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FACTORS INFLUENCING REPRODUCTION IN CAPTIVE VANCOUVER ISLAND MARMOTS: IMPLICATIONS FOR CAPTIVE BREEDING AND REINTRODUCTION PROGRAMS

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Many factors important to reproduction are difficult to quantify for wild mammals, yet an understanding of them is often critical to species' recovery programs, particularly those involving captive breeding and reintroduction. We examined management variables employed by the Vancouver Island marmot captive breeding program during 1998–2005 to determine how such variables influenced production of young and litter sizes. We then tested the ability of factors that were identified as important to predict production of young in the breeding program in 2006. For previously paired animals, production of young was significantly greater when they had been paired with the same mate for $\geq$1 year before the breeding season. When these females had been with a mate for $<$1 year, production of young was more than 2 times greater among 2–4 year olds compared to older age classes. Among previously paired females, 5–7 year olds and those that had produced young previously tended to produce young more often than other categories. Litter size was positively influenced by visual contact between a female and other pairs. For previously paired females, age, the amount of time paired with their mate, and previous production of young accurately predicted 75% of production of young in 2006. We propose that results from our study be combined with genetic considerations to plan future pairings in the breeding program and to assist in the selection of individuals for reintroduction to the wild. Methods reported herein may be applicable to recovery programs for other imperiled mammals.

Key words: age, conservation, experience, familiarity, mammals, marmots, reproduction, rodents

Many factors critical to reproduction are difficult to quantify for wild mammals, especially for species that that are long-lived, exist in low numbers, and occur in areas that are difficult to access. An understanding of these factors is important for all mammals, but especially so for those that are the focus of recovery programs. Captive breeding and reintroduction programs can be powerful tools for aiding species at risk (Baillie et al. 2004; Kleiman 1989), but their success hinges on reliable reproduction among captive (Snyder et al. 1996) and released (Seddon 1999) animals. Research at captive breeding facilities that helps identify factors associated with reproductive success (e.g., Carlstead et al. 1999) can provide information to assist in ensuring success in these programs.

Members of all 14 species of the genus *Marmota*, the largest of the ground squirrels, spend much of their time in burrow systems, using them for hibernation in winter and, during the active season, for copulation, parturition, rearing of young, and escape from predators (Barash 1989). This makes it challenging to conduct detailed studies of these species in the wild. In addition, some marmots are long-lived; individual longevity can be greater than 10 years in Vancouver Island marmots (*Marmota vancouverensis*—Bryant 2005) and yellow-bellied marmots (*M. flaviventris*—Schwartz et al. 1998) and greater than 9 years in hoary marmots (*M. caligata*—Barash 1989). Finally, 4 marmot species are listed as species at risk by the World Conservation Union (IUCN 2006): the bobak marmot (*M. bobak*; Low Risk, Conservation Dependent), the long-tailed marmot (*M. caudata*; Low Risk, Near Threatened), the Menzbier's marmot (*M. menzbieri*; Vulnerable), and the Vancouver Island marmot (Endangered).

As with all mammals, reproduction by marmots may be influenced by numerous factors. For example, examination of data from Vancouver Island and yellow-bellied marmots indicates that age is an important determinant of breeding success, with the youngest and oldest females in a population having a lower probability of reproducing than females in intermediate age classes (Bryant 2005; Schwartz et al. 1998) and with young females producing smaller litters than those in

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older age classes (Bryant 2005). In addition, dominant marmots may suppress the reproduction of subordinates through direct aggressive behavior or by pheromonal activity (Arnold and Dittami 1997; Blumstein and Armitage 1999; King and Allainé 2002; Wasser and Barash 1983). Breeding experience also may influence reproduction (Sydeman et al. 1991), as may familiarity between mates (Tang-Martinez et al. 1993). Although the latter 2 variables have not been examined for marmots, the relatively long life spans, stable social structures (Blumstein and Armitage 1999), and prolonged interlitter intervals (Blumstein and Arnold 1998; Bryant 2005; Holmes 1984; Wasser and Barash 1983) reported for some species suggest that these factors may be important. Finally, among captive animals, elements of enclosure design may influence breeding success (Carlstead et al. 1999).

