Cross-fostering has been used in bird species to evaluate kin recognition and mate choice (Clayton, 1987; Todrank and Heth, 2001; Slagsvold et al., 2002). Fostering has also aided conservation efforts in marsupials (Sterneberg and Rose, 2002), birds (Powell and Cuthbert, 1993; Drewien and Bizeau, 1977), and rodents (Murie et al., 1998).

Cross-fostering of canid pups has several applications for enhancing reproduction in recovery programs of threatened and endangered species. Fostering young can aid conservation efforts by introducing captive-bred young into wild populations to increase the population numerically (US Fish and Wildlife Service, 2004a) or enhance genetic diversity, and provide rearing opportunities for wild young that have been orphaned. Introducing animals into a population as pups allows them to learn natural behaviors, increasing their chances of survival and successful reproduction over animals introduced as adults (US Fish and Wildlife Service, 2004b).

Cross-fostering has been attempted in captive canids during opportunistic events. Fostering attempts have been made in red wolves (*Canis rufus*) with all fostered wolves surviving to weaning (Waddell et al., 2002). In addition, the litter of a female gray wolf (*Canis lupus*) was introduced to another female who had had her pups removed (Goodman, 1990). There have been occasional attempts at cross-fostering canid pups into wild populations. One of two red wolf pups fostered into a wild litter in 1998 survived to weaning (Waddell et al., 2002).

Two captive-born red wolf pups were inserted into a wild litter of two pups in 2002 (US Fish and Wildlife Service, 2004a). Both pups were accepted by the foster mother, remained with the pack, and were seen to exhibit natural behaviors as yearlings. Cross-fostering has also been attempted with Australian dingoes (*Canis familiaris dingo*, pers. comm. L. Corbett) and the endangered African wild dog (*Lycaon pictus*, McNutt personal communication). In 2002, one 6-week-old African wild dog pup was introduced into a litter of five pups. The mother nursed the pup immediately and the pup was still alive two months later.

Thus, there are good indications that cross-fostering can be successful in canids as a population management strategy for threatened and endangered species, and as a tool to facilitate experimental designs. However, information is needed on the success rates and factors influencing success of fostering procedures, especially in threatened species for which controlled studies are logistically difficult. While the coyote (*Canis latrans*) is not threatened, the species makes a good model for other canids. Coyotes share numerous behavioral and physiological attributes with other threatened canids that are relevant to the likelihood of success of fostering, including dominance hierarchies, territoriality, and social suppression of reproduction (e.g., Macdonald and Sillero-Zubiri, 2004). Mating patterns and parental care are often similar among canid species; the pervasive mating system in canids is obligatory monogamy (Kleiman, 1997), canids usually breed once a year, young have a relatively long period of dependency, and bi-parental care is common (Kleiman and Eisenberg, 1973). Since the 1970s, numerous studies have suggested that collaborative care of young may be a fundamental aspect of canid sociology (Macdonald et al., 2004). The use of information gathered on factors influencing fostering success in coyotes for other canids is further warranted by the fact that successful fostering attempts have been made in red wolves and African wild dogs (Waddell et al., 2002; US Fish and Wildlife Service, 2004a; McNutt personal communication). We provide information from a controlled study on the success rates that could be expected from cross-fostering efforts and the effects of fostering on dominance status of litter mates. In addition, we examined the effect of pup age on the probability of acceptance of fostered young.

2. Methods

Coyotes are a monogamous species and it has been shown that mated pairs breed for life (Bekoff and Wells, 1980). Litter sizes generally range between 3 and 12 with both sexes participating in parental care. Pups are weaned between 5 and 7 weeks. Sixteen adult coyote pairs and their litters were maintained in facilities (0.1 ha pens) at the USDA Predator Research Facility, Millville, Utah. Coyotes were fed identical diets obtained from a furbreeders cooperative. All, but 1 parent was captive-bred at the facility, and parents were generally experienced breeders with between 1 and 5 years breeding experience. None of the foster pups were genetically related to foster parents.

