Life history variation in maturation in fluctuating meadow vole populations (*Microtus pennsylvanicus*)

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Successful maturation on the natal area may vary as a function of sex, density, and season in voles and may affect sex ratio manipulation by breeding females. To determine how these factors interact in a microtine population, I live-trapped two *Microtus pennsylvanicus* populations for five years with two different types of traps. I caught large numbers of young shortly after weaning and determined whether they successfully entered the breeding population. Few males matured on the natal grid (12.2%, $N = 1179$), with only 3% maturing in the year of birth and 9% maturing the next year. More females matured on the grid (29.8%, $N = 1207$), with 22% maturing in the year of birth and 8% maturing the next year. Males had the highest probability of entering the breeding population if they were born late in the year and delayed maturation until the next year; females showed the opposite pattern. Maturation on the natal grid in the year of birth during the spring–early summer period was density-independent in males, but strongly density-dependent in females. I found no support for the Trivers-Willard hypothesis that the sex ratio of recruits should be biased to favor the sex most likely to enter the breeding population (daughters early in the breeding season and sons later on): at all times independent of season, a 1:1 sex ratio was observed. I found no support for Cockburn's inbreeding avoidance hypothesis that maturing males should move shorter distances from their natal site at high than at low density to avoid inbreeding; females did move shorter distances at high density.

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Introduction

Organisms living in rapidly changing or occasionally stressful environments can show a large variation in the age at sexual maturity (Nichols et al. 1976, Stearns and Crandall 1984) and this can be a major factor affecting population growth (Cole 1954, Stearns 1976). In small mammals, such as microtines, there is tremendous phenotypic plasticity in the age at sexual maturation and this intrapopulation plasticity is generally regarded as adaptively significant (Anderson 1970, 1980, Schaffer and Tamarin 1973). Dispersal often occurs at the onset of maturation in microtines (Gaines and McClenaghan 1980, Stenseth 1983), and many factors influence the probability of maturation (see reviews by Hasler 1975 and Keller 1985), with major ones being density and

season (Kalela 1957, Schwarz et al. 1964, Koshkina 1965, Keller and Krebs 1970, Krebs and Myers 1974).

Microtines typically show overlapping generations, with a number of litters being produced during a breeding season. Some of these young mature in the year of their birth; others do not. Seasonal variation in maturation may affect the degree of natal philopatry between the sexes. In mammals, females tend to be the philopatric sex (Greenwood 1980; for a review of *Microtus*, see Boonstra et al. 1987). Anderson (1980) proposed that the majority of young males maturing early in the breeding season would disperse from their natal site independent of population density because of competition with adult males for mates. In contrast, young females maturing in the breeding season would remain near the natal site at low densities, but disperse as

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Fig. 1. Population changes in *Microtus pennsylvanicus* on Grid A and the associated changes in percent of young becoming mature residents in the year of birth or in the year after birth. Young born during a year are divided into four periods: May-mid-June, mid-June-July, August, and September-November. Sample sizes given above each period. Non-breeding periods are shaded.

Fig. 2. Population changes in *Microtus pennsylvanicus* on Grid F and the associated changes in percent of young becoming mature residents in the year of birth or in the year after birth. See caption of Fig. 1 for other details.

densities increased. In both males and females, those born near the end of the breeding season would not mature until the next year when many would become breeding residents. To test Anderson's hypothesis, I

examined how the probability of maturing near the natal site varied between the sexes as a function of both season and population density.

An alternative explanation to the proposal that com-

Tab. 1. Percentage of *Microtus pennsylvanicus* maturing on the natal grid. Sample sizes in parentheses.

	Grid	Males	Females
Percentage of young maturing on area over the entire study	A	9.8 (716)	30.3 (736)***
	F	15.8 (463)	29.1 (471)***
Percentage of young maturing:			
– in year of birth	A	2.5	23.9***
	F	4.5	18.0***
– in year after birth	A	7.3	6.4 N.S.
	F	11.2	11.0 N.S.
Percentage of young maturing			
– in year of birth if:			
a) first caught from May-July	A	5.4 (238)	39.7 (282)
	F	5.1 (331)	22.6 (319)
b) first caught from Aug-Nov	A	1.0 (478)	14.1 (454)
	F	3.0 (132)	8.6 (152)
– in year after birth if:			
a) first caught from May-July	A	0.0	0.0
	F	8.8	9.4
b) first caught from Aug-Nov	A	10.7	10.1
	F	17.4	14.5