The endangered Vancouver Island marmot is endemic to Vancouver Island, British Columbia, Canada (Nagorsen 1987), where it is found primarily on south- to west-facing slopes of subalpine meadows ranging from 1,000 to 1,400 m in elevation (Bryant and Janz 1996). Vancouver Island marmots live in colonies that are generally composed of 1 or 2 small family groups (Bryant and Janz 1996; Heard 1977). A typical family group consists of an adult male, 1 or 2 adult females, and a variable number of 2 year olds, yearlings, and young of the year (Heard 1977). Like other marmots, the species has a single breeding season per year, generally commencing shortly after emergence from hibernation (Bryant 1996). This species displays a primarily monogamous mating system, although polygyny may occur (Bryant 1996).

Historic population estimates are vague, but counts from 1972 to the present indicate that the population of Vancouver Island marmots peaked at 250–350 animals in the mid-1980s and then entered a precipitous decline (Bryant and Janz 1996) that may have been linked to forestry practices (Bryant and Page 2005). After the maximum annual population count decreased to 102 animals in 1997, the Vancouver Island marmot captive breeding and reintroduction program was initiated. Between 1997 and 2004, 56 wild-born marmots were taken into captivity (Bryant 2005) with the aim of creating a sustainable captive population that would enable releases of approximately 20 animals per year (Janz et al. 2000). Releases have occurred annually since 2003 and have involved groups varying in size as well as in age and sex composition. As of November 2005, approximately 36 Vancouver Island marmots were thought to reside in the wild, with an additional 121 animals housed in captivity.

As in many recovery programs for endangered mammals, not all captive Vancouver Island marmots reproduce; understanding of why some pairs produce young whereas others do not is limited. In his study on the reproductive rates of captive and wild members of this species, Bryant (2005) found an effect of age on both the probability of production of young and litter size, but no effect of site or previous breeding experience on litter size. However, many factors that may influence reproduction in marmots have not been studied in this species. For example, wild females engage in aggressive encounters (Heard 1977) and only a few of the females in a wild colony produce the majority of offspring (Bryant 1998), suggesting the influence of reproductive suppression. At the same time, observations of aggression between females in adjacent enclosures in captivity suggest that reproduction suppression could potentially influence captive animals housed adjacent to or with sightlines to other pairs.

In this study, we examined a large number of management variables employed by the Vancouver Island marmot captive breeding program to determine how these variables influence the probability of production of young and litter size, and whether these variables can be used to predict future production of young. Our aim was to further understand factors influencing reproduction in Vancouver Island marmots, with the intent of aiding their recovery and potentially that of other imperiled marmot species.

Materials and Methods

Study areas and animals.—Between 1997 and 2006, Vancouver Island marmots were housed at 4 Canadian facilities: the Toronto Zoo in Scarborough, Ontario (hereafter ''Toronto''; 43°49′N, 79°10′W, 143 m), the Calgary Zoo's Devonian Wildlife Conservation Centre in DeWinton, Alberta (hereafter ''Calgary''; 50°49′N, 113°55′W, 1,028 m), Mountain View Conservation Society in Fort Langley, British Columbia (hereafter ''Mountain View''; 49°12′N, 122°27′W, 6 m), and the Tony Barrett Mount Washington Marmot Recovery Centre near Comox, British Columbia (hereafter ''Mount Washington''; 49°45′N, 125°17′W, 1,197 m). Although the animals were housed and managed in captivity for the breeding and reintroduction program and not for the purposes of our study, the care of animals in the program met the guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Captive animals that were 2 years of age or older were usually housed as male–female pairs during the breeding season. Pairing recommendations were based on genetic kinship, specifically the average coefficient of relatedness of any one animal to each living, nonfounder animal in a pedigree (Lacy 1995); possible pairings were evaluated each year by a studbook coordinator. New pairings were typically created toward the end of an active season (before entry into hibernation) and were often preceded by movement of animals among facilities. Otherwise, animals were paired during hibernation or immediately after emergence from hibernation.

