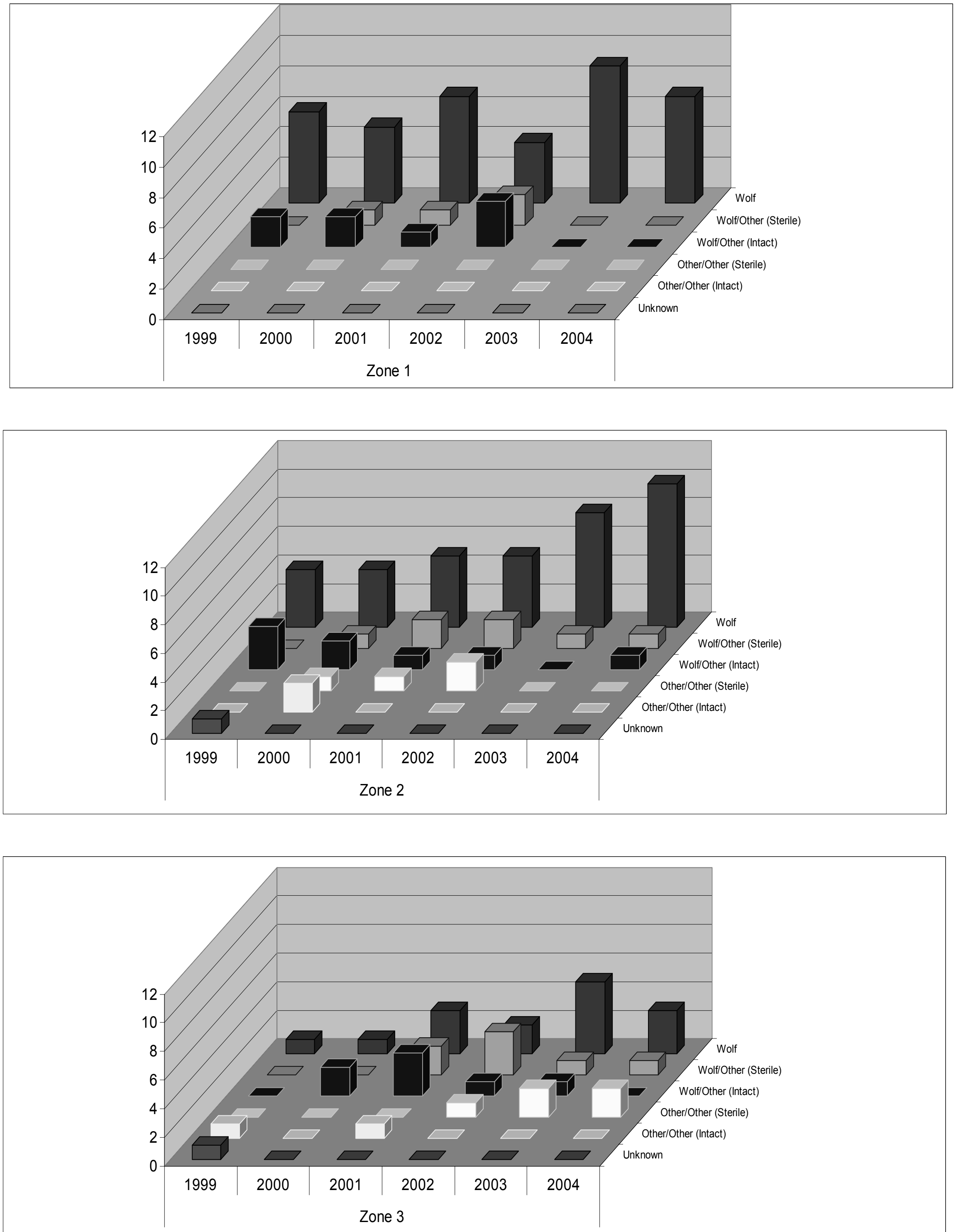

Figure 6. Number and types of breeding pairs in the red wolf recovery area, summarized by current management zone, North Carolina 1999-2004.

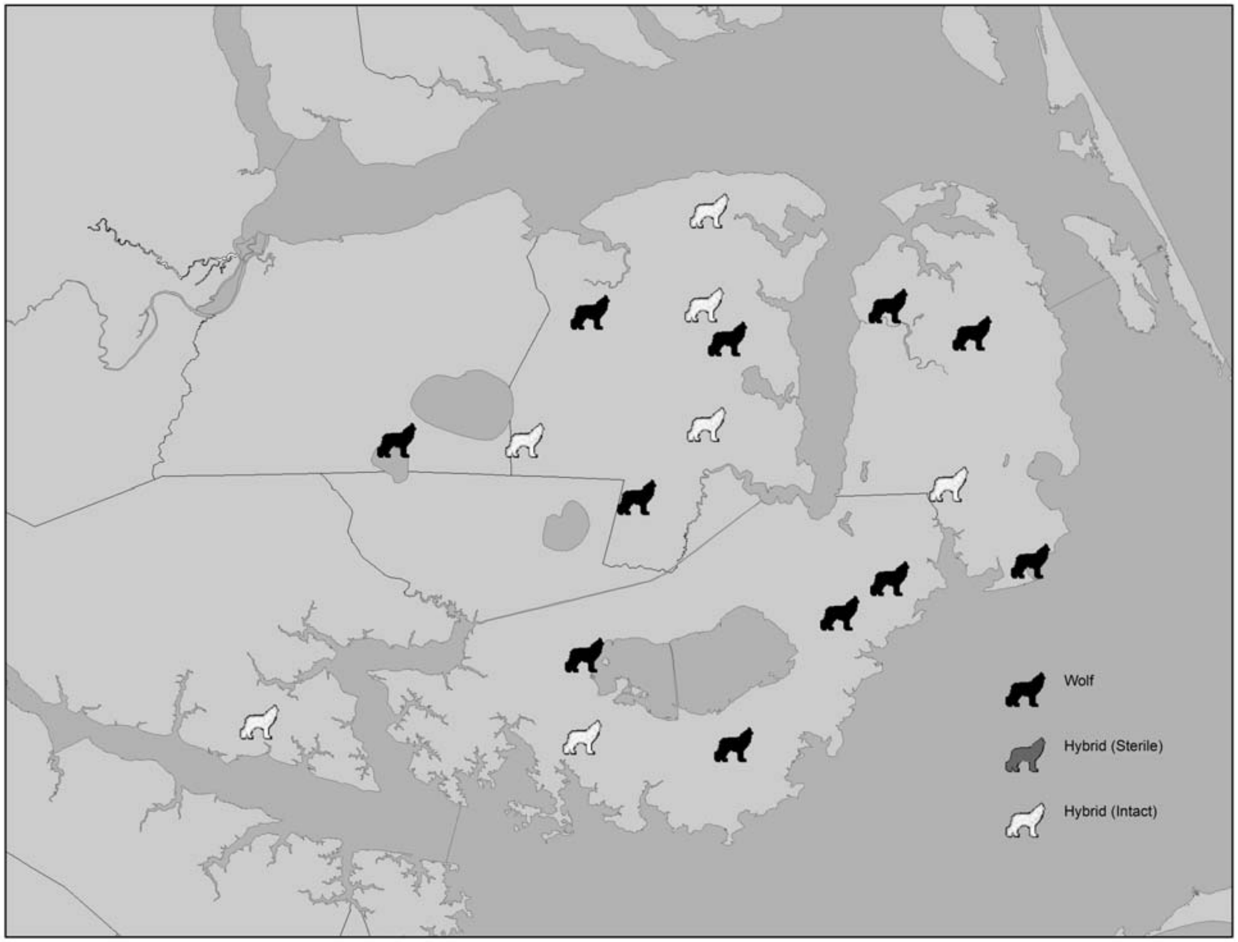

Figure 7. Territorial units in the red wolf recovery area during the 1999 breeding season.

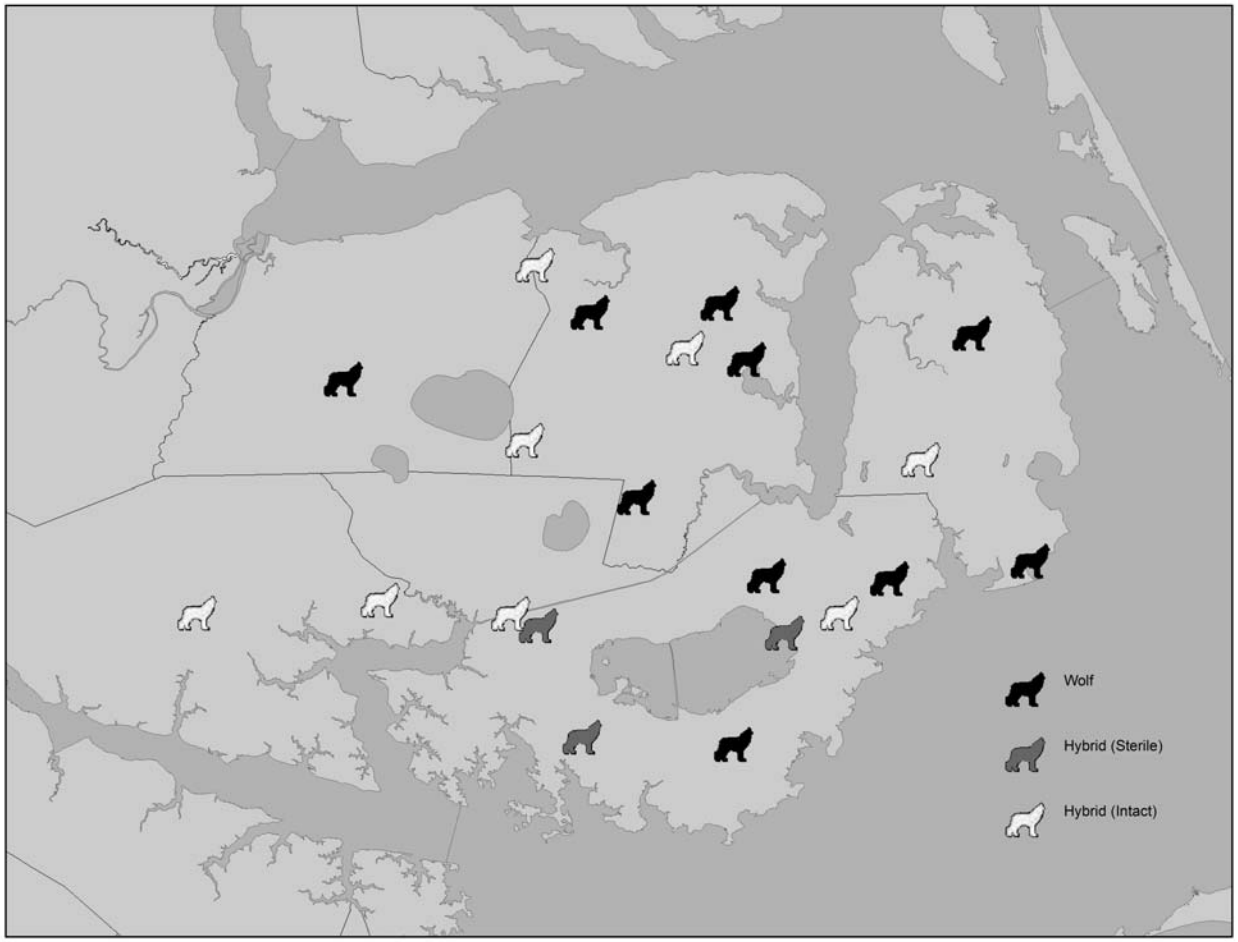

Figure 8. Territorial units in the red wolf recovery area during the 2000 breeding season.

Figure 9. Territorial units in the red wolf recovery area during the 2001 breeding season.

Figure 10. Territorial units in the red wolf recovery area during the 2002 breeding season.

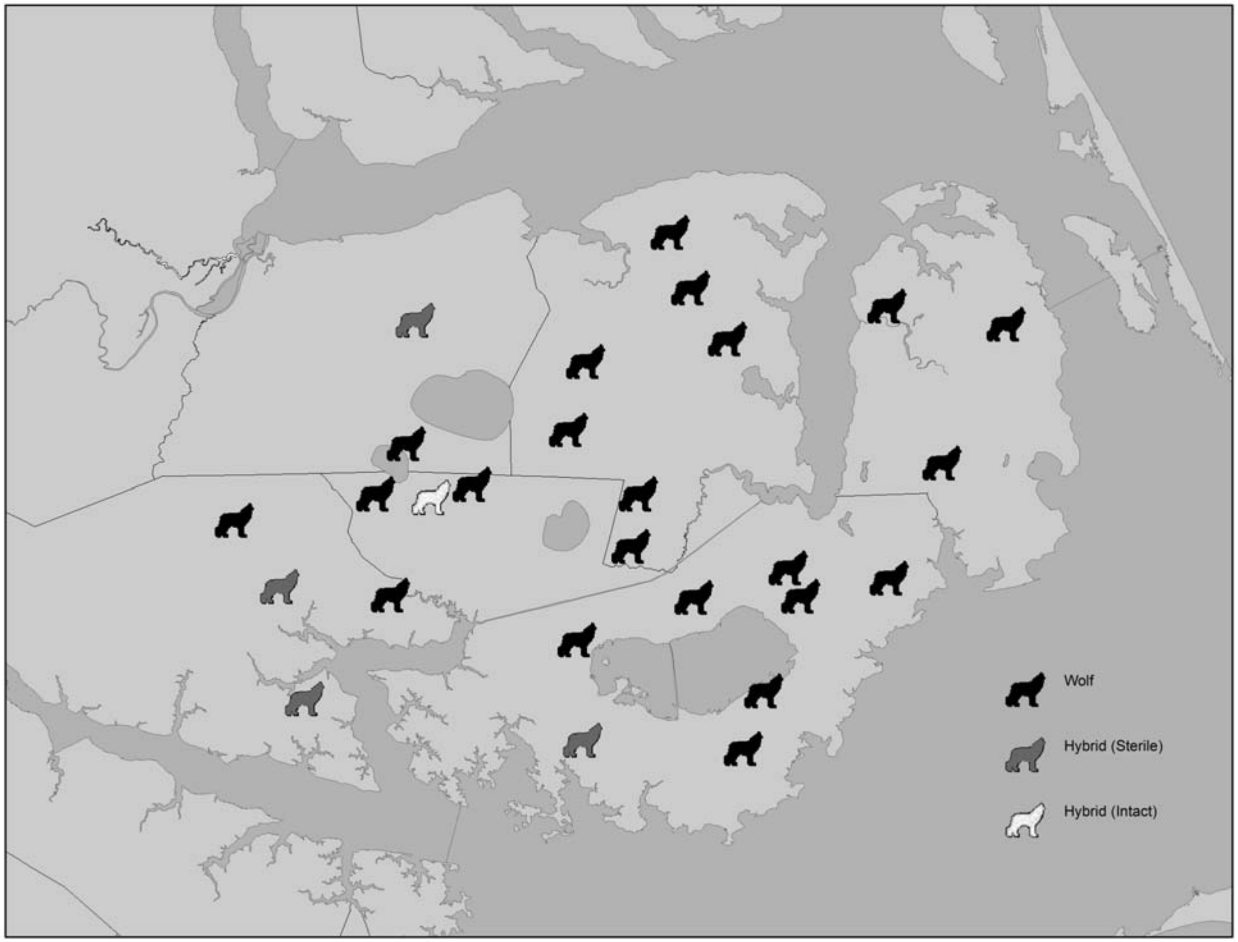

Figure 11. Territorial units in the red wolf recovery area during the 2003 breeding season.

