Reproductive rates of wild and captive Vancouver Island marmots (*Marmota vancouverensis*)

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Abstract: I evaluated reproductive rates of the critically endangered Vancouver Island marmot (*Marmota vancouverensis* Swarth, 1911) using data from captive and wild populations over the 1980–2004 period. Results were similar to those reported for other alpine-dwelling marmots, including the closely related *Marmota caligata* (Eschscholtz, 1829) and *Marmota olympus* (Merriam, 1898). Most females in captivity first bred at age 3 or 4 (T_{breed} = 4.3 years, SD = 1.15, n = 9), an age not significantly different from that observed in the wild (T_{breed} = 3.6 years, SD = 1.2, n = 16). Numbers of pups weaned per litter were similar in captivity (N_{pups} = 3.0, SD = 1.4, n = 25) and in the wild (N_{pups} = 3.4, SD = 1.1, n = 58). Females were capable of weaning pups in consecutive years (46.4%, n = 13) but often skipped 1 year (39.3%, n = 11) or 2 years (14.3%, n = 4) between litters. Two-year-old females weaned pups infrequently (P_{breed} = 0.09, n = 43) and older females were far more likely to breed (P_{breed} = 0.40, n = 200); in neither case were significant captive–wild differences found. The oldest breeding female was 10 years old, but sample sizes for marmots older than 8 years were small and maximum breeding age may be underestimated. Between-litter intervals in captivity (T_{between} = 1.4 years, SD = 0.7, n = 11) were significantly shorter than in the wild (T_{between} = 1.9 years, SD = 0.7, n = 17). Sex ratios of weaned pups did not differ from 1:1 in the wild (female/male = 1.04) but were significantly skewed towards males in captivity (female/male = 0.56). I conclude that reproductive performance in Vancouver Island marmots is limited both by body condition and social constraints.

Résumé : Des données récoltées dans des populations en captivité et en nature de la marmotte de l'île de Vancouver (*Marmota vancouverensis* Swarth, 1911), une espèce fortement menacée, durant la période 1980–2004, ont permis d'estimer les taux de reproduction. Les résultats se rapprochent de ceux obtenus chez d'autres marmottes alpines, en particulier chez les espèces apparentées, *Marmota caligata* (Eschscholtz, 1829) et *Marmota olympus* (Merriam, 1898). Les femelles en captivité se reproduisent pour la première fois à 3 ou 4 ans ($T_{\text{reproduction}}$ = 4,3 ans, ET = 1,15, n = 9), ce qui ne diffère pas significativement des femelles en nature ($T_{\text{reproduction}}$ = 3,6 ans, ET = 1,2, n = 16). Les nombres de petits sevrés par portée sont semblables en captivité (N_{petits} = 3,0, ET = 1,4, n = 25) et en nature (N_{petits} = 3,4, ET = 1,1, n = 58). Les femelles réussissent à sevrer des petits durant deux années consécutives (46,4 %, n = 13), mais elles sautent souvent une année (39,3 %, n = 11) ou deux (14,3 %, n = 4) entre les portées. Les femelles de 2 ans réussissent rarement à sevrer leurs petits ($P_{\text{reproduction}}$ = 0,09, n = 43) et les femelles plus âgées sont plus susceptibles de se reproduire ($P_{\text{reproduction}}$ = 0,40, n = 200), sans différence significative entre la captivité et la nature. La femelle reproductive la plus âgée avait 10 ans, mais la taille des échantillons d'animaux plus vieux que 8 ans est petite et l'âge maximal de reproduction a pu être sous-estimé. Les intervalles entre les portées sont significativement plus courts en captivité ($T_{\text{intervalle}}$ = 1,4 année, ET = 0,7, n = 11) qu'en nature ($T_{\text{intervalle}}$ = 1,9 année, ET = 0,7, n = 17). Les rapports femelles:mâles ne diffèrent pas de 1:1 en nature (femelle/mâle = 1,04), mais ils favorisent significativement les mâles en captivité (femelle/mâle = 0,56). En conclusion, la performance reproductive de la marmotte de l'île de Vancouver est restreinte tant par sa condition corporelle que par ses contraintes sociales.

[Traduit par la Rédaction]

Introduction

Captive-breeding programs are important for a growing list of endangered species (Griffith et al. 1990; Beck et al. 2002). However, genetic, behavioral, and social changes often accompany the transition of wild animals into captivity (Ralls et al. 1979; Gran et al. 1998). Combined with inappropriate housing or environmental conditions, the result is often limited reproductive success, sometimes to the point of unsustainability (Wielebnowski 1998). Few studies have explicitly compared reproductive rates of wild and captive populations of the same species, making it difficult to evaluate the causes of failure or success of captive programs (Snyder et al. 1996). Here I evaluate reproductive rates of captive and wild populations for a critically endangered mammal, the Vancouver Island marmot (*Marmota vancouverensis* Swarth, 1911).

As its name suggests, the Vancouver Island marmot is endemic to Vancouver Island, British Columbia, Canada (Nagorsen 1987). It is the only ground squirrel naturally occurring on that island (Banfield 1977). The natural habitat consists of small subalpine meadows, typically at an elevation of 900–1400 m (Milko and Bell 1986). As is true for all marmot species, the Vancouver Island marmot lives in underground burrows, hibernates during winter, and feeds on a

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variety of grasses and forbs during summer (Barash 1989; Martell and Milko 1986). Historically, colonies have been small, with most containing only a single family group and fewer than five adults (Bryant and Janz 1996). The species remained virtually unknown until the 1970s (Heard 1977), and in 1978 was among the first to be listed as endangered by the newly formed Committee on the Status of Endangered Wildlife in Canada (Shank 1999). Population counts began in 1979 and have continued, with variable coverage and intensity, until the present. Marmots expanded into new habitats created by clearcut logging of high-elevation primary forests during the 1980s; numbers increased to an estimated 300–350 individuals by 1986, with about half of these living in clearcuts (Bryant and Janz 1996). The temporary population expansion was followed by precipitous decline and near-extinction in the wild (Bryant 2000). Fewer than 130 marmots were known to be alive by 2004, including 93 in captivity and ~35 in the wild (unpublished minutes, Vancouver Island Marmot Recovery Team, November 2004).

