Causes and consequences of sex-biased dispersal in Columbian ground squirrel, *Spermophilus columbianus*

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(Accepted: 10 July 2006)

Summary

Dispersal is a fundamental process with wide ranging evolutionary consequences. In birds and mammals, members of one sex typically disperse more frequently, sooner and/or further than members of the other sex. The aim of this study was to examine factors affecting dispersal by yearling male and female Columbian ground squirrels (*Spermophilus columbianus*), and to determine whether inbreeding avoidance, competition or other factors can explain why inter-colony dispersal is more common in males than in females. Males who stayed in their natal colony as adults emerged as yearlings heavier and later from hibernation than males who disappeared in their yearling year, whereas for females, this was not the case. Males who had sisters emerging as yearlings in the same colony were not more likely to leave the colony than males who were alone or with brothers. Further, there was no significant difference in the probability that females would mate with an immigrant compared to a natal male. Finally, three-year-old males who stayed in the colony moved significantly further away from their natal burrow than females of the same age.

I conclude that sex differences in inter-colony dispersal, while promoting outbreeding, are not directly due to inbreeding avoidance, but that inbreeding avoidance may play a role in governing intra-colony dispersal distances. Further, resource competition seems to play a minor role. Aggression by adults against yearling males and the acceptance of yearling females by their mothers may be the proximate cause for male bias in inter-colony dispersal in Columbian ground squirrels. To conclusively demonstrate this effect, however, we need to look at aggression in more detail.

Keywords: Columbian ground squirrels, dispersal, inbreeding avoidance, agonistic behaviour, reproductive success, sex-biased dispersal.
Introduction

Dispersal, the movement of individuals away from their place or group of birth, is virtually universal in both plants and animals. The primary hypotheses advanced to explain why animals disperse are competition for breeding opportunities and other resources and/or genetic benefits of outbreeding (Moore & Ali, 1984; Dobson & Jones, 1985; Pusey, 1987). Interestingly, among birds and mammals, one sex typically disperses more frequently, sooner and/or further than the other (Greenwood, 1980; Dobson & Jones, 1985), however, it is not clear why this should be the case. Mammals in particular tend to exhibit male-biased dispersal (Greenwood, 1980).

Negative effects of strong inbreeding exist in many species (Keller & Waller, 2002). It has often been proposed that inbreeding avoidance is the primary factor underlying sex differences in dispersal distances (Greenwood, 1980; Dobson, 1982; Packer, 1985; Pusey, 1987; Pusey & Wolf, 1996). Especially in polygonous species, females have more to lose by inbreeding than males who invest less and breed with more partners than females do (Thornhill, 1993). While outbreeding is important, however, dispersal costs to the members of the sex that disperse long distances can be high (Waser et al., 1986). Among those species for which dispersal is so costly that it is avoided, inbreeding could be effectively avoided, for example, through kin recognition coupled with mate choice (Potts et al., 1991; Brown & Eklund, 1994).

At the proximate level, aggression due to competition may serve as the main factor driving juveniles away from their natal areas (Christian, 1970; Bekoff, 1977). While inbreeding avoidance, local resource competition and antagonism all provide potential explanations for sex biased dispersal, they are not mutually exclusive.

In this study on Columbian ground squirrels I examined the factors associated with sex-biased dispersal differences and considered whether such effects might be a consequence of inbreeding avoidance or competition. Columbian ground squirrels are ideal for such research in that they are easy to observe, catch and mark. They are found along the Rocky Mountains in south western Canada and north western USA where they live in sub-alpine and alpine open meadows in colonies. Unlike Belding’s ground squirrels (*Spermophilus beldingi*), where all young males disperse before they become reproductively mature (Holekamp, 1984; Nunes & Holekamp,
Causes and consequences of sex biases in animal dispersal

The Columbian ground squirrel is a facultative disperser (Wiggett & Boag, 1992a). Therefore this species is ideal for investigating the reasons why some individuals are philopatric while others disperse. Similar to the Belding’s ground squirrels (Holekamp, 1986), Columbian ground squirrels show an increase in their range of movement shortly before dispersal (Festa-Bianchet & King, 1984).

