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Effects of genetic management on reproduction, growth, and survival in captive endangered pygmy rabbits (*Brachylagus idahoensis*)

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A quarter of all lagomorph species worldwide are threatened with extinction. Captive breeding programs, such as that developed for the Columbia Basin (CB) pygmy rabbit (*Brachylagus idahoensis*), sometimes are implemented as emergency conservation measures to restore small, genetically distinct populations. However, small source populations also may have low genetic diversity, which may influence attributes related to fitness, including growth, survival, and reproduction. We used mixed-effects regression models to explore the influence of genetic pedigree (% CB) on pairing success, growth, and survival during the 10-year captive breeding program at Washington State University, which included controlled pairings and outbreeding with pygmy rabbits from Idaho. Pairing success, juvenile growth, and juvenile survival declined with increasing CB pedigree of 1 or both parents, suggesting inbreeding depression among the small number of related founders. Demographic variables such as age, sex, and previous pregnancies, and environmental variables such as month and temperature at birth also were associated with production of pygmy rabbits. Our study illustrates the difficulty of retaining a unique genome of a small source population while simultaneously producing enough rabbits for restoration into natural habitat as part of endangered species recovery programs.

Key words: *Brachylagus idahoensis*, captive breeding, endangered species, fitness, growth, inbreeding, lagomorph, pygmy rabbit, reproduction, survival

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Despite relatively high potential fecundity, a quarter of lagomorph species worldwide are threatened with extinction (Smith 2008), primarily from habitat loss and fragmentation (e.g., Watland et al. 2007; Farías et al. 2008; Hughes et al. 2008; Litvaitis et al. 2008). When in situ methods of conserving small populations of lagomorphs have failed to slow or stop extirpation, ex situ methods such as translocation or captive breeding have been employed to reestablish or augment native populations (e.g., European hares [*Lepus europaeus*—Stamatis et al. 2007], riparian brush rabbits [*Sylvilagus bachmani riparius*—Williams et al. 2008], European rabbits [*Oryctolagus cuniculus*—Arenas et al. 2006], volcano rabbits [*Romerolagus diazi*—Fa and Bell 1990; Campos Morales 2009], riverine rabbits [*Bunolagus monticularis*—Dippenaar and Ferguson 1994], swamp rabbits [*Sylvilagus aquaticus*—Watland et al. 2007], and Lower Keys marsh rabbits [*Sylvilagus palustris hefneri*—Faulhaber et al. 2006]). Still, to date, captive breeding and restoration of endangered lagomorphs has been met with limited success (Fa and Bell 1990; Dippenaar and Ferguson 1994; Campos Morales 2009).

Although the overall success of reintroduction projects is generally low in mammals ($< 50\%$), a global analysis of 183 species on the *IUCN Red List* found that captive breeding and reintroduction was twice as effective as creating protected areas at improving the conservation status of mammals (Haywood 2011). However, projects using captive-bred animals have been significantly less successful than those using translocation of wild animals (Griffith et al. 1989; Wolf et al. 1996; Fischer and Lindenmayer 2000; Jule et al. 2008). Captive populations require intensive use of resources and are usually small, often with fewer than 20 founders (Witzenberger and Hochkirch 2011), and may face low genetic diversity and inbreeding, which can reduce survival, fecundity, and disease resistance

(Roelke et al. 1993; Charpentier et al. 2008; van Coillie et al. 2008; Rabon and Waddell 2010; Cain et al. 2011). Furthermore, captive-bred animals are usually less well adapted for wild conditions because captive breeding over several generations may create unique selection pressures influencing physiological, behavioral, and evolutionary changes that compromise fitness in natural environments (Robert 2009). However, source populations for translocations often differ genetically from animals in the local restoration area, thus captive breeding may help to retain unique, locally adapted gene complexes that influence fitness (Laikre et al. 2010). Captive breeding may be the only option when rarity precludes translocations from other populations, as in European rabbits (Delibes-Mateos et al. 2008), and fecundity and survival are generally higher in captive than in wild populations, which may speed population recovery (Robert 2009). Thus, a better understanding of the factors influencing success of captive breeding programs for rare or endangered populations of lagomorphs is an urgent priority to guide future conservation decisions.

When attempting to recover populations of Columbia Basin (CB) pygmy rabbit, a federally endangered Distinct Population Segment (United States Fish and Wildlife Service 2003) residing in Washington, the recovery team faced trade-offs in preserving a unique genome and avoiding inbreeding depression. The CB population declined precipitously between 1997 and 2001, resulting in capture of only 16 founders from the last remaining wild population (Becker et al. 2011). These founders were highly related (0.33, between a half and full sibling), and the expected heterozygosity (0.40) at 12 microsatellite loci was low compared to that of pygmy rabbits in the core of the range in Oregon, Montana, and Idaho (0.80). The effective population size of the founders was estimated as < 6 animals (Warheit 2004). Nonetheless, translocation from the core range was rejected as a strategy to recover the CB population, because CB pygmy rabbits had been isolated geographically from the core range for thousands of years (Grayson 1987; Lyman 1991). Mitochondrial DNA sequence data from 307 base pairs of cytochrome *b* demonstrated that CB pygmy rabbits had a single haplotype that was not observed in any other population and differed from other haplotypes by 1–3 base pairs (Warheit 2001). Also, data from 10 nuclear DNA microsatellite loci indicated a high degree of differentiation with pairwise F_{ST} values between CB and other populations of 0.29–0.35. In contrast, F_{ST} values between Oregon, Montana, and Idaho were much lower (0.02–0.05—Warheit 2001; United States Fish and Wildlife Service 2003). Consequently, to produce rabbits for restoration with the unique CB pygmy rabbit genome, a captive breeding program was established in 2001 with the 16 CB pygmy rabbit founders at Washington State University (WSU, Pullman, Washington), Oregon Zoo (Portland, Oregon), and Northwest Trek Zoological Park (Eatonville, Washington). No new CB rabbits were ever found to augment the captive population.