Animals were inaccessible to the public and were housed under quarantine conditions. Enclosure design during the breeding season varied within and among facilities and years. Toronto pairs were housed in areas with indoor enclosures only or areas with indoor and outdoor enclosures, and had access to 1–3 enclosures with surface areas usually between 12.7 and 17.7 m^2 but, before 2002, as small as 4.3 m^2. Enclosures contained 1–3 nest boxes ranging in size from 0.7 × 0.6 × 0.5 m (length × width × height) to 1.2 × 0.6 × 0.6 m. Calgary pairs were housed in areas with indoor and outdoor enclosures, had access to 2–4 enclosures totaling 14.6–29.1 m^2, and were provided with 2 nest boxes that measured 1.2 × 0.8 × 0.6 m or,

TABLE 1.—Variable name, method of categorization, and sample sizes (in parentheses) for program management data collected on 84 pairs of Vancouver Island marmots maintained in the captive breeding program for this species from 1998 to 2005.

Variable	Method of categorization (*n* male, *n* female)
Age	2–4 years (36, 36), 5–7 years (37, 29), 8–10 years (11, 13), 11–13 years (0, 6)
Location	Toronto (25, 25), Calgary (21, 21), Mountain View (21, 21), Mount Washington (17, 17)
Production of young in previous year	No (30, 29), yes (21, 20)
Production of young 2 years previous	No (21, 19), yes (13, 14)
Production of young in any previous year	No (25, 26), yes (29, 27)
Number of enclosures available	1 (7, 7), 2 (41, 41), 3 (23, 23), 4 (11, 11)
Total surface area of enclosures (m^2)[a]	(82, 82)
Number of nest boxes available	1 (7, 7), 2 (56, 56), 3 (12, 12)
Volume of next boxes (m^3)	Small (< 0.4 m^3) only (27, 27), large (> 0.4 m^3) only (20, 20), small and large (28, 28)
Access to outdoor enclosure(s)	No (16, 16), yes (68, 68)
Amount of time housed with current mate	Since current hibernation emergence (10, 10), since end of previous active season (38, 38), 1 year or more (36, 36)
Amount of time housed in current enclosure	Since current hibernation emergence (18, 27), since end of previous active season (16, 23), 1 year or more (30, 24)
Amount of time housed in captivity	Less than 1 year (9,5), 1 year or more (75, 79)
Amount of time housed at current facility	Less than 1 year (23, 15), 1 year or more (61, 69)
Could interact with other pair(s) in adjacent enclosure(s) through mesh walls	No (71, 71), yes (10, 10)
Had sightline(s) to other pair(s) through mesh walls (could or could not directly interact with them)	No (38, 38), yes (43, 43)

[a] Analyzed as continuous variable.

occasionally, $0.9 \times 0.6 \times 0.6$ m. At Mountain View, pairs were housed in areas with indoor and outdoor enclosures, had access to 2–4 enclosures totaling 37.6–126.0 m^2, and were provided with 1–3 nest boxes that were $0.6 \times 0.6 \times 0.6$ m or, occasionally, $0.5 \times 0.6 \times 0.9$ m. The Mount Washington facility had indoor and outdoor enclosures, and pairs had access to 2–4 enclosures totaling 14.4–28.8 m^2 and were provided with 2 nest boxes that were either $0.6 \times 0.6 \times 0.6$ m or $1.2 \times 0.6 \times 0.6$ m.

We compiled program management data on 84 pairings conducted between 1998 and 2005 in which a single male and a single female, each aged 2 years or older, were housed together during the breeding season. Sample sizes were 25 pairs at Toronto (1998–1999; 2001–2005), 21 at Calgary (2000–2005), 21 at Mountain View (2002–2005), and 17 at Mount Washington (2002–2005). When available, data were collected for 16 variables (Table 1); data were obtained from animal care staff at each breeding facility as well as captive breeding program coordinators (see ''Acknowledgments'').

