Seasonal Moulting in Deer Mice (*Peromyscus maniculatus*) in the Rocky Mountains, Alberta

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We recorded seasonal moulting in North American Deer Mice (*Peromyscus maniculatus)* in the Kananaskis River valley, Alberta, Canada, to test the hypothesis that moulting is restricted to the times of year that do not overlap with other high-energy demands, such as reproduction (spring and summer), or with low nutrient availability (winter). Although a seasonal trend showing a peak in moulting in the post-breeding period provided support for our prediction, a low level of continuous moulting did occur throughout the year.

Key Words: North American Deer Mouse, *Peromyscus maniculatus*, moult, seasonal, Kananaskis, Alberta.

Thermoregulation is understood to be the main adaptive function of hair (Ling 1970; Viro and Koskela 1978; Johnson 1984), with the degree of insulation dependent on length and density (Johnson 1984). Hair wears over time, and insulation must be adjusted and/or replaced seasonally (Viro and Koskela 1978; Johnson 1984). In many mammals, hair density increases during winter, allowing more heat retention, and decreases during the summer, allowing more heat loss (Sealander 1951; Johnson 1984). Seasonal colour changes may also occur and are assumed to provide both camouflage and temperature regulation, where light-coloured hair absorbs less heat than dark-coloured hair (Severaid 1945). High-energy expenditure is required for moulting and thus it does not generally coincide with other high-energy demands such as reproduction (Negus 1958) and does not occur at times of insufficient food supply (Stodart 1965; Ling 1970).

Two main types of moult occur in most mammals: maturational (juvenile to adult) and seasonal regeneration. The maturational moult is most obvious, as it commonly includes a colour change. It has been studied in many small mammals, such as Southern Red-backed Voles (*Myodes gapperi,* formerly *Clethrionomys gapperi*; Sare et al. 2005), California Voles (*Microtus californicus*; Ecke and Kinney 1956), and North American Deer Mice (*Peromyscus maniculatus*; Collins 1923). Seasonal regeneration moult in adults, however, has not been studied extensively in any small mammal, and the literature is contradictory in some cases. For example, Osgood (1909) described two moults in Black-eared Mice (*Peromyscus melanotis*), but Collins (1923) suggested continuous moulting with one tentative peak in October and November in Deer Mice from California.

Here, we present data on seasonal moulting in Deer Mice from a northern population to test the hypothesis that moulting is restricted to the times of year that do not overlap with other high-energy demands, such as reproduction (spring and summer), or with low nutrient availability (winter). We expected to find moulting exclusively in the fall, a time of low energy expenditure.

Methods

We collected Deer Mice from three riparian habitats: Porcupine Creek (~1440 m above sea level), Wasootch Creek (~1440 m above sea level), and Evan-Thomas Creek (~1650 m above sea level), all tributaries of the Kananaskis River near Kananaskis Village in the foothills of the Rocky Mountains west of Calgary, Alberta (51°N, 115°W), between June 2007 and August 2008. We used 30–60 Little Critter live mammal traps (Rogers Manufacturing Co., West Kelowna, British Columbia) per site per month, depending on trap success at different times of the year. Traps were insulated with cotton bedding and baited with a mixture of oats and sunflower seeds. They were set at approximately1830 h and checked at approximately 0630 h. Trapping continued until 10–12 male Deer Mice were caught in each trapping session. We focussed on males in order to avoid depleting the population over the long term, but females were captured opportunistically when abundant.

