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Role of Familiarity and Preference in Reproductive Success in Ex Situ Breeding Programs

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Abstract: *Success of captive-breeding programs centers on consistent reproduction among captive animals. However, many individuals do not reproduce even when they are apparently healthy and presented with mates. Mate choice can affect multiple parameters of reproductive success, including mating success, offspring production, offspring survival, and offspring fecundity. We investigated the role of familiarity and preference on reproductive success of female Columbia Basin pygmy rabbits (*Brachylagus idahoensis*) as measured by litter production, litter size, average number of young that emerged from the burrow, and average number of young that survived to 1 year. We conducted these studies on pygmy rabbits at the Oregon Zoo (Portland, Oregon, U.S.A.) and Washington State University (Pullman, Washington, U.S.A.) from February to June 2006, 2007, and 2008. Before mating, we housed each female adjacent to 2 males (neighbors). Female preference for each potential mate was determined on the basis of behavioral interactions observed and measured between the rabbits. We compared reproductive success between females mated with neighbor and non-neighbor males and between females mated with preferred and nonpreferred males. Our findings suggest that mating with a neighbor compared with a non-neighbor and mating with a preferred neighbor compared with a nonpreferred neighbor increased reproductive success in female pygmy rabbits. Litter production, average number of young that emerged, and average number of young that survived to 1 year were higher in rabbits that were neighbors before mating than in animals who were not neighbors. Pairing rabbits with a preferred partner increased the probability of producing a litter and was significantly associated with increased litter size. In captive breeding programs, mates are traditionally selected on the basis of genetic parameters to minimize loss of genetic diversity and inbreeding coefficients. Our results suggest that integrating genetic information with social dynamics and behavioral measures of preference may increase the reproductive output of the pygmy rabbit captive-breeding program. Our findings are consistent with the idea that allowing mate choice and familiarity increase the reproductive success of captive-breeding programs for endangered species.*

Keywords: *Brachylagus idahoensis*, captive breeding, mate choice, mate familiarity, mate preference, pygmy rabbit

Papel de la Familiaridad y la Preferencia en el Éxito Reproductivo en Programas de Reproducción Ex Situ

Resumen: *El éxito de los programas de reproducción en cautiverio se centra en la reproducción constante de animales cautivos. Sin embargo, muchos individuos no se reproducen aun cuando aparentemente están sanos y tienen parejas. La selección de pareja puede afectar múltiples parámetros del éxito reproductivo, incluyendo el éxito de apareamiento, la producción de crías, la supervivencia de crías y fecundidad de crías. Investigamos el papel de la familiaridad y la preferencia en el éxito reproductivo de conejos pigmeo (*Brachylagus idahoensis*) medido en términos de la producción de crías, tamaño de camada, número promedio de juveniles que emergieron de la madriguera y el número promedio de juveniles que sobrevivieron hasta 1 año. Realizamos estos estudios en el Zoológico de Oregon (Portland, Oregon, E.U.A.) y en la Universidad*

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Estatal de Washington (Pullman, Washington, E.U.A.) de febrero a junio de 2006, 2007 y 2008. Antes del apareamiento, alojamos a cada hembra con dos machos adyacentes (vecinos). La preferencia de las hembras por cada pareja potencial fue determinada con base en las interacciones conductuales observadas y medidas. Comparamos el éxito reproductivo entre hembras apareadas con machos vecinos y no vecinos y entre hembras apareadas con machos preferidos y no preferidos. Nuestros resultados sugieren que el apareamiento con un vecino comparado con un no vecino y el apareamiento con un vecino preferido comparado con el de un vecino no preferido incrementaron el éxito reproductivo de las hembras de conejo pigmeo. La producción de crías, el número promedio de juveniles que emergieron y el número promedio de juveniles que sobrevivieron hasta 1 año fue mayor en conejos que eran vecinos antes del apareamiento que en animales que no eran vecinos. El apareamiento de conejos con una pareja preferida incrementó la probabilidad de producir una camada y se asoció significativamente con el incremento en el tamaño de la camada. En programas de reproducción en cautiverio, las parejas tradicionalmente son seleccionadas con base en parámetros genéticos para minimizar la pérdida de diversidad genética y los coeficientes de endogamia. Nuestros resultados sugieren que la integración de información genética con la dinámica social y medidas conductuales de preferencia pueden incrementar la producción reproductiva del programa de reproducción de conejo pigmeo en cautiverio. Nuestros resultados son consistentes con la idea de permitir la selección de pareja y la familiaridad para incrementar el éxito reproductivo de programas de reproducción en cautiverio de especies amenazadas.