Because many animals remained in the captive breeding program for multiple years, the data set included 30 and 31 different males and females, respectively, and 66.7% ($n = 20$) of males and 64.5% ($n = 20$) of females were included in the data set in >1 year. On average, males were included (mean ± *SD*) 2.8 ± 1.9 times and females were included 2.7 ± 1.7 times. It was not possible to include ''individual'' as a variable in analyses because not all individuals were evaluated more than once. Although linear mixed models can incorporate repeated measures, they do so by taking an average of the measures for the individual sample. This is not applicable in our study because, for example, if a female had a small enclosure in 1 year and then a large enclosure in a subsequent year, taking an average of those enclosure sizes results in a loss of meaning for that variable (i.e., it is not useful to know whether a medium-sized enclosure influenced reproduction, because that female was never housed in such an enclosure). Our only other option to control for the lack of independence was to evaluate each animal only once. Because this would result in losing two-thirds of the sample size, we did not feel comfortable trading statistical power for independence. The same pair was rarely housed under the same conditions in multiple years, so the lack of independence was not as great as it could have been. Finally, 60.0% ($n = 12$) of males and 65.0% ($n = 13$) of females that were included in the data set in multiple years showed variation in their breeding performance (i.e., reproduced in some years and not in others). Therefore, it is unlikely that specific individuals substantially biased the outcome of our analyses by being consistently good or consistently poor breeders. Nevertheless, we interpret our results with caution.

Statistical analyses.—We conducted analyses using SPSS version 12.0 for Windows (SPSS Inc., Chicago, Illinois). We used a series of binary logistic regression models (SPSS Inc. 1999) and analysis of variance to analyze the influence of program management variables (Table 1) on production of young and litter size, respectively. All variables except ''surface area of enclosure'' were treated as categorical for a variety of reasons. ''Age'' was treated as categorical because examination of published data (Bryant 2005) indicated a priori that there was no expected linear relationship between age and either pup production or litter size. ''Number of nest boxes'' and ''number of enclosures'' were classified as categorical

variables because they only had a range of 3 and 4 potential values, respectively. ''Nest box size'' was categorical because there were only 2 distinct size ranges, which are classified as ''smaller'' (0.22–0.35 m^3) or ''larger'' (0.43 or 0.58 m^3) in the program. We categorized the variables ''amount of time housed with current mate'' and ''amount of time housed in current enclosure'' because it was biologically meaningful to capture entire breeding seasons. Finally, ''amount of time housed in captivity'' and ''amount of time housed at current facility'' were categorized to provide a broad measure of potential acclimatization periods associated with animal transport. In addition, previous breeding experience (the variables ''production of young in previous year,'' ''production of young 2 years previous,'' and ''production of young in any previous year'') was only evaluated if animals had the opportunity to breed previously (i.e., were 2 years of age or older and paired with a mate who was 2 years of age or older in a previous breeding season).

For logistic regression analyses of the probability of reproducing, categorical variables were ''indicator-variable coded'' (SPSS Inc. 1999) and categories with fewer than 5 cases were excluded from analyses. Because data for the male and female in a pair could differ (e.g., age category of individuals), the 2 sexes were analyzed separately. Individuals were classified as ''produced young'' (1) or ''did not produce young'' (0) in each breeding season based on whether a litter was observed by animal care staff at the breeding facility. For analyses of litter size by analysis of variance (ANOVA), females were classified according to the number of young that were weaned.

Small sample sizes precluded the testing of all variables in a single model. Therefore, each variable was 1st examined separately in univariate analyses. P-values <0.05 were considered significant, but if the P-value for a variable was <0.1 for either males or females, the variable was retained for analysis in the final multivariate models for both sexes. Final multivariate models for production of young were run as backward stepwise binary logistic regressions. P-values < 0.05 were considered significant, but any variables with P-values < 0.1 were retained in the last step of the model.