Discovery of a dispersing subadult male in the village of Coombs provided the initial impetus to breed Vancouver Island marmots in captivity (Munro et al. 1985). That individual and another male were captured and sent to the Okanagan Game Farm (hereinafter “Okanagan”, near Penticton, British Columbia) in September of 1980. A third male and two pups (one male and one female) followed in 1981. The female eventually produced litters in 1985 and 1986. However, financial resources were meager, monitoring efforts were minimal, and housing for the marmots was apparently inadequate. Despite successful reproduction, the last Vancouver Island marmots at the Okanagan facility were seen alive in spring of 1987.

Recognition of declining wild populations inspired a second captive-breeding effort, beginning in 1997 with six animals sent to the Toronto Zoo (hereinafter “Toronto”). Captive populations were later established at the Devonian Conservation Centre operated by the Calgary Zoo (“Calgary”), the privately owned Mountain View Breeding and Conservation Centre (hereinafter “Mountain View”) in Langley, British Columbia, and a facility on Mount Washington, Vancouver Island (the Tony Barrett Mount Washington Marmot Conservation Centre; hereinafter “Mount Washington”).

In this study, I report on reproductive results through summer of 2004 from the wild population and all five captive facilities. My primary objective was to evaluate success of the Okanagan and more modern captive programs in terms of providing conditions suitable for breeding. I also describe reproductive traits of the Vancouver Island marmot in relation to other alpine-dwelling marmot species. My intent was to assess whether Vancouver Island marmots are reproductively similar to other marmots, to evaluate performance of the current captive population, and to provide a benchmark against which future changes in reproductive rates might be compared.

Study areas and methods

Wild populations

The natural habitat of Vancouver Island marmots has been previously described and mapped (Milko and Bell 1986; Bryant 1996; Bryant and Janz 1996). Trapping, tagging, and age-classification methods followed Bryant (1996, 1998) and Karels et al. (2004). I compiled reproductive records from intensively studied colonies (i.e., those in which marmots were tagged and successfully monitored) from 1987 through 2004. Most data were obtained from eight colonies in natural meadows (Green Mountain, Haley Lake, “P” Mountain, “P” Mountain NW, “Big Ugly”, Heather Mountain, Mount Moriarty, and Mount Washington) and four colonies in clearcuts (Sherk Lake, Vaughan road, Green road K44a, and Pat Lake; Fig. 1). The sample from wild colonies represents 249 tagged individuals and 554 marmot-years of observation; approximately half of these records were from females (121 individuals and 291 marmot-years).