Palabras Clave: *Brachylagus idahoensis*, conejo pigmeo, familiaridad con la pareja, preferencia de pareja, reproducción en cautiverio, selección de pareja

Introduction

Captive breeding provides an opportunity to augment declining wild populations and to reestablish extirpated populations (Gilpin & Soule 1986). Reintroduction and population augmentation programs seek to establish genetically healthy (optimal levels of genetic diversity and homozygosity), self-sustaining, captive populations to provide animals for release into the wild (Snyder et al. 1996). For unknown reasons, many individuals in captivity do not reproduce (Carlstead & Shepherdson 1994; Casimir et al. 2007). Typically, captive breeding of endangered species has focused on genetic criteria (Snyder et al. 1996) rather than behavioral criteria such as mate choice and mate competition. However, efforts to create self-sustaining populations of endangered species through captive breeding have been largely unsuccessful. Lees and Wilcken (2009) analyzed 87 mammal populations in zoos and found that 52% were not breeding to replacement and that 67% fell below the threshold of 200 animals recommended to sustain genetic diversity by Baker (2007).

In captive-breeding programs, animals are typically paired for mating to minimize inbreeding and maintain founder representation (i.e., minimize loss of genetic diversity). Such goals usually preclude mate choice (Carlstead & Shepherdson 1994). At the same time, mate choice has been cited as an evolutionary driver of species persistence because it may influence the level of genetic variation maintained within populations (Carson 2003) and affect a population's risk of extinction (Møller 2003). Empirical evidence suggests that female mate choice can directly influence a female's fitness (Andersson & Simmons 2006).

Captive-breeding programs may inadvertently alter perceived mate availability and choice through breeding environments and housing. These changes can affect the reproductive success of a captive population through prefertilization, fertilization, and postfertilization mechanisms (Møller 2003). The effects of eliminating mate choice in a captive population may be evident in the copulation success of pairing. Unsuccessful breeding and low reproductive success as a consequence of matings during which the movement of the female was restricted have been reported in tigers (*Panthera tigris*) (van Bemmel 1968), black rhinoceros (*Diceros bicornis*) (Smith & Read 1992), and kangaroo rats (*Dipodomys merriami*) (Daly et al. 1984). In tree shrews (*Tupaia glis*) (Schreiber et al. 1993) and pygmy rabbits (*Brachylagus idahoensis*) (Elias et al. 2006) paired for mating solely to minimize their genetic relatedness, as few as 20% and 37%, respectively of mating introductions (defined as females and males placed together to facilitate copulation and subsequent fertilization) result in pair formation and subsequent litter production.

Allowing mate choice has also been known to increase number of offspring. For example, wild female guinea pigs (*Galea* spp.) that were allowed to choose among 4 males weaned significantly more offspring than females who were paired with a single male (Hohoff et al. 2003). Free mate choice (simultaneous access to multiple conspecifics of the opposite sex) is also linked to higher reproductive success. Klint and Enquist (1981) found that the number of offspring was higher in free-mated pairs of domestic pigeons (*Columba livia*) than in assigned pairs. Mauritius Kestrels (*Falco punctatus*) (Jones et al. 1995), Puerto Rican Parrots (*Amazona bittata*) (Wilson & Wingfield 1994), and California Condors (*Gymnogyps californianus*) (Cox et al. 1993) produce more offspring per brood when given free choice of mates. Thus, providing mate choice and familiar mates appears to increase reproductive success.

Another potential consequence of reducing or eliminating mate choice in captivity is altering female investment in offspring (e.g., fecundity and egg or birth mass). When a female's ability to choose is constrained, females may not provide as much parental care to offspring (Quader 2005). Female house mice (*Mus musculus*) produce fewer offspring and offspring survival is lower when they mate with nonpreferred males (Drickamer et al. 2003; Gowaty et al. 2003), and females mated to preferred males have litter sizes 31% larger than those mated to nonpreferred males (Drickamer et al. 2000).

Females can discriminate familiar from unfamiliar males and choose their mates accordingly. Females recognize males on the basis of, for example, acoustic (ungulates [Reby et al. 2001]), visual (fish [Zajitschek et al. 2006]), and olfactory (rodents [Rich & Hurst 1998]) signals. Fisher et al. (2003) showed that a female pygmy loris (*Nycticebus pygmaeus*) can be induced to preferentially associate with a particular male by exposing her to his urine for several weeks. Similarly, Roberts and Gosling (2004) manipulated the preferences of female harvest mice (*Micromys minutus*) by inducing males to increase olfactory signaling, thus increasing the familiarity of a particular male to the target female.

