January 2003

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Pages 272-288 in Mech, David L. and Luigi Boitani, eds. Wolves: behavior, ecology, and conservation. University of Chicago Press, 2003.

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"WOLFERS" IN NORTHEASTERN North Carolina were busy on February 5, 1768. Records from the Tyrrell County courthouse read:

> Giles Long and Thomas Wilkinson awarded one pound for a certified wolf scalp; Jeremiah Norman awarded two pounds for certified wolf and wild-cat scalps; Davenport Smithwick awarded one pound for a certified wolf-scalp.

Such was the nature of the war on the wolf: people killed them for money. The belief of the time held that the war was necessary because it was humankind's manifest destiny to tame the wilderness. And for the wilderness to be tame, the wolf had to be exterminated. The wolf was resourceful and hardy, but the wolfers persisted with increasingly sophisticated methods of killing. The war lasted 200 years, and the wolf lost.

History of the Red Wolf

In the late 1700s, naturalist William Bartram traveled throughout the southeastern United States. In his book *Travels* (Bartram 1791), he described the wolf he encountered in Florida:

> Observing a company of wolves (lupus niger) under a few trees, about a quarter of a mile from shore, we rode up towards them, they observing our approach, sat on their hinder parts until we came nearly within shot of them, when they trotted off towards the forests, but stopped again and looked at us, at about two hundred yards distance: we then whooped, and made a feint to pursue them; when they separated from each other, some stretching off into the plains, and others seeking covert in the groves on the shore: when we got to the trees we observed they had been feeding on the carcase of a horse. The wolves of Florida are larger than a dog, and are perfectly black, except the females, which have a white spot on the breast; but they are not so large as the wolves of Canada and Pennsylvania, which are of a yellowish brown colour.

About 60 years later, researchers concluded that the Florida wolf inhabited other southeastern states and that it was structurally different from wolves inhabiting the rest of North America (Audubon and Bachman 1851). Goldman (1944) supported this conclusion after examining a large series of wolf specimens from the southeastern United States. He concluded that all the animals shared important cranial and dental characteristics and assigned them to one species, the red wolf *(Canis rufus)*, which has both red and black phases.

Even though the red wolf was first described during the eighteenth century, the species' natural history remained poorly understood until the latter part of the twentieth century. This lack of understanding was largely due to a lack of interest in studying the species before the 1960s, and by then red wolves were endangered (McCarley 1962).

During the late 1960s and early 1970s, most efforts were directed toward determining the red wolf's status in the wild and identifying individuals to be placed in a captive breeding program. Because of this, our knowledge of red wolves prior to the restoration effort we describe in this chapter (Riley and McBride 1972; Shaw 1975) is based on relatively small samples from remnant and probably atypical red wolf populations. Phillips and Henry (1992) characterized the behavior and ecology of the red wolf using preliminary data from the restoration program. In this chapter, we present a more detailed analysis of these data and compare and contrast our findings, when possible, with the early information on the red wolf.

From the restored population, we know that the red wolf, like the gray wolf, is a monestrous species that typically becomes sexually mature by its second year. From historical data and the restoration to date, we know that litters average three pups (Riley and McBride 1972) and that red wolves live in family groups similar to those of gray wolves (Riley and McBride 1972; Shaw 1975). Data from the restored population indicate that the offspring of a breeding pair are tolerated in their natal home range until they disperse, and that dispersal is apparently related to social factors most typically associated with the onset of sexual maturity.

We have noted some fundamental differences in the prey consumed by the remnant populations of red wolves and the restored population. Principal prey prior to extinction included nutria, rabbits, and rodents (Riley and McBride 1972; Shaw 1975). In contrast, the restored wolves relied on white-tailed deer, raccoon, and rabbits, with resource partitioning evident within packs. Data from the restoration program indicate that dens can be located both above and below ground, and that mortality is due to a variety of factors, including vehicles, parasitism, and intraspecific aggression.

The demise of the red wolf was a result of many factors. Human persecution of wild canids and human settlement of most of the southeastern United States forced the last few red wolves to use marginal habitat in Louisiana and Texas, where they bred with coyotes and suffered heavy parasite infestation (Nowak 1972, 1979; Riley and McBride 1972; Carley 1975; Custer and Pence 1981a; Pence et. al. 1981).

The red wolf was listed by the United States as endangered in 1967, and a recovery program was initiated with passage of the Endangered Species Act (ESA) of 1973. The initial objective of the recovery program was to document the current distribution and abundance of red wolves in Texas and Louisiana. Fieldwork quickly revealed that free-ranging red wolves were rare, while coyotes were common (Riley and McBride 1972; Carley 1975). Red wolf-coyote hybrids were also common (Carley 1975). The U.S. Fish and Wildlife Service (USFWS) concluded that the red wolf could be recovered only through captive breeding and reintroductions (Carley 1975).

Captive Breeding of Red Wolves

In November 1973, a red wolf captive breeding program was established at the Point Defiance Zoological Gardens, Tacoma, Washington. To supply animals to the breeding program, the USFWS captured over 400 canids from southwestern Louisiana and southeastern Texas from 1973 to 1980 (Carley 1975; McCarley and Carley 1979; USFWS 1990). Measurements, vocalization analyses, and skull X rays were used to distinguish red wolves from coyotes and red wolf-coyote hybrids (Carley 1975; Paradiso and Nowak 1971, 1972; Riley and McBride 1972; Shaw 1975), although these criteria had their critics (Jordan 1979). Of the 400 animals captured, only 43 were believed to be red wolves and sent to the breeding facility. The first litters were produced in captivity in May 1977. Some of the pups were believed to be hybrids, so they and their parents were removed from the captive program. Of the original 43 animals, only 14 were considered pure red wolves and became the breeding stock for the captive program (USFWS 1990).

Although Bartram (1791) observed the black phase of the red wolf, he saw very few individuals. Had he viewed more, he would have realized that red wolves most often show a mixture of gray, black, and cinnamon-buff (Goldman 1944). Physically, the red wolf is intermediate to the coyote and gray wolf *(Canis lupus)* (Bekoff 1977a; Mech 1974a; Paradiso and Nowak 1972). The disproportionately long legs and large ears are two obvious features that separate red wolves from coyotes and gray wolves (Riley and McBride 1972).

It is difficult, however, to distinguish red wolves from red wolf-coyote hybrids (Carley 1975). This difficulty, combined with the intermediate morphology of red wolves and the commonness of hybrids, fueled a lasting debate over the taxonomic status of the red wolf (see Wayne and Vilà, chap. 8, and Nowak, chap. 9 in this volume). Some authorities consider the red wolf a full species (Paradiso 1968; Atkins and Dillon 1971; Paradiso and Nowak 1971; Elder and Hayden 1977; Ferrell et al. 1980; Gipson et al. 1974; Nowak 1979), while others consider it a subspecies of the gray wolf (Lawrence and Bossert 1967, 1975) or a hybrid resulting from interbreedings of gray wolves and coyotes (Mech 1970; Wayne and Jenks 1991).

In response, the USFWS conducted an exhaustive review of the issue and concluded that the red wolf is either a separate species or a subspecies of the gray wolf (Phillips and Henry 1992; Nowak 1992a; Nowak et al. 1995). Since then, molecular genetic data from wolves in southeastern Ontario have led Wilson et al. (2000) to contend that the red wolf and eastern timber wolf *(Canis lupus lycaon)* were closely related and shared a common lineage with the coyote until 150,000 to 300,000 years ago. However, Nowak (2002) presented morphological data countering this claim and supporting a taxonomic separation between the red wolf and gray wolf. Some genetic work provides similar evidence (Mech and Federoff 2002). Regardless of its true identity, the red wolf continues to be worthy of recovery efforts.