*** $P < 0.001$

petition between males for mates causes young maturing males to disperse is that these young males are dispersing of their own accord to avoid breeding with relatives (Greenwood 1980, Dobson and Jones 1986). Cockburn (1985) proposed that dispersal of young microtines from the natal site was the result of inbreeding avoidance and was inversely density dependent: at high density, maturing young would not have to move as far to avoid breeding with close relatives. Thus, his hypothesis makes different predictions from Anderson's hypothesis in which male dispersal is expected to be density independent and female dispersal density dependent. To test this hypothesis, I determined the dispersal distance of young animals from the natal area to the site in the trapped population at which they matured on the grid.

If more females than males recruit into the breeding population, parents may increase their fitness by adaptively varying the sex ratio of their young to favor the sex most likely to reproduce (Trivers and Willard 1973, Clutton-Brock and Iason 1986). McShea and Madison (1986) found that the sex ratio of juvenile recruits in a *Microtus pennsylvanicus* population in New York was biased to favor the sex that had the highest probability of entering the breeding population: in the spring, the bias favored females and, in the autumn, the males. To test the generality of these findings, I examined my data

to see whether this relationship occurred in the meadow vole in southern Ontario.

Methods

The study was carried out on two control live-trapping grids at two sites near Toronto, Canada (see Boonstra and Hoyle (1986) and Boonstra and Rodd (1983) for pictures and a description of grids A and F, respectively). Each of these control grids was adjacent to four other grids and the manipulations occurring on these grids and their distances from the control grid are given in the above references. Each grid covered 0.7 ha and had 100 trap points spaced 7.6 m apart and arranged in a 10 by 10 pattern. Longworth live-traps were placed at every trap point and baited with oats; cotton was provided for warmth. Both grids always had at least 150 traps, and grid F had 200 during periods of high density. Each trap point also had a pitfall trap (see Boonstra and Rodd (1984) for details). Both grids were trapped from summer 1978 to spring 1982, with grid A having pitfalls throughout this time and grid F having pitfalls from spring 1979 onwards.

During the main breeding season, both trap types were set at the same time every second week on Wednesday afternoon, checked Thursday morning and afternoon, and again on Friday morning, when they were locked open. In summer, live-traps were set only in the evenings to avoid mortality during the heat of the day. Only live-traps were set during the winter, weather permitting. When first caught, voles were ear-tagged; tag number, location, weight, sex, and sexual condition were noted on each capture and then voles were immediately released. Trappability estimates for these populations are summarized in Krebs and Boonstra (1984) and were always above 50%. Population density estimates were obtained by the Jolly-Seber method.

To examine if young born into the population matured and became residents, I determined the number of young ≤ 22 g which entered the population and what proportion of these subsequently reached maturity. The analysis is based on the critical assumption that these young had just emerged from the nest and entered the nearest trap. Thus, I assume that these young were born on the grid and refer to it as the natal grid. This assumption was tested and confirmed by Boonstra et al. (1987). The weight cutoff is extremely conservative and probably eliminated many animals that were born on the grid but did not enter the trappable population until they were > 22 g. However, I was interested more in obtaining a relatively pure sample of animals born on the grid and not confounding the analysis with animals that might have dispersed onto the grid from elsewhere and subsequently matured. Animals were classified as mature residents only if they were caught at least twice as mature individuals. They were classed as mature if males had scrotal testes and if females were either perforate, lactating, or pregnant.

Tab. 2. Relationship between sexual maturation on the natal grid and population growth and density in *M. pennsylvanicus* as a function of season of birth.

	Population density		Population growth	
	Males	Females	Males	Females
Percentage maturing in year of birth if born in:				
a) spring-early summer	-0.50	-0.88**	-0.41	0.56
b) late summer-autumn	-0.71*	-0.73*	0.48	0.51
Percentage maturing the next year if born in:				
a) spring-early summer	0.36	0.56	-0.20	-0.21
b) late summer-autumn	-0.71*	0.21	0.55	0.11

* $P < 0.05$

** $P < 0.01$

Results

Maturation and residency on grid

Figs 1 and 2 show that there was tremendous variation within and among years in the probability of maturing on the natal grids. In general, males had a much lower probability of maturing on the grid than did females. The probability of maturing within the year of birth declined as the breeding season progressed and the probability of maturing the next year increased. In some years, such as 1980 on grid F, young born in spring and summer behaved more like the young born in autumn of other years in that most delayed maturation to the next year.