After 2 years of unexpectedly low rabbit production at the 3 captive breeding facilities, the CB pygmy rabbit recovery team began a modest outbreeding effort using 4 pygmy rabbits originating from the core range in Idaho to gradually increase genetic diversity, while retaining an average of 75% CB pedigree in the population (i.e., with individuals ranging from 0% to 100% CB) through annual pairing and genetic management plans (Becker et al. 2011). In this study, we conducted a retrospective analysis of captive breeding at WSU from 2001 to 2010. Our objective was to examine the contributions of the CB pedigree (genome) to measures of rabbit production (i.e., pregnancy, litter size, juvenile growth, and survival) relative to other demographic and environmental variables using mixed-effects regression models and model selection. Because of low heterozygosity and high relatedness, we expected pairing success (pregnancies per pairing attempt), litter size, juvenile growth, and juvenile and adult survival in captive-bred pygmy rabbits to decline with increasing % CB pedigree of the pygmy rabbits. We also expected that parents with more experience (older and those with previous pregnancies) would have greater pairing success, litter sizes, and juvenile growth, and that juveniles born at higher temperatures and later in the season would grow faster and survive better.

MATERIALS AND METHODS

Captive population.—The founding captive population of CB pygmy rabbits consisted of 16 rabbits captured from the wild in eastern Washington in 2001–2002 that were housed and bred at WSU, Oregon Zoo, and Northwest Trek Zoological Park. Some rabbits were transferred among facilities each year before the breeding season based on an annual genetic management plan derived from pedigree analysis (Hays and Warheit 2004). Pygmy rabbits from Idaho also were maintained and bred separately in the captive breeding facilities at WSU and Oregon Zoo, initially to develop effective reintroduction techniques (Westra 2004), but beginning in 2003, 4 Idaho rabbits (2 males and 2 females) were included in the CB breeding population creating intercrossed rabbits. In our analysis, we included only CB, Idaho, and intercross rabbits born, bred, or dying at WSU for consistency in record-keeping and husbandry. WSU's Committee for Institutional Animal Use and Care approved all methods under protocol 3097, in accordance with guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

Housing and diet.—Pygmy rabbits were housed in outdoor pens ranging from 4 to 75 m^2 completely enclosed with 1-cm wire mesh with solid or mesh roofs and a layer of 0.5–1 m of compacted soil on the floor. Because of conspecific aggression, rabbits were housed individually except when temporarily paired with a mate, or occasionally in small groups of 2 or 3 in our largest pens. Most pens had a high-definition remote video camera linked to a digital recorder (Open Eye, Spokane, Washington). Average daily outdoor temperatures in Pullman, Washington, were obtained from Weather Underground (Weather Underground 2011).

Rabbits were maintained on balanced grain–forage rabbit pellets fed ad libitum, either purchased commercially or custom-milled at the WSU Animal Sciences Feed Laboratory. Pelleted diets ranged from 16% to 21% crude protein and 30% to 50% neutral detergent fiber. Pelleted diets were supplemented with a variety of fresh greens and big sagebrush (*Artemisia tridentata*) grown in greenhouses on location.

Breeding.—We selected individual males and females for each pairing (i.e., a breeding session when a male was allowed access to a female for potential mating, usually a continuous period of 1–3 days) based on the genetic management plan (Hays and Warheit 2004). We began pairings between mid-February and mid-March, after the males' testes were fully descended. Pairings continued into June, when testes began to regress (Elias et al. 2006).

After each pairing, we monitored females for indications of pregnancy, including digging a natal burrow and using nest materials provided (Elias et al. 2006). In 2002–2003, we attempted another pairing only if no signs of pregnancy occurred by the end of the normal gestation period (i.e., ~ 24 days—Elias et al. 2006), but starting in 2004, we re-paired mates every 1–2 weeks until we saw signs of pregnancy. During the first 2 years of captive breeding, we waited to re-pair rabbits until after juveniles from the previous litter had emerged from their natal burrow and were weaned and removed from the pen. Because rabbits are capable of postpartum estrus (Bautista et al. 2008), from 2005 on, we attempted to maximize the number of pregnancies within a breeding season by pairing females again within a week after giving birth, while their juveniles were still in the natal burrow. In our largest pens, females and males were kept together continuously through the breeding season or until the male was needed to breed with another female. At least 1 male was present in the pen when the female gave birth to allow for postpartum mating. Males remained in the large pens with the females through the end of June. A successful pairing was defined as a pairing that resulted in a confirmed pregnancy.

Pregnancy, birth, and juvenile care.—When a pregnancy was confirmed via behavioral changes, parturition was monitored remotely in pens equipped with video cameras. For females without cameras in their pens, we relied on signs such as fur plucking, disturbance of hay covering the natal burrow entrance, noticeably larger fecal pellets, and trace amounts of blood in the pen to determine that they had given birth (Elias et al. 2006).