Pygmy rabbits are small lagomorphs that occupy arid shrublands with deep sandy-loam soils, in which they dig burrow systems, and dense sagebrush *(Artemisia tridentata tridentata*) (e.g., Weiss & Verts 1984; Gabler 1997; Thines et al. 2004). Pygmy rabbits are highly dependent on sagebrush for food and shelter throughout the year (Orr 1940; Green & Flinders 1980; McAllister 1995). The winter diet of pygmy rabbits may be up to 99% sagebrush (Wilde 1978). The pygmy rabbit is the only rabbit in the United States that digs its own burrows (McAllister 1995).

Pygmy rabbits occur only in the United States and are patchily distributed in southwestern Wyoming and Montana (Campbell et al. 1982), northeastern California (Orr 1940), eastern Oregon (Weiss & Verts 1984), southwestern Utah (Pritchett et al. 1987), central Nevada (Nelson 1909), and southern Idaho (Wilde 1978). Until recently, several isolated populations existed in the Columbia Basin of central Washington (e.g., Lyman 1991; Gahr 1993; Hays 2001). Due to conversion of their habitat to agriculture, between 1997 and 2000, 5 of the 6 known populations in the Columbia Basin were extirpated. By 2001 the only known population was at Sagebrush Flat, near Ephrata, Washington (Hays & Warheit 2004), and apparently it was extirpated by 2003 (Thines et al. 2004). Columbia Basin pygmy rabbits have been geographically isolated from the more widely distributed populations of pygmy rabbits for at least 10,000 years (Hays 2001) and are genetically distinct (Hays & Warheit 2004). Although not classified as a subspecies, they are listed and protected as an endangered distinct population segment (DPS) under the U.S. Endangered Species Act (McAllister 1995). The taxon is one of the 24–35% of lagomorphs worldwide that are declining, endangered, or of long-term conservation concern (Baillie et al. 2004).

The Columbia Basin pygmy rabbit is maintained in 3 small populations in captive-breeding facilities in the Pacific Northwest (Hays & Warheit 2004). Before our study 37% of pygmy rabbit mating introductions were successful and choice of individuals for breeding was based purely on genetic criteria (Elias et al. 2006). Although there have been recent studies on the copulatory behavior and maternal care of pygmy rabbits (Elias et al. 2006), the role of female mate preference and familiarity of females with potential mates has not been studied. We investigated whether the reproductive success of female Columbia Basin pygmy rabbits mated with familiar (neighbor) and preferred males differed from females mated with non-neighbor and nonpreferred males on the basis of litter production, litter size, average number of young that emerged from the burrow, and average number of young that survived to 1 year. We expected that individual females introduced to a neighbor male would have higher reproductive success than individuals introduced to a novel male. We also expected that females that bred with their preferred male would have higher reproductive success than females that bred with their nonpreferred male (Drickamer et al. 2000).

Methods

Study Site and Species

We conducted our study during the breeding season (1 February–1 August) in 2006, 2007, and 2008. Due to decreasing genetic variation in the population and increasing incidence of disease in captivity, in 2006 the species recovery team (U.S. Fish and Wildlife Service appointed team responsible for managing the recovery program) decided to crossbreed the DPS of Columbia Basin pygmy rabbits with pygmy rabbits from a large population in Idaho to increase the fitness of Columbia Basin rabbits. Thus, the subjects of our study were purebred Columbia Basin rabbits and Columbia Basin-Idaho crossbreeds.

We housed pygmy rabbits at the Oregon Zoo in Portland, Oregon, and Washington State University in Pullman, Washington. All subjects in the mate preference versus nonpreference comparison were crossbred rabbits. In the neighbor versus non-neighbor comparisons, all females ($n = 33$) were crossbred, but 3 of 26 males were purebred Columbia Basin rabbits. These males accounted for 6 mate pairings of 54. We define *mate pairings* as the introduction of a specific male to a specific female for the purpose of breeding. Animal care and use guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) were followed by all facility operators.

Due to intraspecific aggression, rabbits were separated from each other except when males were introduced to a female's enclosure for breeding. We housed rabbits in either square (1.8 m × 1.8 m) or rectangular (3.7 m × 1.8 m) mesh enclosures with 0.5–1.0 m of compacted soil substrate. Enclosures were placed in 2 rows such that each enclosure shared a mesh barrier wall with at least 2 others. Each enclosure contained a nest box (60 cm long × 30 cm wide × 30 cm high) filled with alfalfa hay. Enclosures contained sagebrush branches arranged into bushes and artificial burrows constructed from 120-cm lengths of plastic drainage tubing with 7.6-cm openings. All enclosures were exposed to natural light.