Tab. 1 summarizes these data and five points can be made from this analysis. I grouped the maturation data into two periods within a year based on when young were first caught: spring-early summer (May-July) when reproduction was most intense and late summer-autumn (August-November) when reproduction was tapering off and, in some years, absent. First, about three times as many females as males matured on their natal grid. Overall 29.8% of females matured on the area in comparison with 12.2% of males. Second, similar percentages of males eventually matured on the natal grid independent of when they were born (10.5% ($N = 569$) of males born in spring-early summer matured versus 13.6% ($N = 610$) of males born in late summer-autumn ($P < 0.25$)). In females, significantly more matured if they recruited during the spring-early summer (35.8%, $N = 601$) than if they recruited during the late summer-autumn (23.9%, $N = 606$) ($P < 0.001$). Third, overall only 3.3% of males matured on the natal grid in the year of birth and 8.8% delayed maturation until the next year. The opposite occurred in females,

the values being 21.6% and 8.2%, respectively. Fourth, the probability of males maturing on the grid in the year of birth tended to be higher for young entering the traps from May to July (Grid A, $P < 0.001$; Grid F, $P > 0.25$), whereas the probability of maturing on the grid the next year was highest for the young born late in the year (Grid A, $P < 0.001$; Grid F, $P < 0.05$). In females this same trend occurred (year of birth May-July versus August-November comparison - Grid A, $P < 0.001$; Grid F, $P < 0.001$; year after birth May-July versus August-November comparison - Grid A, $P < 0.001$; Grid F, $P > 0.10$). Finally, whereas virtually no young males from the late summer-autumn matured in the year of their birth, a substantial number of females sometimes did. For example, on grid A in 1979, 30% of the females entering the traps in the late summer-autumn period matured, whereas none of those entering in the late summer-autumn of 1980 matured (Fig. 1). In summary, males had a higher probability of maturing on their natal grid if they delayed maturation until the next year; females had a higher probability of maturing on their natal grid if they matured in the year of their birth.

To understand how maturation varied as a function of density and rate of population growth, I correlated the percentage maturing within the year of birth to mean density during the period of maturation and to the instantaneous rate of population growth during that period. In males, there was no relationship between the percentage maturing and the rate of population growth during the period for either the spring-early summer animals (Tab. 2) or the late summer-autumn animals nor between the percentage maturing and the mean population density for the spring-early summer animals (Fig. 3). However, there was significant correlation between the percent maturing in the late summer-autumn and density. However, even in this latter case the rela-

Fig. 3. Relationship between population density in the spring-early summer period and the percentage of young animals recruiting then which matured in the year of their birth. Each point represents one grid in one year.

tionship was relatively weak as the range in percent of males maturing varied only from 0 to 6%. Thus, maturation in males on the natal grid was unrelated to population growth and to density in spring-early summer.

In females there was again no correlation between the percentage maturing and population growth rate, but there were significant negative correlations to density in both spring-early summer (Tab. 2 and Fig. 3) and late summer-autumn. Thus, for young maturing in the year of birth, fewer females matured on their natal grid at high densities, whereas few males matured at any time, regardless of density.

I also correlated the percentage maturing in the year after birth with the mean density during the autumn-winter period (August to March) and with the rate of population growth overwinter from the time of maximum autumn density to the density at the onset of breeding in the next spring. In males there was no correlation to population growth for young entering the population during either period, nor was there a correlation between mean overwinter density and the percentage of the spring-early summer males maturing the next year. However, there was a significant relationship between overwinter density and the percentage of the late summer-autumn males maturing the next year. Since all overwintering animals mature in the spring, this correlation essentially indicates that males survive the winter better when overwintering densities are lower. In females there was no correlation to the rate of population growth for animals entering the population during either period or to overwinter density. Though the latter result is somewhat counterintuitive, especially for the late summer-autumn females, it essentially indicates that a relatively constant percentage of females survive the winter to the onset of breeding the next year (mean = 11.9%, SE = 1.33, N = 8, range = 8–17%).

