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Cross-fostering as a conservation tool to augment endangered carnivore populations

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Cross-fostering offspring with nonbiological parents could prove useful to augment populations of endangered carnivores. We used cross-fostering to augment captive-born and wild-born litters for the endangered red wolf (*Canis rufus*). Between 1987 and 2016, 23 cross-fostering events occurred involving captive-born pups fostered into captive litters (n = 8 events) and captive-born pups fostered into wild recipient litters (n = 15 events). Percentage of pups surviving 3 and 12 months was 91.7% for captive-born pups fostered into captive recipient litters. For pups fostered into wild litters, percentage of pups surviving 5 months was > 94% among fostered pups (pups fostered into a wild red wolf litter or replaced a hybrid litter), pups in recipient litters (wild-born litters receiving fostered pups), and pups in control litters (wild-born litters not in a fostering event) when using pups with known fates. Including pups with unknown fates as deaths, percentage of pups surviving 5 months was > 54% among fostered pups, pups in recipient litters, and pups in control litters. Among wild litters, percentage of pups surviving 12 months was > 82% among fostered pups, pups in recipient litters, and pups in control litters when using pups with known fates. Including pups with unknown fates as deaths, percentage of pups surviving 12 months was > 48% among fostered pups, pups in recipient litters, and pups in control litters. Although survival to 12 months was similar among the groups, average life span was different with pups in control litters living 3.3 years, pups in recipient litters living 4.6 years, and fostered pups living 5.6 years. Of fostered pups surviving > 12 months in the wild, 9 animals whelped or sired 26 litters. Cross-fostering was successful at augmenting litter size for red wolves without any deleterious effects on recipient litters, illustrating fostering as a tool for increasing populations of endangered carnivores.

Key words: augmentation, *Canis rufus*, cross-fostering, population, red wolf, survival

Maintaining or increasing population size is often the key conservation objective for threatened and endangered species. However, many rare or threatened mammalian species may have low birth rates, and low survival and recruitment of young (e.g., Laurenson 1994; Fuller et al. 2003; Groom et al. 2017). Increasing survival rates of young carnivores born into wild populations involves many variables (i.e., sufficient food of high quality, protection from intra- and interspecific predation, disease, human-caused mortality, or extreme weather) that may act independently or in concert with each other (e.g., Mech and Goyal 1995; Fuller et al. 2003; Angerbjörn et al. 2004; Bohling and Waits 2015; Hinton et al. 2017). Although increased survival is essential for population growth, fundamentally a population must produce new individuals to grow.

The red wolf (*Canis rufus*) was declared extinct in the wild in 1980 (U.S. Fish and Wildlife Service 1989) and is currently listed as critically endangered (IUCN 2017). To mitigate the decline of red wolf population numbers, a breeding program was established in 1973 at the Point Defiance Zoo and Aquarium, Tacoma, Washington (Phillips et al. 2004). This managed breeding program, operated under the Species Survival Plan of the Association of Zoos and Aquariums, was developed as a cooperative breeding program to enhance long-term population management for approved species (Hutchins and Wiese 1991). The red wolf Species Survival Plan was designed to function as a source population for initial and ongoing red wolf restoration efforts (U.S. Fish and Wildlife Service 1989). Only 14 individuals were considered "pure" red wolves and were the founders for the red wolf breeding program, with descendants of 12 founders serving as source individuals for reintroduction into the Alligator River National Wildlife Refuge, North Carolina (Phillips et al. 2003).

Low genetic diversity, increased genetic drift, and inbreeding depression can be significant issues whenever low numbers of breeding animals are involved, such as captive breeding programs (Rabon and Waddell 2010) or some wild populations (Brzeski et al. 2014), which can result in reduced litter sizes (Lockyear et al. 2009; Rabon and Waddell 2010). In addition, the expansion of coyotes (*Canis latrans*) into the northeastern North Carolina experimental population area and the risk of hybridization represented another threat to red wolf restoration (Kelly et al. 1999; Stoskopf et al. 2005; Fredrickson and Hedrick 2006; Bohling and Waits 2015). To mitigate introgression of coyote genes into the red wolf population, an adaptive management plan was implemented that 1) sterilized and released coyotes to serve as nonbreeding placeholders (Gese and Terletzky 2015), 2) removed coyotes from the area, 3) translocated red wolves (McLellan and Rabon 2006), and 4) cross-fostered captive-born pups into wild litters (Stoskopf et al. 2005). Combined with intensive field management (Gese et al. 2015) and genomic testing protocols (Miller et al. 2003), wild-born pups could be identified as red wolf, red wolf-coyote hybrid, or coyote, leading to the option of replacing hybrid individuals with red wolf pups from the captive breeding population.