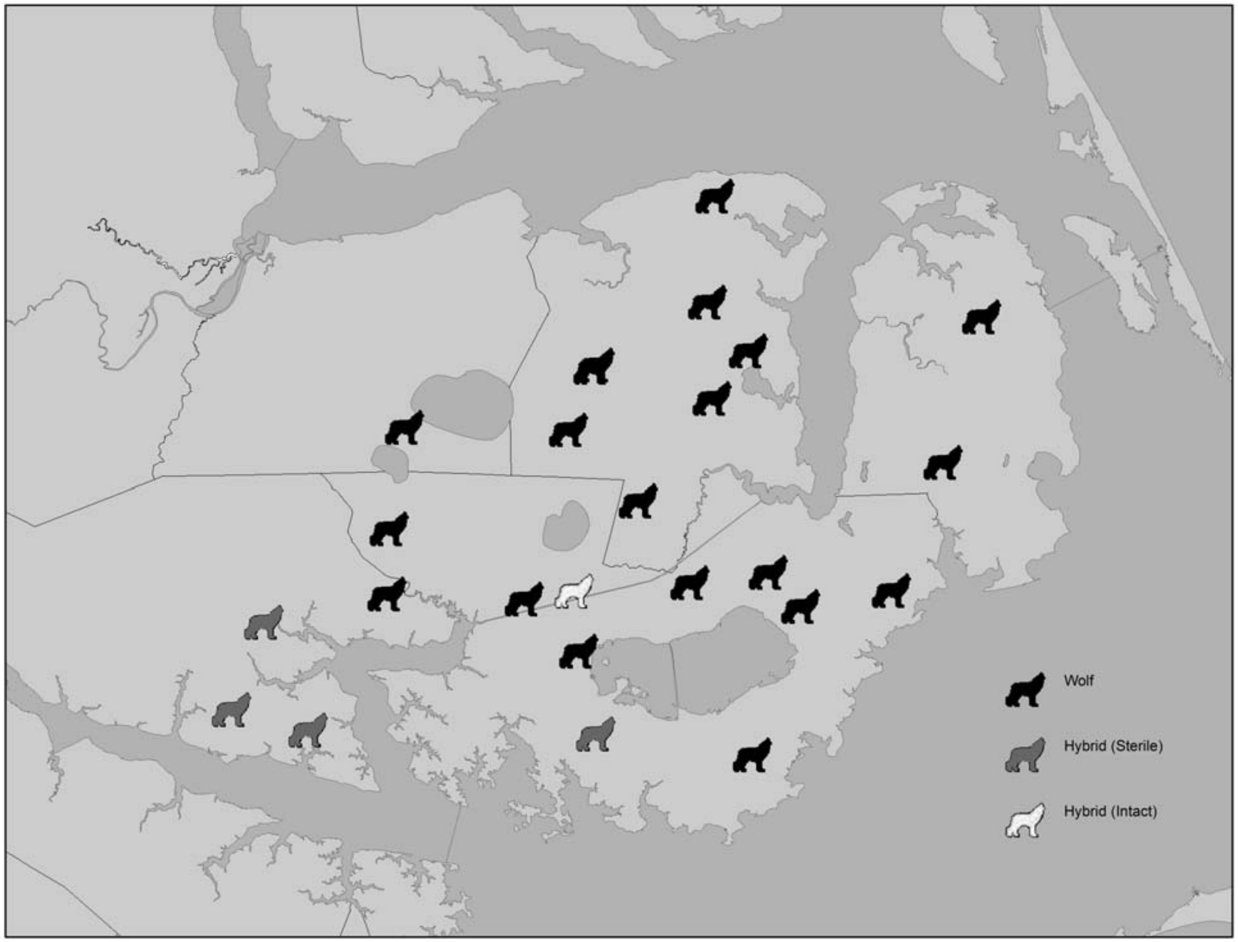

Figure 12. Territorial units in the red wolf recovery area during the 2004 breeding season.

ANALYSIS OF RED WOLF MOVEMENT PATTERNS IN NORTHEASTERN NORTH CAROLINA

> ***Relationship to Infectious Disease Model***
>
> *Elucidating patterns of contact between individuals in the different compartments (X, Y, Z_h, Z_w, and I) of the model is the focus of this chapter. In understanding how a disease is spread, one must understand patterns of contact that then affect the probability of transmission, β. Though this chapter does not directly estimate β, it provides a foundation for understanding movement patterns that may affect β.*

ABSTRACT

Red wolves (*Canis rufus*) and non-wolf canids (coyotes, *Canis latrans,* and coyote-wolf hybrids) in the red wolf recovery area were monitored by radiotelemetry from 1999 through 2004. Locations of individuals were used to look at factors that may facilitate hybridization between wolves and non-wolves. I hypothesized that patterns of movement vary based on type of canid, age, and sex and that these patterns may delineate which animals are at risk of hybridizing. Specifically I hypothesized that 1) wolves and non-wolves use roads, a potential conduit for contact, differently with respect to age and sex of an individual and time of year, 2) wolves and non-wolves have different home range attributes, including area, perimeter, and edge/area ratio, that influence contact rate between individuals, 3) the distance moved between locations varies based on age, sex, and type of canid and that those individuals moving longer distances may be a greater risk of hybridizing and 4) distance moved between an individual's natal den and the den where it was first identified as a breeder varies based on type of canid. In most cases, no differences were detected in home

range attributes or movement patterns of wolves and non-wolves though the small sample size of non-wolves provided limited statistical power.

Key Words: *Canis rufus*, *Canis latrans*, coyote, hybrid, introgression, movement patterns red wolf

INTRODUCTION

Red wolves (*Canis rufus*), once native to the southeastern United States, were nearly extinct in the wild by the late 1960s (McCarley 1959, 1962; Riley and McBride 1972). Years of predator control programs and habitat alteration had reduced the red wolf to a small fraction of its historic range (McCarley 1959, 1962; Riley and McBride 1972). Coyotes (*Canis latrans*), known for being more adaptable and better able to exist in proximity to human disturbance, began to fill the territories vacated by red wolves (McCarley 1959, 1962; Paradiso and Nowak 1971). As coyotes expanded into previously wolf-occupied areas, the opportunity for interaction between the two species presumably increased. As coyotes became more numerous than wolves, wolves presumably encountered coyotes more often than other wolves when searching for mates, breaking down the normal barriers to reproductive isolation between the two species. Hybridization became so extensive that introgression threatened the genetic integrity of the red wolf (Carley 1975, Nowak 1979).

Studies and descriptions of red wolf behavioral ecology from the 1960s and 1970s refer to a remnant population, confined to suboptimal habitat in a small portion of the red wolf's former range (Riley and McBride 1972, Shaw 1975). Red wolves in this remnant population were thought to live in unstable groups averaging less than 2 wolves and to occupy home ranges averaging 44 km^2 (4,400 hectares, Shaw 1975). Red wolves were documented to have different vocalizations and threat expressions than coyotes (Riley and McBride 1972, Shaw 1975). Analyses of scats from the remnant population documented rodents (*Myocastor coypus* and *Sigmodon hispidus*) and lagomorphs (*Sylvilagus* sp.) as major prey items.

To protect the red wolf from extinction through hybridization, wild canids in the area inhabited by remnant red wolves were trapped and evaluated with respect to several criteria indicating genetic integrity. Skull radiographs, knowledge of other canids from the same area, and morphology were all tools used to assess genetic integrity (U. S. Fish and Wildlife Service 1989). Canids that passed this preliminary screening were placed into a captive breeding program so that their offspring could be evaluated for further confirmation of genetic integrity (U. S. Fish and Wildlife Service 1989). Following this deliberate extirpation of the red wolf from the wild, the captive recovery program was managed to maintain long-term genetic viability of the species. With the success of the captive program, red wolves were released on the Alligator River National Wildlife Refuge in 1987 (Parker 1987, Phillips 1994, U. S. Fish and Wildlife Service 1989). This area was well suited for the restoration program because it was federal land in an area within the historic range of the red wolf and was free of coyotes (Parker 1987). Nonetheless, after the initiation of the restoration effort, coyotes expanded their range into the five-county area designated for red wolf recovery. Thus, hybridization again threatened the genomic integrity of the red wolf and again became a serious problem for the recovery program (DeBow et al 1998, Kelly et al 1999).

A Population and Habitat Viability Assessment (PHVA) was convened in April of 1999 to bring together experts with experience useful to developing strategies to save the red wolf (Kelly et al 1999). From this PHVA, an adaptive management plan was developed to address hybridization, considered the most serious obstacle to red wolf recovery (Kelly et al 1999, U. S. Fish and Wildlife Service 2000). As a foundation to understand why hybridization, leading to introgression, occurs, I analyzed telemetry data to look for movement patterns that put wolves at risk of mating with a non-wolf (coyote or coyote-wolf hybrid). Characterizing movement patterns that facilitate pairing between wolves and non-wolves could help refine management strategies to address introgression on a population scale.

Roads are thought to be essential travel corridors for canids in northeastern North Carolina because of the thick pocosins that impede off road travel and, therefore, could serve as conduits of contact. I hypothesized that wolves and non-wolves, especially juveniles, would be closer to the roads during the fall, the time of year associated with many dispersal events. Wolves that are dispersing look to establish a breeding territory of their own and, therefore, are at risk of pairing with a non-wolf.

Documentation of red wolf dispersal events indicate that dispersers average approximately 24 months of age and most often disperse between November and February (Phillips et al 2003). Predispersal forays are common for gray wolves as dispersers begin to explore their surroundings in search of food and breeding vacancies (Mech and Boitani 2003). If juveniles have larger home ranges and thereby increased contact with other canids, they may be the most vulnerable segment of the population to hybridization.

Previous studies have shown that coyotes have smaller home ranges than both red and gray wolves (Andelt 1985, Gese et al 1988, Phillips et al 2003, Mech and Boitani 2003). If coyotes can survive in smaller areas, then it is possible that they could be found in interstitial spaces between wolf territories by having smaller home ranges, longer peripheries, or higher edge/area ratios.

I hypothesized that patterns of movement vary based on type of canid, age, and sex and that these patterns may delineate which animals are at risk of hybridizing. Specifically I hypothesized that 1) wolves and non-wolves use roads, a potential conduit for contact, differently with respect to age of an individual and time of year, 2) wolves and non-wolves have different home range attributes, including area, perimeter, and edge/area ratio, that influence contact rate between individuals, 3) the distance moved between locations varies based on age, sex, and type of canid and that those individuals moving longer distances may be a greater risk of hybridizing and 4) distance moved between an individual's natal den and the den where it was first identified as a breeder varies based on type of canid.

STUDY AREA

The study area encompasses the entire five-county red wolf restoration area, approximately 6,650 km^2 in northeastern North Carolina (Figure 1). Agriculture, including row crops, timber, and pasture, is the predominant land use in this area, though thick pocosins are common. Three national wildlife refuges as well as a Navy and an Air Force bombing range are also found there. The climate is relatively mild with an average annual high of 26˚C and low of 5˚C. Rainfall averages 126 cm per year. For implementation of the adaptive management plan, the recovery area was divided into three management zones

(Figure 1) based on the disposition of non-wolf canids found in each area (Kelly 2000). Zone 1 was maintained free of non-wolves. In zone 2, non-wolves were removed or surgically sterilized by tubal ligation or vasectomy based on management objectives and landowner cooperation. Zone 3 was designated as that area thought to be beyond the capacity for intensive management given available resources.

MATERIALS AND METHODS

Biologists captured canids within the study area using #3, padded, leg-hold traps with offset jaws. Newly captured animals were brought to a central facility for processing that included weighing, collecting morphological measurements, collecting blood for genetic analysis, implanting a passive integrated transponder, and fitting a transmitter collar. When necessary, I surgically sterilized non-wolves by tubal ligation or vasectomy to prevent hybridization while maintaining territorial behavior and pair bonds of sterilized animals (chapter 2 in this volume, Bromley and Gese 2001). Biologists often processed recaptured animals at the site of capture.

A previous analysis determined that with a type I error rate of 0.05, data would be needed on 16 wolves and 16 coyotes to detect a 30% difference between home range sizes of the two species (Kelly 1999). We relocated animals with transmitter collars using both ground and aerial telemetry. We used trucks outfitted with paired, 5-element Yagi antennas and calculated location estimates by triangulation (LOCATE software). Bearings that were more than 15 minutes apart were not used to estimate individual to minimize the influence of movement on the precision of location estimates. Ground telemetry efforts focused on those areas where the recovery program could secure road access, primarily federal land but also areas owned by cooperating land owners. We attempted to collect a similar number of location estimates in each of three 8 hours periods in a day over each month so that data reflected movement and use of space based on time of day. Telemetry using fixed-wing aircraft, however, was usually collected between 7 am and 12 noon due to military airspace restrictions in the study area. We were able to cover a wider area with aerial telemetry than with ground telemetry because we could fly anywhere the canids traveled.

Using the location error method to compare a known location with the estimate of that location, error of ground telemetry averaged 171 +/- 160 m (Zimmerman and Powell 1995). Aerial relocations were plotted on paper maps in the aircraft. Precision of aerial telemetry was quantified by comparing aerial location estimates for 20 transmitter-collars in mortality mode to the location estimated using a recreational grade GPS unit when a biologist retrieved the collar. The median difference between the two types of location estimates for these 20 collars was 661 m. There were an additional 19 locations found in the red wolf program's database with 0 m between the aerial location estimate and the estimate from a recreation grade GPS unit. There is not good information to support that the estimates from the two methods for these 19 collars were independent rather than simply entered simultaneously in the database, so these estimates were excluded from the assessment of precision. We collected 5,333 aerial telemetry locations and 6,986 ground telemetry locations.

Ground and aerial location data were first analyzed separately to determine if a bias existed with respect to proximity to roads. The distance of each location to the closest road was calculated using ArcInfo 9.0 (ESRI, Redlands, CA). Ground telemetry data averaged significantly closer to the road than aerial telemetry locations (t-test with unequal variances, p<.001). Because of this detection bias, ground telemetry data were excluded from the analyses of distance to road and distance moved at 2 to 3 day intervals.

Aerial locations were classified by season, and the average distance to the nearest road was analyzed using a repeated measures ANOVA, first for adults and then combining both adults and juveniles. I analyzed these data to look for differences in proximity to roads based on season or age and only included individuals with at least 5 locations in each of the four seasons in the same year.

Estimates of annual home ranges were calculated using least-squares cross-validation smoothing of the fixed kernel estimator (Animal Movement Extension, Hooge and Eichenlaub 1997) for individuals with at least 20 locations in a given year. Locations from three individuals were used to bootstrap home range size based on the number of locations used to calculate it. The individuals had 155 (female wolf), 140 (female wolf), and 60 (male wolf) locations in a given year. The first two individuals were chosen because they represented the two individuals with the greatest number of locations. The third individual was randomly selected to represent approximately half those number of locations. Starting sample size was 10 for each animal and increased by 5 locations each time until the maximum number of locations was reached for an individual. Ten iterations were done for each sample size.

Some individuals were easier to track from the ground than were others. Those individuals were overrepresented in the sample of individuals with 20 or more locations in a given year, so I used a random numbers table to select individual-year combinations to avoid pseudoreplication. Visual inspection of density plots showed that the distributions were not normal, so I log-transformed the area, perimeter, and edge/area ratio of the 95% home range contour and analyzed each dependent variable using an ANOVA to look for differences due to age, sex, and type of canid (SYSTAT®, Systat Software Inc, Point Richmond, CA).

I calculated the distance moved by individuals over 2 to 6 day intervals, both individually and in two-day pairs, excluding locations from 15 Mar through 1 June, a time when movement can be influenced to a large degree by denning behavior. I also log-transformed these data after visual inspection of the density distribution showed the raw data were not normally distributed. As above, I used randomly selected individual-year combinations of the distances moved at 2 to 3 day intervals in an ANOVA to look for the influence of type of canid, sex, or age on distance moved.