The Reintroduction Program

In 1984, the American Zoological Association (AZA) included the red wolf in its Species Survival Plan (SSP) program. This action helped intensify management of the species in captivity. A population viability assessment (PVA) conducted by the AZA estimated that recovering the red wolf and maintaining 85% of its genetic diversity for 150 years would require retaining at least 330 red wolves in captivity and restoring at least 220 wolves in the wild at three or more sites. This strategy would insure against random events that could wipe out a small population (USFWS 1990) (however, cf. Fuller et al., chap. 6 in this volume).

Long before the red wolf SSP was undertaken, the USFWS had been considering reintroduction. Indeed, the 1974 decision to place the last few wild red wolves in captivity was based on the belief that the animals or their offspring could eventually be reintroduced into the wild.

The red wolf reintroduction program was initiated in 1986. Warren Parker coordinated the effort, and M. K. Phillips was assigned to direct it. An excerpt from Phillips's field journal, written as he began his involvement with the red wolf recovery program, proved especially prophetic:

> I was mesmerized by the adult pair of red wolves racing about the large enclosure at the Point Defiance breeding facility. I knew what a red wolf looked like, but seeing live specimens was revealing in ways I had not anticipated. They acted wild, much more intolerant of people than I expected. And they moved silently as if floating inches above the ground. I was excited by these characteristics because they suggested that these wolves could survive in the wild.

Because previous attempts to translocate gray wolves to Isle Royale National Park (Mech 1966b; Allen 1979), arctic Alaska (Henshaw et al. 1979), and Michigan (Weise et al. 1975) had failed, the USFWS had no protocol for successfully reintroducing wolves. Thus, during 1976 and 1977, the USFWS focused efforts on developing reintroduction methodology (e.g., acclimation, release, and recapture techniques). To assess the relative merits of various approaches to reintroduction, the USFWS released two groups of wild-caught red wolves onto Bulls Island, a 5,000 acre (2,000 ha) component of the Cape Romain National Wildlife Refuge in South Carolina (Carley 1979, 1981). These experiments demonstrated that red wolves acclimated at release sites for 6 months exhibited more restricted movements and higher persistence rates than red wolves released without being acclimated. This finding became the cornerstone of logic that supported the contention that it was feasible to reintroduce red wolves at select mainland sites.

After a failed proposal to use "Land Between the Lakes" in western Kentucky and Tennessee as the first mainland site for restoring red wolves (Carley and Mechler 1983), the USFWS chose the Alligator River National Wildlife Refuge (ARNWR) in northeastern North Carolina as the site for this landmark restoration project. ARNWR includes 120,000 acres (48,582 ha) of coastal plain habitats that are ideal for red wolves. ARNWR supports abundant prey, no coyotes, and few livestock; is bounded on three sides by large bodies of water; is sparsely settled by humans; and lies adjacent to 51,135 acres (20,702 ha) of undeveloped habitat owned by the Department of Defense (DOD) (Lee et al. 1982; Noffsinger et al. 1984; Phillips et al. 1995).

In 1990, the USFWS began adding Pocosin Lakes National Wildlife Refuge to the program to enlarge the restoration area. Pocosin Lakes was also ideal for red wolves because of its large size (110,000 acres or 44,534 ha), remoteness, abundant prey, small populations of coyotes and livestock, and proximity to ARNWR. While the restoration effort is still being carried out, this chapter presents specifics about the project from 1987 through 1994.

Preparations for Wolf Reintroduction

To promote reintroductions of endangered species, Congress amended the ESA in 1982 to allow reintroduced populations to be legally designated as "experimental/nonessential" rather than endangered. That designation allows the USFWS to relax restrictions of the ESA to encourage cooperation from those likely to be affected by the reintroduction (Bean 1983; Fitzgerald 1988; Parker and Phillips 1991).

Before the red wolf reintroduction program was initiated, the USFWS briefed representatives of environmental organizations in Washington, D.C., the North Carolina congressional delegation, the North Carolina Department of Agriculture, the governor's office, local county officials, and local landowners. The U.S. Air Force and Navy were briefed because they conduct training missions in the 40,000 acres (18,000 ha) adjacent to the refuge. Numerous personal contacts were made with local citizens, especially hunters and trappers, in preparation for four public meetings held during February 1986. At these meetings, the experimental/nonessential designation was explained clearly.

Comments resulting from the meetings were integrated into the proposed regulations (Parker et al. 1986). For example, the county government and local sportsmen supported the reintroduction on the condition that hunting and trapping still be permitted. In response, the USFWS decided to permit those activities even though they might result in the accidental "take" of a red wolf. The USFWS decided that the taking of a red wolf would not be prosecuted when it was unavoidable, unintentional, or did not result from negligent conduct, provided that the incident was reported immediately to the refuge manager or other authorized personnel. The USFWS further decided that wolves could be taken by citizens in defense of human life, but not to prevent or reduce depredations (e.g., of livestock or pets). In instances of depredations, citizens were required to contact USFWS or state conservation officers authorized to institute control measures. Without doubt, the flexibility of the experimental/nonessential designation was important in soliciting support for the proposed project.

The wolves we selected for release were taken from the USFWS's certified captive breeding stock. We considered each animal's age, health, genetics, reproductive history, behavior, and physical traits. Before release, we acclimated each wolf in a 225 m^2 (277-$yard^2$) pen at ARNWR. We acclimated the wolves to prepare them for life in the wild and to attenuate their possible tendency to travel widely after release. Acclimation periods were lengthy and averaged 19 months ($n = 42$, range 5 to 49 months), except for three adults, one yearling, and six pups that we acclimated for an average of one month (14 days to 2.5 months). The wolves were either released directly from the acclimation pens or transported to a remote location and released from a shipping container.

Because we were concerned that confinement would increase the wolves' tolerance of humans (a life-threatening trait for wolves about to be released in areas that might be used by some unsympathetic members of the public), we minimized human contact with them during acclimation, hoping to reduce their tolerance of humans. Additionally, we tried to provide the wolves with experiences they would encounter in the wild. For example, we varied the feeding regime to expose the animals to feast-or-famine conditions, and we weaned them from dog food and fed them an all-meat diet. We provided live prey to the first eight wolves we released to give them the opportunity to hone their predatory skills.

To keep the wolves in the area immediately after release and to facilitate their development of predatory skills and knowledge of prey habits, we provided the wolves with supplemental food in the form of deer carcasses placed near the release sites for a month or two after release. This approach was more cost-effective and practical in promoting the wolves' transition to the wild than providing live prey in the acclimation pens. Accordingly, that practice was halted after the first eight releases.

Just before release, we gave the wolves a final health check; administered various vaccines, vitamin supplements, and a parasiticide; took blood samples; determined weights; and fitted the wolves with motion-sensitive radio collars. Since pups were too small to wear radio collars, we implanted abdominal radio transmitters in them at about 10 weeks of age. Most of these animals were recaptured as adults and outfitted with radio collars. In addition, we captured 83% of the known wild-born offspring and outfitted them with radio collars.