Sex ratio

Since the probability of maturing on the area is highest for males if they delay until the year after birth whereas it is highest for females if they mature in the year of birth, mothers may skew the sex ratio of their offspring to favor males late in the breeding season and females early in the season (McShea and Madison 1986). If so, the sex ratio of the young recruiting to the population may shift from one favoring females in the spring-early summer to one favoring males in the late summer-autumn. I obtained the mean sex ratios of recruits ≤ 22 g for grids A and F for both periods (data on Figs 1 and 2). I assume that the sex ratio of these recruits reflects the sex ratio at weaning and that recruitment on the grid provides an index to successful recruitment anywhere. There was no significant deviation from a 1:1 sex ratio for either grid in either period (spring-early summer: grid A 238 males: 282 females, $\chi^2 = 3.72$ and grid F 331:319, $\chi^2 = 0.22$; late summer-autumn: grid A 478:454, $\chi^2 = 0.62$ and grid F 132:152, $\chi^2 = 1.41$).

Though there was a suggestion that more female young entered the population on Grid A in the spring-early summer, the opposite occurred on Grid F. Since females generally have the greatest probability of maturing on the natal grid if they are born during the spring and males have the greatest probability of maturing on the natal grid if they are born during the autumn, I combined the data from both grids and examined only the sex ratios of animals entering at either end of the breeding season: in the spring (May to mid-June) (351: 348) and in autumn (September to November) (492: 488). Again there was no significant deviation from a 1:1 sex ratio. Finally, under conditions of nutritional stress (Trivers and Willard 1973, Myers 1978), mothers may bias their sex ratios to favor female offspring (McClure 1981, Labov et al. 1986). The mothers surviving from the population declines in 1981 on both grids A and F might have been experiencing nutritional or other stresses. However, again there was no detectable bias in the sex ratio of the young entering these populations (49: 48). Thus, there is no evidence for a skewing of sex ratio of recruits within the population at any time.

Dispersal

If dispersal from the natal site is largely a mechanism to avoid inbreeding, then young would have to move shorter distances at higher population densities than at lower densities (Cockburn 1985). To test this hypothesis, I calculated the distance that a young animal moved from its point of first capture on the grid (the natal trap site, Boonstra et al. 1987) to the mean point of all captures on the grid as a mature animal. For each period a mean distance was obtained of all the animals which matured on the grid and this was correlated with the population density during the period of maturation. I recognize that the shape and size of the trapping grids constrained the movements that could be detected and, thus the mean distances may be biased. However, the bias should be constant since neither grid size or shape changed over the course of the study. In males there was no correlation between the distance moved and density for those maturing in the year of birth ($r = -0.38$, N = 7 periods, range of mean distances moved per period 10.1–31.9 m) or for those maturing in the year after birth ($r = -0.45$, N = 8, range 14.6–39.5 m). In females there was a significant correlation for those maturing in the year of birth ($r = -0.90$, $P < 0.01$, N = 7, range 6.2–19.2 m), but not for those maturing in the year after birth ($r = -0.20$, N = 8, range 7.8–22.3 m). Thus, females that mature in the year of birth move shorter distances when densities are high; males do not.

Discussion

These results indicate that the percentage of animals maturing in their year of birth varies greatly among years: during years of high density, fewer mature than

during years of low density (Figs 1 and 2). Similar results have been reported by others (e.g., Krebs and Myers 1974, Wiger 1982, Mihok 1984, Bondrup-Nielsen and Karlsson 1985, Negus et al. 1986). However, no study on microtines has specifically examined the seasonal patterns of maturation in young born into the population and whether they become breeding residents there. My results indicate that of the males maturing on their natal grid in the year of birth during the height of the breeding season, < 6% do so in comparison with 23–40% of females and that males have the highest probability of maturing on their natal grid if they delay maturing until the year after birth (Tab. 1).