From birth until emergence from the natal burrow (~ 15 days—Elias et al. 2006), juveniles were monitored daily using video footage to determine if they were successfully nursing. In pens without video cameras, we left small amounts of hay over the entrance to a natal burrow to determine if the female had opened it during the previous 24 h. Juveniles were normally separated from their mothers within 2 weeks postemergence, depending on whether the dam was aggressive toward emerged juveniles. Juvenile littermates were housed together for 2–12 months, but some individuals and litters were aggressive toward their littermates and were housed separately.

Because juveniles reside in a natal burrow for about 2 weeks after birth, it was difficult to acquire body masses from healthy neonatal juveniles. Still, we obtained body masses from 18 juveniles at birth. After emergence from the natal burrow, most juveniles were weighed approximately weekly, depending on their health and our ability to capture them.

Medical care and postmortem examination.—We measured food consumption, fecal consistency (i.e., firm or loose stools), and behavioral disposition of all pygmy rabbits daily. Sick animals were assessed and treated by a WSU veterinarian, and when animals died, they were routinely submitted to the Washington Animal Disease Diagnostic Laboratory at WSU for gross necropsy and laboratory analyses. Whereas adult rabbits shed spores from coccidia, an intestinal protozoan (*Eimeria brachylagia*), without clinical symptoms (Harrenstein et al. 2006), juveniles were highly susceptible to death from coccidiosis. Beginning in 2003, we administered a variety of coccidiostats prophylactically to adults and juveniles in an attempt to improve survival.

Statistical analyses.—We examined the importance of % CB pedigree in predicting 6 measures of reproduction and survival by creating and selecting models composed of variables expected to influence productivity of breeding rabbits. We examined the probability that a pairing between a male and female produced a pregnancy (i.e., pairing success) using a set of mixed-effect logistic regression models (PROC GLIMMIX—SAS Institute Inc. 2011). To account for multiple pairings within animals, we specified the random effects as individual dams and sires. Our full model included 7 variables, % CB pedigree of dams and sires (0–100%), age of dam and sires (1 or ≥ 2), whether a female had a previous litter that breeding season or not (1 or 0), the month within the breeding season of the pairing (numbered sequentially with February = 1) and the year of the pairing. Because captive breeding over 10 years necessarily employed adaptive changes in diets, housing, breeding strategies, and medical treatments, the factor "year" was treated as a categorical variable and represented unique captive breeding conditions and husbandry practices each year. The variable "month" represented general increases in daylight and temperatures that occurred during the breeding season and was treated as a continuous variable. Age and previous litter were included in the model because we expected older and more experienced parents to have greater pairing success.

We used a set of mixed-effects proportion odds models to examine predictors of 3 categories of litter size—small (1–3), medium (4 or 5), and large (6 or 7) with dam as the random effect. Our full model included 5 variables, including % CB pedigree of dam and sires, dam age, previous litter, and month and year of birth. We expected older dams and dams with more experience that season to have larger litters.

To determine the importance of % CB pedigree on growth rates (g/day) of juveniles 4–26 weeks old (2 weeks postemergence until near adult body mass), we 1st parameterized a growth curve for each juvenile by running a linear regression (PROC REG) on body mass (g) and $\log_e$ of week

Table 1.—Full, intercept-only, and top models (i.e., within 2 ΔAIC of top model) predicting probability of pregnancy per pairing (pairing success), 3 categories of litter size (1-3, 4 or 5, and 6 or 7 neonates per litter), the slope (g/day) of the logarithmic growth curve of juveniles from 4 to 26 weeks of age, probability of survival of from birth to emergence from the natal burrow (15 days), survival from emergence to 1 year, and survival after 1 year on in pygmy rabbits (*Brachylagus idahoensis*) in the captive breeding facility at Washington State University, Pullman, Washington, from 2001 to 2010. Random effects included individual dam, sire, and litter; explanatory variables included percantage Columbia Basin (CB) pedigree of dams and sires (DamCB, SireCB), age of dams and sires (DamAge, SireAge), sex of animal (Sex), whether dams had a previous litter in that breeding season (PrevLitter), litter size (LitterSize), temperature at birth (Temp), and month and year of pairing or birth (Month, Year). Summary statistics provided are sample size (*n*), variables included as random effects, AIC, ΔAIC, Akaike weights (w_is), and number of variables (*k*) in models.