Wolf Releases

Phillips's field journal described the first red wolf release:

> Monday, 9/14/87: weather—clear, cool, and calm during morning; afternoon, light southeast breeze and temperatures in the upper 80's. At 0904 h Warren Parker, John Taylor, Chris Lucash and I departed the houseboat in the small Boston whaler to the South Lake pen. The calm weather made for a smooth ride but added to our anxiety because we knew that wolves 140M and 231F could hear us coming. At 0912 h we turned the engine off and floated the last

50 yards. Chris and I steadied the boat as Warren and John muscled the 110 lb. deer carcass out of the boat and began the wet walk through the sawgrass marsh to the pen. At 0924 h they returned breathless, anxious, and nervous. Both were unusually quiet. Taylor said nothing, but Parker uttered "we did it, we let them go."

From that rather humble beginning grew an aggressive restoration effort that eventually resulted in the release of 63 wolves on 76 occasions from October 1987 through December 1994 (tables 11.1–11.3). We released wolves directly from acclimation pens 46% of the time; for all other releases we transported wolves to remote sites and released them from shipping containers. Each wolf was released once, except for six adults that we released twice and three that we released three times. We defined a release as an initial release or a re-release of a wolf in a different area or with a different social group. Because the intent of the reintroduction was to restore a self-sustaining population, we considered a release successful if the animal eventually bred and raised pups in the wild.

Most initial releases involved adult pairs ($n = 14$) or families ($n = 8$), although additional releases included two siblings, an adult with a yearling, and an adult with a pup. We conducted most releases (71%) between August and October, when pups were 4–6 months old. We define adults as animals over 24 months of age, yearlings between 12 and 24 months of age, and pups less than 12 months of age. The adults we released ranged from 2 to 7 years.

Because wolves are wide-ranging and secretive, radio-tracking was our most important field technique. Thus, capturing wolves to attach or replace radio collars was a common field activity. Once a wolf was captured, we could also implement management actions that had been specifically crafted for that particular wolf (e.g., return to captivity).

Radio-tracking greatly facilitated our determination of wolf movements, results of releases, and fates of wolves. The length of time we telemetrically monitored a wolf depended on the animal's fate and ranged from 0.1 months to 77.1 months ($\bar{x} = 15.4$, SE $= 1.6$). We monitored wolves frequently from the ground and the air. For example, from September 1987 through December 1994 we logged 1,453 hours in fixed-wing aircraft during 755 telemetry flights and recorded more than 10,000 wolf locations. The monitoring was so successful that we determined the outcome of 93% of the releases of captive-born wolves and the fates of 77% of the known wild-born wolves ($n = 66$). We also learned the cause of death for 94% of the wolves that died ($n = 51$). In addition, intensive monitoring allowed us to respond quickly to management issues that arose.

Only 21% of the releases with known outcomes were successful (table 11.1). The successful releases led to eleven adults and three pups establishing themselves and eventually producing pups in the wild (tables 11.1–11.3). One adult female was involved in two successful releases. Successfully restored adults persisted in the wild an average of 22 months, or about two reproductive cycles (table 11.2), whereas adults involved in unsuccessful releases persisted for an average of only about 3 months (table 11.2). Pups involved in successful releases persisted in the wild an average of 61 months, or about five reproductive cycles, whereas pups involved in unsuccessful releases persisted for an average of 7 months (table 11.3).

Success was not affected by the manner of release, as 29% and 25% of the releases from acclimation pens and shipping containers were successful, respectively.

TABLE 11.1. Outcomes of red wolf releases in northeastern North Carolina, September 1987–December 1994

	N		Outcomes			No. individuals involved in
Age, sex	Wolves	Releases	Success[a]	Failure	Unknown	successes
Adult males	16	22	6	16	0	6
Adult females	16	23	6	16	1	5
Male pups	16	16	2	12	2	2
Female pups	15	15	1	12	2	1
Totals	63	76	15	56	5	14

[a] A release was considered successful if the animal raised pups in the wild.

TABLE 11.2. Results of forty-four red wolf releases of known outcomes involving thirty-one adult red wolves

	% of total releases (n = 45)	Families (n = 8)	Pairs (n = 14)	Outcomes[a]					Average ± SD persistence in the wild (months)
				Death		Return to captivity		Free-ranging	
Success[b] (n = 12)	27%	33%	24%	58%	+	33%	+	9%	22 ± 18
Failure (n = 32)	73%	67%	76%	36%	+	57%	+	7%	3 ± 4

[a]Outcomes were determined through 31 December 1994.

[b]A release was considered successful if the wolf raised pups in the wild.

TABLE 11.3. Results of twenty-seven red wolf releases of known outcomes involving twenty-seven pups

	% of total releases (n = 27)	Outcomes[a]			Average ± SD persistence in the wild (months)
		Death	Return to captivity	Free-ranging	
Success[b] (n = 3)	11%	0	0	100%	62 ± 4
Failure (n = 24)	89%	68%	25%	7%	7 ± 7

[a]Outcomes were determined through 31 December 1994.

[b]A release was considered successful if the wolf raised pups in the wild.

Additionally, the type of social group (family versus adult pair) a wolf was released with did not appear to greatly affect the probability of success (see table 11.2).

The eventual fates of the released adults varied. Most adults involved in successful releases eventually died in the wild, whereas adults involved in failed releases were commonly returned to captivity within 3 months after release (see table 11.2). In contrast, the one female and two male pups that were involved in successful releases were free-ranging through December 1994. A higher proportion of pups than adults that failed died in the wild (see table 11.3).

Most successful adults (91%) and 60% of the pups—successful or not—established home ranges that included the release area. Establishment of home ranges began immediately following release; wide-ranging exploratory forays were not common. Only one adult and one pup that eventually bred in the wild did so after establishing home ranges that did not include their release sites. About 30% of the unsuccessful adults established home ranges that included their release sites, whereas the remaining 70% traveled widely immediately after being freed; on average these animals traveled a straight-line distance of 11 ± 4 SD miles (18.3 km ± 6.4 SD km) before dying or being returned to captivity. This trend was much less pronounced for unsuccessful pups, as only 40% of these animals abandoned their release sites immediately after being freed; they traveled an average straight-line distance of 9 ± 3 SD miles (15.5 ± 4.7 SD km) before dying or being returned to captivity.

Because almost all the adults we released were acclimated for lengthy periods, there exists limited opportunity to clarify the effect of acclimation duration on the probability of success and post-release movements. However, some insight can be gained by examining the results of releases involving three adults and seven pups that, for various reasons, were acclimated for an average of only 0.9 months. Two of these pups and one of the adults established home ranges that included the release site and persisted for an average of 28.5 months (SD = 33.1 months). One of these pups survived to sexual maturity and bred.

Of the remaining seven wolves, one experienced an unknown fate, while six others persisted in the wild for only 1.0 month (SD = 0.7 months); none of these animals restricted their movements to the release area. Five of these seven wolves were members of a family that we acclimated and released on Durant Island. Immediately after release, the adult male drowned leaving the island; the adult female wandered widely and was returned to captivity. Following her departure, two of the three pups drowned, and the third disappeared. Possibly the behavior of these wolves resulted from the short acclimation period.

Success: Reproduction and Colonization

> During the telemetry flight on May 5, 1988 I observed adults 211M and 196F. It was the first time in two weeks that 196F was away from what we hoped was her den. She seemed slimmer and spryer than two weeks earlier. As we circled for one last look, a small black ball of fur hurried to keep pace with the adults. The pudgy pup, known officially as 344F but affectionately referred to as "slick and steady," was the first red wolf born in the wild in North Carolina in many decades.

This observation from Phillips's field journal indicated that captive-born red wolves like 211M and 196F could make the transition from captivity to the wild and produce offspring. Indeed, fourteen captive-born wolves and twelve wild-born wolves bred in the wild.