We tested the ability of our final logistic regression models to predict production of young using data on reproductive success in 2006. Using the regression coefficients (B) for each variable retained in the last step of our multivariate models, we calculated the probability of production of young for males and females paired in 2006 according to the following equation (SPSS Inc. 1999):

$$\text{Prob (production of young)} = \frac{1}{1 + e^{-Z}},$$

where $Z = B_{\text{constant}} - B_{\text{var1}}(\text{var1}) + B_{\text{var2}}(\text{var2}) + B_{\text{var3}}(\text{var3}) \ldots$. We then used binary logistic regressions to assess how well these calculated probabilities predicted observed production of young by these males and females. P-values < 0.05 were considered to be significant.

For each variable retained in the last step of our final logistic regression models and the constant created by the model, we present the regression coefficient (B) and associated Wald chi-square statistic, as well as the odds ratio (Exp(B)) with 95% confidence intervals (SPSS Inc. 1999). We present the model chi-square and the area under curve, the latter of which indicates how much variation was explained by the model (SPSS Inc. 1999). We also report the percentage of cases that were correctly predicted from the classification tables. For each significant ANOVA, we present means $\pm$ SE and associated F-statistics.

Results

Determinants of production of young.—Univariate binary logistic regressions revealed that only the variables age, production of young in any previous year, and amount of time housed with current mate (Table 1) had Wald chi-square statistic P-values < 0.1 and hence we only retained these variables in the final multivariate models for males and females. Because inclusion of the variable production of young in any previous year would have excluded any individuals who had not had the opportunity to breed previously from the models, we evaluated those that had not had the opportunity (hereafter ''1st time paired'') separately from those that had (hereafter ''previously paired''). Because, for example, 1 animal in a pair may have been previously paired with a mate whereas the other had not, subsequent sample sizes for male and female analyses sometimes differed.

For animals paired for the 1st time between 1998 and 2005, 4 of 22 males and 4 of 28 females produced young. Wild-born animals over the age of 2 that had been in captivity for <1 year (i.e., animals that had an opportunity to breed in the wild before entering the program) were not included in these analyses. Most 1st-time paired animals were 2–4 years of age (22 of 22 males and 25 of 28 females) and had been housed with their mate since the end of the previous active season (17 of 22 males and 22 of 28 females) and, therefore, the sample sizes for the other categories within these variables were too small to include in logistic regressions. Combining categories to increase sample sizes to the minimum requirement of 5 was not possible for age (no males and only 3 females were older than 4 years of age) and it did not make sense to combine animals that had been paired since the current hibernation emergence with those that had been paired for ≥ 1 year. Therefore, logistic regressions were not used to evaluate the effects of age and amount of time housed with current mate on pup production by 1st-time paired individuals. The percentage of 1st-time paired animals that produced young averaged (mean $\pm$ SD) 18.2% $\pm$ 39.4% for males and 14.3% $\pm$ 35.6% for females across the 8 years we examined.

For previously paired animals, 54 male-seasons (25 of which resulted in young) and 53 female-seasons (25 of which resulted in young) were considered. For male-seasons, only the amount of time housed with the current mate was retained as a significant variable in the last step of the logistic regression model (Table 2). The probability of production of young was significantly greater when previously paired males had been housed with their current mate for ≥ 1 year before the breeding

TABLE 2.—Estimated regression coefficients (*B*) from the last step of backward stepwise logistic regression models predicting production of young in captive Vancouver Island marmots that had been paired with a mate previously. Sample sizes were 54 male and 53 female breeding seasons during 1998–2005. The final model step retained variables with *P*-values ≤0.1. For both sexes, the final model contained a constant and the indicator variable amount of time housed with current mate; for females, the additional indicator variables age and previous production of young in any year were included. For each indicator variable considered, the Wald statistic, odds ratio (Exp(*B*)), and associated 95% confidence interval (95% *CI*) also are shown.