Cross-fostering, the raising of young by nonbiologically related individuals, has the potential to increase population sizes of threatened or endangered species (Kitchen and Knowlton 2006; Stoskopf 2012). Fostering of offspring from natal to surrogate parents has been conducted with Columbian ground squirrels (*Spermophilus columbianus*—Murie et al. 1998), captive coyotes (Kitchen and Knowlton 2006), many bird species (Powell and Cuthbert 1993; Drewien et al. 1997; Oswald et al. 2013), and has been observed without human facilitation in black bears (*Ursus americanus*—Benson and Chamberlain 2006). Fostered young that were raised successfully have been both captive-born (Kitchen and Knowlton 2006) and orphaned in the wild (McNutt et al. 2008). Most research on cross-fostering of canid species has been limited to small sample sizes (< 4 litters) or anecdotal records, although fostering in African wild dogs (*Lycaon pictus*—McNutt et al. 2008), coyotes (Kitchen and Knowlton 2006), and wolves (*Canis lupus*—Schultz et al. 2007; Jansson et al. 2015; Scharis and Amundin 2015) has greatly advanced our understanding of factors required for successful cross-fostering. Kitchen and Knowlton (2006) reported that the age at which captive-born fostered pups were introduced to captive recipient litters influenced survival rates and that fostered pups > 6 weeks old did not survive. Survival of fostered gray wolf pups has been ambiguous. Some pups > 4–5 months old survived into adulthood while other pups, of the same litter, did not survive (Bradley et al. 2005; Schultz et al. 2007). Fostering young pups increases the probability of survival and success. For example, captive-born gray wolf pups that were only 4–6 days old were fostered into captive recipient litters, were readily accepted by the foster female, and had high survival (Scharis and Amundin 2015). The Mexican wolf (*Canis lupus baileyi*) population in the southwestern United States was founded by 7 individuals resulting in a highly inbred population (Harding et al. 2016). Cross-fostering of 2 wild pups (1 female and 1 male) to a wild recipient litter of 3 pups resulted in the survival of all 5 pups for at least 8 months, suggesting that cross-fostering has the potential to increase litter size and subsequently population size of this endangered canid (Harding et al. 2016).

The potential benefits associated with fostering nonmaternal offspring include improved genetic fitness for a population and reduced inbreeding depression (Jansson et al. 2015), in addition to the numerous advantages associated with living in groups (Kokko et al. 2001; Ausband et al. 2016; Lehtonen and Jaatinen 2016). The gray wolf in Sweden is descended from 5 individuals and is highly inbred, but Jansson et al. (2015) suggested that augmentation of wild recipient litters from captive fostered litters should potentially reduce the inbreeding coefficient.

We summarized data on age, litter size, sex ratio, and survival to 3 and 12 months of age for captive-born pups fostered into captive recipient litters, and survival to 5 and 12 months of age for captive-born pups fostered into wild recipient litters. To successfully augment a wild population, fostering should not be deleterious to the recipient litter; therefore, we examined the same parameters for pups within the recipient litter in the wild. In addition, as a "control," we documented the same metrics for an equal number of litters of wild-born red wolf pups not involved in a fostering event (i.e., control litters). These parameters were used to evaluate the success and utility of cross-fostering red wolf pups that were captive-born into litters of captive-born and wild-born red wolves.

Materials and Methods

Red wolf pups involved in fostering events were born and fostered at 11 facilities across the United States: Beardsley Zoo, Connecticut; Brevard Zoo, Florida; Cape Romain National Wildlife Refuge, South Carolina; Dan Nicholas Nature Center, North Carolina; Great Smoky Mountains National Park, Tennessee; Lincoln Park Zoo, Illinois; Miller Park Zoo, Illinois; North Carolina Zoo, North Carolina; Oglebay Zoo, West Virginia; Point Defiance Zoo and Aquarium, Washington; and the Red Wolf Recovery Area, North Carolina. Pups fostered into wild wolf litters were released into 2 locations: 1 fostering event in the Great Smoky Mountains National Park, Tennessee, and 14 fostering events augmenting wild red wolf litters in the Red Wolf Recovery Area located on the Albemarle Peninsula in northeastern North Carolina. For descriptions of the study areas and history of recovery efforts in these 2 sites, see Lucash et al. (1998) for Great Smoky Mountains National Park, Tennessee, and Bohling and Waits (2015) and Gese et al. (2015) for the Red Wolf Recovery Area, North Carolina.