We investigated the success of cross-fostering under two regimes: augmenting litters by adding two pups to existing litters (litters then consisted of two fostered pups and two or three natal pups), and complete litter replacement. All litters were standardized to four or five pups in order to avoid bias of litter size in weight and survival measurements. Thus pups from large litters were augmented into small litters, and in one case, two pups from a large litter were removed from the study. We assessed the success of augmentation for pups at three ages: ⩽1 week (4 litters); 3–4 weeks (3 litters); and 6–7 weeks (2 litters). Efforts were made to augment existing litters with pups of similar ages (difference in ages was ⩽3 days for 1-week augments, ⩽9 days for 3–4-week augments, ⩽4 days for 6–7-week augments, and ⩽6 days for replacements). This also reduced the likelihood of introducing a bias from differences in weights of fostered and natal pups; weights of treatment groups were in fact similar (Fig. 1). Where possible, the

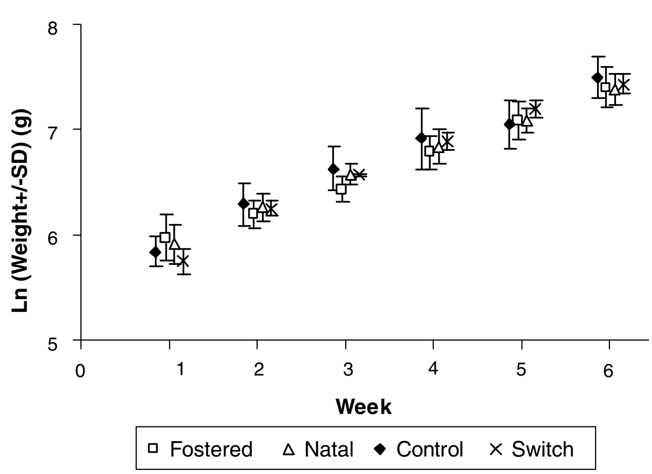

Fig. 1 – Mean weight gains of natal and fostered coyote pups in control, replaced and 1- and 3-week augmented litters. Kitchen and Knowlton: cross-fostering among canids.

sex-ratio of augmented litters was equalized. In addition, four litters were completely replaced when pups were <10 days old and four litters were used as control litters. Adult coyotes remained in the pens during all augmentations and replacements to minimize disturbance.

Pups were marked for individual identification by shaving small patches of pelage from various parts of their bodies. Upon introduction of pups to the foster parents, the initial behavioral response of the parents was monitored by observing interactions of parents with foster pups and with natal pups if present. Growth patterns of all pups were assessed by weighing pups twice a week until 3 weeks of age and once per week thereafter. Pups were monitored through 6 weeks of age, allowing enough time for parents to accept or reject pups. The slope of weekly weight gains of pups within litters was log transformed and compared among the treatments using a autoregressive repeated measures analysis of variance. Pup survival rates were compared among the various treatments. Augmentations of 6–7-week-old pups were discontinued after the first two fostering attempts failed.

We obtained preliminary data on the 6-week dominance status of pups within augmented litters to assess the social effects of fostering. All dominance related interactions (e.g., pins, hip slams, and threats) between pups were recorded during ⩾four 45-minute observation sessions until confidence in dominance rankings was achieved. Observations were made from an observation building to minimize disturbance to animals, and were done in the morning to coincide with a high activity period of the pups. Rankings of fostered versus natal pups were assessed using a Fisher's exact test due to low sample sizes. Both sexes were combined in the rankings as early hierarchies (determined by 6 months of age) are unisex (Walls Knight and Stokes, 1978).

3. Results

Survival of pups in control litters and replaced litters was similar (Table 1), with two deaths in one litter of control pups, and two deaths in one litter of replaced pups. Causes of mortality were not confirmed due to the disappearance of the bodies (coyotes often eat young after death). All natal pups in augmented litters survived. Survival of fostered pups in augmented litters appeared dependent on the age at fostering. All eight pups fostered into four litters before the age of one week survived through the end of the study period (when pups were 6-weeks old). Two of three attempts at cross-fostering 3–4-week-old pups were successful with all four fostered pups in two litters surviving the study period. The two fostered pups in the third litter disappeared within two days. The four pups fostered into two litters (two pups each) at 6–7 weeks of age died within 24 h. Observations immediately following introductions of the 6–7-week-old pups showed that one foster mother continuously carried a foster pup in a normal body grasp for 20 min after which the pup appeared dead. Foster parents of the other litter interacted nonviolently with the foster pups for one hour with no indications of rejection, but the pups were missing the next day. Subsequently, additional augmentations of 6–7-week-old pups were discontinued.