Model	*n*	Random effects	Variables	AIC	ΔAIC	w_i	*k*
Pairing success	483	Dam Sire	DamCB DamAge PrevLitter Year	572.0	0	0.31	4
			DamCB DamAge SireAge PrevLitter Year	573.4	1.4	0.16	5
			DamCB DamAge PrevLitter Month Year	573.9	1.9	0.12	5
			DamCB SireCB DamAge PrevLitter Year	574.0	2.0	0.12	5
			Full model (DamCB SireCB DamAge SireAge PrevLitter Month Year)	577.3	5.3	0.02	7
			Intercept only	603.3	31.3	0.00	0
Litter size	256	Dam	DamAge Prevlitter	357.3	0	0.27	2
			PrevLitter	358.1	0.8	0.18	1
			DamCB DamAge PrevLitter	358.8	1.5	0.13	3
			DamAge PrevLitter Month	359.3	2	0.10	3
			Full model (DamCB DamAge PrevLitter Month Year)	364.4	7.16	0.01	5
			Intercept only	370.5	13.3	0.00	0
Juvenile growth	121	Litter	SireCB Sex LitterSize Month Year	1,067.5	0	0.51	5
			Full model (DamCB SireCB Sex LitterSize Month Year)	1,068.8	1.0	0.31	6
			Intercept only	1,159.4	91.9	0.00	0
Survival—birth to emergence	868	Litter	Full model (DamCB SireCB DamAge PrevLitter Temp Year)	541.6	0	0.20	6
			DamCB SireCB DamAge Temp	541.6	0	0.20	4
			DamCB SireCB DamAge PrevLitter Temp	541.6	0	0.20	5
			DamCB SireCB DamAge Temp Year	542.5	0.9	0.12	5
			DamCB SireCB PrevLitter Temp	542.9	1.4	0.10	4
			DamCB SireCB Temp	543.3	1.8	0.08	3
			Intercept only	656.7	115.1	0.00	0
Survival—emergence to 1 year	435	Litter	Month Year	2,253.6	0	0.39	2
			DamCB Month Year	2,255.4	0.8	0.26	3
			SireCB Month Year		1.8	0.16	3
			Full model (DamCB SireCB Month Year)	2,256.4	2.8	0.10	4
			Intercept only	2,272	18.4	0.00	0
Adult survival	144	Litter	Intercept only	820.4	0	0.25	0
			Full model (DamCB SireCB Sex Year)	827.6	7.2	0.01	4

since birth. We then examined the effect of % CB pedigree of dams and sires, litter size, sex of juvenile, and month and year of birth on the slope of the growth curve using mixed linear models (PROC MIXED). In this model, litter identification was specified as the random effect to account for multiple neonates per litter. We only included slopes of growth curves of juveniles for which we had ≥ 3 measures of body mass. We expected higher growth rates in smaller litters (Rao et al. 1977) and in female juveniles (Swihart 1984).

Because juvenile rabbits often have a period of high mortality when they are weaned and emerge from burrows or nests (Schaal et al. 2008), we examined juvenile survival from birth to emergence (1–14 days) separately from emergence to adulthood (15–365 days). We used a set of mixed-effects logistic regression models to examine the probability of a neonate surviving until emergence, with litter identification as the random effect. Our full model included variables for % CB pedigree of dams and sires, dam age, previous litter, average ambient temperature at birth (°C), and year of birth. We expected neonates from older and more experienced dams to have better survival, and altricial neonates born in colder temperatures to have poorer survival. We were unable to sex most of the neonates that died before emergence, and thus did not include sex in this model.

Finally, we examined the importance of % CB pedigree on survival of juveniles from burrow emergence to adulthood (1 year), and of adults from 1 year until death, using a Cox proportional hazards model (PROC PHREG—Cox 1972), with litter identification as the random effect. The full model for emergence to adulthood included % CB pedigree of dams and sires, and month and year of birth. We were unable to sex many of the juveniles that died in the 1st couple of weeks postemergence, so we did not include sex in our models. The full model for adult survival included % CB pedigree of the dams and sires, sex of animal, and year of birth.

TABLE 2.—Parameter estimates, 95% confidence intervals (95% *CI*s), and Akaike importance weights of model-averaged top models predicting the probability of pregnancy per pairing (pairing success), 3 categories of litter size, the slope (g/day) of the logarithmic growth curve of juveniles from 4 to 26 weeks of age, probability of survival of from birth to emergence from the natal burrow (15 days), and survival from emergence to 1 year in pygmy rabbits (*Brachylagus idahoensis*) ranging from 0% to 100% Columbia Basin (CB) pedigree (genome) in the captive breeding facility at Washington State University, Pullman, Washington, from 2001 to 2010. Coefficients are not provided for the factor "year," which had coefficients for each year from 2001 to 2002. Asterisks (*) denote coefficients with 95% *CI*s that did not overlap 0.

			95% *CI*		
Model	Variable	Estimate	Lower	Upper	Importance weight
Pairing success	Intercept	4.424	3.500	5.353	—
	Dam % CB	−0.027*	−0.034	−0.020	1.00
	Sire % CB	−6e−5	−0.001	0.001	0.22
	Dam age	−0.885*	−1.148	−0.621	1.00
	Sire age	−0.053	−0.211	−0.105	0.22
	Previous litter	0.118	−0.099	0.334	1.00
	Month of pairing	0.044	−0.040	0.127	0.17
	Year of pairing	—*	—	—	1.00
Litter size	Intercept 1	0.350	−0.468	1.168	—
	Intercept 2	3.923	0.914	4.838	—
	Dam % CB	0.001	−0.002	0.004	0.19
	Dam age	0.457*	0.414	0.871	1.00
	Previous litter	−1.238*	−1.587	−0.889	0.74
	Month of birth	−2e−5	−0.030	0.029	0.15
Juvenile growth	Intercept	30.637	27.340	33.934	—
	Dam % CB	−0.013	−0.032	0.007	0.38
	Sire % CB	−0.063*	−0.088	−0.038	1.00
	Sex (Female versus male)	2.402*	1.712	3.092	1.00
	Litter size	−0.239	−0.688	0.210	1.00
	Month of birth	0.085	−0.439	0.609	1.00
	Year of birth	—*	—	—	1.00
Surival—birth to emergence	Intercept	−24.955	−31.627	−19.283	—
	Dam % CB	−0219*	−0.282	−0.156	1.00
	Sire % CB	0.122*	0.072	0.171	1.00
	Dam age	−2.63*	−4.589	−0.677	0.80
	Previous litter	1.399	−0.358	3.160	0.49
	Temperature at birth	0.613*	0.494	0.731	1.00
	Year of birth	—	—	—	0.32
Survival—emergence to 1 year	Dam % CB	−4e−4	−0.002	0.001	0.20
	Sire % CB	−0.002	−0.007	0.002	0.32
	Month of birth	−0.404*	−0.562	−0.246	1.00
	Year of birth	—*	—	—	1.00