	Male breeding-seasons last step (step 5)			Female breeding-seasons last step (step 2)		
	B	Wald	Exp(*B*), 95% *CI*	*B*	Wald	Exp(*B*), 95% *CI*
Constant	−1.5	6.8**	0.2	−3.3	8.1**	0.04
Paired 1 year or more[a]	2.0	9.2**	7.4, 2.0−27.3	2.0	6.4*	7.7, 1.6−37.3
2−4 years of age[b]				2.6	4.3*	13.1, 1.2−148.6
5−7 years of age[c]				1.4	3.2	4.1, 0.9−19.0
Previously produced young[d]				1.5	3.3	4.3, 0.9−21.2
Model χ^2 (*d.f.*)		10.9 (1)			14.9 (4)	
Area under curve		0.67			0.78	

[a] Versus since the end of the previous active season or since the current year's hibernation emergence.
[b] Versus 5–7, 8–10, or 11–13 years of age.
[c] Versus 2–4, 8–10, or 11–13 years of age.
[d] Versus had not previously produced young in any year.
* $P < 0.05$; ** $P < 0.01$.

season (63.6% [$n = 21$] produced young), compared to when they had been paired with their mate for <1 year before the breeding season (19.0% [$n = 4$] produced young). Overall, the amount of time a male had been housed with his current mate correctly predicted production of young 70.4% ($n = 38$) of the time.

For female-seasons, age and the amount of time housed with current mate were retained as significant variables in the last step of the logistic regression model (Table 2). When previously paired females had been housed with their mate for ≥1 year before the breeding season, 63.6% ($n = 21$) produced young (66.7% [$n = 2$] of 2- to 4-year-old females; 63.3% [$n = 19$] of females in older age classes). When these females had been housed with their mate for <1 year before the breeding season, only 25.0% ($n = 5$) produced young (37.5% [$n = 3$] of 2–4 year olds and 16.7% [$n = 2$] of older age classes). Although not quite significant ($P = 0.07$), the variable production of young in any previous year also was retained in the final step of the model. When previously paired females had produced young in any preceding year, 63.0% ($n = 17$) produced young (73.3% [$n = 11$] of 5–7 year olds and 50.0% [$n = 6$] of older age classes). In contrast, only 34.6% ($n = 9$) of females that had not reproduced previously (33.3% [$n = 3$] of 5–7 year olds and 35.3% [$n = 6$] of older age classes) produced young. Overall, for females, age, amount of time housed with current mate, and previous production of young in any year correctly predicted production of young 69.8% ($n = 37$) of the time.

Determinants of litter size.—Mean (± *SD*) litter size among females that produced young was 3.3 ± 1.5 ($n = 33$, range 1–7). Univariate ANOVAs revealed that only the variable sightline to another pair had a significant effect on litter size. Specifically, litter sizes were greater for females that had visual contact with other pairs (3.9 ± 0.3, $n = 18$) compared to females that did not (2.7 ± 0.4, $n = 15$, $F = 6.0$, *d.f.* = 1, 31, $P = 0.02$).

Predicting production of young.—The probability of production of young in 2006 was estimated using data from 20 previously paired males (8 of which produced young) and 24 previously paired females (11 of which produced young). For males, the amount of time housed with current mate did not significantly improve our ability to predict rates of production of young (Table 3); overall, this variable correctly predicted 65.0% ($n = 13$) of production of young. For females, however, age, amount of time housed with current mate, and previous production of young in any year significantly improved our

TABLE 3.—Estimated regression coefficients from logistic regression models predicting production of young in captive Vancouver Island marmots that had been paired with a mate previously. Sample sizes in 2006 were 20 males and 24 females. The model contained a constant and the continuous variable probability of production of young. The Wald statistic, odds ratio (Exp(*B*)), and associated 95% confidence interval (95% *CI*) also are shown.

	Males			Females		
	B	Wald	Exp(*B*), 95% *CI*	*B*	Wald	Exp(*B*), 95% *CI*
Constant	−2.6	2.8	0.1	−2.0	3.7	0.1
Probability of production of young	4.4	2.6	78.5, 0.4−16, 359.6	3.3	4.0*	26.0, 1.1−637.2
Model χ^2 (*d.f.*)		0.0 (0)			8.9 (5)	
Area under curve		0.67			0.78	

* $P < 0.05$.