Finally, I used the square root transformation of the straight-line distance moved between an individual's natal den site and the den site where the animal was first identified as a breeder in a multivariate ANOVA to evaluate the effect of type of canid, age or sex. Again, the raw data were not normally distributed and the square root transformation provided the best fit to a normal distribution.

RESULTS

Eighteen adults and 24 juveniles met the inclusion criteria for the analysis of distance to roads. I combined all canids for this analysis because there were few non-wolves that met the inclusion criteria. In no season were adults or juveniles closer to roads than in other seasons (Table 1). When comparing the data on adults and juveniles distances did not differ due to age.

I calculated home range attributes for 33 adult male wolves, 29 adult female wolves, 14 juvenile male wolves, and 14 juvenile female wolves. I also calculated home range attributes for 9 non-wolf males and 6 non-wolf females. Due to small sample sizes, I combined coyotes (n=5) and coyote-wolf hybrids (n=10) into one group, non-wolves, for home range analyses.

The result of the bootstrapping exercise is shown in Figure 2 and shows that using 20 locations to calculate a home range estimate yielded a similar estimate as obtained using a higher number of locations. For these three individuals, home range estimates averaged 19.1 km^2 +/- 6.1, 14.5 km^2 +/- 2.4, and 18.9 km^2 +/- 7.4. The estimates of home range size did not follow a pattern of increasing until reaching an asymptote. Instead, in all cases, the average home range size reached equilibrium by 20 locations and varied only slightly around that mean.

Home range estimates for wolves ranged from 7.8 to 272.8 km^2 with no statistically significant difference detected due to age or sex (Tables 2 and 3). No statistically significant difference was found between sexes or ages for home range area, perimeter, or the ratio of edge to area with one exception that females had longer home range peripheries than males ($p = 0.044$, Table 3). Home range estimates for non-wolves ranged from 6.4 to 222.4 km^2, also with no detectable differences due to sex. Estimates of home range areas and perimeters were similar between wolves and non-wolves (Table 3).

Distances moved in 2 to 3 day intervals were comparable between wolves and non-wolves, sex, and age classes (Table 4). Wolves and non-wolves moved similar distances from a natal den to the den where the individual was first identified as a breeder (Table 5). No statistically significant differences were found between wolves and non-wolves, ages, or sexes.

DISCUSSION

These analyses describe both wolf and non-wolf movements within the red wolf recovery area. Characterizing movement patterns provides insight into factors that promote canid contact and pairing and, therefore, the possibility of hybridization on the individual level and introgression at the population level. Understanding these factors may help refine management strategies to make the best use of available resources.

Initial analysis of the ground telemetry data showed that the data were biased toward proximity to roads. That is, telemetry locations from the ground were consistently closer to roads than were telemetry locations obtained from the air. This result is not unexpected since the ground telemetry effort was dependent upon the existing network of roads and the range of the truck mounted antennae. Canids may depend on roads in northeastern North Carolina to facilitate travel through the thick pocosins that are common in the area but they were still detected further from roads, on average, when aerial telemetry was employed.

The distance to road analysis was hampered by a small sample size of non-wolves that met the inclusion criteria. I was only able to compare within age classes and not between wolf and non-wolf. More data on non-wolves may have altered the results and interpretation, but the lack of significant difference between juveniles and adults suggests that roads are likely important travel corridors for all canids, regardless of age or season.

My results also suggest that home range sizes are similar between wolves and non-wolves as well as between sexes; thus, non-wolves may have similar spatial requirements. Further analysis of factors affecting home range size would be important for characterizing minimum space requirements of types of canids. If home range characteristics are similar, however, then managers may be able to better characterize availability of the landscape for canid occupancy and thus target management efforts accordingly. That is, small interstitial spaces between known groups may not be suitable areas, even for non-wolves and, therefore, may not function as a reservoir of unknown animals.

When I restricted the analysis of home range attributes to wolves and compared age classes, I found no statistically significant differences. Juvenile red wolves do not appear to have larger home ranges than adults. If juveniles are not roaming over larger distances than adults, then they may not be at increased risk of contact with a non-wolf.

Several explanations are possible for why these analyses failed to yield statistically significant differences. First, it is possible that there is no difference between any of the groups analyzed here. Previous authors have suggested that coyotes and red wolves occupy similar niches (Riley and McBride 1972). If that is indeed the case, then further data collection and analysis will, regardless of sample size, fail to discern a distinction between the two. Second, sample sizes in this study may not be large enough to detect subtle differences that do exist. In this study, we were able to follow only 5 coyotes and 10 hybrids. Because of the low sample size, we combined those two categories into one and still fell just shy of the goal of 16 (Kelly 1999).

The Red Wolf Adaptive Management Plan provided the structure for decisions on the fate of non-wolves caught in the recovery area (Kelly 2000, see also Chapter 2, this volume). Some non-wolves are sterilized and released while others are removed from the population. The implementation of this management plan allows for following sterilized non-wolves, but only in certain parts of the recovery area. The area where red wolves and coyotes likely interface most (Zone 3) is made up of mostly private land and is far from the recovery program's headquarters. These two factors make it logistically difficult to follow animals in this area intensively enough to get the number of locations needed to calculate a home range estimate. The use of other technology such as GPS collars, though these collars are expensive to obtain, could facilitate monitoring in these outlying areas.

More data on non-wolf movement through the recovery area is critically important to distinguish patterns that may exist in the two groups. These analyses serve as a precursor to further characterization of the intricacies of movement patterns and their role in predicting when and where hybridization will occur.

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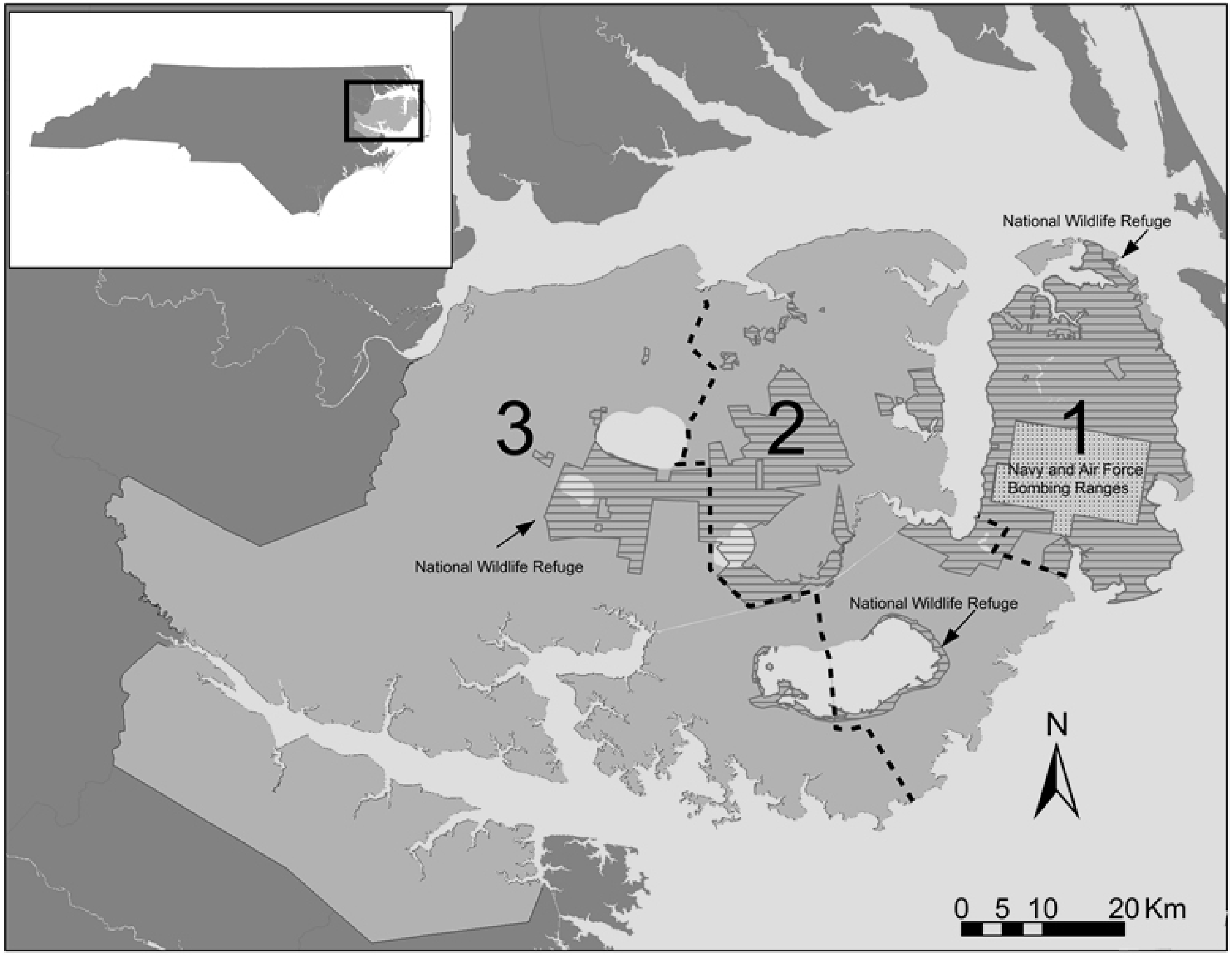
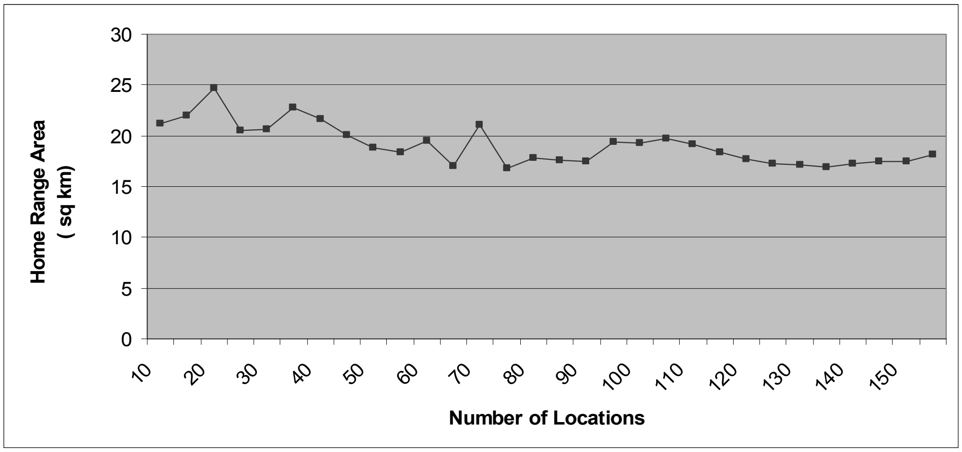
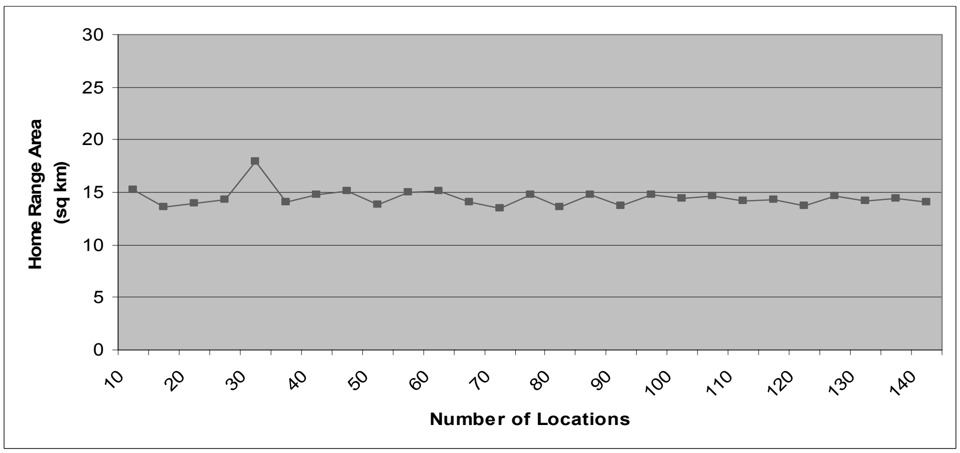


Figure 1. Management zones within the red wolf recovery area in northeastern North Carolina. Zone 1 is maintained as a coyote- and coyote-hybrid-free zone. Non-wolves caught in zone 2 are euthanized or surgically sterilized by tubal ligation or vasectomy based on management objectives and landowner consent. Zone 3 was that area thought to be beyond the capacity of intensive management given available resources.





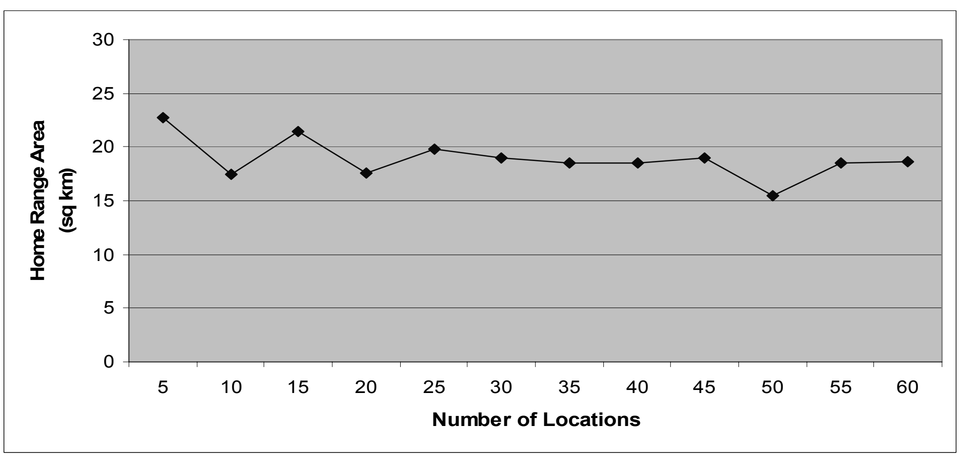


Figure 2. Graphs for three individuals showing home range area (km^2), calculated from 95% kernel contours, as a function of the number of locations used to generate it during bootstrapping. The first two graphs represent data for two different female wolves. The third graph represents data for a single male wolf.

Table 1. Analysis of distance of canids to roads by season and age. Null hypotheses are listed, followed by season (where appropriate), sample size, mean distance (m), standard deviation, and the analysis of variance table for each null hypothesis evaluated.

H_o	Season	N	Mean (m)	Std. Dev	Source	SS	df	MS	F	P
Distance to road does not vary by season for adults.	Jan-Mar	18	315	131.0	Season	44686.78	3	14895.59	1.658	0.188
	Apr-Jun	18	261	52.6	Error	458087.23	51	8982.10		
	Jul-Sep	18	327	134.3						
	Oct-Dec	18	301	124.5						
Distance to road does not vary by season for juveniles.	Jan-Mar	24	301	215.3	Season	159984.86	3	53328.29	1.846	0.147
	Apr-Jun	24	320	103.9	Error	1992952.20	69	28883.37		
	Jul-Sep	24	365	95.0						
	Oct-Dec	24	406	265.8						
Distance to road does not vary by age.					Age	91610.08	1	91610.08	2.284	0.139
					Error	1604526.20	40	40113.16		
Distance to road does not vary by season.					Season	112255.60	3	37418.53	1.832	0.145
					Season*Age	75946.34	3	25315.45	1.239	0.299
					Error	2451035.55	120	20425.30		

Table 2. Summary statistics of home range parameters. Parameters are listed on the left and include home range area (km^2), home range perimeter (km), and the ratio of length of the perimeter of the home range (edge) to the size of the home range. Summary statistics are listed by type of canid, age, and sex and include sample size, mean, and standard deviation.