We recorded rabbit behavior 24 hours/day with a video camera. At the Oregon Zoo we used 4 infrared, high-resolution (600TVL) day–night dome cameras and a high-definition digital recorder (Digimerge, Markham, Ontario, U.S.A.). Video equipment at Washington State University is described in Elias et al. (2006). We fed pygmy rabbits grain-forage pellets, fresh clover, parsley, and sagebrush stem and leaf clippings.

Mating Procedure

In the wild, breeding season for the Idaho pygmy rabbits is from March to May (Elias et al. 2006). We began mate pairing adult pygmy rabbits in mid-February and continued until early July. We based assignment of individuals to mate pairs on a captive-breeding and genetic-management plan (Hays & Warheit 2004) designed to maximize genetic health of the captive population.

Males were introduced to female pens for mating between 10:00 and 11:00. Mating sessions (defined as a pairing of one male and one female from the time males were introduced to females until males were removed from the pen) usually lasted 2–3 d. If either animal's behavior was aggressive, animal care staff removed the male to prevent injury or death. After a breeding session, males were moved back to their enclosures and subsequently were placed with a different female in sequence until all females had been mated. If these pairings did not produce a litter within approximately 24 d, females were reintroduced to the same male or a different genetically recommended male until a pairing resulted in a litter. This method resulted in females having 1–4 mates and 1–6 mating opportunities each breeding season.

We monitored several measures of reproductive success. We did not count copulations because they last 0.1–2 seconds and are thus difficult to detect. We classified mating attempts as successful or unsuccessful on the basis of whether a litter was produced. We classified pairings as litter not produced, litter produced but never emerged (dead young found in natal burrow), young emerged, and young survived for >1 year (i.e., to breeding age [Elias et al. 2006]). If a litter was produced, we counted the number of young.

Neighbor versus Non-Neighbor Males

The non-neighbor test group was composed of animals separated by one or more pens from their potential mate ($n = 25$). The neighbor group consisted of pairs where the enclosure of the male was directly adjacent to that of the female for at least 2 months during the breeding season ($n = 29$). Washington State University had 19 total mate pairings and Oregon Zoo had 35. The neighbor test group was further divided into preferred ($n = 13$) and nonpreferred ($n = 13$) mates on the basis of the behavioral indicators outlined in the next section and were solely composed of animals whose behavior could be monitored remotely. All animals in the breeding program, in theory, may have been in contact because the breeding population is small and the program must control for inbreeding. Thus, for our purposes, neighbors and non-neighbors were defined for the given breeding season. However, none of the mate pairings in this study had successfully produced a litter before this study.

Preferred versus Nonpreferred Male Neighbors

Enclosures of females ($n = 26$) included in mate preference trials were bordered by 2 enclosures that contained 1 male each, and one of the neighboring males was a potential mate for that season. Females were observed and mate preference behavior was scored on the day before a male was introduced to the female. All occurrences of the female behaviors defined below were scored for 4 hours between 16:00 and 09:00. This is the period when rabbits were most active in these facilities. The behavior of 3 females was recorded during the day only. For these females, focal sampling was performed outside the 16:00–09:00 period. Although these females were less active during the day, enough behavior was scored to establish male preference.

We adapted Drickamer et al.'s (2000) method to determine female preference for neighboring males. Ten behaviors were identified as indicators of preference on the basis of observations of staff members caring for the rabbits (B. Elias and R. Lamson, personal communication) and social behaviors reported in New Zealand white rabbits (*Oryctolagus cuniculus*) (Ling-ru et al. 2004): physical contact through the mesh barrier (barrier contact), scent or urine marking along the mesh barrier (barrier mark), contact with barrier in absence of male (barrier investigate), jumping against the barrier, jumping along the barrier, running along the barrier, running along the barrier parallel with male (social barrier run), female within one body length of male, female spinning in 2 or more circles consecutively with the male in close proximity (female spin), and females running in a characteristic z pattern in close proximity to the male 2 or more times (zig zag). All occurrences of these behaviors were recorded along with the identity of the male with whom the behavior was performed. Males were defined as preferred if

Table 1. Values of measures of reproductive success for mate pairings of Columbia Basin pygmy rabbits.