I investigated differences in weight, timing of spring emergence and presence of relatives between yearling animals that stayed within the natal colony and those that disappeared at the expected time of natal dispersal in June and July (Boag & Murie, 1981), when mortality in adults is rare (Neuhaus & Pelletier, 2001). The possibility of inbreeding avoidance being a driving force as a proximate and/or ultimate cause for sex-biased dispersal is specifically discussed looking at reproductive success in males and probability of dispersing. Dobson & Kjelgaard (1985a, b) demonstrated the importance of food availability to both individual life-history traits and population dynamics. If some males stay and some males leave, males in good condition are expected to leave if they are rewarded with an increase in fitness outweighing the expected increase in cost due to inter-colony dispersal. In Arctic ground squirrels (*Spermophilus parryii*), 73% of philopatric squirrels survived, while only between 25-40% of dispersers survived (Byrom & Krebs, 1999); in yellow-bellied marmots (*Marmota flaviventris*) 87% of philopatic individuals, but only 71% of dispersers survived (VanVuren & Armitage, 1994). Similar patterns are expected in Columbian ground squirrels, due to the uncertainty of finding another place to reproduce and the potentially increased mortality during dispersal.

I also compared mating opportunities of males who remained in their natal colony with immigrant males. If the mechanism leading to male-biased inter-colony dispersal is a product of selection favouring inbreeding avoidance, males that stay are predicted to have significantly fewer breeding opportunities than immigrants. Furthermore, if inbreeding avoidance is a proximate cause of male-biased dispersal, one would expect that males, whose female littermates also survived to yearling age, would be more likely to disperse than males who do not have any littermate sisters in the colony. If, alternatively males in better condition stay whereas those in poorer condition leave, and males with littermate sisters are as likely to stay in the colony as males without surviving sisters, inter-colony dispersal is likely to be caused by factors other than inbreeding avoidance (Festa-Bianchet & King, 1984;...
Neuhaus

Waterman, 1992; Wiggett & Boag, 1992a). Several authors have hypothesized that adult aggression against yearlings triggers dispersal in Columbian ground squirrels (Steiner, 1972; Festa-Bianchet & King, 1984; Waterman, 1992; Wiggett & Boag, 1992b).

To evaluate dispersal distances within the colony, I compared distances 3-year-old females and males, the age when most males and all females are reproductively active (Murie & Harris, 1982) moved from their natal site. Because males are territorial and mate primarily with females in their vicinity, I expected males to move further away from the natal den compared to females to promote outbreeding.

Methods
Study area, animals and methods

Data were collected from 1992 to 1999 on two intensively studied neighbouring colonies (distance between the colonies <100 meters) of Columbian ground squirrels in the Sheep River Wildlife Sanctuary of south western Alberta, Canada (114°41′W, 50°40′N; elevation 1550 m). Columbian ground squirrels are active for approximately four months and then hibernate for the remaining eight months of the year (Murie & Harris, 1982; Dobson et al., 1992).

Reproductive, adult male Columbian ground squirrels usually emerge in mid-April, a few days to one week before females, and another 5-7 days before yearlings (Murie & Harris, 1982). All reproductively active animals stay in the same general area inside the colony throughout the active season. Males were considered reproductively active when their scrotum was pigmented (usually age 3 and older) in the spring, while females were considered reproductively active when they went through oestrus (usually age 2 and older; Murie & Harris, 1978). Mating normally occurs within the first week of female emergence from hibernation (Murie & Harris, 1982). Each female is in oestrus for only one day, during which time she will mate with several different males (Murie, 1995). Within a colony females will mate over a period of 2-3 weeks (Neuhaus, 2000a), so there is no pronounced synchrony in female oestrus. Males perform mate guarding, however females usually escape after a short period of time, managing to mate with 2-8 different males, average 3-4 (pers. obs.). The 2-6 (average 3) young emerge from
their natal den 51 days after birth, and once above ground they immediately start to feed on their own (Murie et al., 1980; Murie & Harris, 1982) for the next six to seven weeks before hibernation (Young, 1988). Each individual hibernates on its own (Young, 1990). Juveniles stay in the colony where they were born, delaying dispersal until the following summer when about 65% of yearling males and 35% of yearling females disappear from the colony. Females often stay and start reproducing at age two within close proximity to their mothers (Harris & Murie, 1984; King & Murie, 1985; King, 1989), whereas the majority of males leave the colony as yearlings. Some males remain to reproduce within their natal colony, however, leading to a high potential for inbreeding in this species. Males do not usually start reproducing until they are at least 3 years old, irrespective of whether they were born in the colony or immigrated into it. Because Columbian ground squirrels are a relatively long-lived species (Neuhaus & Pelletier, 2001), it is common that females are still alive when their sons reach reproductive age.