Table 4.—Estimated probabilities (presented in decreasing order) of production of young for previously paired female Vancouver Island marmots in a captive breeding program. Probabilities are based on coefficients from a logistic regression model predicting production of young from a constant and the variable probability of production of young (Table 3), the latter of which was calculated from coefficients from backward stepwise logistic regression models predicting production of young from the variables age, amount of time housed with current mate, and previous production of young in any year (Table 2). 1 indicates membership in the category.

2–4 years of age	5–7 years of age	≥1 year with mate	Previous production of young	Probability of production of young
1	0	1	1	0.74
0	1	1	1	0.67
1	0	1	0	0.63
1	0	0	1	0.55
0	0	1	1	0.45
0	1	1	0	0.43
0	1	0	1	0.33
1	0	0	0	0.28
0	0	1	0	0.21
0	0	0	1	0.17
0	1	0	0	0.17
0	0	0	0	0.13

ability to predict rates of reproduction (Table 3) and, overall, correctly predicted 75.0% ($n = 18$) of production of young.

Table 4 summarizes the effects of age, amount of time housed with current mate, and previous production of young in any year on the probability of production of young by previously paired females. We calculated an adjusted probability of production of young for females by 1st using the equation presented above and regression coefficients for age, amount of time housed with current mate, and previous production of young in any year (Table 2) to calculate a raw probability of production of young, and then by rerunning the same equation but using the regression coefficient for probability of production of young (Table 3). These adjusted probabilities are the values that correctly predicted 75.0% of production of young in 2006. As indicated, a female that is between 2 and 4 years of age, that has produced young previously, and that has been housed with the same mate for at least 1 year has the greatest probability of production of young (0.74) in a given breeding season. In contrast, if that female has been housed with her mate for <1 year, her estimated probability of production of young drops to 0.55. Thus, these analyses provide a valuable tool for assessing the probability of future production of young by females in the captive breeding program.

Discussion

Numerous factors may influence reproduction in mammals. Identifying which factors affect a given species and understanding how they influence reproduction will greatly increase the success of recovery programs for imperiled species, especially programs that incorporate captive breeding and reintroduction. Our study provides the 1st published evaluation of how multiple program-management variables influence production of young and litter sizes in captive-bred marmots, specifically captive-bred Vancouver Island marmots.

In analyses evaluating the probability of production of young in previously paired animals, we detected an effect of the amount of time that individuals in a pair were housed together before the breeding season, female age, and, potentially, production of young by females in any previous year. The positive relationship between the amount of time animals were paired and the probability of production of young suggests that familiarity between mates may enhance breeding success (Radespiel and Zimmermann 2003; Tang-Martinez et al. 1993), perhaps by facilitating cohesive behaviors between members of a pair (Hare 1992, 1994, 1998; King and Allainé 2002; Perrin et al. 1993). This familiarity between mates may be particularly important for species with socially monogamous mating systems (Cezilly and Nager 1996; King and Allainé 2002; Patris and Baudoin 1998). However, although wild Vancouver Island marmots often display single male–single female breeding groups, adult males rarely spend >1 active season at a site (Bryant 1996). There is no information in the published literature about rates of pair turnover for this species. Therefore, it is unclear whether familiarity between mates plays a strong role in successful production of young in wild populations of this species. A study of pair bonds and reproductive success among free-living animals would be informative.

Our results also suggest that, for previously paired females, a reduction in familiarity between mates (i.e., being housed together for <1 year before the breeding season) may negatively influence older age classes more than younger ones. In captive Vancouver Island marmots, the duration of copulatory mounts is positively associated with production of young (Casimir 2005). If captive female Vancouver Island marmots play a larger role than males in determining the duration of matings and young adult females are less likely to reject males or terminate matings than older age classes (Radespiel and Zimmermann 2003), our observed effect may be a reflection of a greater tendency for older females to reject or terminate matings with unfamiliar males compared to younger ones. However, further study is required to elucidate the mechanisms behind our findings and confirm these potential causal relationships.