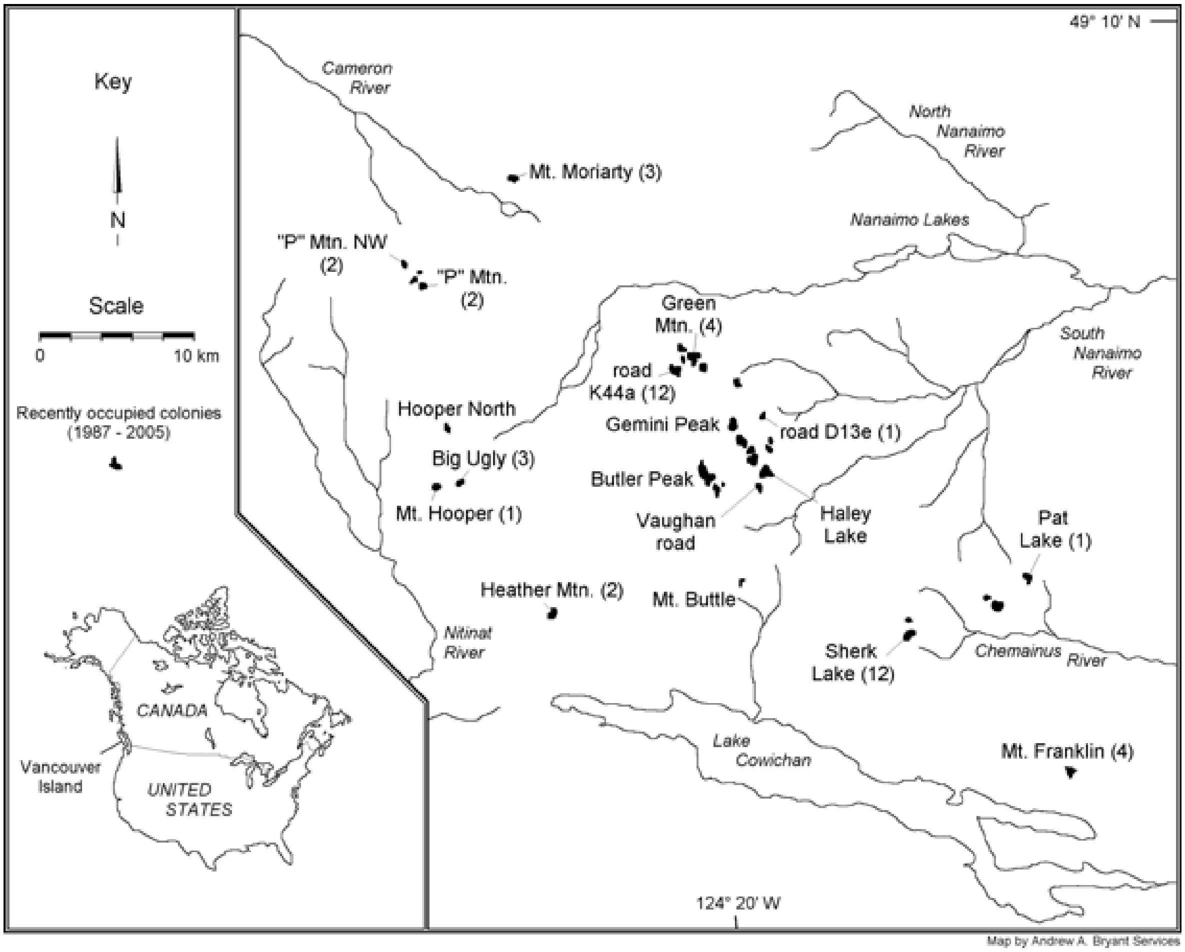
Captive populations

I compiled reproductive records from all five captive facilities where Vancouver Island marmots have been maintained from 1980 though 2004. The early (Okanagan) captive-breeding effort was based on five wild-born animals, two of which were captured as pups. The second captive effort involved larger numbers of animals; 56 wild-born marmots were taken into captivity between 1997 and 2004. The majority of these were first captured as pups (*n* = 31) or yearlings (*n* = 8). Most individuals (*n* = 30) were captured from colonies in regenerating clearcuts, and in three cases the marmot in question was apparently the last surviving member of historically larger colonies. The cumulative sample from captive populations includes records from 124 individuals and 414 marmot-years of observation, with somewhat less than half of these records representing females (48 individuals and 180 marmot-years of observation).

The five captive facilities differed greatly in their design, environmental characteristics, and management philosophies. Vancouver Island marmots in the Okanagan (1980–1987) were housed outdoors in a dry desert environment that experiences hot (>30 °C) temperatures in summers and occasional freezing temperatures and snowfall in winter (Demarchi et al. 1990). Elevation was 490 m. The single enclosure was 12.0 m × 20.0 m in size and was constructed from standard 8-cm wire mesh. Overhead netting (at 3.1 m high) was erected to exclude avian predators. An artificial burrow was constructed from rocks and wood, which marmots soon modified by digging new chambers. The animals were on public display, with adjacent pens containing grizzly bears (*Ursus arctos* L., 1758) and red deer (*Cervus elaphus* L., 1758). No special efforts were made to facilitate or encourage hibernation. Group size varied but approximated that of a natural colony; for example in 1986 the group included an 8-year-old male, a 5-year-old female, a yearling of unknown sex, and four pups produced in that year. The enclosure was apparently inadequate to contain or maintain marmots; an unknown number of marmots escaped, while others died in situ.

Vancouver Island marmots at Toronto (1997 to present) were housed at the animal health care unit, a facility off-limits to the general public. In summer, most marmots were confined within small (2.0 m × 4.0 m × 3.1 m or 4.0 m × 4.0 m × 3.1 m) concrete-floored indoor pens that were equipped with 0.9 m × 1.2 m × 0.8 m nest boxes. Other marmots were housed in 3.0 m × 3.0 m × 3.1 m outdoor pens formerly used for black-footed ferrets (*Mustela nigripes*

Fig. 1. Location of recently occupied Vancouver Island marmot (*Marmota vancouverensis*) colonies in the Nanaimo Lakes region. Numbers of wild-born marmots taken into captivity between 1997 and 2004 are shown in parentheses. The isolated Mount Washington colony is located approximately 95 km to the northwest; consequently $n = 9$ captures from that site do not appear on this map.



Map by Andrew A. Bryant Services

(Audubon and Bachman, 1851)) and cheetahs (*Acinonyx jubatus* (Schreber, 1775)). Outdoor summer temperatures at Toronto rarely exceed 30 °C. In winter, most nest boxes were moved to a climate-controlled (6.0 °C, 70%–75% RH) environmental chamber. Marmots at Toronto were regularly handled for research purposes and to facilitate health examinations. Experience gained after 2001 allowed keepers to adopt a more limited handling policy.

Vancouver Island marmots at Calgary (1998 to present) were located in an arid grassland environment 70 km west of that city. The site experiences hot (>25 °C) summers, cold (<20 °C) winters, and occasional mid-winter melts produced by a phenomenon locally known as the "chinook" (warm winds that occur on the leeward side of the Rocky Mountains). Marmots were housed in modified indoor–outdoor pens previously used for whooping cranes (*Grus americana* (L., 1758)). Individual pens contained an indoor area (3.6 m × 4.5 m × 3.1 m) connected to an outdoor area of similar size through provision of a small (20 cm × 40 cm) door. The intent was to allow marmots the freedom to choose their own thermal "comfort zones". Marmots hibernated and bore pups in metal-clad plywood nest boxes (1.8 m × 0.8 m × 0.8 m) situated within the indoor area. The building was heated but not temperature-controlled. November–April temperatures varied more than at other facilities (mean = 8.7 °C, range = 0.7°–23.6 °C, mean daily $\Delta_{\text{temp.}}$ = 1.7 °C, SD = 1.3 °C, n = 140 days and 3360 hourly measurements). Relative humidity also varied (mean = 28.1%, range = 23.6%–43.7%, mean daily Δ_{RH} = 2.5%, SD = 3.3%, n = 140 days and 3360 hourly measurements). As was the case at Toronto, marmots were not on public display but were occasionally handled for research and health monitoring purposes.