We detected no evidence surviving foster pups were at any disadvantage. Weight gains were similar among pups in all treatments (control, replaced, natal, and fostered pups; $F_{18,75} = 0.62$, $P = 0.87$; Fig. 1). In addition, 6-week dominance hierarchies obtained for 4 litters (3 litters augmented at one week of age, and 1 litter augmented at three to four weeks of age) suggested fostering did not put pups at a disadvantage in terms of the dominance status achieved within the litter hierarchy (Fisher's exact $P = 0.24$; Table 2). Instead, dominance status appeared somewhat correlated to the weights of the pups.

4. Discussion

Our results indicate cross-fostering (either augmenting or replacing litters) of week-old coyote pups is highly successful, with survival and weight gain of fostered pups similar to natal and control pups. In addition, since all natal pups in augmented litters survived, fostering procedures do not appear to have a disruptive effect on the parents' ability to rear a litter.

The success of cross-fostering may be influenced by the ability of the parents to recognize, and their motivation to persecute, unfamiliar individuals in the litter. Possible mechanisms allowing animals to discriminate between kin and nonkin are 'recognition by association', whereby animals learn during rearing to recognize familiar individuals, and 'phenotype matching' where animals discriminate kin and nonkin based on genetic relatedness by comparing

Table 1 – Survival rates for coyote litters and pups in control litters, replacement litters, and litters augmented at 1, 3, and 6 weeks of age

Treatment	Sample sizes (*n*)			Percent surviving		
	Litters	Pups		Litters[a]	Pups	
		Natal	Foster		Natal	Foster
Control	4	20	–	100	90	–
Replaced	4	–	19	100	–	89.5
Augmented:						
At 5–7 days	4	9	8	100	100	100
At 3–4 weeks	3	7	6	100	100	66.7
At 6–7 weeks	2	6	4	100	100	0

a Litter survival based upon survival of ⩾1 pup.

Table 2 – Six week dominance status of natal and cross-fostered coyote pups in augmented litters

Litter	Rank in dominance hierarchy			
	1	2	3	4
1	Fostered (338; 6)	Fostered (374; 6)	Natal (218; 3)	Natal (220; 3)
2	Fostered (378; 2)	Natal (466; 5)	Natal (410; 5)	Fostered (332; 2)
3	Fostered (464; 5)	Natal (426; 2)	Fostered (436; 5)	Natal (416; 2)
4	Fostered (948; 30)	Natal (944; 21)	Fostered (1046; 30)	Natal (818; 21)
% Fostered	100	25	50	25
% Natal	0	75	50	75
Mean wt (g)	532.0	552.5	527.5	444.0

Number in parentheses indicates the weight (g) and the age (days) of the pups on the day augmentations were made.

phenotypes (Halpin, 1991). The mechanism of kin recognition appears to be species-specific and dependent on the mating system and social organization (Ferkin and Rutka, 1990). However, many mammals show recognition by association (Bekoff, 1981; Sherman and Holmes, 1985; Ferkin et al., 1992) indicating that kin recognition may develop by familiarity in early life as opposed to a genetic basis as predicted by kin selection theory (Hamilton, 1964). Our results indicate genetic relatedness is not a necessity for acceptance of young by parents in coyotes.

The decreasing acceptance of pups as their age increased suggests the mechanism of recognition of young by parents, or at least the sensitivity of recognition, changes as the young develop. Temporal changes in recognition ability have also been documented in other taxa. Holmes and Sherman (1982) found high success in fostering ground squirrels (*Spermophilus beldingi* and *S. parryii*) when introductions were made within the first 3 days of age, and concluded mother-offspring recognition did not develop until juveniles were active above the ground. In bank swallows, the 'signature calls' that make chicks individually distinctive do not develop until nestlings are 15–17 days of age (Beecher et al., 1981), and thus that chicks' vocal cues could not become part of a kin template until young are at least 2 weeks old. The flank gland odors that golden hamsters can use to recognize their kin are not produced by juveniles until about 30 days of age (Algard et al., 1966). In thick-billed murres (*Uria lomvia*), cross-fostering experiments revealed that parents were less likely to foster a foreign chick as the chick aged (Lefevre et al., 1998). Our results also suggest litter augmentations in canids should occur at an early age to minimize rejection by foster parents.