There are two major explanations to account for this male recruitment pattern. The first is that males leave their natal grid because they have to – they are driven away at maturation because they are competing with larger adult males for access to mates. The second is that males leave because they want to – they leave to avoid the possibility of mating with related females. My evidence is consistent with the first explanation and hence supports Anderson's hypothesis (see also Myllymäki 1977). Though I was not able to determine whether mortality or dispersal accounted for disappearance of maturing males, other work has demonstrated that dispersal is the major cause for the difference (see Gaines and McClenaghan 1980 and Lidicker 1985 for reviews). In enclosed populations (fenced experimentally or on an island) in several species of *Microtus*, similar percentages of males and females became breeding residents in the populations, whereas in unenclosed populations (control or on the mainland) (as in my study) the bias strongly favored females (Boonstra et al. 1987). My results are also consistent with the second part of Anderson's proposal that males delaying maturation until the next breeding season should have a higher probability of recruiting to the breeding population. The synchronous onset of maturation in the spring of the year in overwintered males which are all reasonably similar in weight, age, and competitive ability allow more of them to become breeding residents (Boonstra and Rodd 1983). In contrast, males maturing in their year of birth do so into an actively breeding population and are at a disadvantage because they are smaller, younger, and presumably competitively subordinate to their fathers and others already there (Christian 1970).

My evidence is inconsistent with the second explanation that males disperse because of inbreeding avoidance for two reasons. First, Cockburn (1985) proposed that movement of males from the natal site should be inversely density dependent: at high density, maturing juveniles would not have to move as far to avoid breeding with close relatives and I found no such relationship among males maturing in their year of birth. Ideally, to test this hypothesis one would have to trap an extremely large area over a population fluctuation, capture young at or near their natal site, and follow their subsequent movements to maturity. Though my test of this hy-

pothesis is relatively weak because of the area of the grids, the grids were sufficiently large to incorporate a wide range in density (grid A–7 to 546 animals on 0.7 ha; grid F–67 to 510). I did not find the predicted relationship in males: the percentage of males maturing on their natal grid in their year of birth was density-independent and, for the small number that did mature on their natal grid, the distance they moved was also density-independent. Second, if inbreeding avoidance was the primary cause of male biased dispersal, I would expect that for males maturing in the year after birth, few should mature on the natal grid since related females would still be resident. However, up to three times as many males successfully matured on the natal grid in the year after birth as matured during the year of birth (Tab. 2). Thus, inbreeding avoidance may be more an effect than a cause of male dispersal (Moore and Ali 1984).

However, Dobson and Jones (1986) have argued persuasively that male-male competition versus inbreeding avoidance may not be mutually exclusive explanations. If young males in a number of species of *Microtus* are forced to remain on the natal grid by enclosures, they can do so and similar proportions of males and females then mature on these grids (Boonstra et al. 1987), but these males still move about two times further than females from the natal trap site at maturation. These data suggest that inbreeding avoidance may still be playing a role in male dispersal. Experiments in which adult males and females are selectively removed before maturation of the young are needed to tease out the relative importance of male-male competition and inbreeding avoidance.

I did find Cockburn's predicted relationship in females: both maturation and dispersal distance of females on their natal grid in their year of birth was density-dependent. However, I suggest that inbreeding avoidance is less likely to be the explanation for the shorter movements of females since the distances between the natal trap site and the site at maturation even at low densities were relatively short (usually < 20 m) and given the large home ranges of males (Madison 1980, Webster and Brooks 1981) these females are likely still to be well within the home ranges of their fathers. Rather, I suggest it was simply female-female competition for space which caused females born during periods of high density to settle nearer to their natal site.

The probability of a young animal successfully recruiting to a breeding population elsewhere after dispersing is likely to be very low. Of the animals that disappeared from grids adjacent to grids A (N = 3342) and F (N = 2781), only 1.4% (38 males and 9 females) and 1.7% (39 males and 9 females) recruited to grids A and F, respectively (Boonstra et al. 1987). Thus, very few tagged animals from nearby adjacent grids successfully entered these populations. In general, breeding vole populations inhibit immigrants from recruiting to

the population (Krebs et al. 1976, Boonstra 1978, Redfield et al. 1978, Baird and Birney 1982, Boonstra and Rodd 1983). Seasonal changes in reproduction may, however, influence the success of a disperser. Danielson and Gaines (1987) found that resident voles (*M. ochrogaster*) were able to inhibit colonization by potential immigrants most effectively during the main breeding season, but not during the nongrowing season when breeding was minimal.