All individuals were regularly live-trapped at approximately weekly intervals using National and Tomahawk live traps (15 × 15 × 48 cm and 13 × 13 × 40 cm mesh) baited with peanut butter. Trapping was most intensive at spring emergence, otherwise the effort was comparable within and among years. Intensive observations throughout the season ensured that no animals were missed during trapping. Weights were taken with Pesola spring scales to the nearest 5 grams. All animals were marked with a numbered ear tag (fingerling fish tags) in each ear on first capture, and additionally received a unique mark painted with black hair dye (Clairol blue-black No. 124) on their backs for identification from a distance. Observations were conducted from 2- to 3-m tall wooden stands with binoculars. During the breeding season (mid April - mid May) up to 4 observers were located on the larger of the two colonies to collect behavioural data. For the remainder of the field season 1-2 observers performed regular scans to obtain approximate dates when individuals disappeared from the colony. One observer did all the trapping and observations on the smaller of the two colonies. Observers were usually able to identify squirrels at distances up to 50 m. Data collected on the same population showed first male precedence in paternity of around 65% of the offspring (Stevens, unpubl. data). Males are only territorial during the mating season whereas females become territorial a few hours after mating and remain territorial until they have weaned their young (Murie & Harris, 1978; Festa-Bianchet & Boag, 1982). Female territoriality has been
described as being mainly for protection of juveniles against infanticide from other lactating females or non-reproducing young males (Festa-Bianchet & Boag, 1982; Stevens, 1998). Observations and trapping during the breeding season enabled me to calculate the exact date of juvenile emergence from their natal burrow. This enabled me to determine maternity by trapping and marking juveniles before they started to interact and mix with other juveniles about 2-3 days after their natal emergence. All yearlings that disappeared between 16 May and 10 July were considered potential dispersers. These dates were used to avoid including squirrels that may have died during a late snowstorm in May 1996 (Neuhaus et al., 1999), or might have stayed but died during hibernation. I could confirm successful dispersal through sightings and/or trappings in other colonies for only a small proportion of those considered to have attempted dispersal.

The use of the term dispersal can be misleading (Dobson, 1982; Thornhill, 1993). Therefore, I define dispersal in this study as movement outside of the natal colony with the possible result of immigrating into another colony. Distances animals moved from their natal burrow were quantified to consider movements of animals within their colony of origin. In this study I termed this movement rather than dispersal.

Yearling spring emergence: body mass and timing

It has previously been shown that early natal emergence date and high body mass of juvenile ground squirrels have a positive impact on survival during the first hibernation (Neuhaus, 2000a, b). In this study, I compared juvenile natal emergence date and weight from the natal burrow of squirrels who survived to yearling age between those who stayed in their natal colony with those who disappeared. Because Columbian ground squirrels stay within their natal colony until after their first hibernation (age = 1), I further compared body mass and timing of emergence in female and male yearling ground squirrels (within two days). For this investigation, I used only squirrels born between 1992 and 1996 from one colony, because timing of emergence differed significantly between the two sites. Furthermore, a potentially confounding litter size manipulation experiment that might have had an impact on body mass of juveniles was carried out on the omitted site. There were a total of 101 squirrels that survived their first hibernation – 60 males and 41 females contributing to this latter analysis. Only animals caught within the first 2 days of their emergence from hibernation were included in the analysis.
In some cases, both female and male yearlings move away from their natal colony, and as population density might play a major role in rates or the intensity of intrasexual competition and aggression, which, in turn, may influence rates of dispersal, it is important to determine colony density. Therefore, I measured densities in the two neighboring colonies described above: one low-density colony with few animals aged two or older (13-24/ha), and one high-density colony (35-45/ha). I measured the adult sex ratio, number of adult animals per ha, and proportion of young of either sex staying in the colony on both sites from 1992-1994.