Captured individuals were taken to the laboratory, where they were euthanized using isoflurane and dissected immediately. Prior to dissection, they were sexed, weighed, and aged, where grey pelage (any amount) indicated juveniles and brown indicated adults. Females were recorded as pregnant, lactating, or non-breeding, and males were recorded as scrotal or non-scrotal. Mass of both testes of males (± 0.001 g) was also recorded as a more precise measure of reproductive status. In

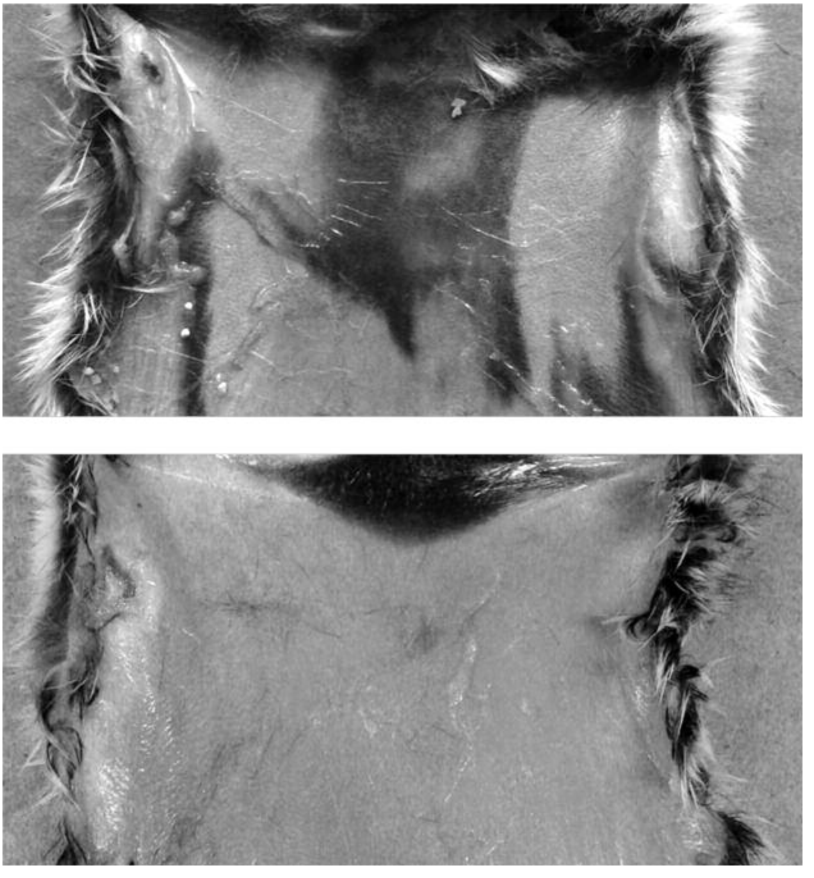

FIGURE 1. Example of moulting pigmentation on the undersides of two Deer Mouse (*Peromyscus maniculatus*) pelts.

other species of mice (e.g., Taiwan Field Mouse, *Apodemus semotus*), spermatogenesis and the mass of reproductive organs have been shown to be correlated (Lee et al. 2001).

We used pigmentation on the underside of the skin to follow waves of new hair growth (Stodart 1965). The skin of each individual was cut along a mid-ventral line, removed, and spread to dry. We then photographed the pigment on the underside of the skin, which showed distinct dark patches in areas of new hair growth (Figure 1). Digital photos of the skins were analyzed for percentage of pigmentation (area of pigmented skin as a percentage of total area) using ArcMap software (ESRI, Redlands, California). We did not examine any pigmentation on the limbs or tail, and any individual with <5% pigmentation was classified as not moulting because small patches of pigmented skin are often associated with wounds that are healing (Viro and Koskela 1978). We sorted skins by month and biological season (breeding season = June to August; post-breeding period = September and October; winter period = November to March; and pre-breeding period = April and May).

We conducted all statistical analyses using SPSS (version 16.0). The data were checked for normality of residuals and homogeneity of variances (Levene's test), and all proportions were arc-sine transformed. Monthly and seasonal analysis of degree of moult within moulting individuals was done using analysis of variance (ANOVA). When the homogeneity of variances was not improved by transformations, we used Welch's ANOVA (Welch 1951) to confirm results. The relationships between proportion of moulting individuals and testes mass and the relationships between degree of moult within moulting individuals and testes mass were analyzsed using linear regression.