The evidence presented in this paper and that summarized above calls into question the pre-saturation – saturation model of dispersal proposed by Lidicker (1975). Pre-saturation or adaptive dispersal (Stenseth 1983) assumes that the motivation for dispersal involves a reasonable probability of recruiting elsewhere; saturation or non-adaptive dispersal does not. However, the motivation for dispersal may be the same irrespective of population density during the breeding season – the 'personal' environment of the animal is saturated and it is forced to move (Anderson 1980). The probability of young males born in spring and early summer recruiting to the breeding population was low and independent of density (Fig. 3). I suggest that their disappearance was directly tied to maturation and enforced dispersal by adult males already there. If pre-saturation dispersal had been involved, I would expect recruitment by young males to be inversely density dependent. Thus, in my study all dispersal of young males maturing in the year of birth may be saturation dispersal. Among young females, the typical pattern is to stay near the natal site and not to disperse (Boonstra et al. 1987) and thus I would suggest that successful pre-saturation dispersal and colonization is rare. However, the success of dispersers will depend on the availability of unoccupied habitat elsewhere. In my study areas, the habitats were relatively uniform and voles were distributed throughout it. Thus, dispersing voles had little opportunity of finding unoccupied habitats. However, in habitat with a mix of optimal and marginal areas, seasonally available dispersal habitat may make successful colonization and breeding by dispersers more likely (Anderson 1980, Stenseth 1983).

McShea and Madison (1986) found that the sex ratio of young *M. pennsylvanicus* at recruitment was biased in favor of females in the early portion of the breeding season and in favor of males near the end of the breeding season. They proposed that this population response was a result of manipulation by the mothers to favor the sex having the highest probability of recruiting to the breeding population. Though they did not have the data to test this interesting idea, evidence from my study is consistent with it: females have the highest probability of recruiting if born in spring–summer and males have the highest probability of recruiting if born in autumn (Tab. 1). In interpreting my data, I am assuming that the low recruitment of males to the breeding population on the natal grid provides an index of how successful they are at recruiting anywhere. If equal proportions of

males and females successfully enter the breeding population, but females do so on the natal grid whereas males mature elsewhere, then these arguments are not relevant. However, the information cited above does indicate that higher dispersal rates by males translate into higher mortality rates, not higher colonization rates. Though sex ratio at birth in some microtines deviates significantly from 1:1 (Fredga et al. 1977, Gileva 1980, Malcolm et al. 1986, Caley et al. 1988), that of *Microtus pennsylvanicus* does not (Myers and Krebs 1971, McShea and Madison 1986, Craine 1987). In contrast to McShea and Madison (1986), I found no deviation from a 1:1 sex ratio at recruitment. There are a number of explanations for the differences between these two studies. First, McShea and Madison (1986) examined the sex ratio for all young entering traps that were ≤ 24 g whereas my cutoff was ≤ 22 g. It is unlikely that the 2 g difference in weight cutoff produced these differences between the studies. Second, differences in trapping technique may be responsible. McShea and Madison used two single capture Spencer traps per station and I used one or two single capture Longworth traps and one multiple capture pitfall trap per station. The pitfall traps are particularly successful in capturing young soon after they leave the nest (Boonstra and Rodd 1984). Since sex ratio at birth is 1:1 and, in my study, at recruitment is 1:1 (from a combined sample size over all years and seasons of 1179 males: 1207 females), McShea and Madison (1986) may not have been catching both sexes equally due to some trappability bias (Myers and Krebs 1971). Finally, the differences between studies may be real and due to some regional effect.

Overall sex ratio adjustment in the population did not occur in my study, though this does not eliminate the possibility that individual females may bias the sex ratio of their offspring based on their own condition and age (McShea and Madison 1986, Caley et al. 1988). Armitage (1987) also found no overall sex ratio adjustment in yellow-bellied marmot populations, but did find adjustment by individual females under certain social conditions and when they were of a certain age. Thus, a more detailed investigation of the birth sex ratios of individual female voles and the fates of their young is warranted. Armitage (1987) found that biasing of sex ratio depended on the mother's probability of giving rise to a matriline: the higher the probability, the more females in the litter. If *Microtus* social structure is based on female kin clusters (Boonstra et al. 1987) which are somewhat similar to those occurring in ground-dwelling sciurids such as marmots, similar biasing of offspring sex ratios by certain mothers may also occur.

These findings suggest three research areas that should receive effort. First, the success of dispersers in colonizing areas already occupied needs more research to resolve the pre-saturation – saturation model of dispersal and the work by Danielson and Gaines (1987) serves as a model. Second, experiments to examine the

role of inbreeding avoidance are needed. Third, biasing of sex ratio of progeny by certain mothers based on their condition or age may occur and we require intensive work to determine this and how it translates into variation in fitness amongst mothers.

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