For each analysis of measures of rabbit production, we evaluated candidate model sets that included all combinations (2^k) of variables included in the full model. We selected our set of top models (i.e., $\leq 2\ \Delta\text{AIC}$ of the top model and $> \Delta\text{AIC}$ of the intercept-only model, where AIC is the Akaike information criterion), and averaged model coefficients for the top models according to Burnham and Anderson (2002). We judged model-averaged coefficients of predictor variables to differ significantly from 0 if the 95% confidence interval based on the associated unconditional standard error did not overlap 0. Akaike importance weights were calculated for each variable included in our top model set by summing Akaike weights (w_is) of all top models that included that variable. Individual animals were only included in the models if data were available for all variables included in the full model. When year was included in the top model set, a post hoc contrast statement was used to compare dependent variables among years of the program.

RESULTS

Over a 10-year captive breeding program, we bred 81 females (12 CB, 11 Idaho, and 58 intercross) and 70 males (14 CB, 7 Idaho, and 49 intercross), resulting in 483 pairings producing 256 litters and 887 juveniles with an overall proportion of males of 0.51. The top models (4) predicting probability of pregnancy within 483 pairings from 2002 to 2010 included the % CB pedigree of dams and sires, age of dam and sires, whether females had a previous litter, month of breeding season, and year of breeding program (Table 1). Pairing success decreased with % CB pedigree of dams and sires, and % CB of dams had among the highest importance weights in the model and a significant model-averaged

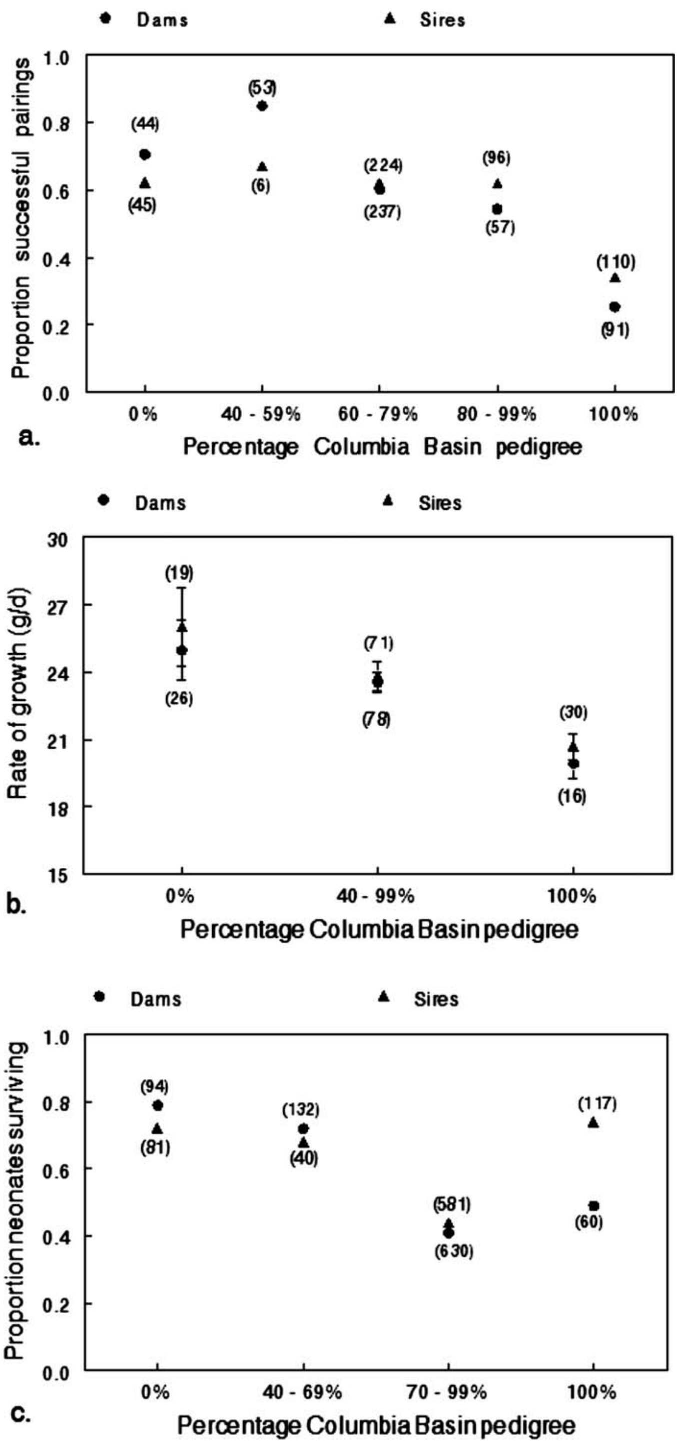

FIG. 1.—Relationship between percentage of the Columbia Basin pedigree of dams and sires and a) proportion of pairings between a male and female resulting in a pregnancy, b) rate of growth (g/day) of juveniles from 4 to 26 weeks of age, and c) proportion of a neonates surviving from birth to emergence from their natal burrows (15 days) in pygmy rabbits (*Brachylagus idahoensis*) at the captive breeding facility at Washington State University, Pullman, Washington, from 2001 to 2010. Sample sizes for dams and sires are indicated in parentheses.