From 1988 through 1994, thirteen adult pairs produced twenty-three litters that contained a minimum of sixty-six pups (table 11.4). The average litter contained three pups (range 1–5). Individual wolves contributed differentially to production. For example, two males (16% of the males that bred) and three females (21% of the females that bred) produced 36% and 42% of the known pups born, respectively. The wolves produced litters in the wild every year except 1989, when no wolves were paired during the breeding season. However, only 28% of the pups were produced during the first 4 years, whereas 65% were produced during the final 2 years (table 11.4).

TABLE 11.4. History of red wolf production in the wild in northeastern North Carolina, 1988–1994

Year	No. of litters	Minimum no. of pups (M.F.?)
1988	2	00.02.00
1989	0	00.00.00
1990	1	01.02.00
1991	4	04.08.02
1992	2	02.02.00
1993	5	12.05.01
1994	9	11.08.06
Totals	23	30.27.09

We estimated parturition dates by noting when the adult pair began showing affinity to a particular area, indicating probable denning. Whelping extended from mid-April through early May, with most litters being produced during late April.

Wild-born wolf 670M was the youngest red wolf to breed; he sired a litter at about 10 months, much earlier than most wild gray wolves (see Mech and Boitani, chap. 1, Fuller et al., chap. 6, and Kreeger, chap. 7 in this volume). In contrast, breeding by yearling coyotes can be significant (Knowlton 1972; Kennelly 1978; Todd, Keith, and Fischer 1981). Male 442, who sired a litter at about 46 months (about 4 years), was the oldest wild-born male to breed, but we had no older wild-born males. The youngest recorded breeding for wild-born females was 22 months ($n = 3$); the oldest wild-born female bred at about 70 months (about 6 years), but we had no older wild-born females.

The limits of breeding age for captive-born wolves largely depended on when they were released. The earliest breeding for a captive-born male was 22 months, and for a female about 46 months. Captive-born male 184 bred at about 82 months (about 7 years) of age, and female 205 at about 106 months (about 9 years) of age.

Despite our best efforts at matchmaking by keeping unrelated adult males and females together in acclimation pens for several months, only four (28%) of the adult pairs that we released together stayed together and produced litters in the wild. Most reproduction resulted from nine pairs that formed naturally in the wild. In seven of these pairs, the adults began consorting about 4 months before the breeding season. The other two pairs were together for 8 and 17 months before successfully breeding. About 80% of the adult pairs that were together during a breeding season produced a litter the following spring ($n = 27$).

We learned little about the persistence of pairs of wild-born wolves because only three females (344F, 358F, and 496F) produced multiple litters. Female 344 had the same mate for all four of her litters, but female 508 had different mates in 1993 and 1994. Female 496 also gave birth to several litters, but we never determined the identity of her mate(s). Captive-born wolves provided more information about pair persistence. Six captive-born wolves produced multiple litters in the wild, including four animals that retained their original mates. The remaining two accepted new mates only after their original mates were returned to captivity or killed. Female 300 and male 319 produced litters in 1990, 1991, and

1992 and remained together during 1993 and 1994 even though they did not produce pups during those years. Two pairs consisting of captive-born wolves that formed in the wild and one captive-born pair we released failed to breed during their first year together, but bred successfully the following year.

Biology of the Restored Wolves

Restoration of the red wolf population allowed us to study many aspects of red wolf biology, natural history, and behavior that had never been investigated before.

Den Characteristics

Three dens we inspected were aboveground nests (Mech 1993b) situated under dense vegetation, where the water table probably precluded underground dens. Through aerial radio-tracking, we learned the locations of twenty other dens that we did not inspect. Most were located along the sides or tops of brushy windrows in agricultural areas where the soil was friable and the water table low. Many were probably underground dens.

The three females that produced multiple litters showed varying patterns of annual den use. For example, 344F used the same den for 4 consecutive years, and 394F for 2 consecutive years. Both dens were burrows. In contrast, female 300 established a new den every year for 3 years, probably because her home range was dominated by swamps and her dens were aboveground nests. Using aboveground nests would make myriad sites available, which would increase the odds that she would den in a different location every year. In addition, she may have needed to do little to prepare the nests for pups, and that may have reduced her affinity for any particular site.

Red wolves routinely used den areas from mid-April until mid-July. For packs consisting of more than an adult pair, we documented all wolves frequenting dens, although we located breeding pairs there the most. By mid-July, wolves began moving more widely and seldom visited the dens.

Fates of Wild-Born Wolves

As of 31 December 1994, 36 (54%) of the 66 wolves conceived and born in the wild were free-ranging, 15 (23%) had unknown fates, 10 (15%) had died, and 5 (8%) had been placed in captivity. By December 1994, the oldest wild-born red wolf was 80 months of age. Wild-born pups persisted significantly longer than wolves we released ($P < .02$). There was no significant difference in average persistence times between captive-born pups and captive-born adults ($P = .14$) (table 11.5).

TABLE 11.5. Persistence time of red wolves involved in the northeastern North Carolina restoration effort, 14 September 1987–31 December 1994

Origin	No. with known fates	Mean ± SD persistence (months)[a]
Captive-born adults[b]	51	8 ± 13
Captive-born pups[b]	27	13 ± 19
Wild-born[c]	44	22 ± 18

[a]Persistence times are minimums because some wolves were free-ranging through December 1994.

[b]There was no significant difference in persistence times between these two samples ($P = .14$, d.f. = 45, Kruskal-Wallis test statistic = 55.15).

[c]Persistence time was significantly different from each of the other two samples (for adults, $P = .01$, d.f. = 57, Kruskal-Wallis test statistic = 87.18; for pups, $P = .02$, d.f. = 49, Kruskal-Wallis test statistic = 72.64).

We placed four wild-born wolves in captivity at the behest of landowners who felt the wolves would eventually cause problems, and another that a farmer thought had been abandoned.

Red Wolf Dispersal

> 11/25/91, Monday: Flew today and located all wolves except 497M, despite a wide-ranging search. I suspect that he's dispersed as did his sister a few days ago.

This entry from Phillips's field journal was an important portent for the restoration program. We documented dispersal from natal ranges by eight male and ten female wolves born in the wild. The lack of a sex bias among red wolf dispersers ($P = .48$, $\chi^2 = 0.50$, d.f. = 1) is consistent with reports for gray wolves (Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Ballard et al. 1987; Fuller 1989b; Gese and Mech 1991; Boyd et al. 1995). Five dispersing males and seven females were members of intact natal packs. On average, these males and females dispersed at about the same age, 27 ± 9 SD months and 23 ± 10 SD months, respectively ($P = .52$, $t = .66$, d.f, = 10). Similar ages have been reported for gray wolves in Minnesota (Mech 1987a), Montana (Boyd et al. 1995), and Alaska (Ballard et al. 1987).

Of the fifteen wolves born in the wild with fates unknown, only 502F dispersed (at 22.5 months of age) before we lost radio contact with her. Of the remaining fourteen, eleven were about 3.5 months old when we lost contact with them. The final three remained in their natal ranges for 13 to 20 months before disappearing.

Six pups dispersed after disruption of their natal pack's social cohesion. Four of these dispersed from their natal ranges within 3 months after we captured and returned their parents to captivity. Two other male pups dispersed within 2 months following the displacement of their father by an unrelated male. Apparently the disruption of social bonds between adults and offspring prompted these pups to disperse at the relatively young average age of 8 ± 1 SD months. Dispersal by small numbers of gray wolf pups has also been documented (Fuller 1989b; Gese and Mech 1991).