We considered the location of source and recipient litters, litter sizes, and age of the pups as initial factors before fostering attempts; age of captive-born pups was known from birth date. We introduced captive-born fostered pups only to captive recipient litters that had successfully raised at least 1 litter to adulthood (Green et al. 2002). History of successfully raising litters of wild recipient parents was not available. We attempted to match as closely as possible the ages of foster pups and pups in recipient litters and in all fostering events; the eyes of fostered and recipient litter pups were closed or had just opened (i.e., pups were 10–14 days old—Kreeger 2003). Fostered pups transferred to captive recipient litters did not have their scents masked nor did animal care staff; however, fostered pups transferred to wild recipient litters were handled by personnel wearing latex gloves.

Captive-born pups fostered into captive recipient litters.—We housed wolves as mated pairs in outdoor enclosures (450–900 m^2) containing natural substrate, foliage, and artificial dens. Half (4 of 8) of the sires and half (4 of 8) of the dams of fostered pups had at least 1 litter before the fostering event. The time between removing a fostered pup from a natal litter to placement into a recipient litter ranged from several minutes to approximately 6 h. Short-duration fostering events required a simple transfer of a fostered pup(s) from one enclosure to another enclosure within the same facility. The event with the longest interval (6 h) required animal care staff from the Brevard Zoo (Florida) accompanying 2 female pups on a commercial airline to a recipient litter at the Beardsley Zoo (Connecticut).

Identification of fostered pups following placement in a recipient litter was possible based on sex (e.g., 1 male pup fostered to recipient den with 3 females) or by a small patch of pelage marked with animal tattoo ink (Ketchum Mfg. Co. Inc., Lake Luzerne, New York). We observed the activity level of all pups daily for 5–7 days following placement in a recipient litter. To assess development, we obtained weights for all pups in recipient litters to ensure neonate growth was consistent among litter mates. Before fostering, we determined that if a fostered pup was isolated from the litter by recipient parents or if consistent weight loss was recorded, the pup would be removed. No fostered pups were rejected other than a single pup that disappeared the day following placement. The percentage of fostered pups surviving to 3 and 12 months of age was the measure of success for the captive fostering events.

Captive-born pups fostered into wild recipient litters.—Reproductive female red wolves in the wild were foot-hold trapped, fitted with a very high frequency (VHF) radiocollar (Telonics, Inc., Mesa, Arizona) and monitored daily from late March to May to identify den sites; fostering events occurred in April and May. Females that were not radiocollared but occupied known den site locations that had previously raised pups, or that were in breeding pairs with stable territories and had an adult female with proven rearing success, were also monitored. All female and male wolves involved with fostering captive pups were born in the wild with the exception of 1 female and 3 males. Additionally, most adults receiving fostered pups in the northeastern North Carolina population had at least 1 litter before the fostering event with the exception of 1 female and 2 males (but were paired with experienced mates). Only the pair involved with the fostering event in the Great Smokey National Park had not raised a prior litter. If a wild litter was genetically determined to be red wolf-coyote hybrids, the hybrid litter was removed and captive-born red wolf pups were placed in the den site (i.e., litter replacement). If a wild litter was considered small in number (but not a hybrid litter), captive-born pups were fostered into the wild litter (i.e., litter augmentation). To avoid facilitating a competitive advantage to either captive or wild pups, we matched the sex ratio and age of the fostered pups as close as possible to the age of the wild-born litter of pups (Kitchen and Knowlton 2006); age of wild-born pups was estimated from body measurements and estimated whelping date. We moved captive-born pups to the den location of the recipient wild litter as soon as possible to promote acceptance of the fostered pups into the litter. We implanted each captive pup with a passive integrated transponder (PIT) tag (Eidap, Inc., Sherwood Park, Alberta, Canada) inserted subcutaneously between the shoulders prior to placement in the den. All capture and handling procedures were in accordance with guidelines endorsed by the American Society of Mammalogists (Sikes et al. 2016).