Vancouver Island marmots at Mountain View (1999 to present) were housed in a facility built expressly for marmots. The design followed the Calgary practice in that enclosures contained both indoor (1.8 m × 3.1 m × 2.5 m) and outdoor areas linked by a "marmot door". Outdoor pens were more spacious than elsewhere (some were 9.2 m × 7.4 m × 3.1 m and others were 4.9 m × 4.6 m × 3.1 m). The intent was to provide marmots with opportunities to dig burrows, eat wild vegetation, and use rocks as they would do in the wild. The climate at Mountain View is moderated by its proximity to the Pacific Ocean, with temperatures occasionally dipping below 0 °C in winter and occasionally exceeding 25 °C during summer (Demarchi et al. 1990). Indoor pens at Mountain View were heated but not climate-controlled. However, resulting temperatures were cooler and varied less than at Calgary (mean = 6.0 °C, range = 4.2–

9.0 °C, mean daily $\Delta_{\text{temp.}}$ = 0.6 °C, SD = 0.7 °C, n = 140 days and 3360 hourly measurements). Relative humidity was higher and more stable than at Calgary (mean = 82.7%, range = 76.1%–86.4%, mean daily Δ_{RH} = 0.5%, SD = 0.5%, n = 140 days and 3360 hourly measurements). The level of marmot handling for research purposes was lower than it was at Toronto or Calgary, particularly during the summer active season.

The Mount Washington facility (2001 to present) was also custom-designed to house marmots. As at Calgary and Mountain View, the basic housing element consisted of an indoor enclosure connected to an outside pen through a small marmot door. The facility is located at an elevation of 1000 m and is close (<1 km) to sites occupied by wild Vancouver Island marmots. The intent was to allow captive marmots to experience natural ambient temperatures and photoperiods in the outside enclosures. Indoor pens were temperature but not humidity-controlled. November–April temperatures varied little and approximated those experienced by hibernating marmots at Toronto (mean = 6.1 °C, range = 4.6–7.4 °C, mean daily Δ_{temp} = 0.4 °C, SD = 0.2 °C, n = 122 days and 2928 hourly measurements). However, relative humidity varied more (mean = 47.7%, range = 24.9%–74.5%, mean daily Δ_{RH} = 0.3%, SD = 0.1%, n = 122 days and 2928 hourly measurements), although they were more stable than at Calgary or Mountain View. A strictly limited access and handling philosophy was practiced. In addition, the location of the Mount Washington facility allowed keepers to provide natural foods such as lupines (*Lupinus latifolius* Lindl. ex J.G. Agardh) and asters (species of *Aster* L.) in addition to the primary diet of dry rodent pellets.

Known-age and presumed-age marmots

Some wild-born Vancouver Island marmots were first captured as pups (n = 108), yearlings (n = 38), or 2-year-olds (n = 32), and were therefore treated as "known-age" individuals. For these age classes, behavior, size, and fur characteristics are diagnostic (Bryant 1996). The remainder (n = 71) were assigned a "presumed age" (i.e., minimum age) at time of first capture. As there is no reliable external or noninvasive means of classifying ages of animals older than 2 years, most adults were assumed to be at least age 3. In a few cases (n = 10), large size and body measurements suggested that animals were at least age 4 (Karels et al. 2004), and I accordingly applied that retroactive adjustment to the data. Subsequent annual records of the same individual were tallied as incremental increases (+1 year) for both known and presumed-age marmots.

Vancouver Island marmots produce only a single litter per year, although they do not necessarily breed every year. Births in the wild occur in late May or early June, with pups first emerging above ground in late June or early July (Bryant 1998). Marmots in captivity typically emerge, breed, and give birth about 5 weeks earlier (Bryant and McAdie 2003). I ignored this variation. For both populations, I considered pups to be age class 0 until after their first hibernation cycle, when they were considered to be yearlings (age class = 1). Two-year-olds were defined as surviving their second hibernation cycle, 3-year-olds as surviving their third, with the same convention being applied to older age classes.

Reproductive rates

I measured five reproductive characteristics: age at first reproduction, litter size, proportion of females that weaned pups, between-litter interval, and sex ratio of offspring. For litter size and probability of breeding, I also evaluated the possible influence of age class. These terms are widely used in the literature (e.g., Schwartz et al. 1998; Stephens et al. 2002), but to avoid misinterpretation I employed the following definitions.

- Age of first reproduction (T_{breed}) is the minimum age of females weaning their first litter. I included records from known-age females in which an adult male was present. Lack of a potential mate precluded use of records from several females in both wild and captive populations. Results therefore reflect an estimate of the age of sexual maturity that is unbiased by population constraints (i.e., inability to find a mate).
- Litter size (N_{pups}) is the number of weaned pups/breeding event from known females. This was simply the largest number of pups seen above ground near the natal burrow in the wild, or seen outside the nest box in captivity. I excluded records of a few wild litters because the female parent could not be positively identified or because pups from adjacent litters could not be distinguished. In captivity, nest-box cameras occasionally suggested that more pups were born than were eventually weaned; I used the weaned estimate for analyses.
- Probability of breeding (P_{breed}) is the proportion of females that weaned pups when an adult (age 3 or older) male was available during the breeding period (i.e., within 3 weeks of spring emergence). For captive marmots, I included females if a male was housed in the same enclosure. For wild marmots, I included all females in a colony if at least one male was present; observations suggested that multiple litters were occasionally sired by a single male (Bryant 1996). I ignored records of females in which enlarged nipples suggested breeding, but no weaned pups were seen. Results therefore reflect the proportion of successful breeders and not pregnancy rates.
- Between-litter interval (T_{between}) is the number of years between litters for individuals that bred more than once. I treated data as ordinal (e.g., female x weaned litters in 1987 and 1988, so the interval was 1 year) rather than continuous (e.g., female x weaned pups on 2 July 1987 and 18 July 1988, so the interval was 1.05 years). Several females bred in the wild prior to being taken into captivity, and some individuals also later bred in captivity. Calculating T_{between} from wild-born and captive-born litters from the same female would require the assumption that capture, transport, and habituation to captivity did not influence breeding frequency. This assumption may be unreasonable, therefore I calculated T_{between} using litters produced only in the wild, or only in captivity, by a given female.
- Sex ratio (female/male) is the ratio of female to male pups. For the captive population, I tallied data provided by the zoos. Data from the wild population were problematic because it was seldom possible to capture all of the pups from particular litters. In addition, sexing young marmots is difficult and observers occasionally watched pups "change sex" between captures. To evaluate the likelihood