Our findings of high dispersal rates for yearlings are similar to those of Fritts and Mech (1981), Peterson, Woolington, and Bailey (1984), and Boyd et al. (1995). All of the wolf populations in these studies were at low density or increasing, intraspecific strife was uncommon, and all occupied areas of relatively high prey densities.

Dispersing red wolves settled new ranges in 1–44 days (average = 9 days, SD = 13 days, $n = 12$). Males and females dispersed similar mean distances of 36 ± 22 SD km and 45 ± 58 SD km, respectively, or 22 ± 13 miles and 27 ± 35 miles ($P = .74$, $t = -.34$, d.f. = 8). Similarly, gray wolves do not show a sex bias in dispersal distance (Ballard et al. 1987; Mech 1987a; Fuller 1989b; Gese and Mech 1991; Mech et al. 1998).

Almost 90% of red wolf dispersers traveled southward or westward to areas without wolf packs that contained good habitat and abundant prey. For most of these animals, established pack territories lay to the north and east. Only one wolf was killed while dispersing; she was hit by a vehicle. The other seventeen dispersing wolves settled new areas; 65% of them eventually paired and produced offspring (table 11.6).

All dispersals occurred between September and March, with 72% between November and February. Gray wolves show a similar peak in dispersal, although some gray wolves disperse at other seasons (Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Ballard et al. 1987; Mech 1987a; Fuller 1989b; Gese and Mech 1991; Boyd et al. 1995; Mech et al. 1998).

Since wolves often dispersed at about the age of sexual maturity, it is likely that was a predisposing factor in dispersal (see Mech and Boitani, chap. 1 in this volume). Dispersal seemed to be an effective means of maximizing genetic fitness, given that 76% of our wild-born animals that dispersed eventually consorted with other canids (usually with other wolves, but also with coyotes; see below), and 70% of the animals eventually produced pups (see table 11.6). Clearly, dispersal facilitates genetic exchange, thus reducing the frequency of inbreeding and associated problems (Mech 1987a; D. Smith et al. 1997; Mech et al. 1998). Boyd et al. (1995) pointed out that dispersal may help to ensure the genetic health of low-density, recolonizing wolf populations.

TABLE 11.6. Fates of seventeen red wolves that dispersed and settled in new areas in northeastern North Carolina, 14 September 1987–31 December 1994

Fate	No. of wolves (M.F.)	Litters produced	Minimum pups produced
Paired and bred	4.7	12	36
Paired but no pups	1.0		
Lived alone	1.2		
Consorted with coyotes	2.0	1	3

Dispersal also greatly affects the politics of wolf restoration. Through dispersal, a wolf population can spread out over a large area fairly quickly. This fact is tremendously important to acknowledge because many opponents of wolf restoration argue that wolves will not stay put, that they will wander widely and establish themselves well beyond the intended area. Regardless of where wolves are released, they are a "fluid" resource that will move about regardless of political boundaries. To be successful, restoration design must take this into account.

Red Wolf-Coyote Interactions

We observed one captive-born female and two wild-born male wolves consorting with coyotes. We returned the female to captivity before she achieved sexual maturity. One male was shot and probably did not sire a litter with a coyote. The other apparently did sire a litter of three hybrid pups during spring 1993. In July we captured two of these pups (both females) and observed the third. All were in poor health from sarcoptic mange (*Sarcoptes scabiei*). We believe the one pup died shortly after we observed it, and we placed the two captured animals in captivity, treated them, and studied their morphological development.

At about 8 months of age, the hybrid pups weighed an average of 12 kg (26 pounds), about the same size as four adult female coyotes we captured in the area (average weight = 13 kg, SD = 1 kg) but much smaller than female red wolves of comparable age (average weight = 18 kg, SD = 2 kg, n = 13). One female acted like the three coyotes we maintained in captivity: she was withdrawn and would often slink around the pen in our presence. The other female's behavior was wolflike: she was bold and ran excitedly around the pen in our presence. Both their physical appearance and their behavior suggested that they were the progeny of a male red wolf breeding a female coyote.

At the outset of the restoration effort we assumed that unmated red wolves would readily breed coyotes because historically they had done so in Texas and Louisiana. In those areas, red wolves were rare and coyotes were common, as discussed earlier. Historical hybridization between red wolves and coyotes could have been due to the fact that wolves encountered far more coyotes than conspecifics. In contrast, in northeastern North Carolina after restoration began, wolves were common and coyotes rare. Indeed, the scarcity of coyotes in northeastern North Carolina was one reason the ARNWR was selected for red wolf restoration. From 1987 through 1994 we captured 106 wolves, but only 4 coyotes. Although our trapping targeted wolves, coyotes would have been captured if they were present.

Even though hybridization between red wolves and coyotes was not a serious problem through 1994, it became so about then (Kelly et al. 1999). A comprehensive population and habitat viability assessment (Kelly et al. 1999) facilitated the development of an adaptive management plan to address the hybridization problem (Kelly 2000). The plan, implemented in April 1999, called for hybridization to be eliminated or reduced by euthanizing or sterilizing coyotes and hybrids and promoting the formation and maintenance of wolf breeding pairs. By 2002 the results were beginning to show that hybridization could potentially be reduced to an acceptable level. Even if this proves to be the case, there is little likelihood of restoring a red wolf population elsewhere without intensive management. There are no suitable restoration areas in the historic range of the red wolf that are not inhabited by coyotes.

As part of the adaptive management plan, intensive genetic, morphological, and ecological research is under way on red wolves and other canids in northeastern North Carolina. Such studies will improve our knowledge of certain aspects of wolf-coyote interactions, including the extent of introgression between the species and the parentage and identity of canids of unknown origin. Such knowledge will help determine whether it is possible to restore the red wolf as a unique taxon functioning as an important component of the southeastern landscape.

Home Range Characteristics

Location data from ninety-six wolves were obtained from aircraft and by triangulation from the ground. Locations per wolf ranged from 2 to 1,085 ($\bar{x}$ = 113, SD = 12). We chose thirteen wolves from three packs to represent the home range size of red wolves at ARNWR. The packs were chosen for the completeness of their data sets. The Milltail, Gator, and Airport packs had established themselves early in the restoration (more than a year before collection of the data we analyzed), were tracked intensively, and occupied significantly different habitats. To ensure more valid comparisons between packs and individuals, wolves with similar temporal distributions of location data were selected. For each wolf's location data, we calculated the 95% minimum convex polygon (Ackerman et. al. 1990). We used the habitat where scats were collected to represent the habitat used by a pack.

Home range sizes averaged 88.5 ± 18.3 SD km^2 (35 ± 7 SD mi^2) for individuals and 123.4 ± 53.5 SD km^2 (48 ± 21 SD mi^2) for packs (table 11.7). Range size differed significantly among packs (F = 17.5, P = .0005). The Gator pack used an area significantly larger than either the Milltail or Airport packs (table 11.7). Although home range size has been positively correlated with pack size in gray wolves (Ballard et al. 1987; Peterson, Woolington, and Bailey 1984; but cf. Mech and Boitani, chap. 1, and Fuller et al., chap. 6 in this volume), habitat type appears to interact with this relationship for the red wolves at ARNWR. The Airport pack, which had the fewest individuals, did have the smallest home range. However, the Gator pack established a home range that was two to three times larger than the home range used by the Milltail pack, even though the Gator and Milltail packs were similar in size (i.e., included four to five animals).