Parameter	Type of Canid	Age	Sex	N	Mean	Std Dev
Home range area (km^2)	Wolf	Adult	Male	33	102	140.9
	Wolf	Adult	Female	29	116	277.7
	Wolf	Juvenile	Male	14	231	322.0
	Wolf	Juvenile	Female	14	313	561.9
	Non-wolf	Adult	Male	9	69	121.2
	Non-wolf	Adult	Female	6	309	530.5
Home range perimeter (km)	Wolf	Adult	Male	33	55	38.2
	Wolf	Adult	Female	29	57	39.9
	Wolf	Juvenile	Male	14	78	65.0
	Wolf	Juvenile	Female	14	75	72.8
	Non-wolf	Adult	Male	9	44	31.4
	Non-wolf	Adult	Female	6	93	79.9
Edge/Area ratio of home range	Wolf	Adult	Male	33	1.11	0.66
	Wolf	Adult	Female	29	1.13	0.73
	Wolf	Juvenile	Male	14	0.93	0.73
	Wolf	Juvenile	Female	14	0.92	0.54
	Non-wolf	Adult	Male	9	1.36	0.73
	Non-wolf	Adult	Female	6	0.81	0.51

Table 3. Hypothesis tests comparing home range parameters. Hypotheses are listed on the left and the associated analysis of variance table follows to the right of each hypothesis.

H_o	Source	SS	df	MS	F	P
Size of home range does not vary by type of canid or sex.	Type of canid	0.341	1	0.341	0.248	0.620
	Sex	4.455	1	4.553	3.303	0.073
	Type of canid * Sex	4.443	1	4.443	3.223	0.077
	Error	100.642	73	0.788		
Within wolves, size of home range does not vary by age or sex.	Sex	0.127	1	0.127	0.072	0.788
	Age	3.760	1	3.760	2.151	0.146
	Sex * Age	0.151	1	0.151	0.087	0.769
	Error	150.357	86	1.748		
The length of the perimeter of the home range does not vary by type of canid or sex.	Type of canid	0.145	1	0.145	0.420	0.519
	Sex	1.444	1	1.444	4.184	0.044
	Type of canid * Sex	1.003	1	1.003	2.907	0.092
	Error	25.189	73	0.345		
Within wolves, the length of the perimeter of the home range does not vary by age or sex.	Sex	0.033	1	0.033	0.075	0.785
	Age	0.391	1	0.391	0.878	0.351
	Sex * Age	0.193	1	0.193	0.434	0.512
	Error	38.300	86	0.445		
Edge/area does not vary by type of canid or sex.	Type of canid	0.041	1	0.041	0.092	0.762
	Sex	0.869	1	0.869	1.941	0.168
	Type of canid * Sex	1.224	1	1.224	2.734	0.103
	Error	32.681	73	0.448		
Within wolves, edge:area does not vary by sex or age.	Sex	0.030	1	0.030	0.056	0.814
	Age	1.726	1	1.726	3.230	0.076
	Sex * Age	0.003	1	0.003	0.005	0.945
	Error	45.959	86	0.534		

Table 4. Analysis of distance moved in 2 or 3 day interval. The null hypothesis is listed followed by the summary statistics that include the sample size, mean, and standard deviation by type of canid, age, and sex. The analysis of variance table to evaluate the null hypothesis is found below the summary statistics.

H_o	Type of Canid	Age	Sex	N	Mean (km)	Std. Dev
Distance moved between locations taken at 2 or 3 day intervals does not vary with type of canid, sex, or age.	Wolf	Juvenile	Male	17	5.4	3.9
	Wolf	Juvenile	Female	10	3.8	2.0
	Wolf	Adult	Male	32	5.7	6.5
	Wolf	Adult	Female	30	4.6	4.2
	Other	Juvenile	Male	1	2.5	
	Other	Juvenile	Female	2	1.0	1.1
	Other	Adult	Male	17	5.6	5.3
	Other	Adult	Female	11	6.7	7.8

Analysis of Variance Table

Source	SS	df	MS	F	P
Type of canid	0.010	1	0.010	0.011	0.916
Sex	0.795	1	0.795	0.852	0.358
Age	0.025	1	0.025	0.027	0.869
Error	108.193	116	0.933		

Table 5. Distance moved from natal den to den where individual was first identified as a breeder. The null hypothesis is followed by the summary statistics that include sample size, mean, and standard deviation by category (characteristic). The analysis of variance table to evaluate the null hypothesis is found below the summary statistics.

H_o	Characteristic	N	Mean (km)	Std Dev
The distance moved from a natal den to the den where the individual is first identified as a breeder does not vary due to type of canid, age, or sex.	Male	15	23.4	17.4
	Female	19	26.8	18.5
	Wolf	29	26.3	17.4
	Non-wolf	5	19.7	21.6

Analysis of Variance Table

Source	SS	df	MS	F	P
Type of canid	1926.518	1	1926.518	0.405	0.529
Age	4334.688	1	4334.688	0.912	0.348
Sex	2447.063	1	2447.063	0.515	0.479
Error	137889.147	29	4754.798		

EVALUATION OF THE IMPACT OF CHANGES IN PARAMETER ESTIMATES ON THE RESULTS OF THE INTROGRESSION MODEL

The purpose of this introgression model is to evaluate the effectiveness of management strategies aimed at increasing the number of immune red wolves (red wolves paired with red wolves) and reducing the number of infectious individuals (non-wolves) in the recovery area. Another important benefit from any modeling exercise is the ability to identify important data that may not have been collected or estimated with confidence. Missing data should not be seen as an impediment to modeling but rather modeling should be seen as a way to identify which missing data are important and, therefore, should be a priority for collecting.

The first step to running this model was to translate the model into words from which equations could be written. Tables 1 and 2 contain the model from Figure 1 translated into words and equations, respectively. I then proceeded to estimate parameters using data collected from 1999-2005, including data analyzed in previous chapters in this dissertation. Table 3 lists the parameters used in the model, an estimate and standard deviation, where available, for each parameter, and how each estimate was generated. See Table 4 for the data used to calculate the estimates. For some parameters, adequate data did not exist to estimate it. Survival rates for non-wolves are not known with certainty and were assumed to be the same as the survival rates for wolves in the same age class. Relatively few data are available on interactions between wolves and non-wolves but these data are important to estimating the effective contact rate, β. In this model, β is the probability that a susceptible individual will become infected and thus represents the rate of movement between the susceptible compartment and the infected compartment of the model (Halloran 1998). Beta, therefore, represents the number of susceptible individuals that pair with a non-wolf and was estimated as the number of wolves newly paired with a non-wolf each year.

It is also possible that some parameter estimates are not an accurate reflection of the true value of the parameter. Further explanation of how the parameter estimates were obtained may help address this concern. The birth rate for red wolves (a_w) was estimated as the number of pups produced divided by the total number of wolf pairs and reflects the production contributed to the wolf pup category by each pair. It is lower than an average litter size because it is adjusted to include the fact that some wolf pairs do not produce pups each year. This estimate was calculated from actual data from the recovery program during the time in question. The birth rate for hybrids and non-wolves was calculated the same way. The data from the program supports a difference in birth rate for wolves, $a_{w,}$ and that for non-wolves, a_h. This difference may be real, or it may be the result of a detection bias or a result of small sample sizes of non-wolves. Since the birth rate for wolves is a function of the total number of wolf pairs, it reflects the fact that the data show numerous instances where wolf pairs were not known to have produced a litter in a given year. Either way, a_w reflects the average number of pups born per female of a territorial pair and not litter size per se.

The rate of red wolf pair formation (b) is the proportion of individuals that move from the susceptible to the immune wolf category. This estimate was also calculated from actual data from the recovery program and represents the proportion of two year old and older wolves that pair with a new wolf in a year. Though this proportion seems high, it is consistent with the turnover in composition of breeding pairs documented by the recovery program.

The natural morality rate of an infectious mate (c_n), the loss of immunity from the loss of a mate to natural causes (γ_n), and the natural mortality rate (μ) are all assumed to be equal and represent the proportion of individuals that die each year due to natural causes. For example, approximately 22% of infected individuals will lose their mate each year due to natural causes.

The management removal rate of an infectious mate (c_m) represents the proportion of infected individuals who will lose their mate each year because the infectious individual is trapped and removed from the population. Similarly, the mortality due to management (μ_m) is the proportion of unpaired, infectious individuals that are removed from the population. These estimates were calculated from actual removals from the population during the study period. There is much variation in these numbers over time, given that densities of non-wolves were greater early in the study period and fewer non-wolves were present and thus subject to removal during the later years.

Survival rates for wolf pups (S_{wp}) and yearlings (S_{wy}) were estimated by another researcher based on data from the recovery program (Dennis Murray, personal communication). These rates represent the proportion of individuals in each category that survive to the next year. Survival rates for non-wolves have not been estimated since known non-wolves are most often removed from the population when found. These rates were assumed to be the same as the survival rates for wolves in the respective category.

The loss of immunity due to management action (γ_m) represents the removal of a sterilized individual from a territorial pair. That is, a sterilized non-wolf that is paired with a red wolf is subject to removal when a red wolf becomes available to replace it. This estimate represents the proportion of wolves that are paired with a sterilized non-wolf that will have that mate removed and was calculated from data from the recovery program.

An infected individual can recover from this "infection" by 1) having its mate die from natural causes (c_n), 2) having its mate die from management actions (c_m), 3) having its mate displaced by a wolf (ν_d), or 4) having its mate sterilized(ν_s). The first two are discussed above. The recovery rate due to displacement represents the proportion of infected individuals that have their mate displaced by a wolf while the recovery rate due to sterilization represents the proportion of infected individuals that have their mate surgically sterilized. Both of these estimates were calculated from data from the recovery program.

Assumptions made in this model include 1) a pair bond remains intact until a member of the pair dies or is displaced, 2) bonded pairs are monogamous, 3) coyotes and coyote-wolf hybrids function similarly in all aspects of the model and are referred to as one group, non-wolves, 4) males and females function similarly in all aspects of the model and are combined for analysis, 5) no immigration occurs from outside the study area nor do individuals disperse outside the study area, 6) no geographic variation exists in how wolves and non-wolves are distributed, 7) no geographic variation exists in parameter estimates, and 8) carrying capacity and the number of breeding territories are not limiting factors in the model.

Biologists use several methods of intervention to control the spread of this "infectious disease". Den work involves the removal of non-wolf litters and is reflected in the model as a decrease in non-wolf pup survival (see chapter 4 this volume). Sterilization rates are reflected in the model as ν_s, the rate of sterilization of intact non-wolves that are mated with red wolves (see chapter 5 this volume). Biologists may also trap and remove non-wolves from the population. These removals may happen at several stages in the model and thus are represented by μ_m (trap and removal of infectious individuals), c_m (removal of a non-wolf that is paired with a wolf), and γ_m (removal of a sterilized non-wolf that is paired with a wolf). For the purposes of this model, I am primarily interested in the effectiveness of sterilization and den work as methods of intervention.

I built a stage-classified matrix combining both wolves and non-wolves (Table 5), using the parameter estimates listed in Table 3 (Lefkovitch 1965). Once this matrix was parameterized, I used the PopTools add-in for Microsoft Excel (version 2.6.9, developed by Greg Hood at the Commonwealth Scientific and Industrial Research Organisation, available online at http://www.cse.csiro.au/poptools/) to analyze the matrix and run an elasticity analyses. Some parameters occur in more than one cell in the matrix (Table 5). Therefore, the analysis was modified to calculate the elasticity of λ to lower-level parameters as described by Caswell (2001). To obtain values for λ, the population growth rate, and the stable category distribution (Leslie 1945), I used the series of equations in Table 2 to calculate the number and proportion of individuals in each category. I ran iterations of the calculations until the category reached a stable point and did not change from one year to the next. I calculated population growth rates for wolves and non-wolves each year as the number of individuals in the current year divided by the total number of individuals in the preceding year. I also calculated an overall population growth rate for each population, wolf and non-wolf, as the total number of individuals in that population when the population attained a stable category distribution divided by the starting number of individuals in that population.

I evaluated 4 different scenarios to reflect various management strategies (Table 6). Scenario 1 evaluates the strategy of no intervention other than trap and removal of adult infectious individuals. Scenario 2 evaluates the impact of den work by decreasing the survival rate of non-wolf pups and yearlings. Scenario 3 evaluates the impact of sterilization with no den work by increasing the recovery rate due to sterilization, ν_s, and by decreasing the birth rate for non-wolves. Since ν_s represents the sterilization of non-wolves that are paired with a wolf, the adjustment of birth rate of non-wolves was necessary to reflect the sterilization of non-wolves paired with non-wolves. That is, ν_s represents movement out of the infected compartment but does not affect the infectious compartment (Figure 1). If no adjustment is made in the birth rate of non-wolves, a_n, then the model would not account for the sterilization of non-wolf, non-wolf pairs, that compartment below the dotted line in Figure 1. Scenario 4 combines the effects of den work and sterilization. I calculated population growth rates and stable category distributions for each population in each scenario. To introduce density-dependence, I modified scenario 4 to account for changes in the rates of pair formation. As the proportion of non-wolves in the population decreases, b should increase and β should decrease. I assumed that β was proportional to the number of wolves and non-wolves, specifically that $\beta = (N_{nw}/N_w)*P$. I calculated this constant P using the total number of wolves and non-wolves in year 1(87 and 21, respectively) and $\beta = 0.11$. I then used P =

0.464 to calculate β for subsequent years and reran scenario 4 to determine population growth rate and the stable category distribution.

Sensitivity and elasticity are methods to evaluate how the outcome of a model will change with small changes in each of the parameters. Sensitivity values reflect how the outcome, in this case the dominant eigenvalue of the matrix is population growth rate (λ), changes with small changes in the value of a specific parameter. Elasticity, on the other hand, evaluates how the outcome changes with small proportional changes in the parameter values. Essentially, elasticity weights sensitivity by the range of the parameter. This difference becomes clear when you consider that the matrix used in this model contains birth rates and mortality rates. Birth rates could vary from 0 to 10, whereas a mortality rate must vary between 0 and 1. A small change of 0.1 is proportionally a larger change in mortality rate than 0.1 is for birth rate.

Caswell (2000) discusses what he terms prospective and retrospective perturbation analyses. Prospective analyses describe the functional relationship between an outcome, in this case the population growth rate λ, and the vital rates used to estimate it. These analyses answer the question of how λ depends on the rates used to estimate it. If you change a particular parameter estimate by this much, then how much does λ change? These analyses do not factor in variation in the rates. Retrospective analyses, however, attempt to describe the relationship between variation in the outcome, in this case λ, and variation in the parameters used to estimate it. A parameter with little to no variation can have little if any effect on variation in λ, even if that parameter was shown to have a high elasticity in the prospective analysis.

Sensitivity and elasticity analyses are prospective analyses that are not based on observed variation in parameters. Elasticity analysis provides particularly powerful information for managers who want to make decisions based on maximum impact for effort. Managers looking to impact population growth, for example, would want to focus their efforts on those parameters shown to have the greatest effect on population growth for the least shift in parameter value. Knowing which parameters population growth rate, λ, responds to the most gives managers the information they need to prioritize field efforts aimed at maximizing impact. In this model, then, an elasticity analysis could be useful to help determine the relative merits of emphasizing den work versus sterilization when the desired outcome is increasing red wolf population growth and decreasing non-wolf population growth.