of mistaken sex assignment, I compared sex ratios calculated from individuals first captured as pups with those that were eventually recaptured, and with those first captured as yearlings.

Statistical analyses

For ordinal data (N_{pups}, T_{between}), I used nonparametric Mann–Whitney tests and Kruskal–Wallis ANOVA to test for differences among groups. For ratio data (female/male, P_{breed}) I used χ^2 tests, and for comparisons of age-specific breeding rates and litter sizes I used parametric ANOVA (Zar 1974). Given the small sample sizes and consequent low power for many analyses, I used an $\alpha = 0.10$ decision rule to evaluate significance. I also evaluated effect sizes for all analyses by calculating Cohen's d, χ^2 contingency coefficients ϕ or C, or r^2 values as appropriate (Cohen 1988).

Results

Age of first reproduction

A total of 25 known-age female Vancouver Island marmots with access to adult males in early spring produced their first litter during the study; 9 of these animals first bred in captivity. Females occasionally weaned pups as 2-year-olds, but this occurred infrequently (16.0%, $n = 4$). Other females first weaned pups at age 3 (20.0%, $n = 5$), 4 (40.0%, $n = 10$), 5 (12.0%, $n = 3$), or 6 (12%, $n = 3$). The distribution of first-reproductive ages did not differ among captive and wild populations ($\chi^2 = 5.11$, df = 4, $P = 0.276$, $C = 0.170$). The mean age of first breeding was slightly but not significantly higher in captive females (4.3 years) than in wild females (3.6 years; Mann–Whitney $U = 99.0$, $P = 0.111$, Cohen's $d = 0.647$).

Given field methods employed, it was impossible to accurately determine ages at which males produced their first offspring in the wild. Behavioral observations suggested that males younger than 3 years were subordinate to older males and did not breed. In no case did observers record females older than 3 years (i.e., reproductive-age females) breeding at colonies where only 2-year-old males were present ($n = 6$ site–year combinations and 21 female-years). In captivity, a single known-age 2-year-old male weaned offspring with a 2-year-old female. In three cases, 3-year-old males successfully bred for the first time with older females (ages 4, 4, and 5), and in three cases, 4-year-old males weaned their first litter with similar-age or older females (ages 4, 4, and 6). Further analysis of the age of first reproduction in males was problematic because managers generally attempted to pair younger females with older males. Thus, while some males were as old as 6, ($n = 1$), 7 ($n = 3$), or 8 years ($n = 1$) when they produced their first pups, the limiting factor in these cases was presumably the availability of breeding-age females.

Litter sizes

Tagged females produced 25 litters in captivity and 58 litters at intensively studied wild colonies during the study. Litters typically consisted of 3 pups (37.3% of cases) or 4 pups (24.1%). Litters of 1, 2, 5, 6, or 7 pups occurred less frequently (8.4%, 15.7%, 10.8%, 2.4%, and 1.2%, respectively). Mean litter size was 3.00 pups (SD = 1.44) in captivity versus 3.38 pups (SD = 1.14) in the wild; the difference was not significant (Mann–Whitney $U = 580.5$, $P = 0.137$, Cohen's $d = 0.307$). Litter sizes did not significantly differ among the five captive facilities (Kruskal–Wallis test statistic = 2.42, $P = 0.660$, $r^2 = 0.046$; Fig. 2*a*).

Litter size varied greatly with year, from a high of 3.89 pups (SD = 0.84, $n = 8$ wild litters) in 1994 to a low of 2.22 pups (SD = 1.48, $n = 4$ wild and 5 captive litters) in 2002. This might reflect weather condition, body condition, or different age of breeders in different years; however, temporal analysis of litter size was confounded by small sample sizes in many years of the study (range = 1–11 litters/year, median = 3 litters/year from 1985 to 2004). Litters produced by first-time breeders (mean = 2.96 pups, SD = 1.04, $n = 25$) were similar to those produced by females known to have weaned pups in previous years (mean = 3.35, SD = 1.13, $n = 34$; Mann–Whitney $U = 373.0$, $P = 0.405$, Cohen's $d = 0.359$).

Probability of weaning pups

Calculating the probability that females wean pups (P_{breed}) requires knowing not only the number of breeding-age females, but also the subset of females with access to potential mates. For example, none of the seven tagged adult females at intensively studied wild colonies in 1995 weaned pups, presumably because no adult males were present. When such records ($n = 36$ female-years) were excluded, the probability of breeding for wild females aged 2 years and older was 0.35 ($n = 164$ female-years). When 2-year-olds, which breed infrequently, were also removed from consideration, P_{breed} increased to 0.41 ($n = 134$ female-years; Fig. 2*b*).