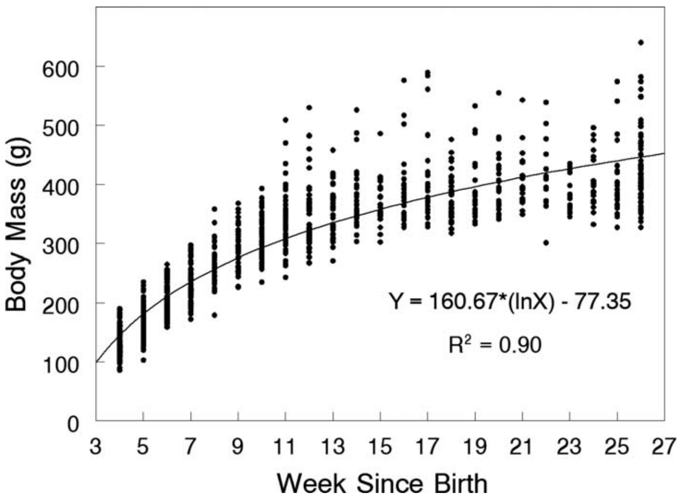

FIG. 2.—Growth from 4 to 26 weeks of juvenile pygmy rabbits (*Brachylagus idahoensis*) born at the captive breeding facility at Washington State University, Pullman, Washington, between 2001 and 2010.

coefficient (Table 2). Probability of pregnancy was nearly 4 times lower in animals with 100% CB pedigree than those with only 50% CB pedigree (Fig. 1a). Pairing success was significantly higher in 2010, the last year of the program, and significantly lower in the first 2 years of the program (all $P < 0.05$).

By breeding females immediately postpartum, we produced an average of 2.7 litters per year per female, with a maximum of 5 per year. Litter size in captive pygmy rabbits ranged from 1 to 9 ($\bar{X} = 4.18 \pm 1.21$ *SD*). The top models (4) predicting litter size category (small, medium, or large) of 256 litters included % CB pedigree of dams, dam age, previous litter, and month of breeding season (Table 1). The % CB pedigree of dams had a relatively low importance weight (0.19) and a nonsignificant model-averaged coefficient. Litter size tended to be larger in dams $>$ 1 year old and in animals that had not had a previous litter that season, and both of these variables had the highest importance weights or significant model-averaged coefficients, or both (Table 2).

Juveniles weighed a mean of 16.4 g ($SD = 0.4$ g) at birth (range 14–19 g; $n = 18$), 81.9 ± 11.1 g ($n = 88$) at emergence (14–16 days), 134.9 ± 22.5 g at 4 weeks ($n = 169$), 360.5 ± 63.2 g at 12 weeks ($n = 63$), and 424.6 ± 60.5 g at 26 weeks of age ($n = 79$) when they reached adult mass. The greatest growth occurred between 4 and 12 weeks (Fig. 2). Top models for juvenile growth (2) included % CB pedigree of dams and sires, litter size, sex, month of breeding season, and year of breeding program (Table 1). Although juvenile growth declined with % CB pedigree of both dams and sires, % CB of dams had a lower importance weight and the confidence interval of the coefficient overlapped 0 (Table 2). Growth rate of juveniles with 100% CB parents was about 20% lower than in juveniles with 100% Idaho parents (Fig. 1b). In addition, growth of 121 juveniles from week 4 to week 26 of age was higher in females ($\bar{X} = 23.4$ g/day $\pm$ 0.7 *SE*, $n = 58$) than in

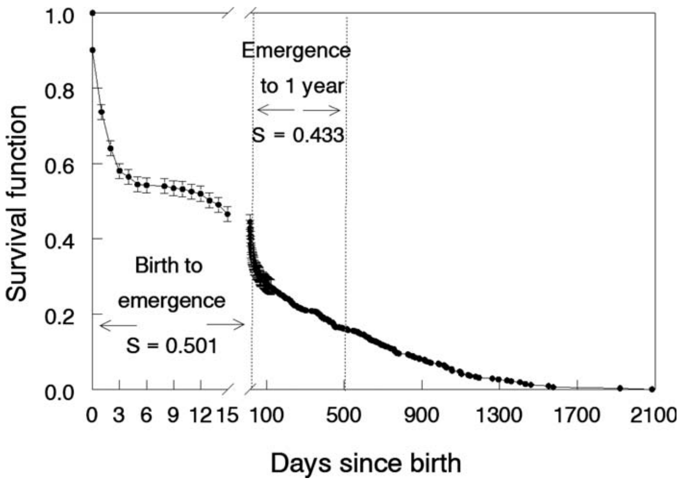

Fig. 3.—Survival (S) of pygmy rabbits (*Brachylagus idahoensis*) born at the captive breeding facility at Washington State University, Pullman, Washington, between 2001 and 2010 from birth to emergence from their natal burrow (15 days), from emergence to 1 year, and after adulthood.

males ($\bar{X} = 22.4 \pm 0.5$ g/day, $n = 62$), and post hoc contrasts indicated that juvenile growth was lower in the first 2 years of the captive breeding program than the later years (all $P < 0.05$).