Although not statistically significant in our models, breeding experience also may have positively influenced production of young and this effect may vary with age among females with previous breeding experience. Breeding experience that is related to age influences litter size in alpine marmots (King and Allainé 2002) and the probability of reproduction in other mammals. For example, in female northern elephant seals (*Mirounga angustirostris*) breeding experience positively influences the probability of successful reproduction for young animals during their 1st few reproductive attempts, but negatively affects success among older animals (Sydeman et al. 1991). In Vancouver Island marmots, breeding experience likely positively influences reproductive skill and proficiency in

females. However, although the absence of successful reproduction in wild or captive Vancouver Island marmots beyond the age of 10 years (Bryant 2005) suggests reproductive senescence by females that are more than a decade old, our results suggest that reproductive potential may begin declining in females that are more than 8 years of age. In contrast to females, age and breeding experience did not influence production of young by males. This may be, in part, an effect of having no males in our oldest age category. However, because the reproductive effort for female marmots is greater than that for males (Barash 1989) it is perhaps not surprising that age and experience effects related to reproduction may be more pronounced in females.

In analyses evaluating litter size, the only effect detected was that the ability to see pairs in other enclosures positively influenced litter sizes. This result is puzzling, especially because sightlines to other pairs had no influence on production of young. We could find no published studies where this or similar variables were examined. It is possible that sightline was correlated to another, untested, variable. Alternatively, small sample sizes may have caused our multivariate analyses to overlook variables that would help explain the relationship. However, it is also conceivable that this relationship reflects elements of social structure in marmot species (Blumstein and Armitage 1999). The social structure of wild Vancouver Island marmots often involves >1 female in a family group and >1 family group in a colony (Bryant and Janz 1996; Heard 1977). Visual contact with other pairs in the captive breeding program may better approximate this social setting, thereby leading to increased reproductive success via larger litter sizes.

In addition to increasing our knowledge of factors that influence production of young in Vancouver Island marmots, we suggest that the results of our study can be used along with genetic considerations to plan future pairings with a high probability of production of young. With regard to the captive breeding program, housing females with the same mate for 2 or more consecutive breeding seasons will maximize their potential for production of young. To this end, it may be advisable to pair yearlings when they emerge from their 1st hibernation to prepare them for breeding as 2 year olds. At the same time, if a male is particularly valuable genetically (e.g., has low mean kinship value relative to other males), we recommend pairing him with a female 7 years of age or younger who has past experience in production of young to maximize his chances of producing offspring.

The true measure of success in a captive breeding and reintroduction program is not simply survival of released animals, but also breeding by the released animals and their offspring (Seddon 1999). Our results have implications for both management objectives. For example, housing pairs in the same enclosure may facilitate mate familiarity before release, thereby potentially increasing social cohesion and survival once animals are released (Bly-Honness et al. 2004; Kleiman 1989). In addition, forming release groups that contain a male–female pair with a high probability of production of young within the captive breeding program also may maximize the potential for production of young once that pair is released.

Like the Vancouver Island marmot, bobak, long-tailed, and Menzbier's marmots all exhibit group hibernation, are socially integrated during the summer (Blumstein and Armitage 1999), and are currently listed as species at risk (IUCN 2006). Like Vancouver Island marmots, long-tailed marmots are most commonly found in apparently monogamous associations in which a few females produce the majority of young and interlitter intervals are >1 year (Blumstein and Arnold 1998). Otherwise, little is known about factors influencing reproduction in these species. Given the general ecological and life-history similarities among social marmot species, we suspect that our results for Vancouver Island marmots may be applicable to recovery programs for these other imperiled species. At a minimum, the methods employed in our study, in particular the development of a quantitative model to assist in maximizing reproductive rates in a predictable manner, may prove useful in recovery programs for endangered mammals.

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