Further, I examined whether the presence or absence of littermates had an impact on the probability of yearlings remaining in their natal colony, by comparing dispersal rate among same- versus mixed-sex litters. Since paternity was not determined, I could not distinguish between full siblings and half siblings. A total of 152 litters in the two colonies with at least one surviving yearling were used for this comparison.

Mating success of adult males and movement of yearlings within the natal colony

Mating success of males who stayed within their natal colony was compared with the success of immigrant males. Immigrant animals were easy to recognize since all resident animals were marked. As an indicator of reproductive success, I used the number of times a male was the first to mate with a female in the morning of her day of mating. Number of matings and identity of the males were monitored by direct observation of females throughout the day they were sexually receptive, starting before emergence of the animals in the morning. First mating is assumed to be a good measure for reproductive success since more than 65% of a female’s offspring are sired by the first male to mate with a female (Stevens et al., 1997, unpubl. data).

Yearling Columbian ground squirrels that stay within their natal colony may move away from the natal burrow, a site determined by observations of the mother during lactation. To estimate the distance individuals moved away from their place of birth, I inspected all trapping locations from 1997 for females and males born in the year 1994. I used the mean location in which the animals were caught during the breeding season as representative of space use and calculated the distance from this point to the place where the
animals emerged as juveniles in 1994. I used only data from 1994/1997 because for 1992 and 1993 I did not have accurate locations of natal burrows, and in 1995 and 1996, there were very few offspring due to poor weather conditions (Neuhaus et al., 1999), and most successful litters were manipulated (Neuhaus, 2000b) in those years, and therefore could not be used in this study.

**Data analysis**

Data were tested for normality and homoscedasticity (SPSS statistical package; Norusis, 1994). Nonparametric statistics were applied where the assumption of normality was not met. I used GLM to compare yearling emergence weight and date at spring emergence. Due to low sample sizes, I used Spearman’s correlation for comparisons between density, sex ratio and as dependent variable the probability of animals to disperse. Because the data were not normally distributed I applied the Mann-Whitney U-test to compare distances travelled by female and male squirrels.

**Results**

A higher proportion of immigrants were males rather than females. Nine of 30 reproductively active males (30%) and 1 of 56 reproductively active females (1.8%) were immigrants from previous years – all other breeders were born in their colony of residence ($\chi^2 = 15.13, p < 0.001, df = 1$).

**Yearling spring emergence: body mass and timing**

Among females and males who survived to yearling age, date and body mass at emergence as juveniles from the natal burrow did not influence the likelihood of the animals disappearing during the expected time of dispersal in June/July as yearlings (GLM males: $F_{1,59}$ date = 0.54, $p = 0.464$; $F_{1,59}$ body mass = 0.60, $p = 0.444$; females: $F_{1,40}$ date = 0.05, $p = 0.818$; $F_{1,40}$ body mass = 1.42, $p = 0.241$). Yearling males who disappeared from their natal colony during dispersal weighed significantly less at spring emergence from their first hibernation (mean $\pm$ SE; 269 grams $\pm$ 6.08 versus 302 grams $\pm$ 21.33 respectively: GLM $F_{1,59} = 4.12, p < 0.047$). Date of emergence from hibernation was also significantly later for males who stayed in the natal
Causes and consequences of sex biases in animal dispersal

colony compared to those who disappeared (mean ± SE; 29 April ± 1.36 versus 10 May ± 4.37 respectively; GLM $F_{1,59}$ date = 10.32, $p = 0.002$). For yearling females, date of emergence (mean ± SE; 1 May ± 2.26 versus 3 May ± 3 respectively) and emergence body mass (mean ± SE; 271 grams ± 5.93 versus 253 grams ± 7.57 respectively) did not differ between those who stayed and survived the second hibernation and those who disappeared before going into hibernation as yearlings (GLM $F_{1,40}$ date = 0.11, $p = 0.738$, $F_{1,40}$ body mass = 0.37, $p = 0.062$). For both male and female yearlings, emergence date and body mass at emergence were significantly positively correlated (Pearson correlation$_{\text{males}}$ = 0.53, $p < 0.01$, Pearson correlation$_{\text{females}}$ = 0.47, $p < 0.01$), indicating that animals emerging later from hibernation weighed more than early emerging animals.