Only one-half of the 887 pygmy rabbits born at WSU survived to emergence (15 days), and survival of 435 juveniles between emergence and adulthood (1 year) was only 0.43 (Fig. 3). Top models (6) for probability of a neonate surviving from birth to emergence included % CB of dams and sires, dam age, previous litter, temperature at birth, and year of program (Table 1). Neonatal survival declined with % CB pedigree of dams (Table 2; Fig. 1c). Although neonatal survival declined as proportion CB pedigree of sires increased from 0% to 99%, 100% CB sires had young with survival rates equivalent to those with < 70% CB pedigree (Fig. 1c), indicating an interaction between CB pedigree of males and females. Therefore, the coefficient for % CB sire was positive when % CB of dam also was included in the model (Table 2). However, most (61%, 19 of 31) of the neonates sired by 100% CB males that did not survive to emergence had dams with 100% CB, and all had dams with ≥ 50% CB, whereas most (72%, 61 of 85) of the neonates sired by 100% CB males that survived to emergence had dams with ≤ 50% CB. Neonatal survival decreased with age of dam and increased with average daily temperature at birth, which ranged from –2°C to 22°C (Table 2).

The top models (3) predicting survival of juveniles from emergence to adulthood included % CB pedigree of dams and sires, and month and year of birth (Table 1). Although juvenile survival tended to decrease with % CB of dams and sires, month and year of birth had the highest importance weights within the top models and were the only variables with model-averaged coefficients with confidence intervals that did not overlap 0 (Table 2). Juvenile survival increased with month of birth (Table 2), doubling between those born in February and those born in June. Juvenile survival generally decreased with year of program, with higher survival in the first 3 years than the last 5 years (all $P < 0.05$). In contrast to juvenile survival, no variables in the candidate model sets explained the survival of 144 adult pygmy rabbits born at WSU after they reached 1 year (i.e., none > 2 ΔAIC of the intercept only model [Table 1]). The mean annual survival of adult rabbits was 0.58 (*SE* = 0.04), and the longest-lived pygmy rabbit born in captivity at WSU survived 2,084 days (5.7 years).

Of the 367 juvenile pygmy rabbits that died at WSU, 180 were necropsied and examined histopathologically, and the cause of death was identified in 111 rabbits. The main cause of death identified was disease, including intestinal infection with acute diarrhea and enteritis of unknown origin (possibly a corona virus, 33%), coccidiosis (25%), and pneumonia (3%). A small proportion of the identified causes of death were likely congenital or developmental, including stillbirth and prematurity (14%) and neurological disorders (3%). The remaining mortality factors may have been environmental, and included vitamin E and Se deficiency (11%), trauma (3%), and exposure (5%).

We were able to determine the cause of death for 93 of 101 adult pygmy rabbits necropsied and 3 that were not necropsied. Like the juveniles, the primary cause of death was disease, including enteritis and acute diarrhea of unknown cause (32%) and mycobacteriosis (41%, caused by *Mycobacterium avium*). The only other significant cause of death was trauma (3%) mostly caused by burrows collapsing and sustained by climbing.

Discussion

Ten years of captive breeding for the endangered CB pygmy rabbit revealed trade-offs in reproductive performance and survival when attempting to retain the unique CB pedigree. Modest outbreeding of Idaho pygmy rabbits with CB pygmy rabbits aimed at maintaining a population averaging 75% CB pedigree increased our success at producing enough captive rabbits to support both a captive breeding population and reintroduction and recovery efforts (Zeoli et al. 2008; Becker et al. 2011). We found that the greater the % CB pedigree of females or males, or both, the lower the probability of pregnancy per pairing, and the slower the growth rate and lower the survival of their offspring. On the other hand, litter size tended to increase with % CB pedigree, but % CB was a less influential predictor in that model. The relative contribution of the pedigrees of male and female parents, and the strength of these effects, differed among the production parameter modeled. The pedigree of the female had a greater negative influence on pairing success compared with that of the male, whereas the pedigree of the sire had a greater negative influence on juvenile growth than that of the dam. Although survival of neonates to emergence from their natal den declined with the % CB of their dams, survival increased with the % CB of their sires, but only for those whose dams had $\leq$ 50% CB pedigree.

We strongly suspect that inbreeding depression within the small, genetically impoverished founding population of CB pygmy rabbits may have influenced reproductive behavior that could affect pairing success, such as receptivity and ovulation. We observed that only a small amount of outbreeding (i.e., $<$ 10% Idaho pedigree) doubled pairing success. In addition, behavioral observations of captive pygmy rabbits at WSU demonstrated that rabbits with 100% CB pedigree took 5 times longer to begin reproductive chases and to copulate after a male was introduced into a female's pen than for male Idaho rabbits (Elias 2004). Furthermore, CB rabbits had twice as many copulations or attempted copulations, and CB males chased females longer before and after copulation than did Idaho males (Elias 2004). Similarly, in endangered volcano rabbits, captive populations had lower genetic and allelic diversity than wild populations (Salomón Sota et al. 2005) and inbreeding was implicated as a potential cause of low reproductive rates (Campos Morales 2009).