	*Pairing type**			
Variable	*neighbors*	*non-neighbors*	*preferred*	*nonpreferred*
Total mate pairings	29	25	13	13
Litters produced	22	8	10	4
Litters emerged	12	3	5	1
Litters survived to 1 year	13	1	5	1
Total young produced	85	23	36	12
Total young emerged	48	3	18	4
Total young survival to 1 year	20	2	16	4
Mean young/litter	4.0 (1.1)	2.9 (1.4)	3.7 (0.9)	2.7 (1.1)
Mean young/litter emerged	2.18 (2.1)	0.38 (0.52)	1.8 (0.6)	1.0 (1.0)
Mean male age (days)	436.6 (163.3)	445.6 (198.9)	408.6 (44.7)	419.2 (46.9)
Mean female age (days)	466.9 (203.6)	532.8 (264.3)	444.2 (65.0)	510.3 (65.5)
Mean male body mass (g)	378.6 (29.7)	379.8 (87.2)	383.4 (7.7)	378.6 (8.1)
Mean female body mass (g)	429.2 (41.6)	430.8 (67.3)	437.5 (10.6)	464.6 (19.5)

**Standard error in parentheses.*

females directed at least 60% of their total behaviors during the 4 hours toward one particular male. If a female did not demonstrate such a preference she was excluded from the study.

The observations were conducted with a single-blind trial protocol, whereby observers were naive to the identity of the male rabbit that would be paired with the female. Females were assigned to be mated with either the preferred or nonpreferred male on the basis of which male was genetically recommended by the species survival plan.

Data Analyses

We report the mean, standard error, and the sample size. The 4 measures of reproductive success were dependent variables: whether a litter was produced (binary), litter size, average number of kits that emerged from the burrow, and average number of young that survived to 1 year. Independent variables were neighbor status (binary) or mate preference status (binary), year breeding was conducted, breeding location (binary), date of mating introduction start (week of the year), female age (weeks), female weight (grams), male age (weeks), and male weight (grams). We included enclosure size and source population (Columbia Basin or cross bred) as variables in the initial statistical model, but they were not significant, so we excluded them from subsequent models.

We used a generalized linear mixed model (GLMM) with a logit link and binomial error distribution to test whether the independent variables explained significant variance in the probability of producing a litter. We used a GLMM with a log link and Poisson error distribution to test whether the independent variables explained significant variance in the average number of young in a litter, the average number of young that emerged, and the average number of young that survived to 1 year. We assumed these response variables have a Poisson distribution given the random effects of female and male identity. We fit models with a maximum-likelihood method. We ran GLMM through a step-wise exclusion method in which the least significant predictor variable ($p \geq 0.05$) was sequentially removed from the model until the final significant model was revealed (McCullagh & Nelder 1989).

Results

Measures of reproductive fitness varied between neighbors and non-neighbors (Table 1). Pairs composed of neighbors s($F_{1,54} = 78.46, p < 0.01$) were associated with increased litter production. More mate pairs of neighbors produced litters than mate pairs that were not neighbors (Supporting Information). Litter size was not significantly associated with any of our independent variables (Supporting Information). There was a significant interaction between neighbor status and the average number of kits that emerged from the burrow ($F_{1,30} = 6.04$, $p = 0.02$). More neighbors had kits emerge than non-neighbors (Supporting Information). More young that survived to 1 year were produced from a pairing with neighbor males ($F_{1,30} = 5.132$, $p = 0.04$) (Supporting Information). No other independent variables were significantly correlated with neighbor status (all p values >0.05).

Measures of reproductive fitness varied between females mated with preferred and nonpreferred males (Table 1). Significantly more females mated to their preferred male produced a litter than females mated to nonpreferred males ($F_{1,26} = 15.89$, $p < 0.001$) (Supporting Information). Female mate preference ($F_{1,14} = 65.05$, $p < 0.001$), female weight ($F_{1,14} = 33.59$, $p < 0.001$), facility location ($F_{1,14} = 24.15$, $p < 0.001$), female age ($F_{1,14} = 15.81$, $p = 0.01$), week of the year mating occurred ($F_{1,14} = 7.49$, $p = 0.02$), year of mating

($F_{1,14} = 5.67$, $p = 0.03$), and male weight ($F_{1,14} = 5.5$, $p = 0.03$) were significantly associated with litter size (Supporting Information). A significantly greater proportion of pairs of older males ($F_{1,14} = 5.19$, $p = 0.04$) (Supporting Information) and heavier females ($F_{1,14} = 4.92$, $p = 0.04$) (Supporting Information) had kits emerge. None of the variables was significantly associated (Supporting Information). Thirty-six young were born to females mated with preferred males; 18 (50%) emerged and 16 (44%) survived to 1 year. Of the 4 litters produced by females mated with nonpreferred males, 1 had kits that survived to 1 year. Twelve young were born to females mated with nonpreferred males; 4 (33%) emerged and 4 (33%) survived to 1 year. No other variables were significantly correlated with mate preference status (all p values >0.05).