Adult sex ratio, density and relatedness

Significantly more yearling males than females disappeared after emergence in spring during the time of expected dispersal in June and July. Of 159 males who emerged as yearlings, 110 disappeared, while only 45 of 131 yearling females disappeared during the same time interval ($\chi^2 = 35.02$, $p < 0.0001$, df = 1).

Sex ratio (females/males) and the proportion of males remaining in their natal colony after the time of natal dispersal both correlated positively with the density of adult animals. In contrast the proportion of females staying in their natal colony was negatively correlated with density of adults (Table 1). Whereas more males stayed in their natal colony with increasing density of adult females, an increasing proportion of females disappeared (Table 1).

Presence or absence of siblings did not affect the likelihood that an individual would stay in its colony or disappear ($\chi^2_{\text{males}} = 0.35$, $p = 0.85$, df = 1; $\chi^2_{\text{females}} = 0.23$, $p = 0.63$, df = 1; Table 2). In litters where at least one sibling survived to yearling age, the sex of this sibling did not affect whether the animal stayed in the colony or not ($\chi^2_{\text{males}} = 0.003$, $p = 0.95$, df = 1; $\chi^2_{\text{females}} = 1.6$, $p = 0.2$, df = 1; Table 2). Also, males and females were not more likely to leave the colony as yearlings when their mother had disappeared (7 out of 10 males disappeared: 70%; while 6 out of 15 females disappeared: 40%) than if she was present in the colony when the animals emerged from hibernation (of 148 males: 30% stayed, 70% disappeared; of 114 females: 67% stayed, 33% disappeared; Fisher’s exact test$_{\text{males}}$ $p = 0.64$; Fisher’s exact test$_{\text{females}}$ $p = 0.4$).
Table 1. Spearman’s correlations between sex ratio of adult Columbian ground squirrels (females per male, age >2), the probability of 159 male and 131 female yearlings to remain in their natal colony to the age of 2+, and overall density of adults (males per ha, females per ha, adult animals per ha; bold indicates a statistically significant correlation with $p = 0.05$ or less).

<table>
<thead>
<tr>
<th>sex ratio</th>
<th>indiv./ha</th>
<th>yearling $\varphi\varphi$</th>
<th>yearling $\sigma\sigma$ staying</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\varphi/\sigma$</td>
<td>0.886</td>
<td>0.657</td>
<td>0.99</td>
</tr>
<tr>
<td>$\sigma/\sigma$</td>
<td>0.886</td>
<td>$p = 0.02$</td>
<td>$p = 0.01$</td>
</tr>
<tr>
<td>$\varphi/\varphi$</td>
<td>0.99</td>
<td>$p &lt; 0.001$</td>
<td>$p = 0.04$</td>
</tr>
<tr>
<td>$\sigma/\varphi$</td>
<td>0.886</td>
<td>$p = 0.02$</td>
<td>$p = 0.01$</td>
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<td>$\sigma/\sigma$</td>
<td>0.657</td>
<td>$p = 0.01$</td>
<td>$p = 0.11$</td>
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</tbody>
</table>

Table 2. Number of yearling male and female Columbian ground squirrels remaining in their natal colony to the age of two depending on the presence or absence of siblings and on sibling sex. Percentages are in brackets. Within each sex there was no significant difference in the proportion of animals staying in the colony depending on the presence or absence of same sex or opposite sex littermates.