Results

We captured 92 adult male Deer Mice; 46 juvenile males and 14 adult females were also captured opportunistically. Samples were collected every month between June 2007 and August 2008, except December

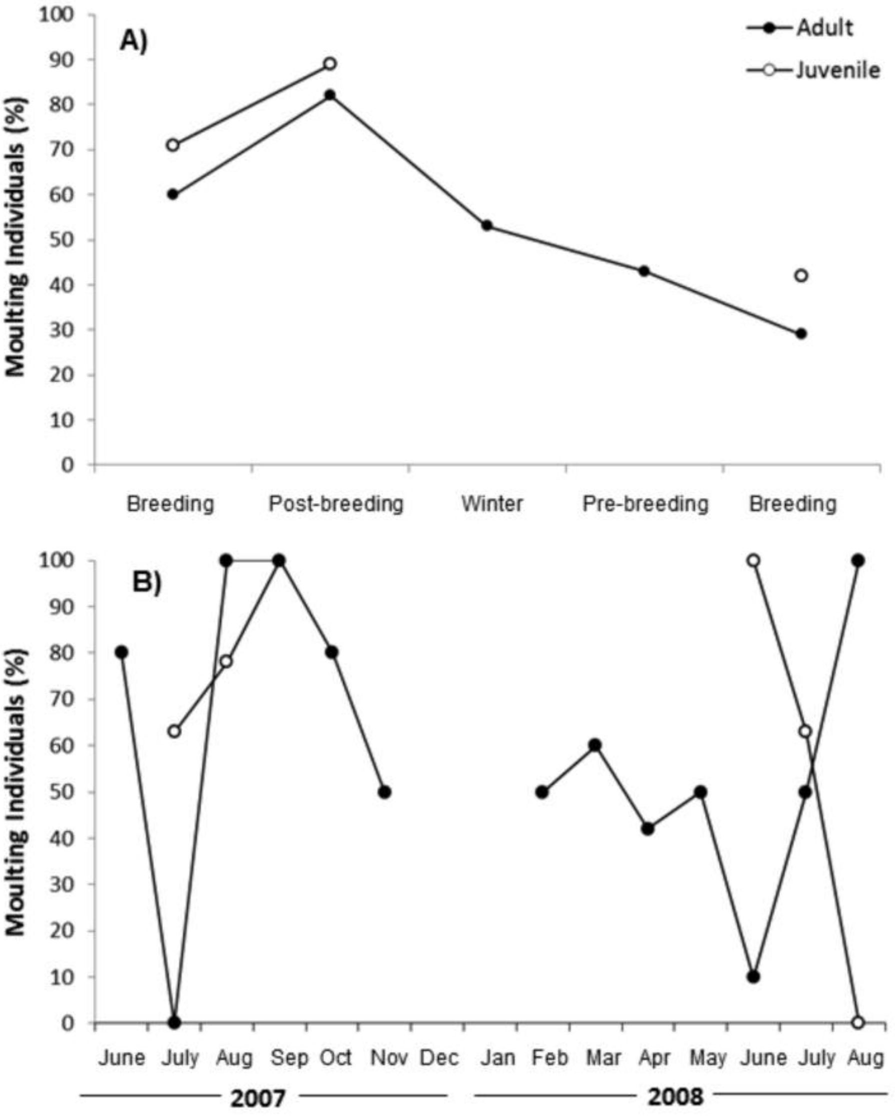

FIGURE 2. Percentage of moulting male Deer Mice (*Peromyscus maniculatus*) by A) biological season, and B) month. Biological seasons were defined as follows: breeding season 2007 = June–August; post-breeding period 2007 = September and October; winter 2007-2008 = November–March; pre-breeding period 2008 = April and May; and breeding season 2008 = June–August.

2007 (due to extreme cold) and January 2008 (due to large snowfalls).