After placing pups into a den, the wild dam was monitored daily by radiotelemetry for 3–5 days to confirm her return to the den site. Although it is common for wild red wolves to move their pups at this age, we continued to observe the movements of the dam remotely and only attempted to verify the survival of the fostered pups during the fall trapping season approximately 5 months following the fostering event. At this time, juvenile wolves were large enough to be safely trapped and equipped with radiocollars. The outcome of captive-born to wild fostering events was considered successful only when a fostered individual was trapped, equipped with a radiocollar, and released at the capture location. If the pups were not captured in the fall, the fate of the pup was classified as "unknown fate." We estimated the number of pups surviving to 5 and 12 months of age for both the fostered pups and the pups in the recipient litter as a measure of success of the fostering event, as well as a measure that cross-fostering is not deleterious to the pups in the recipient litter. Recapturing, radiocollaring, and telemetry flights of fostered and recipient pups continued as part of the overall red wolf monitoring program to assess survival, causes of death, timing and distance of dispersal movements, and reproduction, mainly litter size (Gese et al. 2015). Radiocollared wolves were monitored 2–3 times/week, allowing for the early detection of a mortality signal and facilitating recovery of the carcass to determine the cause of death. If applicable, a field necropsy was conducted, or if the cause of death was not apparent, the carcass was examined by a veterinary pathologist.

Wild-born red wolf pups as "control" litters.—As a comparison to fostered pups and pups in the recipient litters, we evaluated the fate of the pups from an equal number (*n* = 15 litters) of wild-born red wolf litters not involved in a cross-fostering event (i.e., control pups). We then compared the percentage of pups surviving to 5 and 12 months of age, and the life span of pups surviving > 1 year among the 3 categories: fostered, recipient, and control pups. For clarity, fostered pups were pups that were captive-born and placed into a wild red wolf den (either complete replacement of a hybrid litter, or augmentation of an existing red wolf litter). Pups in recipient litters were wild-born pups in which fostered pups were placed. Control pups were wild-born pups that were not involved in a fostering event. The control litters from the Red Wolf Recovery Area were randomly chosen from the entire data set of red wolf litters, but stratified to match the number of fostered litters within each year and management zone (Gese et al. 2015) to reduce the influence of annual and geographical variation in survival rates. Similar to the fostered and recipient pups, the surviving control pups were recaptured, radiocollared, and relocated as part of the overall red wolf monitoring program to assess survival, causes of death, timing and distance of dispersal movements, and reproduction, mainly litter size (Gese et al. 2015). Radiocollared wolves were monitored 2–3 times/week allowing for the early detection of a mortality signal and facilitating recovery of the carcass to determine the cause of death. If applicable, a field necropsy was conducted, or if the cause of death was not apparent, the carcass was examined by a veterinary pathologist.

Statistical analyses.—For captive-born pups fostered into wild litters, we examined differences in the percentage of pups from the 3 treatment groups (i.e., fostered pups, pups in recipient litters, pups in control litters) surviving to 5 and 12 months of age with contingency tables and chi-square tests (Zar 1996). This comparison was performed for pups with known fates (i.e., complete fates), as well as adding pups with unknown fates that were assumed to be deaths. Chi-square tests also were used to examine where dens, in terms of landownership (federal, state, private), of fostered and control litters were located; the proportion of fostered and control pups that dispersed; the proportion of different causes of death between fostered and control pups; and the proportion of landownership (federal, state, private) between fostered and control pups in relation to where they died. We determined landownership using state GIS databases (Gese and Terletzky 2015). Differences in litter size, age at the time of dispersal, and distance of dispersal movements between fostered and control pups were determined with a Student's *t*-test (Zar 1996).

Results

Captive-born pups fostered into captive recipient litters.—There were 8 events involving 12 fostered pups between captive-born red wolf pups and captive-born red wolf recipient litters (Table 1). The mean age of fostered pups was 10.7 ± 2.7 days (*SD*) with the youngest pups 8 days old and the oldest pups 16 days old. Single pups were the most common (62.5%) number of pups fostered, followed by 2 fostering events with 2 pups (25.0%), and a single fostering event involving 3 pups. There was an equal sex ratio (6 F:6 M) among the 12 fostered pups. The mean age of pups in captive recipient litters was 8.9 ± 5.6 (*SD*) with the youngest litters 4 days old and the oldest litter at 19 days old. Recipient litters, before fostering pups, consisted of 3 litters of a single pup, 3 litters of 3 pups, 1 litter of 2 pups, and 1 litter of 4 pups. The sex ratio of the 18 pups in recipient litters was 7 females to 11 males (Table 1). The largest age difference between fostered pups and recipient litter pups was 7 days with the fostered pups being older. Including the fostered pups, the sex ratio of the 30 pups in recipient litters was 13 females to 17 males.