<table>
<thead>
<tr>
<th>Litter composition</th>
<th>survived to age two</th>
<th>disappeared between age one and two</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>single survivor</td>
<td>8 (40)</td>
<td>12 (60)</td>
</tr>
<tr>
<td>two or more same sex</td>
<td>9 (43)</td>
<td>12 (57)</td>
</tr>
<tr>
<td>mixed sex</td>
<td>16 (42)</td>
<td>22 (58)</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
</tr>
<tr>
<td>single survivor</td>
<td>11 (61)</td>
<td>7 (39)</td>
</tr>
<tr>
<td>two or more same sex</td>
<td>12 (80)</td>
<td>3 (20)</td>
</tr>
<tr>
<td>mixed sex</td>
<td>25 (63)</td>
<td>15 (37)</td>
</tr>
</tbody>
</table>
Mating success of adult males and movement of yearlings within the natal colony

Males who were born in the colony achieved a similar number of first matings (mean 1.66 ± 1.9) as males who immigrated into the colony (mean 2 ± 0.6). Out of 35 first matings observed, 23 were obtained by 14 males born in the colony and 12 were obtained by 6 immigrant males (z = −0.14, p = 0.9). In other words, 70% of all reproductively active males were born in the colony, attaining about 66% of the first matings, while only 30% were immigrants getting 34% of first matings. Among animals who stayed in the natal colony, three-year-old females stayed significantly closer to their natal area (16 m ± 3, 95%CI = 10-23) than males of the same age (54 m ± 15, 95%CI = 20-87; U-Test, z = −2.6, p < 0.01).

Discussion

Natal dispersal differs between male and female individuals in most animal species. I investigated why male Columbian ground squirrels are more likely to leave their natal colony than female ground squirrels (Festa-Bianchet & King, 1984; Waterman, 1992; Wiggett & Boag, 1992a, b), and what differences can be observed in dispersal movements between the sexes for individuals remaining in the natal colony.

Yearling spring emergence: body mass and timing

Male Columbian ground squirrels that disappeared as yearlings in spring, when natal dispersal takes place, emerged with lower body mass earlier from hibernation in spring than the males who stayed in their natal colony. This result is not consistent with the findings of Wiggett & Boag (1992a) who reported no differences in body mass or timing of emergence between dispersing and non-dispersing male Columbian ground squirrels within a population in the same general vicinity of my study site. This difference is likely attributable to the authors pooling data from inter-colony dispersers with intra-colony dispersers. Foremost, the date of emergence played a major role in determining whether or not males were likely to stay in their natal colony. I assume that yearling males who are in good body condition remain in hibernation as long as possible, waiting for good forage to appear and
Neuhaus

avoiding predation and intraspecific aggression. Males who did not disperse emerged from hibernation on average on 10 May, when mating was usually over, whereas the average male that disappeared emerged a week earlier when some females were still mating. Once mating is over, adult males become less aggressive (Murie & Harris, 1978), which allows the later emerging yearling males to avoid agonistic behaviour from adult males. Females, however, become territorial just after mating and stay aggressive until a few days after their young emerge in June. Aggression is stronger against yearling males than against yearling females by both sexes of adult Columbian ground squirrels (Festa-Bianchet & King, 1984). For adult males, yearling females likely represent potential future mates and are therefore treated less agonistically than yearling males who are potential future competitors. Females may be more aggressive toward yearling males than females because of selective tolerance of philoptaric female kin (King, 1989), and the potential infanticidal tendencies of non-reproductive males (Festa-Bianchet & King, 1984; Stevens, 1998; but see Hare, 1991). While it is possible that daughters are also a potential threat in terms of infanticide (Stevens, 1998), the benefits of female kin clusters with less aggression (King, 1989) and even increased reproductive success (Neuhaus et al., 2004) likely outweigh this risk – at least at lower densities when infanticide is less common (J.O. Murie, pers. comm.). Several authors have suggested that aggression is the main trigger for natal dispersal in this species (Steiner, 1972; Festa-Bianchet & King, 1984; Waterman, 1992; Wiggett & Boag, 1992b). It has been argued, at least in baboons, that aggression is usually higher in new groups than in the natal group (Packer, 1985; Harvey & Ralls, 1986). In Columbian ground squirrels, however, aggression is seasonal and dispersing animals disperse after mating, and shortly before the new young emerge, around mid-June at the peak of aggressive behaviour by females. Immigration is mostly observed several weeks later in early July after juvenile emergence. Danger of infanticide regresses rapidly after emergence of the young when females are no longer territorial. Agonistic behaviour by both adult males and adult females is rare at this time when all animals are fattening up for the next hibernation. Immigrating animals have enough time to establish themselves, before and just after hibernation. Where yearling dispersers spend the few weeks between emigration and immigration is unknown.