Table 7 shows the results of the elasticity analysis. Under scenario 1, changes in the birth rate of non-wolves and the survival rates of non-wolf pups and yearlings would have the most effect on the growth rate of the combined population of wolves and non-wolves. When den work is used to decrease the survival rate of non-wolf pups and yearlings, the birth rate of wolves and the survival of wolf pups and yearlings are highly influential but the rate of red wolf pair formation has the greatest influence (scenario 2). If instead sterilization is used, the results do not change much at all (scenario 3). When den work and sterilization are combined, the results change slightly but the order of influence remains unchanged (scenario 4).

Table 8 shows the stable category distribution reached under each of the scenarios. Under scenario 1, the population is entirely non-wolf individuals with almost half of the population made up of non-wolf pups. Management intervention as described in any of the three other scenarios results in a population that is more than 80% red wolf individuals. Scenario 2 results in 12% hybrid pups but few other non-wolves. Scenario 4 is most effective at reducing the population of non-wolves. The result is a population growth rate for non-wolves of less than 1 and a population that is less than 5% non-wolves. Nearly one-third of the population in each scenario is comprised of susceptible individuals. The high proportion of susceptible individuals is to be expected given that any adult wolf without breeding status in a pair or pack is considered susceptible.

Figure 2 shows population growth rate for wolves and non-wolves as it changes from year to year for each of the management scenarios. Wolf population growth initially decreases before increasing and leveling off, around 10 to 15 years. Non-wolf population growth rate initially increases then decreases before leveling.

For the first scenario evaluation, I used parameter estimates that reflect no den work or sterilization. The only management intervention is in the mortality rate of adult non-wolves that are trapped and removed from the population. Under this scenario, the birth rate of non-wolves, survival rate of non-wolf pups, and survival rate of non-wolf yearlings all showed equal elasticities (Table 7). The rate of management removal (μ_m) has very low elasticity and decreasing the rate of non-wolf production and survival would have much more of an impact on decreasing non-wolf population growth (λ). The population growth rate for this scenario was 1.57, a large and implausible figure (Table 8). Nearly 48% of this population would be non-wolf pups and 19% of the population would be non-wolf adults (Table 8).

For scenario 2, I estimated the impact of den-work by decreasing non-wolf pup and yearling survival. The rate of non-wolf pup survival was extremely low to represent the removal of most non-wolf litters within the red wolf recovery area (Table 6). Under this scenario, three parameters reflecting pup production and juvenile survival, this time wolf instead of non-wolf, again show equal elasticity but the rate of red wolf pair formation shows a higher elasticity (Table7). The population shifts from predominantly non-wolf pups to predominantly wolf with only 14% non-wolves (Table 8).

Scenario 3 estimates the effect of sterilization by sterilizing mates of infected wolves and by decreasing the birth rate of non-wolves from 3.88 to 1.0 (Table 6). This estimate allows for some non-wolf reproduction to occur in the restoration area but at approximately 25% of the previous rate of reproduction. The results of the elasticity analysis are very similar to the results obtained under scenario 2 (Table 7). The population growth rates are similar as is the combined percentage of non-wolves in the population (Table 8). There is a difference, though, in the distribution of the population in the non-wolf categories (Table 8). Though approximately 14 % of the population is non-wolf under either scenario, most of the non-wolf population is hybrid pups in scenario 2 where as the non-wolf population is evenly distributed across the non-wolf categories in scenario 3 (Table 8).

Finally, scenario 4 estimates the combined impact of den work and sterilization. While the elasticity results are similar to scenarios 2 and 3, the combined effect on non-wolf population growth rate reduces λ to 0.97 (Table 8). Under this scenario, non-wolves make up only 3% of the total population. If the variable β based on the equation $\beta = (N_{nw}/N_w)*P$ reflects some effect of density dependence, then the non-wolf population growth rate under scenario 5 was reduced to 0.84 and the wolf population growth rate increased to 1.16. The resulting population was entirely wolf.

Den work, at the rates in scenario 2, and its corresponding impact on non-wolf survival were equally effective at decreasing the population growth rate of non-wolves as sterilization at the rate in scenario 3, when compared to the population growth rate of non-wolves in scenario 1. Both management strategies resulted in similar population growth rates of wolves. The synergy of the two together had an even greater impact on non-wolf λ than either strategy alone.

The value of the non-wolf λ obtained under scenario 1 is high and biologically unlikely. A λ of 1.0 denotes a stable population that is not expanding or shrinking. To have λ of 1.11 is possible but 1.57 is highly unlikely. Because this model includes no density dependence, the model population can grow without, for example, any increased mortality or decrease in reproduction from the lack of suitable habitat availability. In reality, as the population expands, there is likely to be increased inter- and intraspecific strife as well as fewer available territories.

Some research suggests that high variation in rates could be more influential in a model than a rate with high elasticity (Gaillard et al 1998). Mills et al (1999) explore the relationship between elasticity and variation and conclude that though elasticity analysis can prove useful, the results should be interpreted with an understanding of the underlying variation possible in the vital rates. Variation in vital rates could alter the results of the elasticity analysis and thereby change the qualitative ranking of which rates should be targeted for management action. Ehrlen et al (2001) argue that elasticities are accurate under a wider range of scenarios than that suggested by Mills et al (1999) and that providing simple statistics can provide information on how often elasticities yield inaccurate information and how large the discrepancies can be. Mills et al (2000) caution that because elasticities do not describe variation in vital rates, elasticities alone are not sufficient to predict which rates are most important and influential in affecting population growth rate.

We know that there is a large amount of variation in most of the parameters used in this model. These rates may have been estimated with low precision, may vary naturally, and may vary over both time and location. For example, the rate of sterilization was high early in the time period discussed here (1999 through 2005) but decreased as fewer breeding non-wolves were caught and as wolves began to fill breeding vacancies. Removal of adult infectious individuals from the population followed a similar pattern. More of these adults were removed early in the implementation of the current management strategy than are removed now, mainly because of the effectiveness of controlling non-wolf and hybrid reproduction within the study area. The proportion, as opposed to the absolute number, of individuals removed may actually be higher now than in the early years of the program. This result would be expected as the number of individuals may decrease but proportionally more of them are removed. That is, if only three non-wolves existed and all three were removed, the proportion removed would be 1.0. If, as could be the case early in the recovery effort, the number of non-wolves were higher, say 10, and 5 were removed, the proportion removed would be 0.5. The red wolf adaptive management plan utilizes zones of gradated management intensity and thus different parameter estimates would be expected for each management zone (Kelly 2000). Management removal rates of non-wolves are higher in some zones than others due to the relative densities of wolves and non-wolves in the zone and the management objective for each zone.

Caswell (2000) argues that the impact of changing parameters can be best understood through elasticity analysis rather than an investigation of the contribution to variance in λ. Thus, to understand which parameters should be targeted for management intervention, an elasticity analysis provides useful information. Mills et al (2001) argue, however, that the distinction Caswell (2000) makes between prospective and retrospective analysis is not helpful and potentially "misleading" (p. 282). Rather, they suggest including in any elasticity analysis information on whether variation is included and how the variation was quantified. Certainly this model would benefit from further examination of elasticities and their relationship to the natural variation in demographic rates (how the rates vary over time) as well as the impact of precision of the estimation of vital rates (how well the estimate of the rate reflects the actual value of the rate).

When interpreting this model and its results, one must keep in mind the assumptions of the model and resulting limitations. This model is fairly simplistic and does not account for geographic variation in management strategies, a key component of the red wolf adaptive management plan (Kelly 2000). This model also does not allow for immigration or emigration, sociality or dispersal, or the limitation in available habitat. Though wolves are not likely to immigrate from outside the recovery area, non-wolves are. This fact makes controlling non-wolves in the study area slightly more complicated than in this model that does not allow immigration. Integrating multiple versions of the matrix, one for each management zone, would allow the variation of parameters across zones and, therefore, a more realistic description of the population that is elucidated by this model.

Another limitation of this model is the lack of density dependence in the parameters. Undoubtedly, many of the parameters are in fact density dependent. As the population of wolves increases and the population of non-wolves decrease, the rate of wolves pairing with wolves (b) should increase while the effective contact rate (β) should decrease. If there were no non-wolves present, the effective contact rate would, by definition, be 0. Fewer management removals (μ_m and c_m) would be required at lower population densities of non-wolves though the proportion of non-wolves removed may actually increase. That is, as there are fewer and fewer non-wolves, the absolute number of removals may decrease but the relative proportion may increase. A similar argument could be made for the recovery rate due to displacement (ν_d) and sterilization (ν_s).

Another stage could be included that would allow for an individual to be considered immune because it is a member of a pack or susceptible because it is dispersing. Limiting the number of breeding pairs due to constraints in availability of suitable habitat would also strengthen the model. These types of considerations are being addressed in more traditional demographic models being built for use in evaluating the effectiveness of the current red wolf management strategy. As designed, this model shows that the persistence of immune wolves combined with a high rate of red wolf pair formation are important to expanding the population of red wolves. Controlling non-wolf survival rates, primarily through den work, combined with sterilization of non-wolf adults is extremely effective at controlling the population growth rate of non-wolves in this model. If, indeed, the rates of wolf pair formation and hybrid pair formation are density dependent, the model suggests that the management strategies outlined here would be even more effective in decreasing the non-wolf population and expanding the red wolf population.

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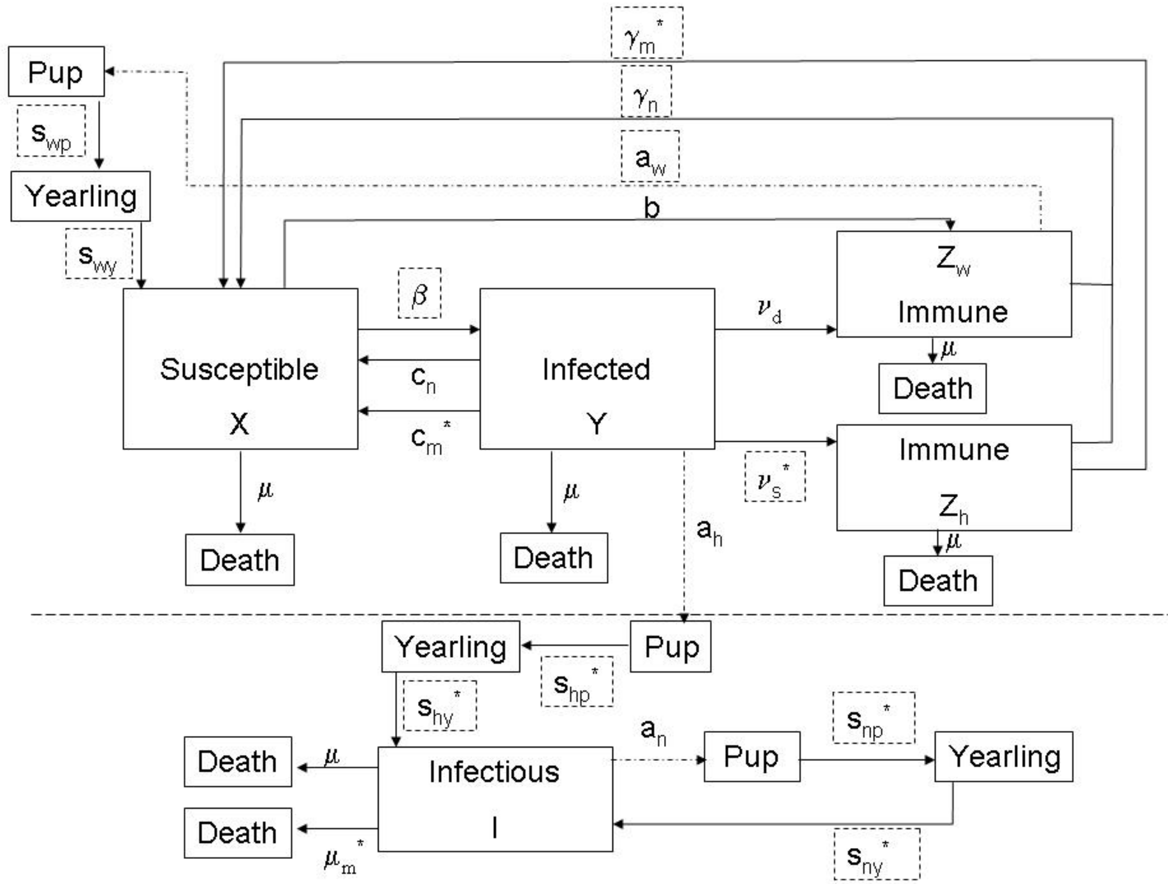
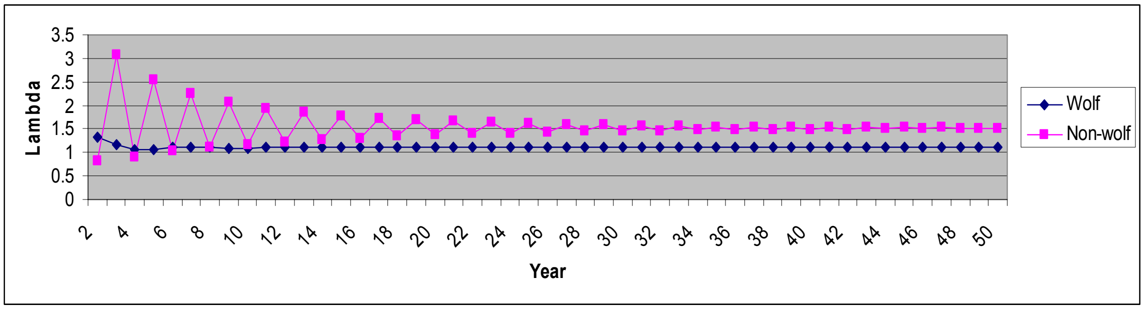
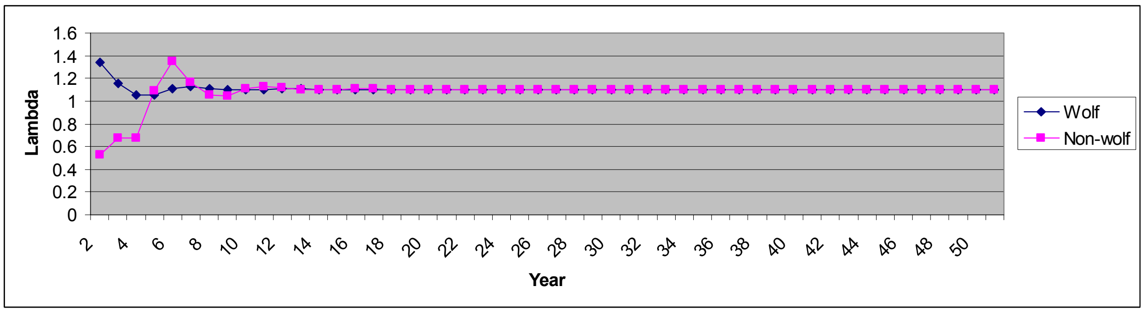


Figure 1. Diagram of the introgression as a disease model. Parameters outlined in dotted lines represent those rates specifically addressed in other chapters of this dissertation. Parameters marked with an asterisk represent potential intervention opportunities. The model above the dotted line depicts the wolf population while the model below the dotted line depicts the non-wolf population.