Discussion

Pairs of neighbors produced more litters, had more young emerge, and had a greater number of young survive to 1 year. Our results suggest that a lack of familiarity between mates (i.e., being housed apart before and during the breeding season) may negatively affect reproductive success of female pygmy rabbits. This is consistent with the finding that mate familiarity with a female increases mating success and production of offspring (Fisher et al. 2003; Roberts & Gosling 2004).

Columbia Basin pygmy rabbits live in aggregations and are territorial. Home ranges of females may overlap. It is thought that males visit multiple females burrows during the breeding season, the only period during which females tolerate conspecifics near their burrows (Gahr 1993). In the European rabbit (*Oryctolagus cuniculus*), a species with a social structure similar to that of the Columbia Basin pygmy rabbit, territory is maintained in the field by scent marks including glandular secretions (Mykytowycz & Hesterman 1975), fecal mounds (Mykytowycz & Hesterman 1975), and urine (Bell 1981). The submandibular cutaneous glands of dominant male rabbits produce more secretions than those of other individuals within the social group, and these animals also show more scent-marking behavior than other rabbits (Mykytowycz & Hesterman 1975). Similarly, male house mice that frequently remark scent marks in their territory were selected more often as mates than males that did not (Roberts & Gosling 2004). Because Columbia Basin pygmy rabbits also are territorial in the field, females may choose familiar males, or males that have a familiar scent, as an indicator of male fitness.

We believe 2 months is a sufficient amount of time to establish mate familiarity because males were placed in February and mated in April. However, it may require significantly less time to establish familiarity. It would be helpful to understand the factors that influence familiarity so that breeding programs could manipulate them for maximum reproductive success. For example, if animals could become familiar with each other on the basis of scent alone, it would allow managers to familiarize mates before introduction, even when animals are housed in separate facilities.

Female mate preference correlated positively with a pair's reproductive success. For example, females mated to nonpreferred males produced fewer litters than females mated to preferred males. This is consistent with the results of studies of mice (*Mus domesticus*) (Drickamer et al. 2000; Drickamer et al. 2003), fruit flies (*Drosophila pseudoobscura)* (Anderson et al. 2007), wild guinea pigs (*Galea musteloides*) (Hohoff et al. 2003), pigeons (*Columba livia domestica*) (Klint & Enquist 1981), pipe fish (*Syngnathus typhle*) (Sandvik et al. 2000), and Mauritius Kestrels (*Falco punctatus*) (Jones et al. 1995). Although our sample sizes constrained our ability to analyze young produced by pygmy rabbit pairs in this study, if Columbia Basin pygmy rabbits follow patterns similar to house mice, management-induced constraints that inhibit or prevent females from mating with preferred males may result in reduced reproductive success. Mate choice is thought to be an important source of evolutionary change (Drickamer et al. 2000); hence, it may affect both physiological and morphological traits in progeny and the dynamics of social behavior.

The role of familiarity and preference in reproductive success of laboratory species has been demonstrated experimentally. Our results expand the list of species in which mate choice affects reproductive output, but also demonstrates the practical importance of mate choice in the pygmy rabbit ex situ breeding program. These findings may be applicable to many of the endangered species currently maintained in captive-breeding programs. Although genetic criteria are important in the choice of individuals for breeding, we believe more attention should be focused on the behavioral parameters that affect the reproductive success of these populations.

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Supporting Information

The GLMMs of neighbor versus non-neighbor for litter production (Appendix S1), litter size (Appendix S2), young emerged (Appendix S3), and young survival to 1 year (Appendix S4) are available online as are the GLMMs of preferred versus nonpreferred for litter production (Appendix S5), litter size (Appendix S6), young emerged

(Appendix S7), and young survival to 1 year (Appendix S8). The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Anderson, W., K. Yong-Kyu, and P. Gowaty. 2007. Experimental constraints on mate preferences in *Drosophila pseudoobscura* decrease offspring viability and fitness of mated pairs. Proceedings of the National Academy of Sciences of the United States of America **104:**4484–4488.

Andersson, M., and L. W. Simmons. 2006. Sexual selection and mate choice. Trends in Ecology & Evolution **21:**296–302.