The overall percentage of fostered pups surviving in the recipient litters to 3 months of age was high (91.7%; 11 of 12 pups). This single unaccounted pup may have been eaten by the recipient litter dam, although 1 of the 2 siblings from this individual's natal litter was stillborn and the other disappeared 8 days postpartum. Thus, this pup may have been medically compromised; however, the cause of mortality could not be verified because of the disappearance of the body 1 day following insertion into the recipient den. The percentage of fostered pups surviving to 12 months of age remained 91.7% (Table 1).

Captive-born pups fostered into wild recipient litters.—There was a total of 15 events involving 31 captive-born pups fostered into wild recipient litters (Table 2). Four recipient litters were

Table 1.—Age, litter size, and sex ratio of fostered pups and pups in recipient litters, and percent surviving of captive red wolf (*Canis rufus*) pups fostered into captive recipient litters.

Fostered pups			Pups in recipient litter			Combined litter			% fostered pups surviving	
# fostered	Sex ratio (F:M)	Age (days)	# prior to event	Sex ratio (F:M)	Age (days)	Final # pups	Final sex ratio (F:M)	Age difference (days)[a]	@ 3 months old	@ 12 months old
1	1:0	11	3	0:3	11	4	1:3	0	100	100
3	1:2	8	1	0:1	7	4	1:3	+1	100	100
1	0:1	8	2	2:0	10	3	2:1	−2	100	100
1	1:0	16	3	0:3	19	4	1:3	−3	100	100
2	1:1	11	3	2:1	4	5	3:2	+7	100	100
2	2:0	14	1	0:1	11	3	2:1	+3	100	100
1	0:1	9	4	3:1	4	5	3:2	+5	0	0
1	0:1	11	1	0:1	7	2	0:2	+4	100	100

[a] Age difference is the number of days older or younger the fostered pups were as compared to pups in the recipient litter.

Table 2.—Age, litter size, sex ratio, and percent pups surviving of fostered pups and pups in recipient litters for events involving captive red wolf (*Canis rufus*) pups fostered into wild recipient litters. NA: not applicable, as this was a hybrid litter and all pups were removed.

Fostered pups					Pups in recipient litter					Combined litter		
# pups	Sex ratio (F:M)	Age (days)	% survive to 5 months	% survive to 12 months	# pups	Sex ratio (F:M)	Age (days)	% survive to 5 months	% survive to 12 months	Final # pups	Final sex ratio (F:M)	Age difference (days)[a]
2	0:2	5	50	50	3	1:2	9	100	100	5	1:4	−4
5	2:3	11	100[b]	100[b]	NA	NA	NA	NA	NA	5	2:3	NA
2	1:1	14	100	100	2	0:2	15	100	100	4	1:3	−1
1	1:0	17	100	100	4	0:4	18	100[c]	50[c]	5	1:4	−1
1	1:0	18	100	100	2	1:1	4	100	100	3	2:1	+14
4	3:1	15	100	75	NA	NA	NA	NA	NA	4	3:1	NA
1	1:0	7	100	100	1	0:1	6	Unk	Unk	2	1:1	+1
2	2:0	7	100[d]	100[d]	1	0:1	6	Unk	Unk	3	2:1	+1
2	2:0	7	Unk	Unk	3	1:2	11	100[e]	100[e]	5	3:2	−4
2	1:1	7	100	100	2	1:1	11	100[d]	100[d]	4	2:2	−4
2	1:1	13	Unk	Unk	2	2:0	14	100[d]	100[d]	4	3:1	−1
2	2:0	13	Unk	Unk	NA	NA	NA	NA	NA	2	2:0	NA
2	1:1	7	Unk	Unk	3	2:1	7	100[f]	100[f]	5	3:2	0
1	1:0	10	100	100	2	2:0	11	100[d]	100[d]	3	3:0	−1
2	2:0	10	Unk	Unk	NA	NA	NA	NA	NA	2	2:0	NA

[a] Age difference is the number of days older or younger the fostered pups were as compared to pups in the recipient litter.
[b] Known fate of 3 out of 5 pups.
[c] Known fate of 2 out of 4 pups.
[d] Known fate of 1 out of 2 pups.
[e] Known fate of 2 out of 3 pups.
[f] Known fate of 1 out of 3 pups.