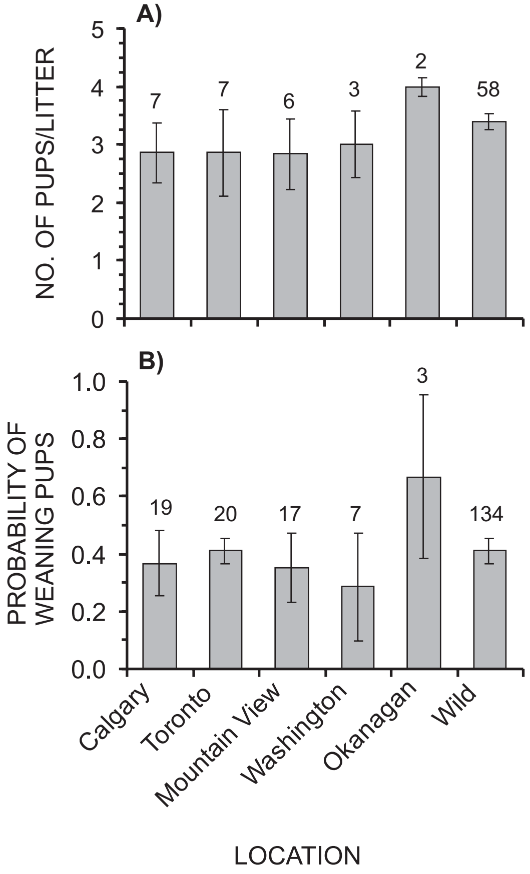
At first glance the probability of breeding by females aged 2 years and older was very low in captivity ($P_{\mathrm{breed}} = 0.24$, $n = 105$ female-years). However, as with the wild population, there were multiple occasions ($n = 26$ female-years) in which no adult males were housed with females during the early-spring mating period; exclusion of these records increased P_{breed} to 0.32 ($n = 79$). Removal of records from 2-year-olds further increased P_{breed} to 0.38 ($n = 66$), a rate not significantly different from that seen in the wild ($\chi^2 = 0.40$, df = 1, $P = 0.524$, $\phi = 0.045$). Despite the range of environmental conditions experienced by Vancouver Island marmots, P_{breed} did not differ significantly among the five captive facilities ($\chi^2 = 1.40$, df = 4, $P = 0.844$, $C = 0.021$).

Age-specific influences upon litter size and breeding probability

Age-specific sample sizes were generally insufficient to compare wild and captive reproductive rates for particular age classes, but pooled data from captive and wild populations were informative. Two-year-old females weaned fewer pups/litter (1.75 pups/litter, SD = 0.50, $n = 4$) than did adults aged 3–10 (3.34 pups/litter, SD = 1.22, $n = 79$). The difference between groups was highly significant (Mann–Whitney $U = 280.0$, $P = 0.007$, Cohen's $d = 1.716$). ANOVA showed no significant differences in litter sizes weaned by females older than 2 years ($F_{[7,71]} = 0.792$, $P = 0.596$, $r^2 = 0.072$), although three 10-year-old females weaned relatively small litters (Fig. 3*a*).

Two-year-old females displayed a lower probability of breeding ($P_{\mathrm{breed}} = 0.09$, $n = 43$ female-years) than did older

Fig. 2. Number of weaned pups/litter (A) and probability that an adult female Vancouver Island marmot weaned pups in a given year (B) by location. Data are means and SE. Sample sizes are shown. Data from 2-year-old females (n = 3 litters) and from site–year combinations in which no male was available (n = 62 female-years) have been excluded.

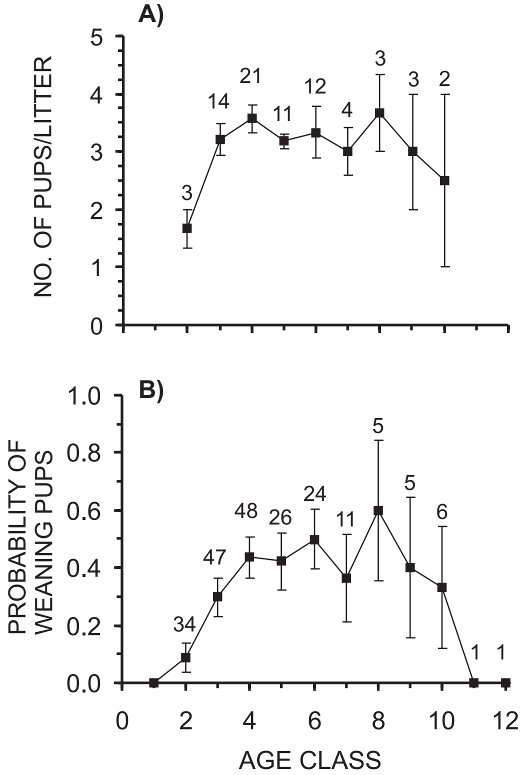


females (P_{breed} = 0.39, n = 200); again the difference was highly significant (χ^2 = 14.35, df = 1, P < 0.001, ϕ = 0.243; Fig. 3*b*). There was no significant difference in P_{breed} for females older than 2 years (ANOVA, $F_{[11,188]}$ = 0.983, P = 0.463, r^2 = 0.054). However, it may be biologically significant that three females that lived past the age 10 in captivity did not breed (n = 5 marmot-years).

Between-litter intervals

A total of 24 females bred more than once during the study, including 5 females that produced at least 3 litters either in the wild (n = 3) or in captivity (n = 2). A single female produced five litters, including one born in the wild and four later born at Calgary. Exclusion of between-litter intervals from Vancouver Island marmots that encompassed movements between the wild and captivity, or contained years in which no potential mate was available, left a useable sample of n = 28 between-litter records from 22 females.