Animal Care and Use Committee. 1998. Journal of Mammalogy **79:**1416–1431.

Baillie, J., C. Hilton-Taylor, and S. Stuart 2004. 2004 IUCN red list of threatened species: a global assessment. International Union for Conservation of Nature, Gland, Switzerland.

Baker, A. 2007. Animal ambassadors: an analysis of the effectiveness and conservation impact of ex situ breeding efforts. Pages 139–154 in A. Zimmermann, M. Hatchwell, L. A. Dickie, and C. West, editors. Zoos in the 21st century: Catalysts for conservation? Cambridge University Press, Cambridge, United Kingdom.

Bell, D. J. 1981. Chemical communication in the European rabbit: urine and social status. Pages 271–279 in K. Meyers and C. D. McInnes, editors. Proceedings of the World of Lagomorph Conference (1979). University of Guelph, Guelph, Ontario.

Campbell, T. M., T. W. Clark, and C. R. Groves. 1982. First record of pygmy rabbits (*Brachylagus idahoensis*) in Wyoming. Great Basin Naturalist **42:**100.

Carlstead, K., and D. Shepherdson. 1994. Effects of environmental enrichment on reproduction. Zoo Biology **13:**447–458.

Carson, H. L. 2003. Mate choice theory and the mode of selection in sexual populations. Proceedings of the Royal Society B: Biological Sciences **100:**6584–6587.

Casimir, D. L., A. Moehrenschlager, and R. M. R. Barclay. 2007. Factors influencing reproduction in captive vancouver island marmots: implications for captive breeding and reintroduction programs. Journal of Mammalogy **88:**1412–1419.

Cox, C. R., V. I. Goldsmith, and H. R. Engelhardt. 1993. Pair formation in California condors. American Zoologist **33:**126–138.

Daly, M., M. I. Wilson, and P. Behrends. 1984. Breeding of captive kangaroo rats, *Dipodomys merriami* and *D. microps*. Journal of Mammalogy **65:**338–341.

Drickamer, L., P. Gowaty, and C. Holmes. 2000. Free female mate choice in house mice affects reproductive success and offspring viability and performance. Animal Behavior **59:**371–378.

Drickamer, L., P. Gowaty, and D. Wagner. 2003. Free mutual mate preferences in house mice affect reproductive success and offspring performance. Animal Behavior **65:**105–114.

Elias, B. A., L. A. Shipley, R. D. Sayler, and R. S. Lamson. 2006. Mating and parental care in captive pygmy rabbits. Journal of Mammalogy **87:**921–928.

Fisher, H. S., R. Swaisgood, and H. Fitch-Snyder. 2003. Odor familiarity and female preferences for males in a threatened primate, the pygmy loris *Nycticebus pygmaeus*: applications for genetic management of small populations. Naturwissenschaften **90:**509–512.

Gabler, K. I. 1997. Distribution and habitat requirements of the pygmy rabbit (*Brachylagus idahoensis*) on the Idaho National Engineering and Environmental Laboratory. Ph.D. dissertation. Idaho State University, Pocatello.

Gahr, M. L. 1993. Natural history, burrow habitat use, and home range of the pygmy rabbit of Sagebrush Flats, Washington. M.S. thesis. University of Washington, Seattle.

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: processes of species extinction. Pages 19–34 in M. E. Soule, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts.

Gowaty, P., L. Drickamer, and S. Schmid-Holmes. 2003. Male house mice produce fewer offspring with lower viability and poorer performance when mated with females they do not prefer. Animal Behavior **65:**95–103.

Green, J. S., and J. T. Flinders. 1980. Habitat and dietary relationships of the pygmy rabbit. Journal of Range Management **33:**136–142.

Hays, D. 2001. Washington pygmy rabbit emergency action plan for species survival. Addendum to Washington State recovery plan for the pygmy rabbit (1995). Wildlife Program, Washington Department of Fish and Wildlife, Olympia.

Hays, D., and K. Warheit. 2004. Columbia Basin pygmy rabbit captive breeding and genetic management plan. Washington Department of Fish and Wildlife, Olympia.

Hohoff, C., K. Franzen, and N. Sachser. 2003. Female choice in a promiscuous wild guinea pig, the yellow-toother cavy (*Galea musteloides*). Behavioral Ecology and Sociobiology **53:**341–349.

Jones, C., W. Heck, R. Lewis, Y. Mungroo, G. Slade, and T. Cade. 1995. The restoration of the Mauritius Kestrel *Falco punctatus* population. Ibis **137**(Suppl.):S173–S180.