determined to be hybrids and these pups were removed. Thus, the fostered pups were considered litter replacements. The other 11 events involved litter augmentation (i.e., adding fostered pups to an existing red wolf litter). The mean age of fostered pups was 10.8 ± 3.7 days with the youngest pups at 5 days old and the oldest pups at 18 days old. Pairs of pups were the most common (56.2%) number of pups fostered, followed by a single pup being fostered (31.2%), 3 pups in 1 event, and 5 pups in another event (Table 2). The number of captive-born pups fostered had more females than males (21 F:10 M). The mean age of pups in wild recipient litters was 10.9 ± 4.2 days with the youngest litter at 4 days old and the oldest litter at 18 days old. The largest age difference between the fostered pups and the wild recipient litter pups occurred when the fostered pups were 14 days older. Before having the hybrid pups removed and the fostered pups added, the mean size of wild recipient litters was 3.4 (± 2.1 *SD*) pups and ranged from litters with a single pup to a litter with 9 pups. However, after removing the 4 recipient litters determined to be hybrids, the mean litter size was 2.4 (± 0.8) pups at the time of fostering. For the wild recipient litters, the sex ratio was 10 females to 15 males (Table 2). The resulting litter size containing fostered and recipient pups ranged from 2 to 5 pups, well within the range of litter sizes for red wolves (Lockyear et al. 2009).

The fate of 8 pups fostered into the 15 wild litters was unknown at 5 and 12 months of age (Table 2). Overall, the percentage of "known fate" pups fostered into wild red wolf litters, or replacing hybrid litters, surviving to both age 5 and 12 months was high (Table 3). However, if pups with unknown fates are considered deceased, then the percentage of fostered pups surviving to 5 and 12 months was lower (Table 3). Unfortunately, the fate of some pups remained unknown as they were never recaptured in the recovery area. One litter with complete survival information had 1 fostered pup die before 3 months of age, but a second fostered pup survived to at least 12 months. Both pups were handled 28 days after placement in a recipient den; however, 1 pup disappeared after movement of the litter by the recipient parents (Table 2). Notably, of 16 fostered pups known to survive > 12 months of age, these individuals lived to an average age of 5.6 years, and 9 animals whelped or sired a total of 26 litters in the wild.

Table 3.—Percentage of fostered, recipient, and control red wolf (*Canis rufus*) pups with known fates and unknown fates assumed to be deaths surviving to 5 and 12 months of age.

Fate Treatment group	*n* pups	% surviving to 5 months	% surviving to 12 months
Known fate			
Fostered	18	94.4	88.9
Recipient	15	100	93.3
Control	35	100	82.0
Known fate and unknown fate assumed dead			
Fostered	31	54.8	51.6
Recipient	25	60.0	56.0
Control	66	59.1	48.5

Since cross-fostering is meant to assist population recovery of this endangered carnivore, we examined whether augmenting existing litters could be deleterious to the recipient litter. For pups of known fate in the recipient litters, the percentage of pups surviving to 5 months (100%) and 12 months (93.3%) was similarly high as the fostered pups (Table 3). When considering the pups with unknown fates as deaths, the percentage of pups in the recipient litters surviving to 5 months (60%) and 12 months (56%) was similar to the percent survival of the fostered pups. Of 15 recipient pups known to survive > 12 months of age, these individuals lived to an average of 4.6 years of age.

Why some fostered individuals survived far into adulthood, while others did not live to 12 months of age is not readily apparent (Table 2). The percentage of fostered pups surviving to 12 months of age within the 4 litters that were replacements for the hybrid litters that were removed (i.e., no competition from a recipient litter) was 85.7% (6 of 7 pups) for pups with known fates, and 46.1% (6 of 13 pups) when including pups with unknown fates. For 8 litters of fostered pups that were equal to (0 age difference), greater than (> 1 day age difference), or only 1 day different (−1 day age difference) from the pups in the recipient litter, survival to 12 months was 100% (7 of 7 pups) for pups with known fates and 58.3% (7 of 12 pups) when including pups with unknown fates. For the 3 litters in which the fostered pups were much younger than the recipient litter (i.e., −4 days age difference), the number of known fate pups surviving to 12 months of age was 75% (3 of 4 pups) and when including pups with unknown fates as deaths, the percent survival was 50% (3 of 6 pups).