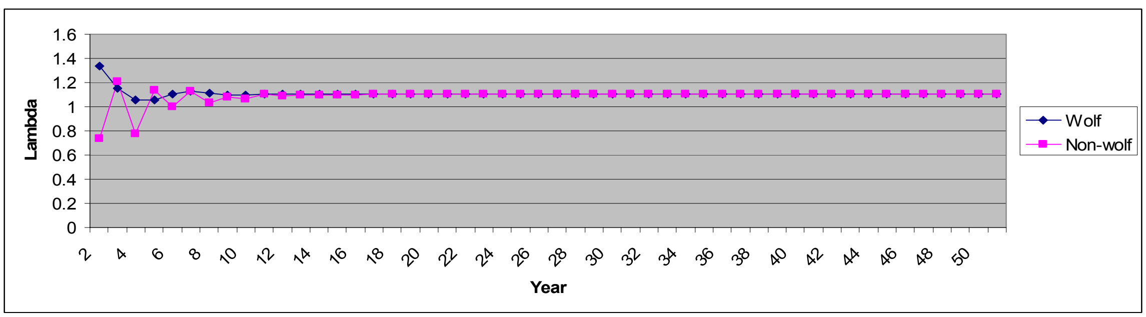
Scenario 1



Scenario 2



Scenario 3



Scenario 4

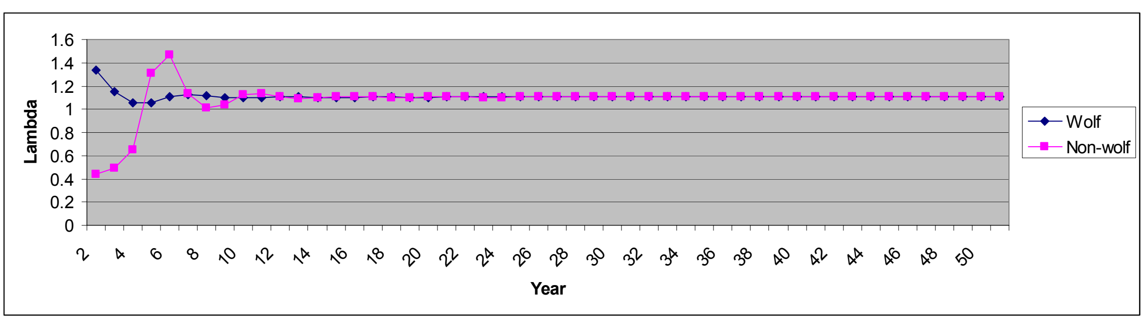


Figure 2. Lambda (λ) for wolf and non-wolf populations by year for each of 4 scenarios. Scenario 1 represents no den work or sterilization. Scenario 2 represents den work but no sterilization. Scenario 3 represents sterilization but no den work. Scenario 4 represents the use of both den work and sterilization as management strategies.

Table 1. The introgression model translated into words, defining the inputs and outflows for each compartment.

Susceptibles (X) next year =	Susceptibles this year+new two year old wolves + Immune that lose mate naturally + Immune that lose mate due to management + Infected that lose mate naturally + Infected that lose mate due to management - Susceptibles that pair with wolf - Susceptibles that pair with intact nonwolf - Susceptibles that die
Infected (Y) next year =	Infected this year + Susceptibles that pair with intact nonwolf - Infected that lose mate due to management - Infected that lose mate naturally - Infected whose mate is sterilized - Infected whose mate is displaced by wolf - Infecteds that die
Immune (wolf, Z_w) next year =	Immune (wolf) this year + Susceptibles that pair with a wolf + Infecteds whose mate is displaced by wolf - Immune (wolf) who lose mate naturally - Immunes (wolf) that die
Immune (hybrid, Z_h) next year =	Immune (hybrid) this year + Infecteds whose mate is sterilized - Immunes (hybrid) that lose mate naturally - Immunes (hybrid) that lose mate due to mgmt - Immunes (hybrid) that die
Infectious (I) next year =	Infectious this year + new two year olds from Infectious + new two year olds from Infected - Infectious that die due to management - Infectious that die naturally

Table 2. The introgression model translated into equations using symbols to define inputs and outflows for each compartment.

$$X_{t+1} = X_t + (G_t{*}s_{w,t}) + (\gamma_n{*}Z_{w,t}) + (\gamma_n{*}Z_{h,t}) + (\gamma_m{*}Z_{h,t}) + (c_n{*}Y_t) + (c_m{*}Y_t) - (b{*}X_t) - (\beta{*}X_t) - (\mu{*}X_t)$$

$$Y_{t+1} = Y_t + (\beta{*}X_t) - (c_m{*}Y_t) - (c_n{*}Y_t) - (\nu_s{*}Y_t) - (\nu_d{*}Y_t) - (\mu{*}Y_t)$$

$$Z_{w,t+1} = Z_{w,t} + (b{*}X_t) + (\nu_d{*}Y_t) - (\gamma_n{*}Z_{w,t}) - (\mu{*}Z_{w,t})$$

$$Z_{h,t+1} = Z_{h,t} + (\nu_s{*}Y_t) + (\gamma_n{*}Z_{h,t}) - (\gamma_m{*}Z_{h,t}) - (\mu{*}Z_{h,t})$$

$$I_{t+1} = I_t + (G_{n,t}{*}s_n) + (G_{h,t}{*}s_h) - (\mu{*}I) - (\mu_m{*}I_t)$$

Table 3. Parameter table. This table defines the parameters, the abbreviation (Abb) used in the model, an estimate (Est) of the parameter, the standard deviation (SD) of that estimate, and how the estimate was obtained.

Parameter	Abb	Est	SD	How obtained
Birth rate for red wolves (#pups produced/total # wolf pairs)	a_w	2.77	0.63	Estimated from data on litter sizes
Birth rate for hybrids	a_h	3.88	3.17	Estimated from data on litter sizes
Birth rate for non-wolves	a_n	3.88	3.17	Assumed same as birth rate of hybrids
Rate of red wolf pair formation	b	0.22	0.12	Estimated from data on composition of breeding pairs
Natural mortality rate of infectious mate	c_n	0.22		[1]Estimated from monitoring data by another researcher
Management removal rate of infectious mate	c_m	0.32	0.42	Estimated from data on composition of breeding pairs
Survival rate of wolf pups to yearlings	s_{wp}	0.68		[1]Estimated from monitoring data by another researcher
Survival rate of wolf yearlings to two year olds	s_{wy}	0.79		[1]Estimated from monitoring data by another researcher
Survival rate of hybrid pups to yearlings	s_{hp}	0.68		Without intervention, assumed same as wolf
Survival rate of hybrid yearlings to two year olds	s_{hy}	0.79		Without intervention, assumed same as wolf
Survival rate of non-wolf pups to yearlings	s_{np}	0.68		Without intervention, assumed same as wolf
Survival rate of non-wolf yearlings to two year olds	s_{ny}	0.79		Without intervention, assumed same as wolf
Loss of immunity (loss of mate due to natural cause)	γ_n	0.22		[1]Estimated from monitoring data by another researcher
Loss of immunity (loss of mate due to management action)	γ_m	0.05	0.11	Estimated from data on composition of breeding pairs
Natural mortality rate	μ	0.22		[1]Estimated from monitoring data by another researcher
Mortality due to management	μ_m	0.64	0.18	Estimated from trapping and disposition data
Recovery rate due to displacement	ν_d	0.02	0.03	Estimated from data on composition of breeding pairs
Recovery rate due to sterilization	ν_s	0.21		[2]Estimated from data on composition of breeding pairs
Effective contact rate	β	0.11	0.09	Estimated from data on composition of breeding pairs

[1]Dennis Murray, personal communication

[2]The estimate of ν_s and μ_m were adjusted so that the proportion of individuals leaving the infected and infectious categories, respectively, did not exceed 1.0. Because the estimates represent averages for many years, these averages did not necessarily sum to 1.0. This adjustment was necessary to keep more individuals from leaving the category than existed in the category. The elasticity analysis showed little if any elasticity to ν_s , and μ_m was adjusted to account for the presence of undetected individuals.

Table 4. Estimates for each parameter by year and the overall mean and standard deviation as calculated from the recovery program data.

	a_w		a_h		b	β	c_m	γ_m	μ_m	ν_d	ν_s
Year	Number of Wolf Litters	Average Litter Size	Number of Hybrid Litters	Average Litter Size	Rate of Wolf Pair Formation	Effective Contact Rate	Infectious Mates Removed	Sterile Mates Removed	Infectious Individuals Removed*	Displacements	Infectious Mates Sterilized*
1999	11	2.82	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
2000	10	3.40	n/a	n/a	0.11	0.17	0.00	0.00	0.52	0.00	0.38
2001	15	2.33	n/a	n/a	0.22	0.16	0.13	0.00	0.88	0.09	0.63
2002	11	3.64	3	3.00	0.11	0.26	0.00	0.30	0.82	0.00	0.83
2003	22	1.77	1	5.00	0.42	0.00	0.80	0.00	0.94	0.00	0.40
2004	20	2.65	0	0.00	0.35	0.03	1.00	0.00	1.00	0.00	1.00
2005	15	2.73	2	7.50	0.13	0.05	0.00	0.00	1.00	0.00	1.00
Overall	104	2.76	6	3.88	0.22	0.11	0.32	0.05	0.86	0.02	0.71
Std Dev		0.63		3.17	0.12	0.09	0.42	0.11	0.16	0.03	0.26

*The estimate of v_s and μ_m were adjusted so that the proportion of individuals leaving the infected and infectious categories, respectively, did not exceed 1.0. Because the estimates represent averages for many years, these averages did not necessarily sum to 1.0. An elasticity analysis showed little if any elasticity to v_s , and μ_m was adjusted to account for the presence of undetected individuals.

Table 5. The Leslie matrix used for elasticity analysis of impact of parameters on population growth rate, λ.

	Wolf Pups	Wolf Yearlings	Susceptibles	Infected	Immune Wolf	Immune Sterile	Infectious	Infected Pups	Infected Yearlings	Infectious Pups	Infectious Yearlings
Wolf Pups	-	-	-	-	a_w	-	-	-	-	-	-
Wolf Yearlings	S_{wp}	-	-	-	-	-	-	-	-	-	-
Susceptibles	-	S_{wy}	$1-\beta-b-\mu$	c_n+c_m	γ_n	γ_m	-	-	-	-	-
Infected	-	-	β	$1-c_n-c_m-\nu_d-\nu_s-\mu$	-	-	-	-	-	-	-
Immune Wolf	-	-	b	ν_d	$1-\gamma_n-\mu$	-	-	-	-	-	-
Immune Sterile	-	-	-	ν_s	-	$1-\gamma_m-\mu$	-	-	-	-	-
Infectious	-	-	-	-	-	-	$1-\mu-\mu_m$	-	S_{hy}	-	S_{ny}
Infected Pups	-	-	-	a_h	-	-	-	-	-	-	-
Infected Yearlings	-	-	-	-	-	-	-	S_{hp}	-	-	-
Infectious Pups	-	-	-	-	-	-	a_n	-	-	-	-
Infectious Yearlings	-	-	-	-	-	-	-	-	-	S_{np}	-

Table 6. Summary of parameter estimates used in each of 4 scenarios in an elasticity analysis of the population matrix. Scenario 1 represents no den work or sterilization. Scenario 2 represents den work but no sterilization. Scenario 3 represents sterilization but no den work. Scenario 4 represents the use of both den work and sterilization as management strategies.

		Estimate Used			
Parameter	**Abbrev**	**Scenario 1**	**Scenario 2**	**Scenario 3**	**Scenario 4**
Birth rate for red wolves (#pups produced/total # wolf pairs)	a_w	2.77	2.77	2.77	2.77
Birth rate for hybrids	a_h	3.88	3.88	1.00	1.00
Birth rate for non-wolves	a_n	3.88	3.88	1.00	1.00
Rate of red wolf pair formation	b	0.22	0.22	0.22	0.22
Natural mortality rate of infectious mate	c_n	0.22	0.22	0.22	0.22
Management removal rate of infectious mate	c_m	0.32	0.32	0.32	0.32
Survival rate of wolf pups to yearlings	s_{wp}	0.68	0.68	0.68	0.68
Survival rate of wolf yearlings to two year olds	s_{wy}	0.79	0.79	0.79	0.79
Survival rate of hybrid pups to yearlings	s_{hp}	0.68	0.05	0.68	0.05
Survival rate of hybrid yearlings to two year olds	s_{hy}	0.79	0.25	0.79	0.25
Survival rate of non-wolf pups to yearlings	s_{np}	0.68	0.05	0.68	0.05
Survival rate of non-wolf yearlings to two year olds	s_{ny}	0.79	0.25	0.79	0.25
Loss of immunity (loss of mate due to natural cause)	γ_n	0.22	0.22	0.22	0.22
Loss of immunity (loss of mate due to management action)	γ_m	0.05	0.05	0.05	0.05
Natural mortality rate	μ	0.22	0.22	0.22	0.22
Mortality due to management	μ_m	0.64	0.64	0.64	0.64
Recovery rate due to displacement	ν_d	0.02	0.02	0.02	0.02
Recovery rate due to sterilization	ν_s	0	0	0.21	0.21
Effective contact rate	β	0.11	0.11	0.11	0.11

Table 7. Summary of elasticities for each parameter under each scenario summarized in Table 6. Scenario 1 represents no den work or sterilization. Scenario 2 represents den work but no sterilization. Scenario 3 represents sterilization but no den work. Scenario 4 represents the use of both den work and sterilization as management strategies. Since they reflect the same parameter under different circumstances, c_n, γ_n, and μ were all treated as one parameter, μ, for elasticity analysis.

		Elasticity			
Parameter	**Abbrev**	**Scenario 1**	**Scenario 2**	**Scenario 3**	**Scenario 4**
Birth rate for red wolves (#pups produced/total # wolf pairs)	a_w	0	0.147	0.149	0.149
Birth rate for hybrids	a_h	0	0	0	0
Birth rate for non-wolves	a_n	0.321	0	0	0
Rate of red wolf pair formation	b	0	0.198	0.196	0.187
Natural mortality rate of infectious mate	c_n	-	-	-	-
Management removal rate of infectious mate	c_m	0	0.007	0.004	0.005
Survival rate of wolf pups to yearlings	s_{wp}	0	0.147	0.149	0.149
Survival rate of wolf yearlings to two year olds	s_{wy}	0	0.147	0.149	0.149
Survival rate of hybrid pups to yearlings	s_{hp}	0	0	0	0
Survival rate of hybrid yearlings to two year olds	s_{hy}	0	0	0	0
Survival rate of non-wolf pups to yearlings	s_{np}	0.321	0	0	0
Survival rate of non-wolf yearlings to two year olds	s_{ny}	0.321	0	0	0
Loss of immunity (loss of mate due to natural cause)	γ_n	-	-	-	-
Loss of immunity (loss of mate due to management action)	γ_m	0	0	0.001	0.001
Natural mortality rate	μ	0.008	0.074	0.061	0.072
Mortality due to management	μ_m	0.022	0	0	0
Recovery rate due to displacement	ν_d	0	0.002	0.002	0.002
Recovery rate due to sterilization	ν_s	0	0.001	0.001	0.001
Effective contact rate	β	0	0.035	0.030	0.032

Table 8. Summary of the stable category distribution and population growth rate (λ) reached under each of 4 scenarios analyzed during an elasticity analysis. Scenario 1 represents no den work or sterilization. Scenario 2 represents den work but no sterilization. Scenario 3 represents sterilization but no den work. Scenario 4 represents the use of both den work and sterilization as management strategies. Scenario 5 represents the use of both den work and sterilization as management strategies (i.e., scenario 4) as well as density-dependence of b and β.

	Scenario 1	**Scenario 2**	**Scenario 3**	**Scenario 4**	**Scenario 5***
Wolf Pups	0	0.28	0.28	0.31	0.36
Wolf Yearling	0	0.17	0.17	0.19	0.21
Susceptibles	0	0.27	0.28	0.30	0.28
Infected	0	0.03	0.03	0.03	0
Immune Wolf	0	0.11	0.11	0.12	0.15
Immune Sterile	0	0	0.01	0.01	0
Infectious	0.19	0	0.03	0	0
Hybrid pups	0	0.12	0.03	0.03	0
Hybrid yearlings	0	0.01	0.02	0	0
Nonwolf pups	0.48	0.01	0.03	0	0
Nonwolf yearlings	0.33	0	0.02	0	0
λ (wolf)	1.11	1.12	1.12	1.12	1.16
λ (nonwolf)	1.59	1.12	1.10	0.97	0.84

APPENDICES

Appendix A. Summary of data on sterilized non-wolf canids in the red wolf recovery area, North Carolina, 1999-2004.