The observed differences in rates of disappearance between males and females highlights the relationship between body condition, timing of emergence from hibernation as yearlings and the decision to leave the colony in
Causes and consequences of sex biases in animal dispersal

males but not in females. The correlation between body mass and date of emergence in males and females leads to the hypothesis that yearling animals who are not reproductively active stay in hibernation as long as their body condition allows. This is probably (1) to avoid aggression and harassment by territorial males, and (2) to wait until forage is of higher quality and increased quantity while reducing the danger of exposure to late snow cover (Neuhaus et al., 1999). In adult animals the opposite is the case; not only do males who have to establish a mating territory emerge from hibernation as early as weather and body condition allow, early emergence is also advantageous for females because the earlier they mate, the higher the likelihood their offspring survive to yearling age (Neuhaus, 2000a).

The strong trend toward heavier yearling females being more likely to stay in the colony than light yearling females shows that we cannot rule out a similar relationship between body condition and the probability of staying in the colony as observed in yearling males.

Adult sex ratio, density, and relatedness

Because the density of adult females, adult males, and total adults are not independent of each other, I concentrate on the correlations between the probability of yearlings staying in their natal colony and the different densities and sex ratio. Increasing female density was accompanied by more female-biased sex ratios as well as a shift in the likelihood of males and females staying in their natal colony. In all years, and in both colonies, the majority of males disappeared (62-84%) and the majority of females stayed (55-84%). The proportion of yearling males staying was positively correlated with female density and the proportion of yearling females staying was negatively correlated with female density. That females have an increasing tendency to leave their natal colony with increasing density (female, male and overall density), whereas males are more likely to stay, is probably due to females being more sensitive to habitat quality and social factors than males who might be encouraged to stay due to increased mating opportunities (Ostfeld, 1985; Sandell et al., 1990; Aars & Ims, 2000). With higher female density, one would also expect the number of unrelated or less related mates to increase for males born within the colony. One can assume that if the density exceeds a certain threshold, where it has a strong impact on body condition, yearling males may be more inclined to disperse. While density effects
across entire colonies apparent in this study prompt interesting interpreta-
tions, we have essentially no understanding of the scale over which density
of individuals may affect individual decisions regarding dispersal.

Males were not more likely to leave their natal colony when they had
littermate sisters around than when this was not the case, again suggesting
that a direct link between inbreeding avoidance and dispersal is lacking.
Males in polygynous species experience little or no costs of inbreeding; i.e.,
producing inbred offspring does not affect the number of outbred offspring
a male can produce, and so selection on males to avoid inbreeding is relaxed
relative to females, who bear a significant cost of inbreeding depression.

The strong trend toward a higher proportion of females staying in the
colony when sisters are present than when there are no siblings, or where
there are just brothers (Table 2), may be due to the increased reproductive
success of 2-year old females in female kin clusters (Neuhaus et al., 2004).
The conclusion that littermate presence influences disappearance is tentative,
however, owing to the small litter sizes employed in my research.

Further, one could also argue that to assess whether or not an individual
has opposite-sex littermates present, it has to be able to recognize kin; if
an individual can recognize kin it would be more efficient to remain in the
colony, avoiding matings with close kin, than to disperse, as long as there
are enough potential mating partners available. However, discrimination of
littermates from non-littermates cannot be automatically equated with kin
recognition and there might be other mechanisms working in mate choice.