The proportion of moulting males peaked in August and September 2007 and August 2008, and it decreased over the fall, winter, and spring months, reaching a minimum in June 2008 (Figure 2). The proportion of moulting juveniles that had been born in 2007 increased over the summer and peaked in September 2007. Among biological seasons (Figure 2), the proportion of moulting individuals peaked during the post-breeding period and was at a minimum during the breeding season of 2008, both for adult-only samples and for juveniles born in 2007. The 2008 breeding season had a lower proportion of moulting individuals than the 2007 breeding season.

The trend in degree of moult among moulting individuals (amount of pigmentation) was similar to the proportion of moulting individuals, both monthly and

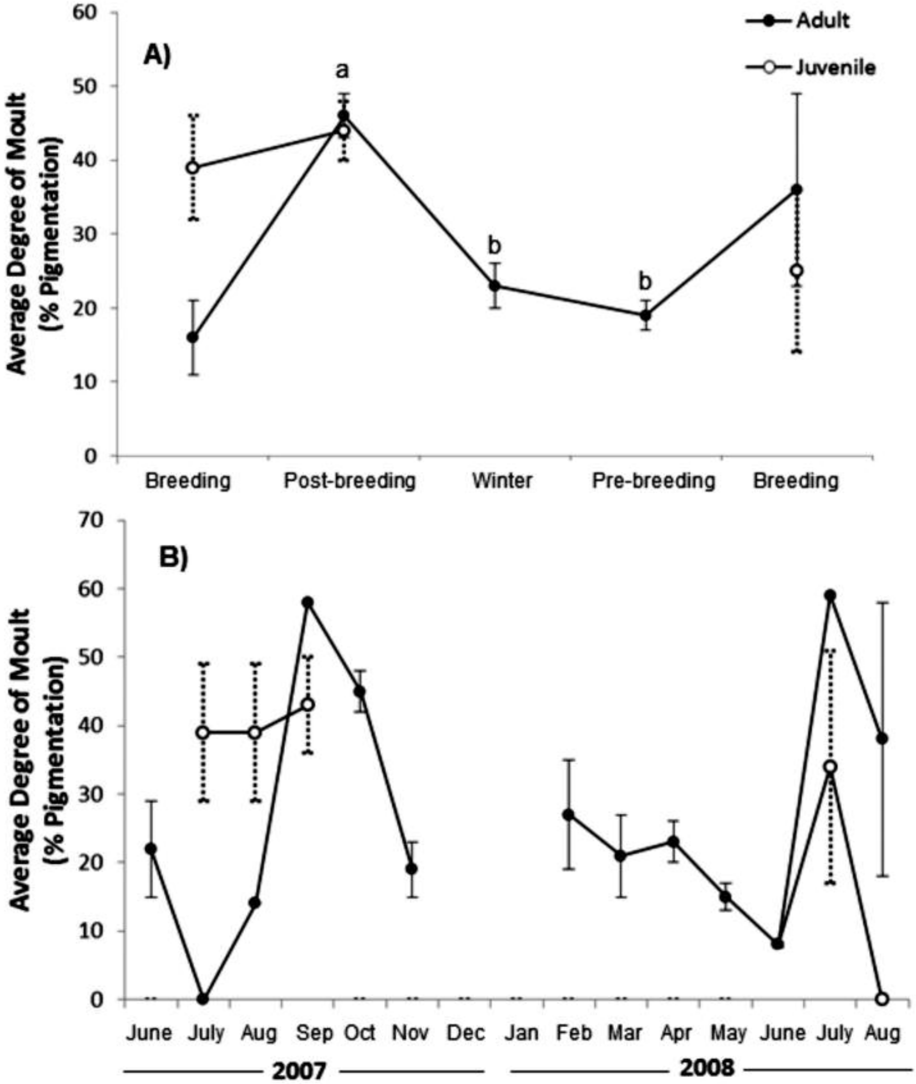

FIGURE 3. Average degree of moult (± SE) by A) biological season, and B) month, among moulting male Deer Mice (*Peromyscus maniculatus*). Biological seasons were defined as follows: breeding season 2007 = June–August; post-breeding period 2007 = September and October; winter 2007-2008 = November–March; pre-breeding period 2008 = April and May; and breeding season 2008 = June–August.