ID	Sex	Date Sterilized	Fate	Member of a Breeding Pair?	Fate Date	Survival Days	Currently Monitored?
20094	F	6/26/1999	Unknown COD		10/1/2000	463	No
20132	F	3/17/2000	Gunshot	2000, 2001	5/30/2001	439	No
20134	F	3/25/2000	Gunshot (Suspected)		12/28/2000	278	No
20136	F	4/4/2000	Intraspecific		6/9/2000	66	No
20137	M	4/8/2000	Euthanized		5/9/2002	761	No
20138	M	4/11/2000	Lost Contact		3/3/2003	1056	No
20170	M	1/25/2001	Current	2003, 2004	**8/1/2004**	1284	Yes
20181	M	5/8/2001	Euthanized		2/7/2003	640	No
20189	F	6/18/2001	Lost Contact	2002, 2003	7/28/2003	770	No
20192	F	9/11/2001	Intraspecific	2002	11/8/2002	423	No
20198	M	1/22/2002	Gunshot	2002	12/18/2002	330	No
20199	F	2/5/2002	Euthanized	2002	5/9/2002	93	No
20206	M	4/2/2002	Current	2004	**8/1/2004**	852	Yes
20243	M	2/10/2002	Current		**8/1/2004**	903	Yes
20255	M	6/16/2003	Euthanized		10/18/2003	124	No
30081	M	5/25/1999	HBC		1/16/2000	236	No
30083	M	6/11/1999	Unknown COD	2000	12/13/2000	551	No
30093	M	6/22/1999	Gunshot		2/28/2000	251	No
30113	F	10/26/1999	Euthanized		7/19/2001	632	No
30129	F	3/9/2000	Euthanized	2002	2/27/2003	1085	No
30130	M	3/7/2000	Euthanized	2000, 2001, 2002	7/31/2002	876	No
30133	M	2/26/2000	Mange	2000	4/20/2001	419	No
30139	F	4/14/2000	Heartworms	2000, 2001, 2002	11/14/2002	944	No
30140	F	4/14/2000	Euthanized	2000, 2001, 2002	5/4/2002	750	No
30141	M	4/27/2000	Current	2001, 2002	**8/1/2004**	1557	Yes
30145	M	11/16/2001	Gunshot	2000	12/13/2003	757	No
30158	F	5/23/2000	Gunshot		12/1/2001	557	No

Appendix A (continued).

ID	Sex	Date Sterilized	Fate	Member of a Breeding Pair	Fate Date	Survival Days	Currently Monitored?
30159	F	7/24/2000	Lost Contact		12/28/2000	157	No
30161	F	8/29/2000	Gunshot (Suspected)		2/4/2001	159	No
30172	M	2/20/2001	Gunshot	2001	1/14/2002	328	No
30182	M	5/9/2001	Euthanized	2003	7/23/2004	1171	No
30183	F	3/27/2001	Euthanized		5/4/2002	403	No
30236	M	10/15/2002	Current		**8/1/2004**	656	Yes
30237	F	11/18/2002	Euthanized		4/1/2004	500	No
30240	M	12/4/2002	Current		**8/1/2004**	606	Yes
30248	M	3/15/2003	Euthanized		6/30/2004	473	No
30262	M	1/16/2004	Current		**8/1/2004**	198	Yes
30263	M	2/2/2004	Current		**8/1/2004**	181	Yes
30273	M	3/30/2004	Lost Contact		5/11/2004	42	No
30274	M	4/1/2004	Current		**8/1/2004**	122	Yes
30275	M	4/1/2004	Current		**8/1/2004**	122	Yes
30277	F	4/6/2004	Current		**8/1/2004**	117	Yes
30905	F	5/21/1999	Euthanized	2000, 2001, 2002, 2004	4/22/2004	1798	No
40163	F	9/11/2000	Unknown COD	2001	5/23/2002	619	No
40196	M	10/23/2001	Euthanized	2002, 2003, 2004	5/6/2004	926	No
50131	F	3/10/2000	Euthanized	2002	7/23/2002	865	No
50173	F	2/20/2001	Current	2001, 2004	**8/1/2004**	1258	Yes
50180	M	4/9/2001	Euthanized		7/19/2002	466	No
50232	F	10/23/2002	Current	2003, 2004	**8/1/2004**	648	Yes

Appendix B. Summary data of sterilized animals in the red wolf recovery area, North Carolina, 1999 -2004.

Sex	Number
M	27
F	22

Year of Sterilization	Number
1999	6
2000	16
2001	11
2002	8
2003	2
2004	6

	All	Euthanized	Current
Ave survival days	590	723	654
Range	42 to 1798	93 to 1798	117 to 1557
Median	551	695	648

Appendix C. Average distance, in meters, to road by individual and type of telemetry location in the red wolf recovery area, North Carolina, 1999-2004.

ID	n (Aerial)	Distance (Aerial)	n (Ground)	Distance (Ground)
10331	12	224.38	17	155.87
10505	29	310.28	37	224.52
10508	39	284.12	163	236.14
10582	25	233.80		
10593	10	128.73		
10647	1	924.02		
10662	61	1575.29	28	1315.72
10673	37	290.48		
10674	22	389.92	1	29.72
10675	59	247.06	25	240.21
10746	52	206.79	344	229.47
10747	54	1728.42	25	1391.60
10748			4	287.36
10752	7	370.27		
10756	56	229.34	13	250.43
10759			1	241.40
10768	51	202.86	199	243.37
10771	31	363.66		
10781	24	417.19		
10795	57	383.01	12	272.34
10797	26	149.15	51	186.30
10798	37	290.85	26	290.52
10799	3	559.30		
10803	1	181.86		
10808	40	375.65		
10815	12	180.50		
10852	1	20.21		
10874	53	263.05	234	224.44
10878	9	336.11		
10880	47	204.49		
10884	9	248.06		
10888	21	315.61	6	150.16
10889	8	212.64		
10890	3	630.07		
10894	17	403.05		
10900	5	255.24		
10904	74	205.55	384	235.21
10907	5	331.78		
10929	7	403.33		
10930	22	234.76	2	258.41
10933	3	155.95		
10944	3	218.51		

Appendix C (continued).

ID	n (Aerial)	Distance (Aerial)	n (Ground)	Distance (Ground)
10945	1	559.02		
10946	141	308.20	5	309.37
10947	100	225.65	68	188.62
10948	44	413.28		
10949	39	180.55	275	236.15
10950	19	402.82		
10951	5	524.25	1	116.29
10952	63	377.89	14	368.04
10969	54	298.39	88	202.43
10970	7	618.03		
10973	8	316.48	2	215.14
10977	66	273.03	13	191.61
10978	86	212.06	200	242.97
10979	26	163.83		
10980	126	252.66	5	195.42
10982	4	231.47		
10985	60	270.96	16	255.17
10986	7	228.57		
10987	35	223.02	382	227.43
10992	54	305.43	119	286.03
10995	3	66.15		
10998	18	316.23		
11001	92	303.98	210	243.06
11022	10	192.13		
11026	3	343.08		
11027	3	161.03		
11028	55	365.89	11	285.12
11030	46	417.50	13	420.04
11031	25	259.75	84	219.12
11032	35	244.71	73	186.09
11033	9	584.78		
11034	34	310.25	1	408.56
11035	106	266.80	163	226.15
11036	62	495.45		
11037	71	504.95	6	206.75
11038	15	247.20	4	189.70
11039	68	313.93	84	193.75
11040	13	260.14	2	120.53
11042	2	359.25		
11043	1	268.39		
11044	45	292.19	1	433.48
11045	77	367.50	288	323.14
11048	70	365.73	240	317.32
11049	24	354.92		

Appendix C (continued).

ID	n (Aerial)	Distance (Aerial)	n (Ground)	Distance (Ground)
11051	83	241.14	95	199.64
11052	19	227.94	10	202.05
11053	62	480.42	15	332.29
11055	12	398.33		
11059	35	379.20	269	286.24
11068	41	359.22		
11069	33	411.95	4	111.32
11070	7	285.88	2	477.98
11071	4	186.15		
11073	55	428.32		
11074	5	222.82		
11075	8	270.33		
11080	20	744.29		
11085	85	318.34	64	225.98
11086	3	126.00	8	136.88
11087	11	306.26	2	128.07
11100	33	341.45		
11101	10	300.83		
11102	7	525.92		
11104	14	198.81	69	204.11
11105	53	527.93	11	640.59
11106	19	478.24		
11107	14	415.51		
11108	44	540.37		
11109	16	443.55	1	139.37
11110	1	1310.66		
11112	57	270.29	13	207.80
11114	16	328.12	7	240.35
11115	19	246.37	8	185.30
11117	2	58.35		
11132	21	256.78	157	258.71
11133	1	320.73	33	222.59
11134	4	432.47	22	143.14
11135	8	308.97	74	299.08
11136	29	336.26	105	323.38
11140	16	300.03		
11148	58	431.77	20	308.20
11149	38	332.22	33	210.58
11152	10	610.08		
11162	34	401.24	11	261.46
11163	54	372.42	118	309.05
11164	17	217.46	1	34.71
11165	57	264.40	34	153.48
11166	23	260.84	143	214.69

Appendix C (continued).

ID	n (Aerial)	Distance (Aerial)	n (Ground)	Distance (Ground)
11167	14	243.07	2	121.37
11168	46	235.80	110	213.12
11169	50	431.30	10	202.12
11170	30	312.08	139	229.54
11171	8	374.06	20	214.28
11173	2	472.63	5	222.71
11176	1	455.51	5	254.12
11177	11	227.67	2	93.72
11178	6	209.44		
11180	13	423.29		
11181	5	234.86		
11183	9	348.87	67	240.43
11184	24	416.53	3	206.35
11185	39	310.37	26	160.55
11186	20	612.32		
11187	1	443.02		
11188	6	366.69	3	283.57
11190	27	396.33	1	199.57
11199	14	311.66	69	212.36
11202	10	296.32	73	225.83
11205	11	432.08	49	256.68
11207	44	313.78	5	214.80
11233	3	297.33	59	133.79
11234	7	289.28	113	179.87
11235	4	345.81	88	242.72
11236	4	170.04	61	252.92
11237	10	354.41	49	275.43
11243	1	358.19		
11259	1	427.22		
11293			21	235.56
11294	2	280.68		
11295	2	1047.30	10	232.91
11296			22	200.81
20075	12	186.51		
20076	8	561.24		
20094	7	138.25		
20132	3	305.61		
20134	2	351.66		
20137	26	341.96	48	241.37
20138	42	313.87	81	251.81
20170	23	432.20		
20181	18	213.58	126	215.08
20189	16	392.27		
20192	15	329.43		

Appendix C (continued).

ID	n (Aerial)	Distance (Aerial)	n (Ground)	Distance (Ground)
20198	13	301.49		
20199	3	173.44	15	323.87
20206	20	510.59		
20243	11	351.28		
20255	25	320.74	7	221.07
30074	7	735.16	3	541.74
30081	6	1167.25		
30083	8	1190.85		
30093	6	377.02		
30113	5	644.14	1	36.41
30119	6	179.45		
30120	4	308.25		
30121	21	338.08		
30124	2	170.78		
30126	43	294.62		
30129	38	294.42		
30130	22	484.89		
30133	16	302.75		
30139			123	324.73
30140	5	402.96		
30141	2	554.61	146	300.35
30142			1	224.12
30143	4	214.57		
30144	3	235.28		
30145	18	467.04		
30155	17	215.49		
30156	2	115.73	3	101.67
30157	5	138.67		
30158	5	435.12		
30159	4	315.67		
30161	6	273.51		
30172	3	210.67		
30182	64	304.37	3	67.07
30183	6	530.55		
30203	103	277.54	5	235.61
30205	25	360.81	11	394.35
30212	1	320.03		
30214	49	202.29	31	221.66
30215	24	207.61	134	214.33
30219	1	320.03		
30236	19	463.80		
30237	37	329.23	2	617.09
30240	13	351.81		
30248	19	335.43		

Appendix C (continued).

ID	n (Aerial)l	Distance (Aerial)	n (Ground)	Distance (Ground)
30905	16	1332.68		
40163	13	476.27		
40196	8	298.14		
50131	48	400.21	67	249.38
50173	8	718.87		
50180	29	313.70	86	193.57
50232	8	294.84		

Appendix D. Distance to road for aerial locations of adult canids (minimum 5 locations each season) in the red wolf recovery area, North Carolina, 1999-2004.

ID	Year	Sex	Age	Species	n (season1)	Distance (season1)	n (season2)	Distance (season2)	n (season3)	Distance (season3)	n (season4)	Distance (season4)
10675	1999	1	3	1	5	167.77	14	193.43	13	244.09	12	154.51
10880	1999	1	3	1	11	113.87	18	222.15	11	261.54	7	211.81
10947	2003	1	3	1	12	267.38	10	192.88	16	296.98	7	243.04
10980	2002	1	3	1	5	165.33	6	226.87	8	279.86	6	273.38
11032	2001	2	3	1	6	252.43	6	318.81	5	206.12	7	247.17
11035	2003	2	3	1	6	340.14	10	266.81	5	287.40	6	165.74
11037	2003	2	3	1	10	656.82	8	263.04	7	373.29	10	654.24
11039	2002	2	3	1	14	479.39	8	217.65	8	236.93	6	273.38
11045	2001	2	3	1	10	324.20	6	266.78	7	335.77	8	478.60
11048	2001	1	3	1	10	322.69	5	301.45	7	360.10	8	478.60
11051	2002	2	3	1	10	274.91	20	240.74	6	252.88	7	216.25
11069	2002	1	3	1	5	401.33	12	278.57	6	828.80	6	370.91
11085	2002	2	3	1	20	406.95	16	302.84	10	332.66	7	304.34
11165	2003	2	3	1	15	233.50	12	285.95	16	276.72	11	262.81
11168	2002	1	4	1	8	208.36	5	201.29	7	280.60	8	263.72
30126	1999	1	3	3	6	410.73	15	277.08	12	307.32	10	236.02
30203	2000	2	3	3	5	252.13	8	404.23	11	345.66	13	272.89
30237	2003	2	4	3	8	402.75	11	233.27	13	370.58	5	315.22

Sex: 1 = male
2 = female

Species: 1 = wolf
2 = non-wolf

Age: 1 = pup
2 = juvenile
3 = adult
4 = adult, but exact age unknown

Appendix E. Distance to road for aerial locations of juvenile canids (minimum 1 location each season) in the red wolf recovery area, North Carolina, 1999-2004..