Comparison of fostered, recipient, and control litters.—We analyzed data from 15 litters containing 66 wild-born red wolf pups as the "control" group for comparison to the fostered pups and pups in recipient litters. The percentage of pups surviving to 5 months of age was similar among fostered pups, pups in recipient litters, and pups in control litters when using pups with known fates ($\chi^2_2 = 3.042$, $P = 0.218$; Table 3) and was similar across groups when including pups with unknown fates as deaths ($\chi^2_2 = 0.199$, $P = 0.905$; Table 3). The percentage of pups surviving to 12 months of age also was similar among fostered pups, pups in recipient litters, and pups in control litters when using pups with known fates ($\chi^2_2 = 1.308$, $P = 0.520$; Table 3) and was similar across groups when including pups with unknown fates as deaths ($\chi^2_2 = 0.420$, $P = 0.810$; Table 3). Even though the percent of pups surviving to 12 months of age was similar among the 3 groups, life span differed ($F_{2,58} = 4.49$, $P = 0.015$) with pups from the control litters living an average 3.3 years (± 1.97 *SD*; $n = 32$ pups), recipient pups living to a mean of 4.6 years (± 2.62; $n = 14$ pups), and fostered pups living to an average of 5.6 years (± 3.16; $n = 15$ pups).

The greatest difference among the groups was the fostered pups living 2.3 years longer than the control pups. We examined several factors that may explain this disparity. First, we examined where dens were located as differences in landownership could create more risky landscapes. Results showed similar use of federal, state, and private lands between the 2 cohorts (Table 4). Second, we examined if smaller litter sizes could give pups a competitive advantage later in life, and found that the fostered litters were slightly smaller than the control litters (Table 4). Third, we examined the possible influence of dispersal since dispersal into unfamiliar areas carries a decrease in survival. We had anticipated that the control pups would have a higher dispersal rate, but found the percentage of pups dispersing was dissimilar with more fostered pups dispersing from their natal home range (Table 4). The age at which the pups dispersed and the distance they dispersed was similar (Table 4). Last, we examined aspects of mortality and found the causes of mortality were similar between fostered and control pups (Table 4), suggesting that different life spans were not related to agents of mortality. Human-caused sources of mortality included gunshot, foul play, poisoning, trapping, and vehicle collisions. The type of landownership where pups were killed also was similar between fostered and control pups (Table 4), suggesting equal exposure to risk on the landscape.

Discussion

The survival of captive-born red wolf pups fostered into captive and wild recipient litters was high for animals of known fate. When we considered red wolf pups with unknown fates as having perished, then the percentage of pups surviving to

Table 4.—Landownership at the den, litter size, dispersal rate, age at dispersal, distance of dispersal, causes of mortality, and landownership at death site for fostered and control red wolf (*Canis rufus*) pups, with test statistic and *P*-value.

Metric	Fostered pups	Control pups	Test statistic	*P*-value
Landownership at den (%)				
Federal	43	60	$\chi^2_2 = 1.64$	0.44
State	7	0		
Private	50	40		
Litter size (*n* pups)	3.7 ± 1.2	4.4 ± 1.5	$t = 1.36$	0.09
Dispersal rate (%)	75	45	$\chi^2_1 = 4.13$	0.042
Age of dispersal (months)	17.6 ± 5.3	20.9 ± 11.7	$t = -0.91$	0.18
Distance of dispersal (km)	29.5 ± 17.0	30.9 ± 15.2	$t = 0.05$	0.48
Causes of mortality (%)				
Human	71.2	67.7	$\chi^2_2 = 0.09$	0.95
Natural	14.4	14.7		
Unknown	14.4	17.6		
Landownership at death site (%)				
Federal	7.1	2.9	$\chi^2_2 = 0.48$	0.79
State	7.1	5.9		
Private	85.7	91.1		

12 months of age declined, but was still greater than 50% survival. Stoskopf (2012) surmised that 30–35% survival to maturity among a cross-fostered litter was a positive contribution to a population. Most individuals fostered from captivity into wild red wolf litters were known to have survived past weaning, remained with their surrogate pack, and several demonstrated movement and dispersal behaviors comparable to wild-born red wolves. For example, following dispersal from her natal home range, 1 fostered female red wolf died at 23 months of age from complications associated with pregnancy. This individual's fostered male sibling also dispersed from his natal range and sired a litter of 8 pups.

Overall, of the fostered red wolf pups known to have survived a year in the wild, these individuals lived to an average age of 5.6 years, and several of these animals produced or sired litters in the wild as adults. The several fostered pups growing to adulthood, successfully mating, and producing wild red wolf litters indicate the utility of cross-fostering, as these individuals learned the behavioral skills necessary to survive and reproduce, thereby contributing to the red wolf population. Equally important to the recovery of any endangered species was the finding of similar survival rates among the pups in the recipient litters, further demonstrating that fostering was not deleterious to the existing wild litter that received the fostered pups.