Mating success of adult males and dispersal of yearlings within the natal
colony

The small number of immigrating animals from outside the colony, relative
to the number emigrating from the colony, means that a large proportion of
males likely die during dispersal. Survival to reproductive age in males who
stay in their natal colony until after their second hibernation is quite high
(72%; Neuhaus & Pelletier, 2001). This suggests high costs of inter-colony
dispersal in terms of mortality or ability of finding another colony. That cost
may be too high to make it worthwhile to disperse to avoid inbreeding if there
is a chance of reproducing successfully within the natal colony (Waser et al.,
1986). Males who stayed in their natal colony to reproduce were as likely to
have first matings with a female (a good indicator of reproductive success)
Causes and consequences of sex biases in animal dispersal

As immigrant males. Because females seem to be able to avoid matings with unwanted males (pers. obs.), one would expect that kin recognition would be a more efficient means of avoiding inbreeding than inter-colony dispersal (Waser et al., 1986; Blouin & Blouin, 1988; Keller & Arcese, 1998). Further, if females left the natal colony as yearlings it would be extremely unlikely for them to get large enough and to establish a territory in time to reproduce successfully before the age of three, whereas if they stay in their natal colony they have a good chance of breeding successfully as two year olds, and potentially even as yearlings (Neuhaus et al., 2004). In contrast, males are usually not reproductively active until they are at least three years of age even if they stay in their natal colony (Boag & Murie, 1981; Neuhaus & Pelletier, 2001).

The distances moved within the colony differed significantly between males and females once they reached the age of three, which is when males usually become reproductively mature. This result is consistent with those of Murie & Harris (1984) who found males moving further away from their natal burrow as yearlings. One cause of the observed sex difference in distances moved away from the natal burrow might be that females are attracted to their own mother and sisters (King & Murie, 1985; King, 1989), having a higher reproductive success than females that do not have close kin in their vicinity (Neuhaus et al., 2004). It could also prove advantageous for males to leave the proximity of mothers and sisters when females actively avoid inbreeding with close kin.

Conclusions

Whereas male-biased inter-colony dispersal in Columbian ground squirrels may promote outbreeding, my results suggest that outbreeding is probably an artefact of other factors promoting male-biased dispersal. While this remains to be tested, I suggest that the proximate cause leading males to leave their natal colony is eviction by adult females and perhaps adult males in that only yearling males coming out of hibernation late and in good body condition (high body mass) are able to remain resident. Hence, the observed differences in inter-colony dispersal behaviour between females and males would be attributable primarily to female territorial behaviour aimed to increase safety of her offspring, coupled with the less agonistic behaviour of
Neuhaus females towards their own yearling females promoting kin clustering. The high expected mortality of disappearing males and the relatively high potential reproductive success of males staying in their natal colony reduces the likelihood that males should leave to avoid inbreeding. I suggest that in Columbian ground squirrels, outbreeding is, a by-product of the few animals that find and establish themselves in a new colony after aggression by adults declines in late June and July. That said, a selective advantage of outbreeding cannot be dismissed entirely as having contributed to the evolution of sex-differential dispersal given the well documented advantages of outbreeding relative to inbreeding in terms of birth weight, survival, reproduction, resistance to disease, predation and environmental stress (Crnokrak & Roff, 1999; Keller & Waller, 2002).

Acknowledgements

For help in the field I thank N. Blatter, N. Duvoisin, T. Grau, D. Haase, P. Herzig, A. Jaun, A. Lüscher, T. Lloyd, J. Murie, B. Reutter, S. Stevens, B. Studholm, S. Thiele, and P. Wittwer and numerous field assistants collecting data for J.O. Murie and S. Stevens in 1992 and 1993. Thanks go to J. Murie and S. Stevens who let me use data they collected over the years while supported by NSERC. The author is supported by the Swiss National Science Foundation and the commission for travel grants of the Swiss Academy of Science SANW. I especially thank T.J. Karels, J.O. Murie, K.E. Ruckstuhl, A.F. Russell, G. Pelchat, J. Hare and an anonymous referee for their constructive comments and discussions on earlier drafts. The University of Calgary Kananaskis Field Stations provided space and facilities. The research was conducted under animal use protocols from the Biosciences Animal Care Committee, University of Alberta, and the Life and Environmental Sciences Animal Resource Center, University of Calgary.

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Causes and consequences of sex biases in animal dispersal


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