ID	Year	Sex	Age	Species	nseas1	distseas1	nseas2	distseas2	nseas3	distseas3	nseas4	distseas4
10977	1999	1	2	1	6	147.92	13	261.36	11	250.78	13	387.12
10986	2000	2	2	1	1	163.37	2	245.53	3	302.46	1	38.19
11068	2001	1	2	1	1	138.28	1	255.29	1	331.70	1	368.24
11069	2001	1	2	1	1	138.28	1	255.29	1	331.70	1	321.46
11073	2001	2	2	1	1	136.11	2	214.70	1	331.70	4	867.35
11074	2001	1	2	1	1	136.11	1	255.29	1	331.70	2	195.49
11075	2001	2	2	1	1	136.11	2	206.95	1	331.70	2	344.85
11085	2001	2	2	1	3	393.22	4	314.66	1	323.34	4	269.64
11087	2001	1	2	1	2	316.00	4	421.43	1	301.23	2	275.30
11106	2001	1	2	1	6	608.08	7	438.12	4	480.86	1	356.17
11107	2001	1	2	1	3	530.37	2	418.00	1	482.63	7	379.44
11112	2001	1	2	1	3	158.64	3	146.09	1	351.57	7	317.27
11114	2002	2	2	1	2	324.89	1	394.46	3	216.92	9	363.14
11162	2002	2	2	1	9	397.79	13	472.23	1	252.64	2	295.43
11180	2003	2	2	1	5	271.14	4	385.56	2	438.95	1	1417.75
11184	2003	1	2	1	9	535.14	5	228.39	7	461.80	3	268.66
11185	2003	1	2	1	2	133.57	5	340.53	18	333.58	14	295.01
11186	2003	1	2	1	1	839.54	1	308.10	7	550.02	11	658.96
11190	2003	2	2	1	4	757.81	3	457.90	6	336.66	11	299.77
11199	2003	1	2	1	1	301.21	6	279.27	2	329.66	3	331.72
11202	2003	2	2	1	1	301.21	5	274.79	2	329.66	2	314.37
11205	2003	1	2	1	1	110.90	2	388.91	1	535.85	4	512.52
11237	2003	1	2	1	3	232.79	1	543.64	1	535.85	4	410.63
30129	2000	2	2	3	1	17.65	1	180.69	5	290.72	5	463.77

Sex: 1 = male
2 = female

Species: 1 = wolf
2 = non-wolf

Age: 1 = pup
2 = juvenile
3 = adult
4 = adult, but exact age unknown

Appendix F. Home range characteristics of canids in the red wolf recovery area, North Carolina, 1999-2004.

Year	ID	Species	Sex	Age	Number of Locations	Area 95	Perim 95	Edge/Area 95	Log Area 95	Log Perim 95	Log Edge/Area 95
1999	10582	1	F	3	25	19598	26967	0.73	9.9	10.2	0.97
1999	10756	1	F	3	22	84093	54296	1.55	11.3	10.9	1.04
1999	10880	1	F	3	50	73811	57075	1.29	11.2	11.0	1.02
1999	10977	1	M	2	47	52116	44605	1.17	10.9	10.7	1.01
1999	10985	1	F	3	40	57095	66165	0.86	11.0	11.1	0.99
1999	30126	2	M	3	43	27516	43778	0.63	10.2	10.7	0.96
2000	10331	1	M	3	21	64554	53021	1.22	11.1	10.9	1.02
2000	10662	1	M	3	24	67332	56298	1.20	11.1	10.9	1.02
2000	10746	1	M	3	50	26146	31027	0.84	10.2	10.3	0.98
2000	10747	1	F	3	22	58190	59771	0.97	11.0	11.0	1.00
2000	10904	1	F	3	63	9952	19970	0.50	9.2	9.9	0.93
2000	10946	1	M	3	30	272862	125446	2.18	12.5	11.7	1.07
2000	10980	1	M	3	36	186541	104419	1.79	12.1	11.6	1.05
2000	30203	2	F	3	40	213256	122388	1.74	12.3	11.7	1.05
2001	10505	1	F	3	45	12406	28120	0.44	9.4	10.2	0.92
2001	10675	1	M	3	25	17291	30915	0.56	9.8	10.3	0.94
2001	10797	1	F	3	20	7964	19241	0.41	9.0	9.9	0.91
2001	10798	1	F	3	20	63316	45320	1.40	11.1	10.7	1.03
2001	10808	1	F	3	20	55767	49747	1.12	10.9	10.8	1.01
2001	10874	1	M	3	67	39497	34870	1.13	10.6	10.5	1.01
2001	10949	1	F	3	89	19190	28670	0.67	9.9	10.3	0.96
2001	10969	1	M	3	69	24623	29632	0.83	10.1	10.3	0.98

Species: 1 = wolf
2 = non-wolf

Age: 2 = juvenile
3 = adult

Appendix F (continued).

Year	ID	Species	Sex	Age	Number of Locations	Area 95	Perim 95	Edge/Area 95	Log Area 95	Log Perim 95	Log Edge/Area 95
2001	11028	1	F	3	23	80512	60491	1.33	11.3	11.0	1.03
2001	11032	1	M	3	74	48002	50829	0.94	10.8	10.8	0.99
2001	11039	1	F	3	53	100110	65394	1.53	11.5	11.1	1.04
2001	11045	1	F	3	119	56832	55789	1.02	10.9	10.9	1.00
2001	11085	1	F	2	44	52850	50792	1.04	10.9	10.8	1.00
2001	11104	1	F	3	72	42171	36590	1.15	10.6	10.5	1.01
2001	11134	1	F	2	21	13910	21560	0.65	9.5	10.0	0.96
2001	11135	1	M	2	22	28819	37652	0.77	10.3	10.5	0.97
2001	11148	1	F	2	20	14986	26442	0.57	9.6	10.2	0.94
2001	20138	2	M	3	48	68014	68299	1.00	11.1	11.1	1.00
2001	20181	2	M	3	40	23356	26630	0.88	10.1	10.2	0.99
2001	30129	2	F	3	20	222429	80189	2.77	12.3	11.3	1.09
2001	30139	2	F	3	59	7602	18933	0.40	8.9	9.8	0.91
2001	50131	2	F	3	52	102598	58851	1.74	11.5	11.0	1.05
2001	50180	2	M	3	68	61955	49437	1.25	11.0	10.8	1.02
2002	10768	1	M	3	81	31577	41236	0.77	10.4	10.6	0.97
2002	10795	1	M	3	29	83579	71271	1.17	11.3	11.2	1.01
2002	10948	1	M	3	38	194442	78319	2.48	12.2	11.3	1.08
2002	10952	1	F	3	36	46015	46132	1.00	10.7	10.7	1.00
2002	10978	1	F	3	93	27828	36547	0.76	10.2	10.5	0.97
2002	10992	1	M	3	28	24650	33582	0.73	10.1	10.4	0.97
2002	11031	1	M	3	24	19114	28747	0.66	9.9	10.3	0.96
2002	11035	1	F	3	102	109576	89206	1.23	11.6	11.4	1.02
2002	11036	1	F	3	26	26656	32766	0.81	10.2	10.4	0.98
2002	11051	1	F	3	73	96240	60151	1.60	11.5	11.0	1.04

Appendix F (continued).

Year	ID	Species	Sex	Age	Number of Locations	Area 95	Perim 95	Edge/Area 95	Log Area 95	Log Perim 95	Log Edge/Area 95
2002	11053	1	M	3	34	63305	53270	1.19	11.1	10.9	1.02
2002	11069	1	M	3	33	121073	76591	1.58	11.7	11.2	1.04
2002	11100	1	F	3	27	106929	55207	1.94	11.6	10.9	1.06
2002	11105	1	F	3	37	141368	91422	1.55	11.9	11.4	1.04
2002	11132	1	F	2	82	20522	24305	0.84	9.9	10.1	0.98
2002	11133	1	M	2	21	36171	33071	1.09	10.5	10.4	1.01
2002	11163	1	F	2	84	9377	20098	0.47	9.1	9.9	0.92
2002	11164	1	M	2	20	106622	73834	1.44	11.6	11.2	1.03
2002	11168	1	M	3	83	31236	35771	0.87	10.3	10.5	0.99
2002	11170	1	F	3	68	25935	35296	0.73	10.2	10.5	0.97
2002	20137	2	M	3	24	28877	28241	1.02	10.3	10.2	1.00
2002	20199	2	F	3	20	59677	54646	1.09	11.0	10.9	1.01
2002	30205	2	M	3	21	23010	32681	0.70	10.0	10.4	0.97
2002	30214	2	F	3	42	25058	26994	0.93	10.1	10.2	0.99
2002	30215	2	M	3	60	13832	22613	0.61	9.5	10.0	0.95
2003	10508	1	F	3	86	7891	25136	0.31	9.0	10.1	0.89
2003	10947	1	M	3	86	17435	26676	0.65	9.8	10.2	0.96
2003	10987	1	M	3	133	16131	21195	0.76	9.7	10.0	0.97
2003	11001	1	M	3	118	23720	32887	0.72	10.1	10.4	0.97
2003	11037	1	F	3	35	38422	44677	0.86	10.6	10.7	0.99
2003	11048	1	M	3	128	27568	39018	0.71	10.2	10.6	0.97
2003	11059	1	F	3	62	9872	28641	0.34	9.2	10.3	0.90
2003	11108	1	M	3	22	52655	41551	1.27	10.9	10.6	1.02
2003	11112	1	M	3	27	65990	54293	1.22	11.1	10.9	1.02
2003	11136	1	M	3	60	55162	43858	1.26	10.9	10.7	1.02

Appendix F (continued).

Year	ID	Species	Sex	Age	Number of Locations	Area 95	Perim 95	Edge/Area 95	Log Area 95	Log Perim 95	Log Edge/Area 95
2003	11165	1	F	2	82	116963	78477	1.49	11.7	11.3	1.04
2003	11166	1	M	3	129	51719	37797	1.37	10.9	10.5	1.03
2003	11169	1	M	3	21	24412	38655	0.63	10.1	10.6	0.96
2003	11171	1	M	2	24	40530	38623	1.05	10.6	10.6	1.00
2003	11183	1	M	2	74	63548	53362	1.19	11.1	10.9	1.02
2003	11184	1	M	2	21	216597	92132	2.35	12.3	11.4	1.07
2003	11185	1	M	2	44	173595	84717	2.05	12.1	11.3	1.06
2003	11199	1	M	2	77	56191	59032	0.95	10.9	11.0	1.00
2003	11202	1	F	2	82	55805	60283	0.93	10.9	11.0	0.99
2003	11205	1	M	2	56	27023	40694	0.66	10.2	10.6	0.96
2003	11207	1	F	2	32	118495	59822	1.98	11.7	11.0	1.06
2003	11233	1	F	2	50	12173	20327	0.60	9.4	9.9	0.95
2003	11234	1	F	2	103	20812	26777	0.78	9.9	10.2	0.98
2003	11235	1	F	2	83	11656	15283	0.76	9.4	9.6	0.97
2003	11236	1	M	2	55	9416	20237	0.47	9.2	9.9	0.92
2003	11237	1	M	2	49	30130	43605	0.69	10.3	10.7	0.97
2003	20255	2	M	3	23	42708	50361	0.85	10.7	10.8	0.98
2003	30141	2	M	3	24	6375	18198	0.35	8.8	9.8	0.89

Appendix G. Distance moved (meters) in 2-3 day intervals by canids in the red wolf recovery area, North Carolina, 1999-2004.

ID	Sex	Age	Species	Year	Log 2-3 Distance
10505	2	3	1	2001	9.98
10508	2	3	1	2002	6.36
10582	2	3	1	1999	7.49
10662	1	3	1	2002	6.41
10746	1	3	1	2003	6.47
10747	2	3	1	2000	8.72
10752	1	3	1	1999	9.11
10756	2	3	1	2000	8.62
10781	1	3	1	1999	9.09
10795	1	3	1	2003	8.98
10797	2	3	1	2000	7.78
10798	2	3	1	2001	9.29
10808	2	3	1	2001	7.59
10874	1	3	1	2002	5.52
10878	2	3	1	1999	7.35
10880	1	3	1	1999	8.60
10930	1	3	1	2000	8.36
10944	1	3	1	1999	7.65
10946	1	3	1	2000	9.15
10947	1	3	1	2002	7.94
10948	1	3	1	2002	8.46
10949	2	3	1	2000	8.25
10950	1	3	1	2001	8.32
10973	2	2	1	1999	8.86
10977	1	2	1	2000	8.79
10978	2	3	1	1999	8.03
10979	1	3	1	1999	7.09
10980	1	3	1	2001	10.37
10985	2	3	1	2001	8.22
10986	2	2	1	2000	8.16
10987	1	2	1	2000	7.91
10992	1	3	1	2001	10.02
10998	1	2	1	2000	8.22
11001	1	3	1	2002	8.34
11022	1	2	1	1999	6.62
11028	2	3	1	2001	8.50
11030	2	3	1	2003	8.25
11031	1	3	1	2001	7.50
11034	1	3	1	2002	8.51
11035	2	2	1	2000	7.39
11036	2	3	1	2003	6.76
11037	2	3	1	2002	4.58

Sex: 1 = male; 2 = female   Age: 2 = juvenile; 3 = adult   Species: 1 = wolf; 2 = non-wolf

Appendix G (continued).

ID	Sex	Age	Species	Year	Log 2-3 Distance
11038	2	3	1	2000	7.92
11039	2	3	1	2003	7.82
11044	2	3	1	2003	8.67
11045	2	3	1	2000	7.92
11048	1	3	1	2002	8.29
11051	2	3	1	2000	8.62
11052	1	3	1	2002	6.62
11053	1	3	1	2003	8.94
11055	2	3	1	2001	8.10
11069	1	3	1	2002	7.99
11073	2	3	1	2002	8.76
11080	1	3	1	2000	7.54
11085	2	3	1	2002	9.46
11100	2	3	1	2002	8.51
11102	1	3	1	2000	9.21
11105	1	2	1	2001	9.21
11106	1	2	1	2001	8.57
11107	1	2	1	2001	7.46
11108	1	3	1	2001	7.52
11109	2	3	1	2001	6.44
11112	1	3	1	2002	7.22
11114	2	2	1	2002	8.43
11115	1	3	1	2003	8.73
11117	1	3	1	2003	9.15
11132	2	3	1	2003	8.20
11140	2	2	1	2002	7.51
11148	2	2	1	2002	8.67
11149	1	2	1	2002	9.78
11152	2	3	1	2003	8.43
11163	2	3	1	2003	8.57
11164	1	2	1	2002	8.47
11165	2	3	1	2003	8.23
11166	1	2	1	2002	8.37
11167	1	3	1	2002	8.22
11168	1	3	1	2003	8.23
11169	1	3	1	2003	7.69
11171	1	2	1	2003	7.59
11173	2	2	1	2003	7.59
11178	1	2	1	2003	8.67
11180	2	2	1	2003	8.67
11184	1	2	1	2003	8.67
11185	1	2	1	2003	8.36
11186	1	2	1	2003	8.50

Appendix G (continued).

ID	Sex	Age	Species	Year	Log 2-3 Distance
11190	2	2	1	2003	7.42
11205	1	2	1	2003	8.98
11207	2	2	1	2003	8.33
11237	1	2	1	2003	8.01
20138	1	3	2	2002	8.36
20170	1	3	2	2001	9.95
20189	2	3	2	2002	7.48
20192	2	3	2	2002	8.83
20198	1	3	2	2002	9.55
20199	2	3	2	2002	7.83
20206	1	3	2	2003	7.97
20243	1	3	2	2003	8.91
20255	1	3	2	2003	8.81
30120	2	2	2	1999	7.48
30121	1	3	2	2000	6.48
30126	1	3	2	1999	7.72
30129	2	3	2	2001	9.66
30130	1	3	2	2002	7.69
30133	1	2	2	1999	7.83
30143	2	2	2	1999	5.65
30145	1	3	2	2003	7.98
30155	2	3	2	2000	7.73
30157	1	3	2	2000	9.26
30161	2	3	2	2000	10.19
30182	1	3	2	2000	6.56
30203	2	3	2	2000	8.95
30205	1	3	2	2003	8.64
30214	2	3	2	1999	7.81
30215	1	3	2	2002	7.33
30236	1	3	2	2002	8.17
30237	2	3	2	2003	8.41
30248	1	3	2	2003	7.73
50131	2	3	2	2002	7.95
50173	2	3	2	2003	6.87
50180	1	3	2	2001	8.72