Why the control pups had a lower life span compared to the fostered and recipient pups remains unclear. Where the pups were placed, when they dispersed, how far they dispersed, what they died from, and where they died did not appear to be factors determining the observed difference in life span between fostered and control pups. Whether the slight difference in litter size among the fostered litters translated to longer life span remains a possibility. Therefore, we concluded that while survival up to 12 months of age was similar between the cohorts, why fostered animals lived on average 2 years longer than the control animals requires further investigation.

The release of adult red wolves from the captive program to initiate new packs or supplement the wild population has had mixed success (van Manen et al. 2000; Phillips et al. 2003; Gese et al. 2015). Furthermore, acclimation to humans and human-related activates may have resulted in increased mortality risk (e.g., vehicle collision, gunshot—Hinton et al. 2017). Regardless of the age when captive-born individuals were introduced into a wild population, mortality risks were unavoidable for free-ranging animals. Introducing pups from captivity into wild red wolf litters can provide fostered individuals the benefit of learning survival and social skills from wild parents and other pack members, can be used as replacements for hybrid (red wolf-coyote) litters, and can augment population size in the recovery area and potentially facilitate increased genetic diversity in an inbred population. The recovery program also successfully fostered a litter of pups from one wild litter following the death of the breeding female into another wild litter, thereby keeping that litter alive and integrated into the wild population.

Kitchen and Knowlton (2006) recommended cross-fostered coyote pups be placed in recipient litters as young as possible (< 1 week) to facilitate acceptance by the pack. In our study, the pups that did not survive to 5 months were not older than 9 days, nor was the age difference between the fostered pups and the recipient litter pups more than 9 days. Conversely, we recorded a 16-day-old pup was successfully accepted into a captive recipient litter and an 18-day-old pup was successfully accepted into a wild recipient litter. The fostering success of pups older than a week but younger than 3 weeks suggests that the age of fostering is more plastic than previously thought. We did not attempt cross-fostering with pups older than 18 days, so we were not able to assess the oldest day at which fostering could be successful. However, Kitchen and Knowlton (2006) reported that fostered coyote pups > 6 weeks old did not survive in their recipient litter.

Stoskopf (2012) made several recommendations to reduce den disturbance (e.g., scent transfer, timing insertions when adults are away from the den, minimizing the number of personnel involved on-site) and thereby increase the success of fostering pups into wild litters. We further recommend the fostered pups be well fed (i.e., bottle fed) before insertion as they cry when hungry and could potentially attract predators while the recipient female is away from the den. We also recommend minimizing the time spent at the den to avoid overly disturbing the parents and risk abandonment of the litter, and consider the weather conditions at the time of fostering (e.g., dry conditions if the pups are in a day bed exposed to the elements, rather than in an excavated den). To ensure success and survival of cross-fostered pups, we recommend that pups be fostered between the ages of 4 to 21 days (but urge using pups < 14 days old, if possible), and that fostered pups be of similar age to the recipient litter (Kitchen and Knowlton 2006; Stoskopf 2012). The similar survival rates among the fostered pups that varied in age relative to the recipient litter, or had no competition from a recipient litter, indicated there was no competitive advantage when the fostered pups were similar in age or older. However, the numbers of litters were small, thereby inference was limited, and future investigations among other canid species are warranted.

We concluded that cross-fostering was successful at augmenting litter size for red wolves without any deleterious effects on recipient litters, illustrating cross-fostering as a potential management tool for increasing populations of other endangered carnivores. Most research on cross-fostering of canid species has been limited to small sample sizes or anecdotal records, although fostering in African wild dogs (McNutt et al. 2008), coyotes (Kitchen and Knowlton 2006), and gray wolves (Schultz et al. 2007; Jansson et al. 2015; Scharis and Amundin 2015) has advanced our understanding of the factors required for successful cross-fostering within these canid species. We demonstrated that cross-fostering red wolf pups was an effective rearing technique that has assisted captive and wild population management and could complement other management strategies (Stoskopf et al. 2005; Gese et al. 2015; Gese and Terletzky 2015) when supplementing endangered canid populations is required. Cross-fostering pups also could provide a simple process for maintaining genetic diversity of both captive and wild populations where units are disjunct from one another.

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