Fig. 3. Age-specific number of weaned pups/litter (A) and probability that an adult female weaned pups in a given year (B) for Vancouver Island marmots. Data are means and SE, using records from locations where a possible mate was present. Records from captive and wild populations were pooled.



Females weaned pups in consecutive years (46.4%, n = 13) or skipped 1 year (39.3%, n = 11) or 2 years (14.3%, n = 4) between reproductive events. The distribution of between-litter intervals differed between captive and wild populations (χ^2 = 5.09, df = 2, P = 0.078, C = 0.154). Specifically, between-litter intervals were shorter in captivity (mean = 1.36 years, SD = 0.67, n = 11) than in the wild (1.88 years, SD = 0.70, n = 17) (Mann–Whitney U = 54.5, P = 0.045, Cohen's d = 0.759). With only n = 11 records, it was not possible to test for differences in between-litter intervals among the five captive facilities.

Sex ratio of pups and yearlings

A total of 108 wild-born pups were captured from 1987 through 2004. In 27 cases pups were never recaptured and it was therefore impossible to verify the accuracy of original sex determination. On four occasions pups were recaptured in later years and found to have been misidentified at time of first capture. In three cases males were mistaken as females, and in one case a female was erroneously recorded as a male. In 77 cases the original sex determination was verified, producing a success rate of 77/81 (95%). Few older animals were found to have been misidentified at time of first capture; the exception being two 2-year-old males that were initially identified as females when captured and sent to the Okanagan captive facility in 1980.

After incorporating corrections based on recaptures, numbers of female and male pups captured in the wild produced a sex ratio of 1.04 (55/53). Conceivably this estimate might be biased by gender-specific probabilities of capture or misidentification by field personnel. However, exclusion of the 27 cases in which pups were never recaptured produced a similar ratio (female/male = 0.93 (39/42)), as did records

Table 1. Reproductive traits of several populations of wild alpine-dwelling marmots (genus *Marmota*).

Variable and species	Location	*N*	Mean	SD	Range	Source
Weaned pups per litter						
M. flaviventris	Colorado	265	4.10	0.10	1–8	Schwartz et al. 1998
M. olympus	Washington	24	4.00	1.18	2–6	Barash 1973
M. caligata	Montana	4	3.75	0.50	3–4	Barash 1974
M. caligata	Washington	5	3.60	0.90	3–5	Barash 1980
M. caligata	Alaska	13	3.10	0.80	2–5	Holmes 1984
M. vancouverensis	Vancouver Island	7	3.40	1.71	1–6	Milko 1984
M. vancouverensis	Vancouver Island	58	3.38	1.14	1–6	This study
M. vancouverensis	Vancouver Island	5	3.00	0.50	3–4	Heard 1977
M. marmota	Germany	126	3.47	1.47	1–6	Stephens et al. 2002
M. marmota	France	4	3.10	1.40	3–4	Barash 1976
M. marmota	France	26	2.62	0.50	2–5	Allainé et al. 1994
M. caudata	Pakistan	15	4.20	1.14	2–6	Blumstein and Arnold 1998
Age at first breeding (years)						
M. flaviventris	Colorado	119	3.02	0.10	2–6	Schwartz et al. 1998
M. olympus	Washington	24	3.62	0.79	3–6	Barash 1973
M. vancouverensis	Vancouver Island	16	3.56	1.15	2–6	This study
Between-litter interval (years)						
M. caligata	Alaska	9	3.33	0.71	2–4	Holmes 1984
M. olympus	Washington	88	2.10	0.30	2–3	Wasser and Barash 1983
M. vancouverensis	Vancouver Island	17	1.88	0.70	1–3	This study
M. caudata	Pakistan	5	1.40	0.55	1–2	Blumstein and Arnold 1998
Probability of weaning pups (0–1)						
M. caligata	Washington	10	0.50			Barash 1980
M. caligata	Alaska	36	0.36			Holmes 1984
M. flaviventris	Colorado	646	0.41			Schwartz et al. 1998
M. vancouverensis	Vancouver Island	134	0.41			This study
M. marmota	France	50	0.52			Allainé et al. 1994
M. marmota	Germany	161	0.48			Stephens et al. 2002
M. caudata	Pakistan	84	0.19			Blumstein and Arnold 1998

from animals first captured as yearlings (female/male = 1.07 (16/15)). I conclude that relatively few young marmots were mistakenly sexed at time of first capture and that the sex ratio of wild Vancouver Island marmots approximates 1:1.

The 67 pups born in captivity had little chance of being misidentified given repeated handling by experienced veterinarians. The observed sex ratio was skewed towards males (female/male = 0.56 (24/43)), a value significantly different from 1:1 ($\chi^2 = 5.39$, df = 1, $P = 0.020$, $\phi = 0.284$), and from that observed in the wild ($\chi^2 = 3.81$, df = 1, $P = 0.051$, $\phi = 0.148$). Sex ratios were not significantly different among the five captive facilities ($\chi^2 = 4.29$, df = 4, $P = 0.232$, $C = 0.060$), although they varied from 0.25 (4/16) at Toronto to 1.25 (5/4) at Mount Washington.

Reproductive rates of Vancouver Island marmots compared with other species

Reproductive rates of wild Vancouver Island marmots were generally similar to those reported for other species of alpine-dwelling marmots (Table 1). Litter sizes were slightly smaller than those reported for the yellow-bellied marmot (*Marmota flaviventris* (Audubon and Bachman, 1841)), but approximated those reported for the closely related hoary marmot (*Marmota caligata* (Eschscholtz, 1829)) and the alpine marmot (*Marmota marmota* (L., 1758)). Age of first reproduction and between-litter intervals were nearly identical to those observed in the Olympic marmot (*Marmota olympus* (Merriam, 1898)). If one excluded 2-year-old females, the probability of weaning pups was also very similar to that reported for most other species and populations.