seasonally (Figure 3). Although we excluded 6 of 14 months from monthly statistical analysis and the two breeding seasons from seasonal analysis (because of low sample sizes of adult males and a low proportion of moulting individuals, respectively), we were still able to detect an effect of season. Degree of moult within moulting adult males differed among months ($F_{6,35}$ = 4.47, P = 0.002) and biological seasons ($F_{2,34}$ = 15.57, P < 0.001; Figure 3). The degree of moult among moulting adult males decreased with increasing testes mass (R^2 = 0.11, $F_{1,45}$ = 5.35, P = 0.026), but there was no relationship between testes mass and the proportion of moulting individuals by month (R^2 = 0.10, $F_{1,12}$ = 1.15, P = 0.306).

Adult females were captured in November 2007, June 2008, and July 2008. None of the six females sampled in November and only two of eight females sampled in June and July were moulting, indicating a low rate of moulting in summer.

Discussion

Although a seasonal trend showing a peak in the post-breeding period occurred in adult males, some continuous moulting also occurred throughout the year. Our data agree with Collins (1923), who described continuous moulting in Deer Mice in California. But, unlike Collins (1923), we found a distinct post-breeding peak, providing some support for the assumption that moulting should occur during the non-breeding season, when energy demands are low. However, the constraints appear relative rather than absolute.

Viro and Koskela (1978) found a similar moulting peak in post-breeding Eurasian Harvest Mice (*Micromys minutus*) in a northern environment in Finland. Other species of the genus *Peromyscus*, however, appear to have two seasonal moults per year, e.g., *P. melanotis* in Mexico (Osgood 1909) and *P. boylii* (Brush Mouse) in Missouri (Brown 1963). These warmer and more temperate environments may provide an earlier surge of resources that permits a spring moult that is not evident in more northern species. At our study site in the Rocky Mountains of Alberta, vegetation begins to grow as late as mid-May and begins dormancy as early as mid-August. This short growing season probably does not provide sufficient time for two moulting events per year for small mammals in addition to reproduction.

Testes mass, a proxy for reproductive activity, showed a negative relationship with degree of moult, also supporting the prediction of little overlap between these two energetically costly events. A similar relationship between testes mass and moulting was observed in Eastern Cottontails (*Sylvilagus floridanus*; Spinner 1940). Therefore, although we found that moulting did occur during the breeding season, the degree of moult varied with breeding status: adult male Deer Mice putting energy into enlarged testes moulted less frequently and to a lesser degree than non-breeding male Deer Mice.

These data also help to explain the discrepancy in moulting events between the breeding seasons of 2007 and 2008. Breeding, as defined by scrotal males, began quite early in 2008 (some time in March) and ended early (some time in August), while in 2007 it ended in September. The early onset of breeding in 2008 most likely permitted an earlier onset of moulting toward the end of the season, whereas the still active reproductive status of the Deer Mice in August 2007 probably caused them to postpone moulting.

Juvenile male Deer Mice showed a similar trend to adults during the breeding season, although they were moulting more intensely (more area of the skin was pigmented) than adults—a sign of the post-juvenile moult. By October, most samples were young-of-the-year adults. The occurrence of a moulting peak during the post-breeding period within this cohort suggests that they undergo two successive moulting events before winter. This is especially true of those born early.

In general, moulting occurred at a low level throughout the year, with a more intense post-breeding peak evident in the fall. This indicates that the energetic cost of hair replacement may be low enough that a low level of moulting can be sustained even during the most resource-poor times, but the energetic cost may be high enough to drive the majority of individuals to moult at times of low energy demand and high resource abundance.

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