Klint, T., and M. Enquist. 1981. Pair formation and reproductive output in domestic pigeons. Behavioral Process **6:**57–62.

Lees, C. M., and J. Wilcken. 2009. Sustaining the Ark: the challenges faced by zoos in maintaining viable populations. International Zoo Yearbook **43:**6–18.

Ling-ru, C., J. P. Garner, and J. A. Mench. 2004. A behavioral comparison of New Zealand white rabbits (*Oryctolagus cuniculus*) housed individually or in pairs in conventional laboratory cages. Applied Animal Behaviour Science **85:**121–139.

Lyman, R. L. 1991. Late quaternary biogeography of the pygmy rabbit (*Brachylagus idahoensis*) in eastern Washington. Journal of Mammalogy **72:**110–117.

McAllister, K. R. 1995. Washington state recovery plan for the pygmy rabbit. Washington Department of Fish and Wildlife, Olympia.

McCullagh, P., and J. A. Nelder 1989. Generalized linear models. 2nd edition. CRC Press, Boca Raton, Florida.

Møller, A. P. 2003. Sexual selection and extinction: why sex matters and why asexual models are insufficient. Annals of Zoology Fenn **40:**221–230.

Mykytowycz, R., and E. Hesterman. 1975. An experimental study of aggression in captive European rabbits, *Oryctolagus cuiculus* (L), with appendix on method of multivariate analysis of data by Dudzinski, M.L. & Edwards, C.B.H. Behaviour **52:**104–123.

Nelson, E. W. 1909. The rabbits of North America. North American Fauna **29:**11–314.

Orr, R. T. 1940. The rabbits of California. Occasional Papers of the California Academy of Sciences **19:**1–227.

Pritchett, C. L., J. A. Nilsen, M. P. Cofeen, and H. D. Smith. 1987. Pygmy rabbits in the Colorado River drainage. Great Basin Naturalist **47:**231–233.

Quader, S. 2005. Mate choice and its implications for conservation and management. Current Science **89:**1220–1227.

Reby, D., M. Hewison, M. Izquierdo, and D. Pépin. 2001. Red deer (*Cervus elaphus*) hinds discriminate between the roars of their current harem-holder stag and those of neighbouring stags. Ethology **107:**951–959.

Rich, T. J., and J. L. Hurst. 1998. Scent marks as reliable signals of the competitive ability of mates. Animal Behaviour **56:**727–735.

Roberts, S. C., and L. M. Gosling. 2004. Manipulation of olfactory signaling and mate choice for conservation breeding: a case study of harvest mice. Conservation Biology **18:**548–556.

Sandvik, M., G. Rosenqvist, and A. Berglund. 2000. Male and female mate choice affects offspring quality in a sex-role-reversed pipefish.

Proceedings of the Royal Society B: Biological Sciences **267:**2151–2155.

Schreiber, A., L. Kolter, and W. Kaumanns. 1993. Conserving patterns of genetic diversity in endangered mammals by captive breeding. Acta Theriologica **38:**71–88.

Smith, R. L., and B. Read. 1992. Management parameters affecting the reproductive potential of captive, female black rhinoceros, *Diceros bicornis*. Zoo Biology **11:**375–383.

Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone, and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. Conservation Biology **10:**338–348.

Thines, N. J., L. A. Shipley, and R. D. Sayler. 2004. Effects of cattle grazing on ecology and habitat of Columbia Basin pygmy rabbits (*Brachylagus idahoensis*). Biological Conservation **119:**525–534.

van Bemmel, A. C. V. 1968. Breeding tigers *Panthera tigris* at Rotterdam Zoo. International Zoo Yearbook **8:**60–63.

Weiss, N. T., and B. J. Verts. 1984. Habitat and distribution of pygmy rabbits (*Syvilagus idahoensis*) in Oregon. Great Basin Naturalist **44:**563–571.

Wilde, D. B. 1978. A population analysis of the pygmy rabbit (*Sylvilagus idahoensis*) on the INEL site. Ph.D. dissertation. Idaho State University, Pocatello.

Wilson, B. S., and J. C. Wingfield. 1994. Seasonal and interpopulational variation in plasma levels of corticosterone in the side-blotched lizard (*Uta stansburiana*). Physiological Zoology **67:**1025–1049.

Zajitschek, S. R. K., J. P. Evans, and R. Brooks. 2006. Independent effects of familiarity and mating preferences for ornamental traits on mating decisions in guppies. Behavioral Ecology **17:**911–916.