Cross-fostering could be considered successful as a conservation tool if the fostered individuals survive and reproduce within the population. Fostered animals have reproduced in red wolves; one male fostered into the population in 2002 bred in 2004 and one female fostered in the same year became pregnant (US Fish and Wildlife Service, 2004b). Reproductive success in canids is often correlated with dominance status within the resident pack (e.g., Peterson et al., 2002), and studies in birds have found that fostering can negatively influence an individuals chance of achieving dominant status (Hansen and Slagsvold, 2004). However, our observations indicated that fostering did not put coyote pups at a disadvantage in achieving dominant status within the litter. Thus, fostered coyotes initially accepted by foster parents may increase recruitment into the population. Our results are based on low sample sizes, however, and further research is needed to fully assess the effects of fostering, weight, and age on dominance status in coyote pups.

Successful cross-fostering would also facilitate certain types of research. The ability to readily cross-foster young would increase the potential for a wide range of studies that have previously been difficult to conduct in canids. Such studies may involve issues such as kin recognition, mate choice, and the examination of genetic versus environmental influences on behavior. Cross-fostering also allows for standardized litters (litters of similar size, sex ratios, etc.) to be created which may reduce experimental biases in studies.

Our results demonstrate cross-fostering could be a successful management technique for increasing recruitment to populations of endangered canids, introducing genetic diversity into populations suffering inbreeding depression, or for use as a research tool to generate standardized litters for research purposes. Our results, however, suggest success is highly correlated with the age at which young are introduced into foster litters.

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REFERENCES

Algard, F.T., Dodge, A.H., Kirkman, H., 1966. Development of the flank organ (scent gland) of the *Syrian hamster*. American Journal of Anatomy 118, 317–326.

Beecher, M.D., Beecher, I.M., Hahn, S., 1981. Parent–offspring recognition in bank swallows. II. Development and acoustic basis. Animal Behaviour 29, 95–101.

Bekoff, M., 1981. Mammalian sibling interactions: genes, facilitative environments and the coefficient of familiarity. In: Gubernick, D.J., Klopfer, P.H. (Eds.), Parental Care in Mammals. Plenum Press, New York, pp. 307–346.

Bekoff, M., Wells, M.C., 1980. The social ecology of coyotes. Scientific American 242, 130–148.

Christian, J.J., Lemunyan, C.D., 1958. Adverse effects of crowding on lactation and reproduction of mice and two generations of their progeny. Endocrinology 63, 517–529.

Clayton, N., 1987. Mate choice in male zebra finches: some effects of cross-fostering. Animal Behaviour 35, 596–597.

Drewien, R., Bizeau, E.G., 1977. Cross-fostering whooping cranes to sandhill crane foster parents. In: Temple, S.A. (Ed.), Endangered Birds-management Techniques for Preserving Threatened Species. University of Wisconsin Press, Madison, WI, pp. 201–222.

Ferkin, M.H., Rutka, T.F., 1990. Mechanisms of sibling recognition in the meadow voles. Canadian Journal of Zoology 68, 609–613.

Ferkin, M.H., Tamarin, R.H., Pugh, S.R., 1992. Cryptic relatedness and the opportunity for kin recognition in microtine rodents. Oikos 63, 328–332.

Goodman, P.A., 1990. In: A History of Wolf Park 1972–1999Ethology Series, vol. 5. Institute of Ethology, North American Wildlife Park Foundation, Battle Ground, Indiana.

Halpin, Z.T., 1991. Kin recognition cues in vertebrates. In: Hepper, P. (Ed.), Kin Recognition. Cambridge University Press, Cambridge, pp. 220–258.

Hamilton, W.D., 1964. The genetical theory of social behavior. Journal of Theoretical Biology 7, 1–52.