This disparity was probably a function of the produc-

TABLE 11.7. Home range estimates of free-ranging red wolves in northeastern North Carolina

				Dates tracked	
Pack	*n*	km²	mi²	Begin	End
Milltail					
205F	105	35.1	13.7	10/04/90	09/30/91
331M	110	37.2	14.5	10/04/90	09/30/91
351F	42	76.9	30.0	10/05/90	01/24/91
394F	106	58.6	22.9	10/04/90	09/30/91
$\bar{x}$	4	52.0	20.3		
SE	4	9.9	3.9		
Composite	363	98.9	38.6	10/04/90	09/30/91
Gator					
300F	109	190.5	74.4	10/04/90	09/30/91
319M	103	199.9	78.1	10/19/90	09/30/91
442M	82	108.2	42.3	10/19/90	09/30/91
443F	89	197.5	77.1	10/19/90	09/30/91
444F	63	98.7	38.6	02/08/91	09/30/91
$\bar{x}$	5	159.0[a]	62.1		
SE	5	22.7	8.9		
Composite	446	225.8	88.2	10/04/90	09/30/91
Airport					
313F	115	39.4	15.4	10/04/90	09/17/91
328M	92	44.9	17.5	10/04/90	06/30/91
426M	93	29.4	11.5	10/04/90	07/15/91
430F	118	34.4	13.4	10/04/90	09/30/91
$\bar{x}$	4	44.9	17.5		
SE	4	3.3	1.3		
Composite	418	45.6	17.8	10/04/90	09/30/91
Overall					
Individual $\bar{x}$	13	88.5	34.6		
SE		18.3	7.1		
Composite $\bar{x}$	3	123.4	48.2		
SE		53.5	20.9		

[a] Different from the other packs ($P < .05$, Fisher's least significant difference test).

tivity of habitat. Of 893 scats attributed to the Gator pack, 99% ($n = 888$) were collected in pine-hardwood habitats where prey is relatively scarce (Lee et al. 1982; Noffsinger et al. 1984; M. K. Phillips, unpublished data). In contrast, 71% and 98% of the scats attributed to the Milltail and Airport packs, respectively, were collected in agricultural habitats where prey were abundant (Lee et al. 1982; Noffsinger et al. 1984; M. K. Phillips, unpublished data). Variation in home range size due to prey density has also been observed in gray wolves (Ballard et al. 1987; Wydeven et al. 1995; Fuller et al., chap. 6 in this volume), coyotes (Gese et al. 1988), and bobcats (Litvaitis et al. 1986).

Home range sizes for red wolves in Texas were similar to those in North Carolina, ranging from 25 km² to 130 km² (10–51 mi²) (Riley and McBride 1972; Shaw 1975). Overall, red wolf home ranges appear to be intermediate to coyote ranges, which vary from 4 km² to 84 km² (1.5–34.6 mi²) (Andelt 1985; Gese et al. 1988; Sargent et al. 1987), and gray wolf territories, which range beyond 2,600 km² (1,015 mi²) (see Mech and Boitani, chap. 1 in this volume).

Food Habits

Between 27 November 1987 and 11 March 1993, we collected and analyzed 1,890 red wolf scats. When possible,

TABLE 11.8. Analysis of 1,890 red wolf scats collected in northeastern North Carolina, November 1987–March 1993

Prey species	% of biomass[a]
White-tailed deer	43
Raccoon	31
Lagomorph	13
Rodent	11
Domestic ungulate	2

[a]Raw data converted as per Weaver 1993.

scats were assigned to individual wolves, or packs, via radioisotope marking (Crabtree et al. 1989) or intensive tracking of the wolf.

Scat content analyses based on the percentage of scats containing a given item, commonly referred to as frequency of occurrence or percent frequency, are biased (Kelly 1991). Accordingly, we used Weaver's (1993) model to refine our scat analysis and estimate the proportions of various prey red wolves consumed. Although Weaver's model was developed for gray wolves, its application to red wolves is tenable, with the caveat that prey smaller than snowshoe hares will probably be overestimated (Kelly 1991, 66).

White-tailed deer, raccoons, and marsh rabbits constituted 86% of the red wolves' diet (table 11.8). These results differ from previous reports about red wolf food habits. Nutria, rabbits, and cotton rats were the primary prey of red wolves in Texas (Shaw 1975; Riley and McBride 1972).

Differences in prey consumption by pack were evident at ARNWR. The Milltail pack consumed more small prey (rodents and rabbits) than the Gator pack, which consumed more large prey (deer and raccoons) (table 11.9). This difference in food habits was related to the abundance and distribution of prey. While rabbits and rodents were abundant in the agricultural fields used by the Milltail pack, they were uncommon in the pine-hardwood swamps used by the Gator pack (Lee et al. 1982; Noffsinger et al. 1984; M. K. Phillips, unpublished data).

Rodents were consumed more by juvenile wolves than by adults, and analysis of the scats from the Milltail pack indicates a decrease in rodent consumption with age (table 11.10). A similar pattern of prey use was not evident for the Gator pack. However, resource partitioning similar to that manifested by the Milltail pack was documented among members of coyote packs in Yellowstone National Park (Gese et al. 1996).

The differential use of prey by the Milltail and Gator packs may have played a role in determining their home range sizes (see above). If the predominance of agricultural habitat in the Milltail pack's range provides enough prey variety to allow the pack to partition prey resources, their home range should be smaller than it would be otherwise (Harestad and Bunnell 1979). Additionally, the relatively abundant and diverse prey in the Milltail pack range may explain why this pack was able to produce and raise an average of 4.0 pups per litter ($n = 3$), whereas the Gator pack produced and raised an average of only 2.3 pups per litter ($n = 3$).

Mortality

Of the 135 red wolves involved in the restoration effort, 51 (38%) died while free-ranging, most during the first year after release or birth (table 11.11). The first wolf to die was female 231, whose death prompted this entry in Phillips's field journal:

TABLE 11.9. Analysis of 494 and 831 scats from two red wolf packs in northeastern North Carolina, November 1987–March 1993

	Milltail pack		Gator pack	
Prey species	% of biomass[a]	% of scats	% of biomass[a]	% of scats
White-tailed deer	25	29	40	43
Raccoon	38	52	46	59
Lagomorph	14	25	8	15
Rodent	19	38	2	8
Domestic ungulate	—	—	1	—

[a]Raw data converted as per Weaver 1993.

TABLE 11.10. Mammalian prey consumed (% of biomass[a] and % of scats below) by wolves of different ages[b] as determined from analysis of scats collected from two red wolf packs in northeastern North Carolina, November 1987–March 1993

	Milltail pack: Age of wolf		Gator pack: Age of wolf		Milltail pack: Age of wolf (months)			
Prey species	Juvenile $n = 17$	Adult $n = 191$	Juvenile $n = 46$	Adult $n = 390$	≤24 $n = 23$	24–48 $n = 29$	48–72 $n = 88$	>72 $n = 208$
White-tailed deer	14	21	42	39	17	17	23	21
	18	26	56	46	22	24	30	26
Raccoon	15	59	31	51	11	16	42	56
	24	74	46	69	26	35	61	70
Lagomorph	3	9	13	9	2	7	9	8
	12	20	20	15	9	21	19	19
Rodent	62	9	1	1	66	57	25	14
	71	19	9	6	74	69	40	24

[a]Raw data converted as per Weaver 1993.

[b]Ages were based on isotope labeling of scats from known individuals or from intensive tracking of known individuals (see text).