The % CB pedigree of dams was associated with low survival of neonates, especially before emergence and weaning when the dam was caring for young. As noted in captive breeding programs for other lagomorphs (Fa and Bell 1990; Dippenaar and Ferguson 1994; Campos Morales 2009), juvenile mortality of pygmy rabbits was extremely high, especially in the 1st few days of life. Inbreeding may have influenced the dam's nursing behavior, milk yield, or milk quality, which may account for early mortalities in lagomorphs (Rashwan and Marai 2000; Schaal et al. 2008). Additionally, juvenile growth rates of 100% CB sires were about 20% lower than those of 100% Idaho rabbits. Other studies have found negative correlations between inbreeding and mass or growth rate (White 1972; Moura et al. 2000).

Despite intensive veterinary care and monitoring, one-half of the known mortalities of juveniles and adults in our facility were caused by disease, especially coccidiosis and enteritis. Similar diseases also were the primary cause of high mortality in captive volcano rabbits (Hoth and Granados 1987), but disease was not a leading cause of death in captive-reared European rabbits (Arenas et al. 2006). Adult pygmy rabbits in the captive breeding facility were unusually susceptible to avian tuberculosis (Harrenstein et al. 2006), caused by a ubiquitous mycobacterium that typically only affects animals with compromised immune systems. Because adult rabbits with 100% CB pedigree in our captive breeding program had a less vigorous lymphocyte response compared with animals with a mixture of CB and Idaho pedigree (Harrenstein et al. 2006), the low genetic diversity within the captive CB population may have contributed to high adult and juvenile mortality from disease. High mortality from disease may have been compounded by the necessity of housing rabbits on soil during the period from breeding through lactation because pygmy rabbits were unable to successfully raise young without a soil substrate for digging natal burrows (B. A. Elias, in litt.).

Survival of neonates while in their natal burrows was strongly related to outdoor temperatures at birth. No information is available about the effects of temperature and neonatal survival in wild pygmy rabbits, but natal burrows constructed in 0.5–1 m of soil above ground in our captive facility may not have provided an adequate thermal environment for neonates in the colder months early in the breeding season. Juveniles born later in the breeding season also had a greater survival to adulthood. Delaying breeding until temperatures are warmer, providing climate control, or providing deeper soil may improve neonatal survival in captive pygmy rabbits, although this delay would reduce the number of litters that could be produced per animal per season.

Demographic variables such as sex and age were important in explaining reproductive performance of captive pygmy rabbits. Despite our expectation that older animals (those that had survived 1 breeding season) would be more productive because they may have more energy reserves and more experience, we found that pairing success and survival of neonates was lower for older dams or sires, or both, although older dams did produce larger litters. Females that had a previous litter that breeding season were more likely to become pregnant during a pairing and to produce neonates that survived until emergence, but produced a smaller litter. In contrast, Stott et al. (2008) found that litter size increased with the number of litters produced per female per year in European rabbits, and Rashwan and Marai (2000) found that shortening the birthing interval increased mortality in domestic rabbits. Female juveniles grew faster and had a higher adult mass, but sex was not related to adult survival.

Finally, pairing success, juvenile growth, and juvenile survival all varied with year of the captive breeding program. Juvenile survival was higher in early years of the program, potentially before some pathogens were introduced to, and compounded within, the captive colony. On the other hand, pairing success and juvenile growth were higher in later years, possibly reflecting advances in adaptive management such as diet, housing, cleaning protocols, and medical care designed to improve rabbit production. Because husbandry practices were completely or partially confounded with year, we were unable to examine their individual effects on production. Furthermore, discerning cause-and-effect relationships is difficult in a captive breeding program for an endangered species, which necessarily precludes formal experimentation that could be harmful to some individuals.

In conclusion, declining or endangered species most in need of emergency captive breeding programs are often similar to the CB pygmy rabbit—small populations with low genetic diversity and high genetic differentiation from possible sources for translocation (Brekke et al. 2010; Rabon and Waddell 2010; Cain et al. 2011; Karsten et al. 2011; Roberts et al. 2011). Consequently, difficult trade-offs (e.g., demographic, facility logistics, and financial expenses) often must be balanced to adaptively manage population genetics, population size, and production of enough new animals to support both a captive population and reintroduction efforts (van Heezik et al.

2005; Zeoli et al. 2008; Robert 2009). In our study, a modest level of outbreeding of CB pygmy rabbits with a genetically distinct population that had higher genetic diversity and larger populations improved pregnancy rates, juvenile growth, and juvenile survival. The default assumption that distinct population segments contain genetic complexes well adapted to local ecological conditions frequently may be offset by the potential for inbreeding depression in populations with low genetic diversity. Thus, we recommend that captive breeding efforts for rare or endangered species consider outbreeding as a potential response even early in recovery programs when fitness measures suggest compromised reproductive performance and survival. Under ideal circumstances, to increase the chances of success in captive breeding of endangered lagomorphs, we recommend frequent monitoring of size and genetic diversity of declining populations of concern and establishing captive breeding programs before such populations become as small and isolated as the CB pygmy rabbit. Captive breeding programs starting with a large number of unrelated founders that are supplemented annually with new founders and continue for a minimal number of generations ($<$ 20) to avoid rapid evolutionary processes associated with adapting to conditions in captivity can be a key component of restoring endangered lagomorphs (Robert 2009; Witzenberger and Hochkirch 2011). We conclude conserving short-lived, relatively r-selected species, as may characterize numbers of lagomorph species, is challenging, especially when information on reproduction, population and landscape genetics, and associated fitness values is limited or nonexistent. Conservationists must therefore be prepared for the necessity of rapid adaptive management of captive populations, even when critical biological information is limited.

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