Hansen, B.T., Slagsvold, T., 2004. Early learning affects social dominance: interspecifically cross-fostered tits become subdominant. Behavioral Ecology 15, 262–268.

Holmes, W.G., Sherman, P.W., 1982. The ontogeny of kin recognition in two species of ground squirrels. American Zoologist 22, 491–517.

Huck, U.W., Banks, E.M., 1980. The effects of cross-fostering on the behavior of two species of North American lemmings, *Dicrostonyx groenlandicus* and *Lemmus trimucronatus*: II Sexual behavior. Animal Behaviour 28, 1053–1062.

Kleiman, D.G., 1997. Monogamy in mammals. The Quarterly Review of Biology 52, 39–69.

Kleiman, D.G., Eisenberg, J.F., 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Animal Behaviour 21, 637–659.

Lefevre, K., Montgomerie, R., Gaston, A.J., 1998. Parent–offspring recognition in thick-billed murres (Aves: Alcidae). Animal Behaviour 55, 925–938.

Macdonald, D.W., Creel, S., Mills, M.G., 2004. Canid society. In: Macdonald, D.W., Sillero-Zubiri, C. (Eds.), Biology and Conservation of Wild Canids. Oxford University Press, Oxford, pp. 85–106.

Macdonald, D.W., Sillero-Zubiri, C., 2004. Wild Canids – an introduction and dramatis personae. In: Macdonald, D.W., Sillero-Zubiri, C. (Eds.), Biology and Conservation of Wild Canids. Oxford University Press, Oxford, pp. 85–106.

McGuire, B., 1988. Effects of cross-fostering on parental behavior of meadow voles (*Microtus pennsylvanicus*). Journal of Mammalogy 69, 332–341.

McNutt, J.W. 2002. Fostering of wild dog pups. Personal communication to F.F. Knowlton.

Murie, J.O., Stevens, S.D., Leoppky, B., 1998. Survival of captive-born cross-fostered juvenile Columbian ground squirrels in the field. Journal of Mammalogy 79, 1152–1160.

Peterson, R.O., Jacobs, A.K., Drummer, T.D., Mech, L.D., Smith, D.W., 2002. Leadership behavior in relation to dominance and reproductive status in gray wolves, *Canis lupus*. Canadian Journal of Zoology 80, 1405–1412.

Powell, A.N., Cuthbert, F.J., 1993. Augmenting small populations of plovers: an assessment of cross-fostering and captive-rearing. Conservation Biology 7, 160–168.

Sherman, P.W., Holmes, W.G., 1985. Kin recognition: issues and evidence. In: Holldobler, B., Lindauer, M. (Eds.), Experimental Behavioral Ecology. Fisher Verlag, New York, pp. 437–460.

Slagsvold, T., Hansen, B.T., Johannessen, L.E., Lifjeld, J.T. 2002. Mate choice and imprinting in birds studied by cross-fostering in the wild. In: Royal Society of London Proceedings. Biological Sciences 269, 1449–1455.

Sterneberg, B., Rose, R. 2002. Cross-fostering for marsupial conservation. In: Advances in Ethology; Special Issue: Contributions to the 4th International Symposium on Physiology and Behaviour of Wild and Zoo Animals, vol. 37, Berlin, Germany, 29 September – 2 October. p. 75.

Todrank, J., Heth, G., 2001. Rethinking cross-fostering designs for studying kin recognition mechanisms. Animal Behaviour 61, 503–505.

US Fish and Wildlife Service, 2004a. Fostered red wolf recaptured and released. Red Wolf News 5:1, US Fish and Wildlife Service, Manteo, NC.

US Fish and Wildlife Service, 2004b. Exciting Year for Red Wolf Pups. Red Wolf News 5:2, US Fish and Wildlife Service, Manteo, NC.

Waddell, W., Behrns, S., Lucash, C., McLellan, S. 2002. Intraspecific fostering in the red wolf (Canis rufus). Poster at Carnivores 2002, Monterey, Calilfornia.

Walls Knight, S., Stokes, A.W., 1978. Dominance Hierarchies of Captive Coyote Litters. Final Report to the US Fish and Wildlife Service. Utah State University, Logan, UT.