TABLE 11.11. Number (percentage) of thirty-six captive-born red wolves released in northeastern North Carolina dying, and causes of death, 14 September 1987–31 December 1994

	No. months after release					
Cause	1	2	6	12	>12	Totals
Vehicle	5 (14)	3 (8)	1 (3)	3 (8)		12 (33)
Intraspecific aggression	5 (14)					5 (14)
Malnutrition and parasitism				4 (11)	3 (8)	7 (19)
Drowning	3 (8)		1 (3)			4 (11)
Shot	1 (3)					2 (6)
Miscellaneous causes[a]	1 (3)			1 (3)	4 (11)	6 (17)
Totals	15 (42)	3 (8)	2 (5)	9 (25)	7 (20)	36 (100)

[a]Includes uterine infection (1), suffocation (1), pleural effusion and internal bleeding from unknown causes (1), handling accident (1), and unknown (2).

> 12/18/88, Friday: It was cold, clear, and windy all day. At 1530 we found 231F dead on the beach about 1 mile south of Long Shoal point. We had last located her on December 11 about 2 miles west, but weather had prevented monitoring since then. We found her laying on her side. She had obviously been dead for some time as the tides had nearly covered her with sand.

Female 231 died because of internal bleeding and fluid in her chest from an unknown cause. Most other deaths were caused by vehicles (30%), malnutrition and parasitism (27%), or intraspecific aggression (12%) (see Mech and Boitani, chap. 1, and Fuller et al., chap. 6 in this volume). In addition, four wolves drowned, four were shot, one died of complications from a uterine infection, one choked on a raccoon kidney, one was poisoned, and one died during a handling accident. The causes of death of three wolves were unknown.

Because two paved highways bisect ARNWR, we expected vehicles to be an important source of mortality. To reduce vehicle strikes, the North Carolina Department of Transportation erected red wolf road-crossing signs. In addition, we produced public service announcements on local radio to alert motorists to the presence of wolves.

Despite the fact that the captive-born wolves had little or no experience hunting, none died solely from an inability to feed itself. Those that were malnourished were either very old or also suffered heavy parasite infestations (see Kreeger, chap. 7 in this volume). For example, wolves 300F and 319M, who had been together for almost 5 years and were 8 and 7 years old, respectively, died from malnutrition within 4 months of each other. Both possessed heavily worn teeth, and we supposed that they had grown too old to hunt successfully (but see Mech 1997).

Four other wolves, all from one pack, died from malnutrition and parasitism by ticks *(Dermacentor variabilis* and *Amblyomma americanum)* and intestinal worms *(Ancylostoma caninum* and *Dioctophyme renale)*. Another wolf, adult 358M, succumbed to sarcoptic mange. We also captured three pups, sired by 358M, that harbored large numbers of *Sarcoptes scabiei* and were in marginal condition. We treated them with parasiticides for 18 to 21 days and released them; they survived at least through December 1994. Two wild-born pups died at 10 and 11 months, respectively, from complications of demodectic mange *(Demodex canis)*, which has not been reported before for red or gray wolves (see Kreeger, chap. 7 in this volume). Mange, ticks, and intestinal worms were known causes of mortality for naturally occurring red wolves in Texas and Louisiana (Riley and McBride 1972; Carley 1975; Custer and Pence 1981a; Pence et. al. 1981).

Five wild-born wolves that presumably died from malnutrition were littermates whose only parent (383F) was killed by a vehicle when they were about 40 days old. Despite extensive searches, we were unable to locate the litter after 383F's death. Because of their young age, we presumed that they all died.

Intraspecific aggression led to the deaths of five recently released wolves that entered the territories of established wolves. Possibly these inexperienced captive-born wolves were unaware of the grave consequences that sometimes accompany trespass (Mech 1994a; Mech et al. 1998). The other death from intraspecific aggression involved a 33-month-old, wild-born female killed by her pack, apparently in competition over the only breeding-age male in the area. This is one of the few records of a wild red or gray wolf killed by close relatives (see Mech and Boitani, chap. 1 in this volume).

Four wolves drowned, including a female pup accidentally captured in a foothold trap set for a bobcat. The other three were from a pack we acclimated on Durant Island, as mentioned earlier.

The four wolves that were illegally shot included two captive-born and two wild-born animals. Two of them had been mistaken for coyotes, which can be legally harvested in North Carolina. Over 90% of the red wolf deaths were accidental or natural.

Management during Restoration

From the outset of the restoration program, intensive management of the wolves was necessary to ensure quick establishment of a breeding population and adequate resolution of wolf-human conflicts. Most management required capture of wolves for reasons discussed below. We made 110 captures of 45 (71%) of the 63 captive-born wolves and 125 captures of 59 (83%) of the 71 wild-born wolves. We accomplished 195 of these captures (83%) using foothold traps (Mech 1974b). We also modified acclimation pens to act as traps for 27 captures (11%) of 12 captive-born wolves and 1 wild-born wolf. The remaining 13 captures involved a variety of techniques, including dart guns, box traps, and nets.

On 42 occasions the solution we adopted for the management problem at hand was to return a wolf to captivity or translocate the animal to another area before re-release. We returned one pup to captivity because of concern for its welfare; a farmer had found it and believed it had been abandoned. We placed two wild-born wolves in captivity because they were malnourished and harbored significant parasite infestations. Intraspecific aggression prompted four captive-born wolves to wander widely, which forced us to return them to captivity. Decisions to recapture these wolves were based on judgments that their future movements would continue to be wide-ranging and that it was likely that they would be involved in negative encounters with humans.

We returned six wolves to captivity on seven occasions for breeding because their mates had died or, in one case, had been returned to captivity. We removed another wolf from the wild to breed her so as to improve the representation of a rare genetic lineage.

Conflicts with people led to twenty-eight (70%) of the incidents that prompted us to return wolves to captivity or translocate them. Eighteen of these incidents involved captive-born wolves that, for mostly unknown reasons, frequented small areas inhabited by people. Although these animals rarely caused actual problems, their mere presence was unacceptable to the residents. In contrast, the ten incidents involving wild-born wolves resulted from the animals colonizing uninhabited private land. Even though they did not cause problems, their presence was unacceptable to the landowners, who requested their removal.

These management issues and a few others that did not involve the public were resolved without significantly injuring the wolves or inconveniencing residents. We were able to manage the wolves successfully because radio collars allowed us to determine their whereabouts almost at will. Knowledge of a wolf's location simplified all aspects of management.

The importance of managing wolves successfully during restoration cannot be overstated. For wolf restoration to succeed, the public must support, or at least tolerate, the program, and managing wolves successfully is one way to generate and maintain support and tolerance. Because successful management is so important, all or most wolves involved in a restoration effort should be radio-collared during the first several years of the program.

Capturing wolves was not the only intensive management strategy we employed to ensure establishment of the red wolf population. For example, during the first 2 years of the project, when the population consisted of just a few wolves, we implemented a parasite control program that prevented or ameliorated parasitism in selected wolves (Phillips and Scheck 1991). As the population grew, however, it become extremely laborious to continue this effort, and the importance of individual wolves decreased, so we terminated the parasite control program.

Conclusions

The red wolf restoration program progressed considerably from 1987 to 1994. As of June 2002, approximately a hundred red wolves (all wild-born animals), distributed in twenty packs, inhabited a restoration area that had grown to encompass about 680,000 ha (1.7 million acres). From the project's inception through June 2002, free-ranging wolves had given birth to 281 pups over four generations (USFWS, unpublished data).

The restoration area is now composed of 60% private land and 40% public land, which includes three national wildlife refuges. Since 1988 we have officially integrated about 78,800 ha (197,000 acres) of private land into the restoration area through cooperative agreements, at a total cost of $3,951 per year for 5 years (Phillips et al. 1995).