Discussion

The modern captive-breeding program for Vancouver Island marmots has been publicly described as "failing" (e.g., Toronto Globe and Mail, 3 December 2003). This seems unwarranted. Indeed, while sample sizes remain small, my results suggest that Vancouver Island marmots in captivity bred at rates similar to those observed in the wild. I found no significant differences in age of first reproduction, litter size, or probability of breeding between wild and captive populations.

The literature suggests considerable variation in reproductive rates among species of marmots (e.g., Barash 1989; Armitage 2000). Blumstein and Armitage (1998) interpret this variation as being related to "social complexity", with the more social alpine-dwelling species generally taking longer to mature, and producing smaller litters in which they make higher levels of parental investment. On average, yellow-bellied marmots reach sexual maturity relatively early, produce large litters, and breed frequently (Schwartz et al. 1998). Golden marmots reach sexual maturity relatively late, breed infrequently, and produce large litters (Blumstein and Arnold 1998). The three closely related North American species (Vancouver Island marmot, Olympic marmot, and hoary marmot) display intermediate and very similar reproductive characteristics, a result that perhaps reflects their close evolutionary affinity (Steppan et al. 1999; Kruckenhauser et al. 1999).

There would seem to be no basis for imagining that Vancouver Island marmots have somehow become reproductively "deficient", or that reduced reproductive rates were responsible for declining wild populations. Both captive and wild marmots typically produced litters containing 3 or 4 pups. Two-year-olds produced smaller litters and bred infrequently, while older females bred at consistent rates until at least age 10. No marmot bred after that age, but sample sizes remain small and maximum reproductive age in Vancouver Island marmots may be underestimated. Females were physiologically capable of breeding in consecutive years but often skipped a year or more between litters. All of these traits are typical of other populations and species of socially complex alpine-dwelling marmots (Barash 1989; Schwartz et al. 1998; Lenti Boero 1999; Stephens et al. 2002).

However, some of the results from Vancouver Island marmots raise interesting questions. One issue concerns the sex ratio of weaned pups, which did not differ from 1:1 in wild populations but was significantly skewed towards males in captivity. Several studies on alpine marmots have reported male-bias in weaned pups (Allainé et al. 2000; Stephens et al. 2002), with Allainé (2004) interpreting this as being related to cooperative breeding. Specifically, it was suggested that sex ratios will be skewed toward "helpers" (i.e., subordinate nonreproductive males) if these are absent from the social group. This is an intriguing hypothesis, which, if true for Vancouver Island marmots, might suggest that they not be housed as pairs. Certainly housing marmots in larger groups might have additional benefits. For example, a growing body of literature suggests that reproductive rates and fitness of offspring might be enhanced by allowing captive individuals to choose their own mates (Gran et al. 1998). However, there is little evidence for the existence of nonreproductive male "helpers" in wild Vancouver Island marmot social groups (Bryant 1998) and I consider the cooperative breeding explanation to be unlikely. An alternative explanation of male-biased sex ratios comes from the Trivers–Willard model, which predicts that females in better body condition will tend to produce sons, while females in poorer condition will tend to produce daughters (Trivers and Willard 1973; Carranza 2002). Distinguishing among these possibilities would be a fruitful area for further study, because male-biased sex ratios will slow the growth of the captive population and, consequently, the rate at which animals can be returned to the wild.

Vancouver Island marmots in captivity experienced environmental conditions quite different from those experienced by their wild counterparts. One apparent consequence of this was altered timing and duration of hibernation; captive marmots typically emerged 5 weeks earlier in the spring and immerged 6 weeks later in autumn (Bryant and McAdie 2003). However, neither the increase in the length of active seasons nor provision of unlimited food apparently resulted in reproduction at younger ages. Breeding rates among captive 2-year-old females were very low, just as they were in the wild. In no case were older adult females present in the same social group in which 2-year-olds bred, which may suggest reproductive suppression (Wasser and Barash 1983). Reproductive suppression has been postulated for several other marmot species (e.g., Hackländer and Arnold 1999; Armitage 2003; Hackländer et al. 2003). This possibility requires further study, specifically in terms of identifying the spatial, social, and environmental contexts that might minimize suppression and therefore maximize reproductive output in captivity.

Between-litter intervals were significantly shorter for captive females, a trend that may reflect better body condition. In captivity, unlimited food was provided and the summer growth season was longer by 11 weeks. In addition, while the five captive facilities differed in their environmental characteristics, in no case were Vancouver Island marmots exposed to weather extremes of the magnitude believed to significantly influence breeding rates in wild populations of marmots (Blumstein and Foggin 1997; Van Vuren and Armitage 1991; Schwartz and Armitage 2005). Thus, while it is conceivable that age of first breeding might be limited by reproductive suppression, it would also appear that captive marmots can tolerate a wide range of environmental conditions without altering the frequency of breeding.

The modern effort to maintain and breed Vancouver Island marmots in captivity has resulted in an encouraging degree of success to date. Presumably these efforts will continue to provide a source of marmots for return to the wild, and ultimately lead to the restoration of wild populations (Janz et al. 2000). However, the program is still very much in its infancy, and there remain several important unanswered questions concerning optimal group sizes in captivity, variation in sex ratios, and the extent to which reproductive suppression could be managed by enclosure design or other means. Finally, more work is needed to evaluate how captivity may alter behavior, and whether this may eventually reduce the likelihood of successful reintroduction.

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