The red wolf restoration program has generated benefits that extend beyond the immediate preservation of red wolves, positively affecting local citizens and communities, larger conservation efforts, and other imperiled species (Phillips 1990). Indeed, the program is an effective model for restoring other controversial endangered carnivores, such as gray wolves, African wild dogs, and black-footed ferrets.

The red wolf program also illustrates that the designation of a population as "experimental/nonessential" can be beneficial for wide-ranging species introduced into areas not designated critical habitat, or where an introduced population may expand into nonpublic land not designated critical habitat. The experience gained by reintroducing red wolves suggests that such a designation would help other introduction programs succeed.

However, the red wolf program also serves as an example of a potential overrelaxation of regulations under the experimental designation. Despite the utility of the original final rule that resulted from the experimental designation, local opposition to the red wolf program during the early 1990s prompted the USFWS to modify it (Henry 1995). The revised rule requires the USFWS to remove wolves from private land at the behest of the landowner if possible, even if the only problem is the mere presence of the animal(s). A similar rule has been adopted by the Mexican wolf recovery program (Parsons 1997). The revised red wolf rule also contains a provision that allows issuance of a permit for landowners to take red wolves (for simply being present) after USFWS efforts to remove the animals have concluded.

Regulations that provide landowners such flexibility are potentially inappropriate for at least two reasons: first, because they are nearly impossible to implement effectively as the wolf population grows because of the difficulties of responding simultaneously to a large number of landowners, and second, because they might establish a precedent that could be used to argue for the removal of individuals from other populations of endangered species (both reintroduced and naturally occurring) inhabiting private land. However, given that traditional wildlife management concepts and attendant regulations assume that wildlife is public property and not subject to removal from private property in the absence of a problem, concern that the red wolf rule might establish a precedent may be moot except for specific situations involving reintroduced predatory species that are perceived to conflict with private interests.

Certainly local opposition to the red wolf and Mexican wolf reintroduction programs greatly affected the regulations governing management of the wolves. Indeed, the recovery program coordinators and Phillips (for the red wolf project) assumed from personal knowledge of local politics and sentiments that more restrictive rules would have significantly hindered and possibly caused the termination of the project (V. G. Henry, personal communication, 1994; D. R. Parsons, personal communication, 1996). Additionally, there was a need to clarify regulations for the red wolf program so that they accurately reflected long-standing commitments made by the USFWS that wolves that inhabited private land would be removed if so desired by the landowner. The revised regulations published in 1995 may have contributed to the widespread local support for red wolf recovery (Quintal 1995; Mangun et al. 1996).

Nonetheless, it has been argued that the 1995 regulations were excessively relaxed (Phillips and Smith 1998) and may have contributed to the current level of hybridization by allowing wolves to be managed in a manner that continually disrupted their social affinities (Kelly and Phillips 2000). Phillips and Smith (1998) believed that the argument that relatively relaxed regulations were necessary to ensure successful restoration of red wolves is contrary to experiences from reintroduction of gray wolves to central Idaho and Yellowstone National Park (YNP). Local opposition to these programs was substantial, but the authors of the regulations did not provide landowners a level of flexibility similar to that afforded landowners affected by red wolf reintroductions.

It is true that the central Idaho and YNP projects were much less dependent on private land than the red wolf project. However, throughout the planning period for the gray wolf projects, landowners expressed grave concern over problems that would arise if wolves came to inhabit private property. And during the first two years of the YNP project several contentious management incidents arose involving wolves and private land (Phillips and Smith 1998). Nonetheless, the relatively restrictive regulations in no way hindered resolution of those incidents nor the maturation of the two projects; both are viewed as unqualified successes (Bangs and Fritts 1996; Phillips and Smith 1996).

During the restoration program several important points became apparent:

1. Acclimating and releasing captive-born adults in a manner that predisposed them to remain near the release site and establish a home range there seemed to increase the chances that the wolves would breed in the restoration area. Furthermore, it simplified the task of initial telemetric monitoring and management.
2. Given that the manner of release (i.e., directly from an acclimation pen versus transport to a distant site and release from a shipping container) did not affect success, we concluded that it was most cost-effective to use a central facility for acclimation rather than a multitude of remote sites.
3. Most releases failed to result in the wolf breeding in the wild, so numerous releases over an extended period were required. This fact and the differential pup production by a few individuals emphasize the importance of individual wolves early in the program. Accordingly, it was appropriate during the first few years of the project to monitor and manage the wolves intensively to ensure their survival. Similar results have been reported for other restoration projects (Griffith et al. 1989).
4. Even though most captive-born wolves did not contribute to population growth, a large enough number (at least 18% of the total number released) did to serve as the catalyst for population formation. Indeed, fourteen captive-born wolves were involved in the production of at least 50% of the pups born from 1987 through 1994. Clearly captive-born red wolves were appropriate "seed stock" for restoring a free-ranging population.
5. Our matchmaking of captive pairs was not very effective. Of the fourteen adult pairs we released, only 28% remained together and produced pups in the wild. Most reproduction during the first 7 years resulted from nine pairs that formed naturally in the wild.
6. Maintaining radio contact with free-ranging wolves was essential to determining the fates of individual animals and for resolving management issues.
7. The management flexibility afforded by the experimental/nonessential designation was critical in soliciting and maintaining support for the restoration effort from local citizens and state and federal agencies. This flexibility also provided field biologists with the latitude necessary to resolve conflicts in innovative and cost-effective ways.
8. Because red wolves traveled long distances, dispersal greatly affected the politics of restoration. It is critical when designing a wolf restoration program to realize that the wolf population will occupy a large area, regardless of political boundaries.

9. Significant land use restrictions were not necessary for wolves to survive. Indeed, the rather lenient hunting and trapping regulations for the refuge remained unchanged or were further relaxed during the experiment. The lack of land use restrictions facilitated the integration of private land into the program, which greatly increased the area wolves could inhabit, which facilitated population growth. The prognosis for landowners and red wolves to coexist is good, since the wolves do not fit their stereotypical image and are not a threat to personal safety and landowner rights.
10. It will be necessary to study the extent of introgression between red wolf and coyote populations and to actively manage both to prevent hybridization. Intensive management seems to be the only way to ensure the coyotes will not again genetically "swamp" red wolves.
11. Most management issues that arose resulted in extensive press coverage, which promoted the perception that wolves are less manageable and more difficult to live with than other wildlife. This perception may subside as local residents become accustomed to living with wolves and as the species becomes less "newsworthy." However, we feel that wolf conservation will continue to be controversial as discussions shift from whether to restore the species to how best to manage free-ranging populations. A similar trend has been predicted for conservation of gray wolves in the northern Rocky Mountains (Bangs and Fritts 1996).
12. A well-trained and dedicated field crew with appropriate expertise was crucial to program success. Administrative continuity also facilitated success. The importance of these two aspects of the program should not be overlooked. Reintroduction programs using captive-born animals are especially sensitive to staff changes and administrative inefficiencies because they are long-lived, because they require that many difficult decisions be made in crisis situations, and because mistakes with small populations can be hard to reverse (Miller et al. 1996).
13. Red wolves can flourish in a wide variety of habitats, and there is sufficient habitat available in the southeastern United States to meet the population objectives of the Red Wolf Recovery Plan (USFWS 1990), assuming that the problem of hybridization between red wolves and coyotes can be resolved. Much of that area, however, is privately owned. Consequently, recovery of the red wolf is not dependent on setting aside undisturbed habitat, but rather on overcoming hybridization with coyotes and the political, logistical, and emotional obstacles to human coexistence with wild wolves.